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PREFACE TO REVISED EDITION

The accumulation of the facts of science, as well as the interpretation, evaluation, and application of these facts, is a continuing process. It must follow, then, that the teaching of science cannot remain a static procedure and that new texts of science must from time to time be written.

This textbook of botany represents the authors' ideas of some of the gradual changes in objectives, content, emphasis, sequence, and procedure in general botany that are necessary to incorporate effectively appropriate new discoveries in science and their various applications to human welfare. For anyone to assume that these features of general botany are already standardized is to close one's eyes to the continual increase of new material available for general botany courses as well as to a scientific consideration of the problems of teaching.

Present-day botanists, moreover, cannot escape responsibility for some share in a general educational program for students and laymen. Many students of diverse interests elect general botany as their sole requirement for a course in science; a smaller number will enroll because of a desire for special training in the subject, still others merely because it is one of the science requirements in the college program. We cannot meet our obligations to these students merely by insisting that they memorize what scientists have discovered or by trying to tell them what the scientific method is and what may be accomplished by it. For the scientific method to become meaningful and a habit of procedure, the students must experience it repeatedly and see it exemplified as a normal part of classroom procedure as well as a *fait accompli* in the literature they are required to read.

As all botanists are fully aware, plants are complex systems influenced by and in turn influencing other systems of their immediate environment, both animate and inanimate. There can be no clear appreciation of the fundamental interrelations among these dissimilar systems without some basic knowledge of the organization of the structures and the nature of the processes inherent in them. In short courses in botany much of the time in the classroom must necessarily be devoted to acquir-

ing this preliminary background. For that reason we have included in the textbook numerous discussions of various kinds of interrelations for further consideration outside of class.

Botany is primarily a concrete science and is most effectively approached through a first-hand study of plants. We have found class discussions while observations are being made a most satisfactory approach. A workbook is available as a convenient aid in some of the class periods and as a means of further suggestions for work outside class periods. The textbook has been written primarily to supplement what is observed and discussed. It is intended to help students review, organize, amplify, and correct their own observations, inferences, and ideas, whether they obtained them first-hand or by hearsay. We have tried to interfere as little as possible with the teacher who prefers to have students observe and discuss plant phenomena before books are consulted. *Nearly every chapter has been written with the assumption that it will not be read by the student until the instructor thinks that the student's own observations and inferences should be supplemented by what is written.* The sequence of topics within a chapter is not always the best one to follow in observation and oral discussion.

Since there is no fixed standard of knowledge and procedure that one may rely upon indefinitely and in all circumstances, we have tried to present a cross section of what appears to us to be in keeping with the immediate present. We believe that there is a body of basic information, scientific inferences, and points of view about the plant part of our environment that is as important a background for students who intend to major in any phase of plant science as it is for that much larger group of students who are taking the course in botany as part of their general education. Our aim has been to help the students organize that background and appreciate some of the numerous interrelations of plants and of plants and animals, particularly man. It is of course impossible to incorporate in a book of this size all the information demanded by students while they are comparing observations and inferences. Furthermore, some of the information needed is best supplied by the teacher, either directly or through the assignment of specific observations or references.

Many general topics are not discussed completely in any one place in the book, as they are in an encyclopedia. Here only so much of a topic as is needed is discussed when first introduced. In later chapters further information is added from time to time as it becomes appropriate.

The general course may begin at different seasons of the year, when readily available plant materials may differ greatly. For that reason the first five chapters contain discussions of materials which are useful in approaching the study of plants under different conditions. As the background of information increases in subsequent chapters, the interrelations discussed become more intricate and the student is expected to participate more and more intelligently in discussions involving a knowledge of structural systems of cells or of whole plants, of sequences of events in the development of a plant or of the whole life cycle, of the intimate relations of chromosomes and hereditary factors, of the interrelations of physiological processes and development, of physiological processes and environment, or of a combination of all these phenomena.

Material from all the artificial subdivisions of botany is included not because we intended to survey the entire field, but because the synthesis of material from all phases of botany is necessary to give a student a general perspective of his relations to his plant environment.

In keeping with the scientific attitude we have persistently tried to maintain a terminology and phraseology consistent with the views of special students in the various phases of botany, and to avoid language patterns characteristic of abandoned ideas and interpretations. Procedures in teaching that help students learn to educate themselves by means of observations accompanied by the drawing and evaluation of inferences necessarily include a concurrent regard of precision in the use of language. There is no place in these procedures in botany for the perpetuation of such language patterns as those characteristic of the early concepts of the food of plants, of nutrients, of personification and deification, of structures and processes *for* this and that purpose, of stimulus and response, and of statements in which the subject could not possibly perform the action denoted by the verb. Since the text is to be used *following* class discussions, we hope we have not departed too often from the precision expected of the students.

Another of our aims has been to help students thoughtfully arrive at reasonable and usable concepts rather than memorize proposed definitions, and to come to the realization that much of our knowledge about plants is in reality a summation of *best inferences,* i.e., inferences which are often referred to as scientific conclusions, principles, definitions, natural laws, and in many instances as facts. If there is a recognizable limit to a course in general botany it must be related to the time when students have learned what can be done with facts, have become accus-

tomed to a scientific approach, and are able to consider plants from about as many general points of view as the instructor can, but in less detail.

The authors are grateful for the criticisms they have received since the first publication of this book. Many suggestions have been helpful in clarifying both subject matter and presentation. Suggestions which would have necessitated departures from our primary aims, such as more detailed discussions of structures or further analysis of experimentally unsolved problems, have been accepted by citing references that may be consulted. We are concerned chiefly with helping general botany students acquire certain basic facts and an awareness of scientific procedures that they may retain and use throughout life, rather than with attempting to familiarize them temporarily with all the detailed facts about plants that specialists know and use in their work. General botany is not the last course in botany for those who become interested in some special phase of plant science.

The major changes in the second edition include a comprehensive revision of the index, the correction of errors, simplification of discussions and terminology, and the inclusion of some new illustrations and references, and of new facts and ideas that have been contributed by the thousands of research workers in the many specialized fields of plant science.

ACKNOWLEDGMENTS

The authors are deeply indebted to their associates at The Ohio State University and Northwestern University, to Dr. O. F. Curtis of Cornell University, to Dr. C. L. Wilson of Dartmouth College, and to Dr. W. F. Loehwing of the State University of Iowa for their sympathetic and helpful criticism of the original manuscript.

The illustrations have been secured from many sources, and are properly credited to those who have furnished the photographs, negatives, and materials from which photographs were made. We are particularly indebted to the World Book Company for permission to use some of the drawings and illustrations in the *General Botany* published by them. Through the courtesy of the U.S. Forest Service, the U.S. Soil Conservation Service, the U.S. Department of Agriculture, and the New York Botanical Garden, it has been possible to obtain photographs suitable for illustrating the various vegetation types of North America and some of the features described in other chapters. Miss Jane Roller, of Washington, D.C., has made many of the new drawings. Mr. Eugene B. Wittlake has made some of the diagrams and most of the photomicrographs. Mr. Gordon Crowl, Mr. Fred Norris, and Mr. Clyde Jones have made photographs of experiments, cultures, and some landscapes especially for this book.

The greatest debt of all, of course, is to the thousands of fellow scientists who cannot be mentioned individually but whose scientific efforts have supplied humanity with an ever-increasing fund of valuable data and scientifically evaluated conclusions free for all to use. A relatively few references appear at the end of certain chapters. The instructor will be able to add others equally good.

E. N. T.
H. C. S.
L. H. T.

Columbus, Ohio
Evanston, Illinois
September 1, 1952

TEXTBOOK OF BOTANY

CHAPTER I

PLANT SCIENCE

Every animal is in some way dependent upon plants every moment of its life. One may well begin the study of botany by inquiring into the ways in which man and other animals of his own community are dependent upon plants and plant products, or are otherwise influenced by plants. This local survey may be extended into other communities and geographic regions. If the inquiry is also projected into historic and prehistoric records one may learn how plants and a knowledge of plants have played a significant and at times a decisive role in the advance and decline of civilizations in many parts of the world.

Everywhere man and other animals use plants directly as food, or eat other animals that feed on plants. Directly or indirectly all animals are dependent upon plants as the source of food. During the growth of the animal a part of this food is transformed by physiological processes into the substances of which the body is composed. A larger part of it is oxidized within the tissues of the animal, and energy is liberated. As a result of this liberated energy the temperature of the body of the animal is often maintained above that of its surroundings, and the animal is also able to move about and to do other kinds of work.

Through the burning of such plant derivatives as wood, coal, petroleum and gas in furnaces or engines man secures light, heat, electricity, and mechanical energy by which he has been able to modify his immediate environment, supplement his own ability to move about, and transport materials and supplies wherever they are needed or desired. These two products of green plants—food substances and chemically bound energy—are indispensable to all living organisms.

There are also certain substances derived from plants which are essential to the health and well-being of all animals—for example, the vitamins and the mineral elements chemically bound in organic compounds.

With the progress of civilization many other plant products have become indispensable or at least highly desirable. From plants we obtain the materials of which most of our houses are built, finished, and fur-

nished. Much of our clothing is made from plant fibers. Paper and rubber made from plant products have increased our means of communication and transportation. Many of our beverages and some of our important medicines contain plant derivatives. A large part of the population earns a living by supplying itself and the rest of society with plant parts or plant products.

Certain of the larger plants are used to beautify our homes, to decorate the landscape, and in other ways to add to the enjoyment of living. We use trees to protect us from intense heat and light. Forested areas have become the centers of many forms of sport and recreation. They are also continuous sources of cover and food to countless animals both large and small. Plants not only hold the soil against erosion by wind and water, but they improve its texture and composition; and myriad microscopic plants contribute to its fertility.

But the relation of plants to animals is not wholly beneficent. Weeds, for example, decrease the yield of crops and greatly increase the labor of cultivating them. Many plants contain toxic and irritating substances that cause suffering, illness, or the death of human beings and other animals. Certain microscopic plants may invade the tissues of the animal body and lead to disease and death. Others cause diseases and destruction of the larger plants, and still others grow on commercial food products in shipment and storage and lessen their value or destroy them. Such plants test the ingenuity of every generation of human beings to devise means of avoiding, controlling, or eradicating them.

The value of plant science to society has been increasingly appreciated as knowledge of plants has advanced. The farmer who plants a field; the orchardist who attempts to secure a crop of fruits; the florist who seeks the production of ornamental plants and flowers; the forester who tries to obtain a profitable yield of timber on a tract of land; the gardener who supplies our markets with edible and succulent leaves, stems, and roots; industrialists who seek to find new sources and new forms of plant products to meet our social needs; and the conservationists who strive to preserve our soils from wind and water erosion and to rescue our disappearing fish and game animals—all these find themselves confronted by an often bewildering array of problems that lie within the field of *plant science*, or *botany*.

Many of these problems have been solved by a study of the structures, the chemical composition, the physiological processes, the heredity, and

the life histories of plants; or by a study of plants in relation to soil and climatic conditions. Other problems have been solved through the discovery of facts about the growth and chemical diversity of bacteria and fungi, their various effects on the growth of other organisms, and the means of controlling their development.

Numerous unsolved problems remain. That society recognizes the need of continued and far-reaching research with plants is attested by its maintenance of forest and agricultural research stations in every country and in nearly every state and province throughout the world. Through the years these institutions have provided an increasingly important addition to research by teachers and graduate students in colleges and universities. As a result of these investigations each generation has an increased wealth of botanical knowledge available for both personal and social needs. Through instruction one may readily learn how to select and apply a portion of this accumulated knowledge.

Thus far we have stressed the importance of plants and of the science of plants mainly in relation to human economics, occupations, health, and the survival of all animals. The general desire of man to know and interpret his environment and to speculate about himself and his environment must also be emphasized here. Plants are a conspicuous and important part of that environment. In addition to the interrelations of plants and animals there are many important relations among plants themselves, between plants and their physical environments, and between the parts of each individual plant. These interrelations have been and still are interpreted on the basis of several diverse assumptions ranging from magic to science. Throughout the ages some of these interpretations, whether obtained in the classroom or elsewhere, whether correct or incorrect, have become a part of the general outlook and culture of everyone. A study of plants as part of a general education would be quite inadequate unless it included interpretations of these interrelations based on present scientific knowledge and method. In the chapters that follow we shall find that an understanding of these interrelations on the basis of evidence is not only a matter of personal interest, but one that is both desirable and necessary for the welfare of society.

What is a plant? When we pull weeds in a garden, mow the grass on a lawn, enjoy the shrubs and trees in parks and forests, we readily recognize these living organisms as *plants*. Stale bread and fruit may be covered with *mold* (Fig. 1). We have all seen other *fungi* (Fig. 2) in the form of mushrooms in fields and woods. The surfaces of ponds and moist

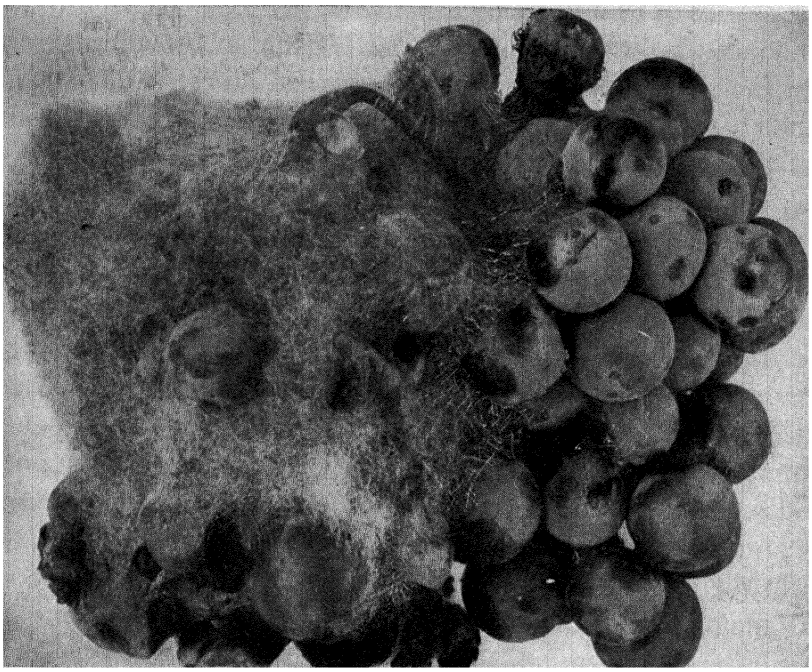

FIG. 1. A common mold on a bunch of grapes. Photo from U. S. Department of Agriculture.



FIG. 2. One of the common edible mushrooms (*Coprinus*). Photo from W. G. Stover.

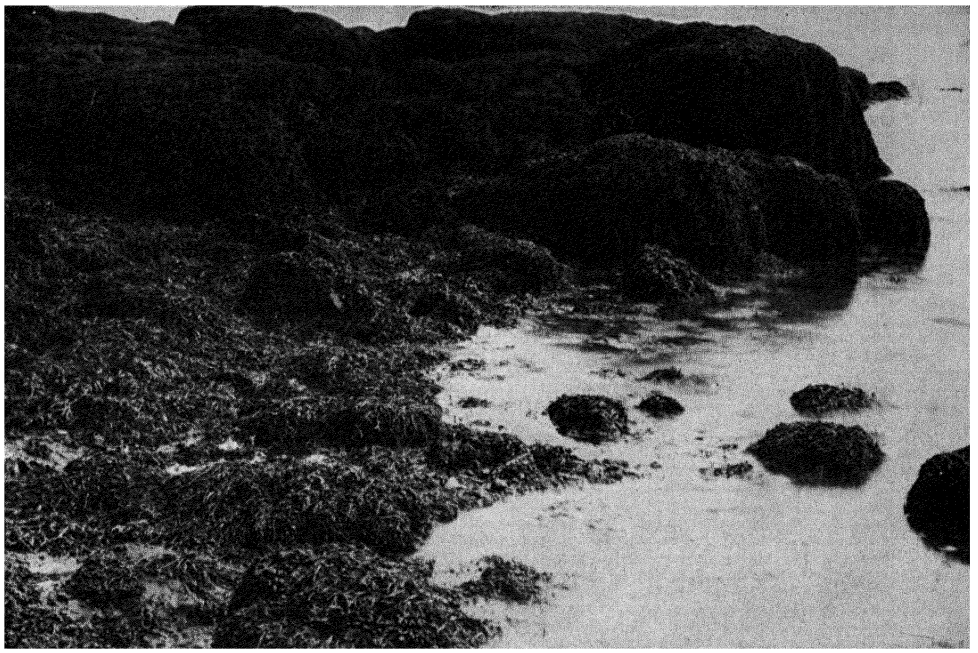

FIG. 3. Brown seaweeds (*Algae*) on rocks at low tide, New York Harbor. Photo from New York Botanical Garden.

soil at times become green with "pond scums"—microscopic plants that may be distinguished as *algae*. Those who have visited the seashore are familiar with "seaweeds," which are other and larger kinds of algae (Fig. 3). Tree trunks and rocks that have long been exposed to the weather are often partially covered by gray-green or highly colored patches of *lichens* (Fig. 4). Everyone who even occasionally strolls on forest trails distinguishes some of the *mosses* (Fig. 5) and *ferns* (Fig. 6). Much of the decay of plant and animal products, and many of the diseases of both plants and animals are due to the presence of *bacteria* (Fig. 7). *All these organisms are plants.*

On first thought it may seem rather easy to answer the question: What is a plant? But we may be thinking only of such plants as trees, shrubs, and herbs, and of such animals as men, dogs, and birds. When we include in our survey mosses, algae, fungi, bacteria, and numerous kinds of one-celled animals, the observable differences among plants are often far more striking than those between certain plants and certain animals. This fact makes it surprisingly difficult to list any group of qualities that are characteristic of plants alone.

Similarity of plants and animals. The larger plants differ from the



FIG. 4. Lichens growing on a vertical rock face. Photo by C. H. Jones.

larger animals in so many ways that they not only are readily distinguished but are commonly thought to be quite unrelated. To suggest that horses and trees have certain characteristics in common may seem absurd. But students of living organisms have found that many of the processes in plants and animals are either identical or essentially similar if the basis of comparison is *limited to certain fundamental features.* Among the microscopic organisms are many that resemble animals quite as much as they resemble plants; and except for the many things one may learn about plants and animals in trying to do so, it would be futile to try to classify them strictly in either category. The reader may be content to call a certain object a plant because it looks like a plant. One's concept of what looks like a plant, however, is dependent upon the various kinds of plants he has seen and recognized as such.

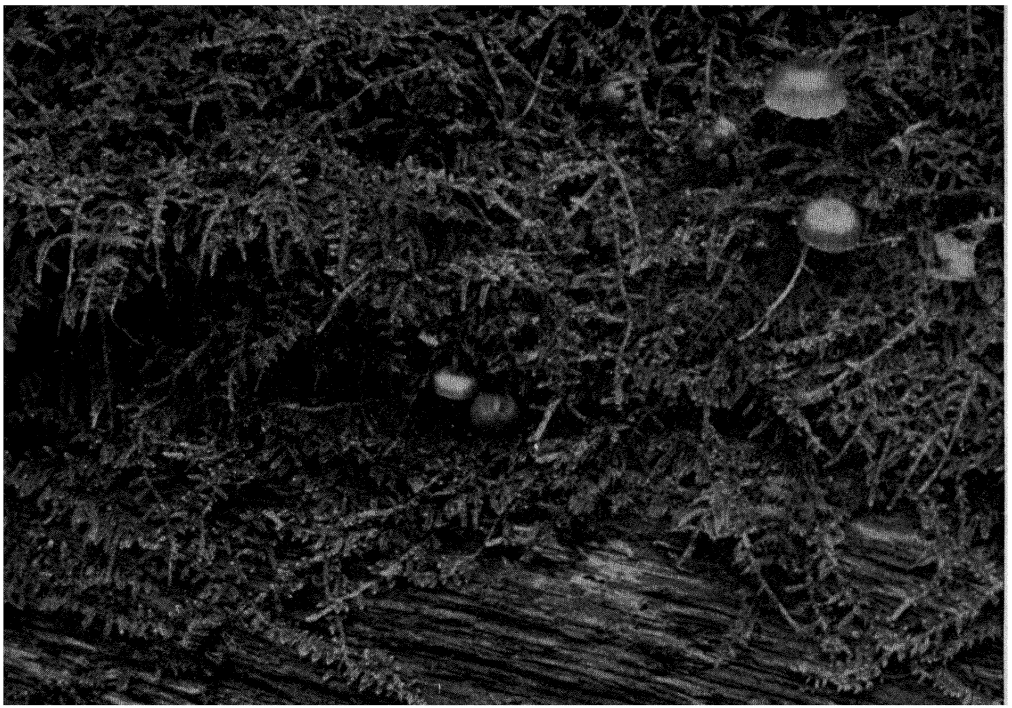

FIG. 5. A mat of moss plants (*Hypnum*) on a decaying log. Several "mushrooms" are also present. Photo by E. S. Thomas, Ohio State Museum.

Concepts versus definitions. Perhaps you will be amazed to learn that even botanists cannot give you an acceptable definition of the term *plants*. How much disturbed should you be? Since you are an animal, would it be reasonable to expect you to know what an animal is? Can you give an acceptable definition of the term *animals*? Even if definitions can be given when a new subject in botany is opened up for discussion, it may be well to postpone them, for there are almost always excellent opportunities for you to discover for yourself certain things about the phenomenon in question. Shortly you may discover that, although you have not learned to make an acceptable definition, you have acquired usable concepts which you can continue to enlarge as your knowledge and understanding increase. In this way you will become able to help formulate, evaluate, and apply definitions rather than merely memorize them. A definition may be faulty. Moreover, there are many plant phenomena about which we must be content with reasonable concepts—for example, growth—as well as plant and animal.

The biological sciences. Knowledge that pertains to plants or animals



FIG. 6. Polypody fern on a cliff edge. Photo by C. H. Jones.

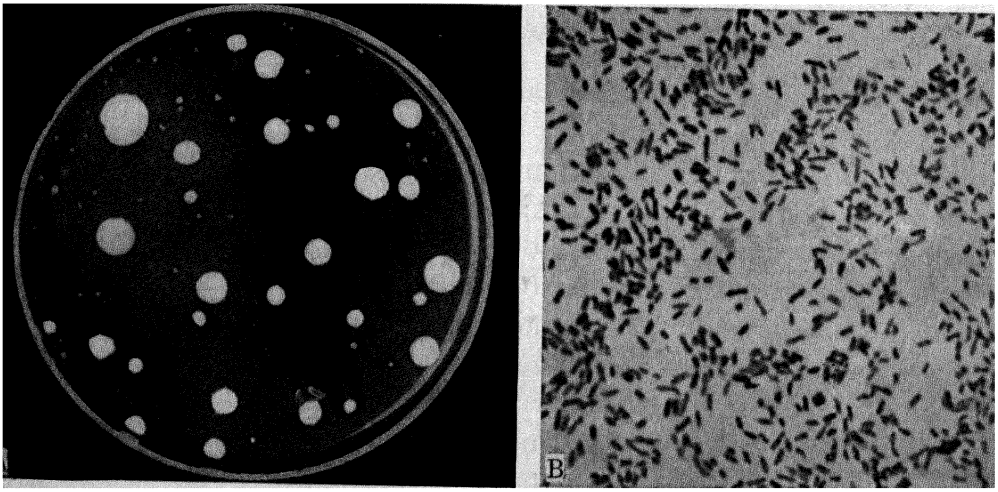

FIG. 7. A, photograph of masses or colonies of bacteria that have grown on agar in a petri dish; B, bacteria of fire blight from a similar culture when magnified about 2000 times.

or to both is called *biological science*. The range of biological information that has accumulated through the centuries—but more especially during the last hundred years—is now so extensive that no one person is entitled to be called a *biologist* in the sense that he is a master of the whole field. The facts and principles that have been or may be derived from the study of plants are called *botany*, and the knowledge similarly gained from the study of animals constitutes *zoology*.

Because of the great diversity of structures and life relations among the many species of both plants and animals, botanists and zoologists have difficulty in viewing their subjects as wholes. Most botanists have become especially interested in some one or only a few of the many phases of the subject, such as the classification of plants, their physiology, their structure, life histories, diseases, heredity, geography, or geological history. This specialization has certain advantages in research and in practice. But the behavior of plants, in the broadest sense, results from interactions among processes characteristic of many special fields of study. Thus in the interpretation of plant phenomena we are forced to seek an ever-widening background of biological, physical, and chemical knowledge.

In a general study of plants we shall be concerned not with the special phases of the subject, but with that general background which experience seems to indicate is most worth while to anyone. We may begin our study as indicated at the beginning of this chapter, or we may prefer to go into the field and learn to distinguish plants from other objects in our environment. The plants growing all about us are just as important objects of study where they grow as are the materials carried to the laboratory, and they may be studied much more frequently and leisurely. These are two possible methods of approach for beginners. In Chapters II to VI several other approaches to the study of plants are suggested; any of them may be preferred to the ones suggested in this chapter.

CHAPTER II

THE PARTS OF PLANTS

The principal parts, or organs, of the more familiar seed-bearing plants may be distinguished in a bean plant as it develops from the seed that is planted to the seeds that are harvested. This life cycle from seed to seed includes part of two life histories, or generations, of beans; for like a human being each bean plant begins its existence as a single cell. The young plant, or embryo, already visible in the seed developed from a fertilized egg. After the germination of the embryo in the seed the rest of the life history of the bean plant as well as the development of the embryos of the next generation may be completed in a few weeks. Some of the structural changes that occur in a growing bean plant may be visualized by studying Figs. 8 and 9, but much more can be learned by planting several bean seeds and watching the changes that occur in the plants from day to day.

Within the seed coat is an embryo consisting of a short stalk (the hypocotyl) and a pair of very large, thick, leaf-like structures (the cotyledons) which are at the first node. At the apex of the hypocotyl is a terminal bud (the plumule), and at the other end is a root tip from which the primary root develops.

Two or three days after the seed is planted, the primary root begins to elongate. It breaks through the seed coat and penetrates into the soil. From the primary root lateral roots grow more or less horizontally. The young plant is now firmly anchored, and the rapid growth of the hypocotyl lifts the cotyledons well above the soil surface.

As the cotyledons increase slightly in size the broken seed coats fall away. From the plumule a stem bearing leaves begins to develop. A lateral bud soon becomes visible in the axil of each leaf. Each bud consists of a stem tip bearing embryonic leaves. The first true leaves that develop at the second node of this stem are simple, opposite, and heart-shaped. From the terminal bud another stem segment (internode + 3rd node) grows, and from this third node only one leaf forms—this time a leaf of three leaflets. Growth in height continues by the development of

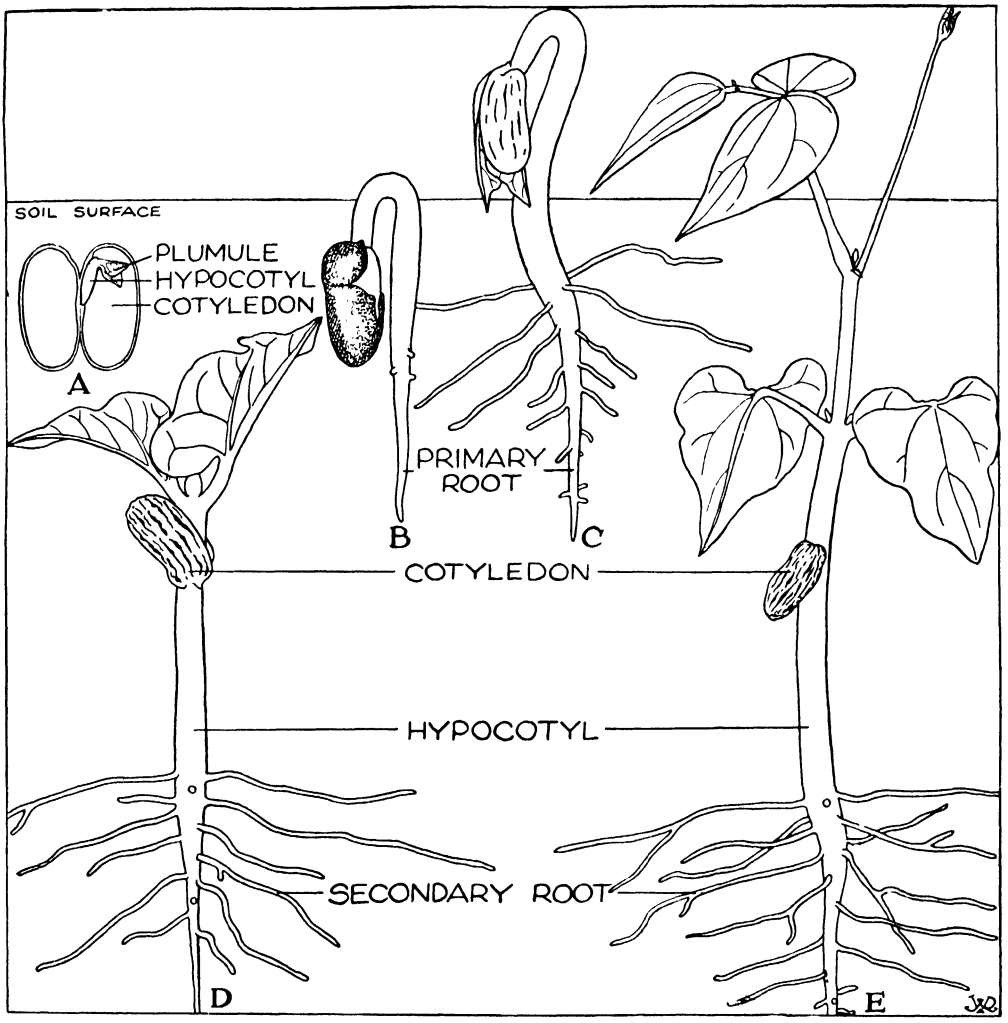

FIG. 8. Early stages in the development of a bean plant.

additional stem internodes and new leaves at the nodes until 5 or 6 leaves are formed. In the meantime, leaf-bearing branches may also be developing from the lower lateral buds. These four distinct parts—the *roots*, the *hypocotyl*, the *stems*, and the *leaves*—constitute the vegetative organs of the plant. Internally they are all interconnected by veins, or vascular bundles (Fig. 10).

Usually after the formation of leaf-bearing branches, another type of branch that bears flowers appears. Within a few days a pod, or fruit, begins to develop from the pistil of the flower. As the pod increases in size, seeds develop in it and soon enlarge to the size of the seed that was

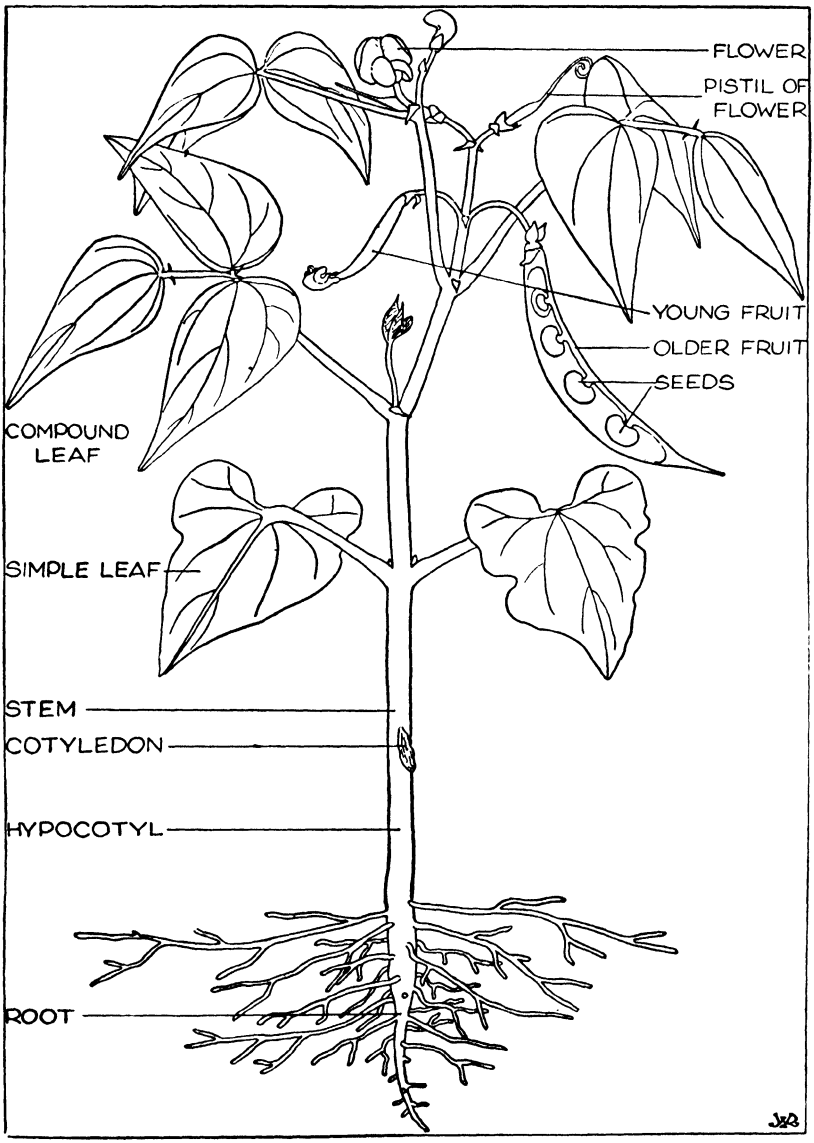

FIG. 9. Diagram of older bean plant: stem with leaves and flowers, and with fruits (pods) of various ages from the pistil. The seeds are borne within the fruits.

planted. When the seeds are mature the life cycle of the bean plant is complete. The *flowers*, *fruits*, and *seeds* are often spoken of as the reproductive organs of the plant in contrast to the vegetative body made up of roots, hypocotyl, stems, and leaves. The major part of the various food-making processes occur in the vegetative organs. Other processes in reproductive structures result in the formation of seeds. Growth and

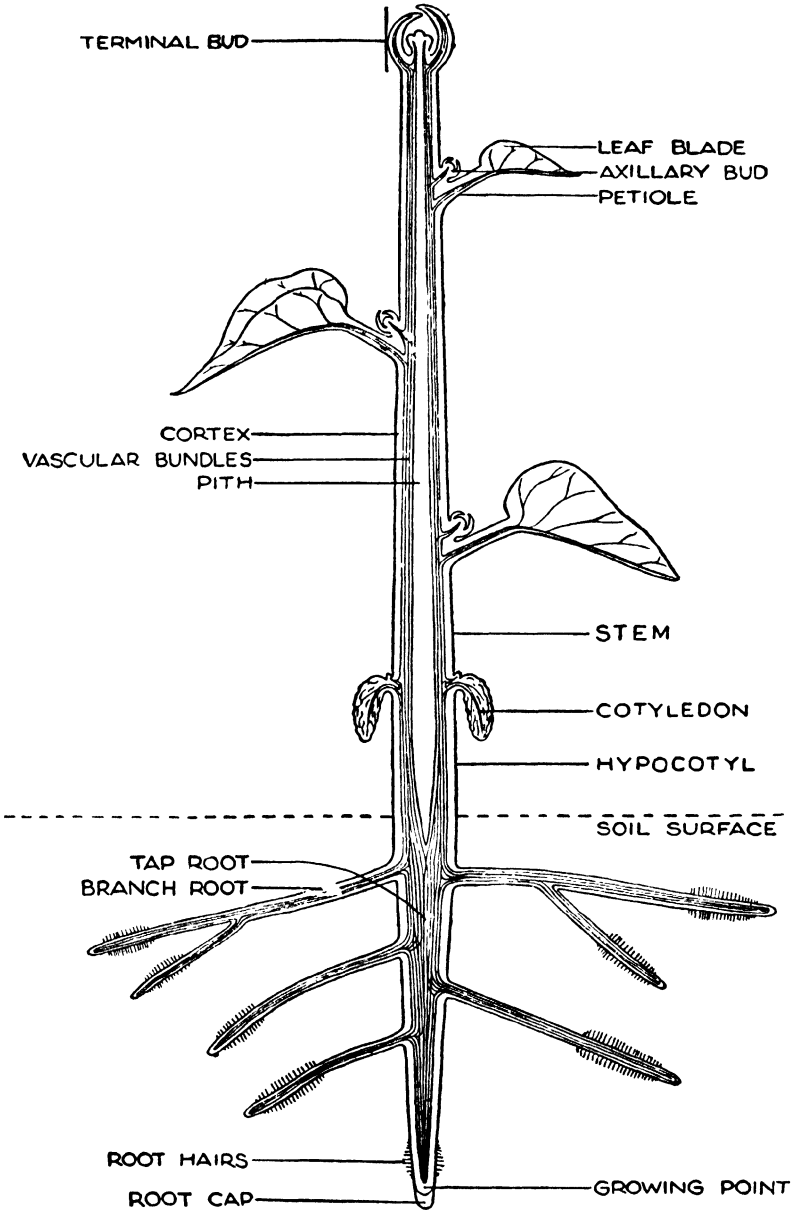

FIG. 10. Diagram of some external and internal structures of a seed plant.

the utilization of food occur in all organs of a plant. Every generation of a seed plant is in general a repetition of the same orderly sequence of vegetative structures followed by reproductive structures.

From past experience you probably have formed general ideas of these several parts of plants. But if these ideas are vague they will not be

useful in either reading or discussion. To regard a leaf merely as the part that is green, a root as the part in the ground, and a seed as what one plants is quite inadequate. If enough plants are examined it will be discovered that any of these organs may be green, any of them may be found underground, and all of them are planted by man. A stroll on the campus or in nearby gardens and conservatories for the purpose of learning to distinguish the parts of plants will be much more profitable than a search for technical book definitions.

Roots, for example, are usually thought of as cylindrical, more or less tapering, underground structures. From observations of tropical plants in conservatories, of mature vines growing on walls, and of mature corn plants in a field one will learn that roots are not always underground. Stems are still more variable in form. They usually are aerial cylindrical structures, but some develop below the soil surface and may become greatly thickened like the tuber of Irish potato. Among the lateral outgrowths of stems are the leaves. Only in a few plants will leaves be found originating from other organs. There are myriad forms of leaves, but generally they are flat organs with a very large surface compared with their weight. Leaves above the surface of the soil are usually green during at least part of the year. Beginning with such general ideas, one may readily build more accurate and usable concepts of these organs through further personal observations.

Flowers are of every size from a twentieth of an inch to three feet in diameter, and of every color, often of superb and startling mixtures of colors. Usually flowers are easily recognized, but careful observation is needed to decide what is the flower in the flowering dogwood, Indian paintbrush, calla lilly, jack-in-the-pulpit, snowball, poinsettia, and hydrangea. Brightly colored parts are not found exclusively in flowers. Nor are flowers always brightly colored, as may be discovered by examining flowers of grasses, sedges, and several kinds of trees.

Fruits usually develop from the pistils or from the pistils and adjoining parts of flowers. The name fruit is applied to a great variety of structures, such as the dry fruits of the grasses, and "sticktights," as well as the succulent berries of the grape and tomato, the fleshy apples and pears, the pumpkins and melons, the firm green fruits of the walnut and of osage orange. To obtain some notion of the remarkable variety of fruits it is best to observe the transition from flowers to fruits on many kinds of plants at any time such observations can be made in the field or greenhouse.

Seeds develop from certain structures in the pistil of the flower and are borne inside the fruit. They may be very minute; they rarely exceed a few inches in length. Their most general characteristic is the presence of a firm coat or shell surrounding an embryo plant from which an adult plant may develop more or less like the plant on which the seed was borne.

Length of vegetative period. The bean plant matures in a few weeks; that is, the formation of reproductive organs takes place after a relatively short vegetative period. The vegetative period of plants may be either long or short; it depends both on the kind of plant and on the environ-

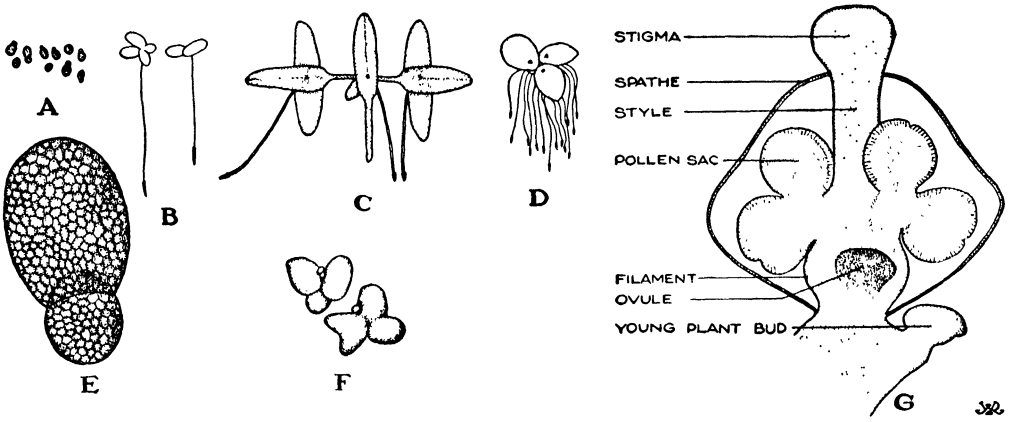

FIG. 11. The duckweeds are the smallest of the flowering plants: A, *Wolffia Columbiana*; B, *Lemna minor*; C, *L. trisulca*, and D, *Spirodela polyrhiza*, natural size; E, *Wolffia*, enlarged; F, flowers of *L. trisulca* on floating plants, natural size; G, a flower of *L. minor*, much enlarged. F and G drawn from photographs by W. H. Camp and L. E. Hicks.

ment. Some of the autumn flowering plants start from seeds in the spring. Some grasses, clovers, primroses, and carrots start from seeds in late summer and remain in the vegetative condition until the second summer. The so-called century plant grows vegetatively 20 to 30 years before it bears flowers, fruits, and seeds. Woody plants grow vegetatively from a few to many years, and then for many succeeding years reproduce during each growing season. In later chapters it will be shown how the vegetative period of a plant may be lengthened or shortened by such external factors as light, temperature, moisture, and soil salts.

We have referred thus far only to the more familiar seed-bearing plants, most of which have the seven principal plant organs in one form or another. Some seed plants lack one or more of these organs. Some of

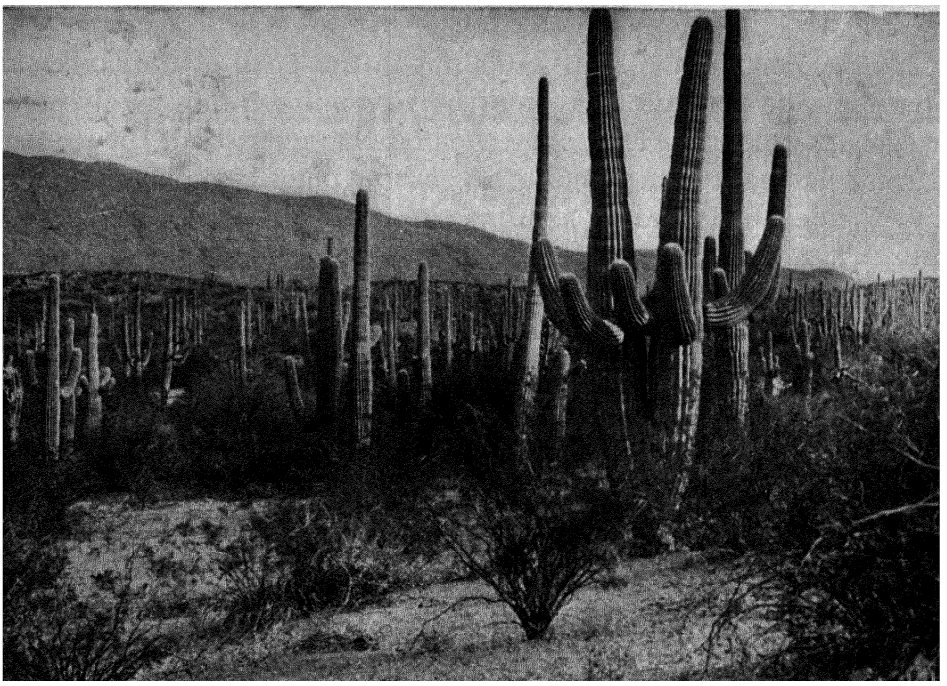

FIG. 12. The stems of the giant cactus do not bear leaves. Some of the shrubs in this desert scene have leaves only during rainy periods. Photo by U. S. Forest Service.



FIG. 13. A flower and buds of *Rafflesia*, a root-parasite in the East Indies. The species pictured above occurs in the Philippines. A species in Sumatra closely resembles it in form and habit and has flowers three feet in diameter. Photo from Philippine Bureau of Science.

the duckweeds have a small globose body with no distinction of root, stem, or leaf; others have a flattened body with a well-formed simple root; all of them have flowers, fruits, and seeds (Fig. 11). The well-known Spanish "moss" of the South has no roots (Fig. 223, page 508). Many cacti are notable for the absence of leaves (Fig. 12). In some plants, such as the dandelion and the common plantain, the stem is merely a small flattened cone at the top of the root. The tropical parasitic plant *Rafflesia* has neither roots nor leaves—just a short stem, a flower, a fruit, and seeds (Fig. 13).

Ferns have roots, stems, and leaves but no flowers, fruits, or seeds. The pond scums and seaweeds (algae) have none of these organs, and certainly there are no organs closely resembling them among the fungi. It is evident that none of these organs is essential to all plants, but they are generally present in seed-bearing plants. As we shall see later, certain fundamental processes are usually associated with each of them but are not necessarily limited to them.

CHAPTER III

LEARNING TO NAME PLANTS

We shall not get very far in the study of plants without studying them in the field and greenhouse. In order to observe and discuss plants intelligently, we must have appropriate names for them. Many common plants have local names which may suffice for ordinary conversation. But the names applied in one community may be different from those in another. Furthermore, the same name is often used for quite different plants in other localities. Many other plants lack common names. To overcome these difficulties scientific names have been given to all the known *species* of plants, and by agreement these names are used and understood by botanists everywhere.

Botanists have recognized and named more than a quarter of a million species of plants. As a beginning it will be sufficient to know some of the local seed-bearing plants. Many plants can be recognized readily by their leaf and stem characters. For the recognition of others, flowers, fruits, and seeds may have to be observed. Names of plants may be obtained from others who know them or from published "keys." To make the simplest keys or to use those made by others, it is necessary to examine the external features of leaves and stems and become acquainted with the terms that are applied to their parts, forms, and arrangements.

The parts of a leaf. If one examines a leaf, such as that of Japanese quince, it is evident that it consists of a broad, thin *blade*, a narrow cylindrical *petiole*, and at the base of the petiole a pair of small appendages, the *stipules*. A leaf consisting of these three parts is frequently called a *complete leaf*. The primary parts of a complete leaf, then, are the blade, petiole, and stipules (Fig. 14).

The stipules are usually small structures; but some of them, such as those of pansy, Japanese quince, and garden pea, are large and blade-like. Those of buckwheat and smartweed are *sheaths* surrounding the stem for some distance above the point of attachment. Stipules of the greenbrier are *tendrils*, and those of the black locust are *spines*.

Some leaves have no apparent petioles and are described as *sessile.* The leaves of many grasses, such as those of oats, wheat, and bluegrass, have neither petioles nor stipules; the blades are attached to the stem by a *sheath* which may be long or short. At the top of the sheath is a collar-like extension called the *ligule.* The ligule of the bamboo and certain other grasses may consist merely of several long bristles.

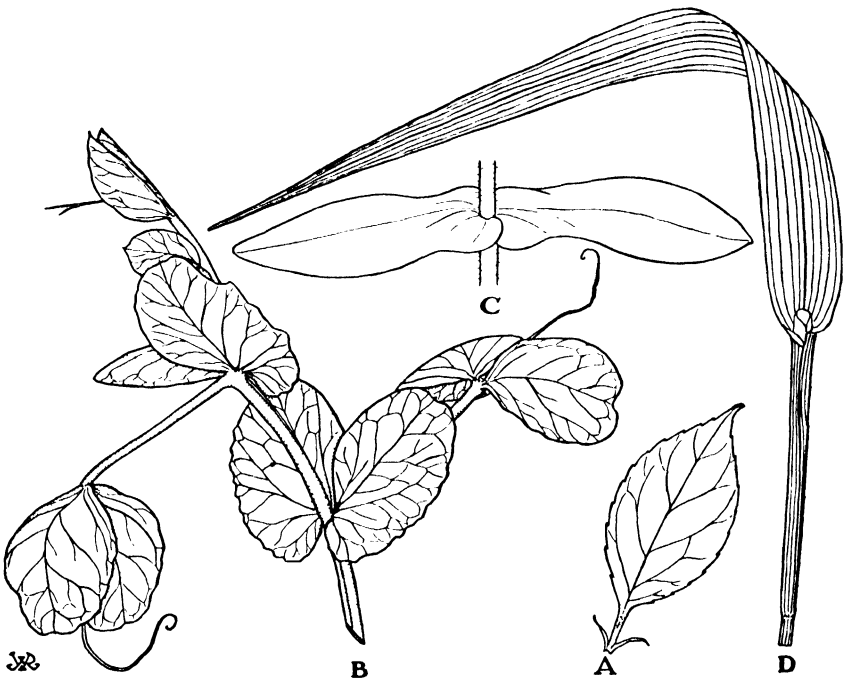

FIG. 14. Diagrams of some parts of leaves. A, blade, petiole, and stipules of apple leaf; B, stem of pea bearing leaves composed of two large stipules, leaflets, and a terminal tendril; C, sessile leaves of zinnia; D, blade, ligule, and sheath of a grass leaf.

The needle leaves of such trees as pines and spruces appear superficially to be quite unlike those of broad-leaved trees. The leaves of pines and larches are in clusters, or *fascicles*, at the end of short *dwarf branches.* Spruce, fir, and hemlock have solitary leaves. The leaves of arbor vitae are small *scales* oppositely arranged on the stem.

The veins. The most conspicuous structures of an elm leaf are the veins. The large vein near the middle of the blade is the *midrib.* In a maple leaf there are several prominent veins which are called the *principal veins.* In general, the smaller veins form a network and unite with larger veins, which in turn connect with the midrib or the principal

veins. These larger veins are smallest at the apex and margin of the leaf and gradually become larger toward the middle and base of the blade.

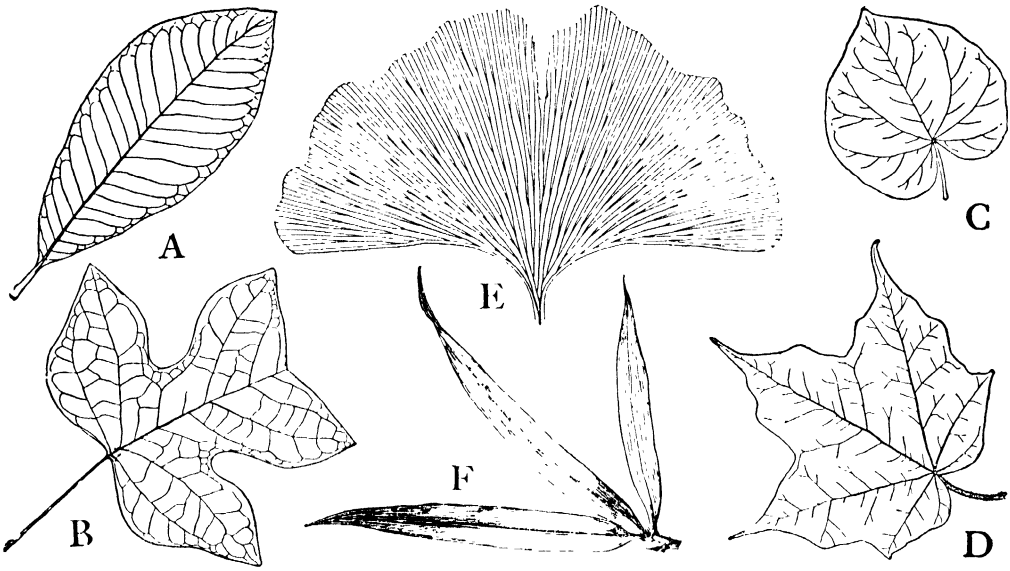

FIG. 15. Arrangement of the larger veins. The leaves of magnolia (A) and tuliptree (B) exemplify pinnate venation; red bud (C) and black maple (D), palmate venation. Veins may also be parallel as in the bamboo (F) or dichotomous as in the ginkgo (E). From drawings by C. H. Otis, Mrs. A. E. Hoyle, and C. J. Chamberlain. Fig. E from *Textbook of Botany* (Coulter, Barnes, and Cowles), Amer. Bk. Co.

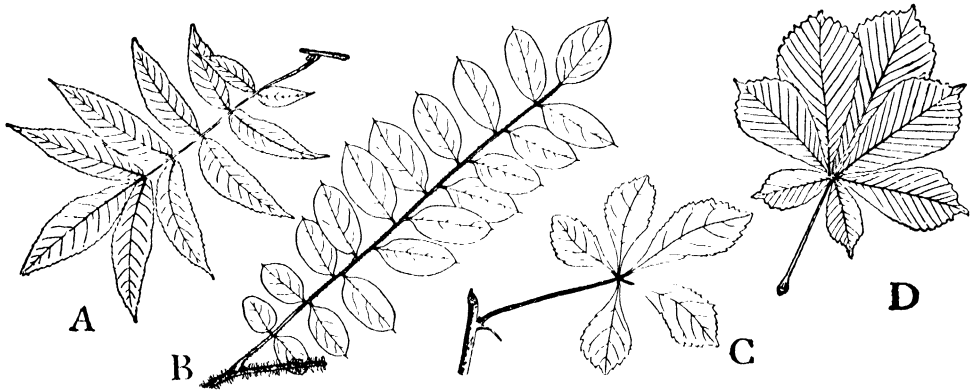

FIG. 16. The leaves of bitternut hickory and clammy locust are pinnately compound (A-B). Those of Aralia and horse chestnut are palmately compound (C-D). From drawings by Mrs. A. E. Hoyle and E. B. Wittlake.

The arrangement of the veins of a leaf is termed *venation*. There are four general arrangements of the *principal veins* in leaves that are easily

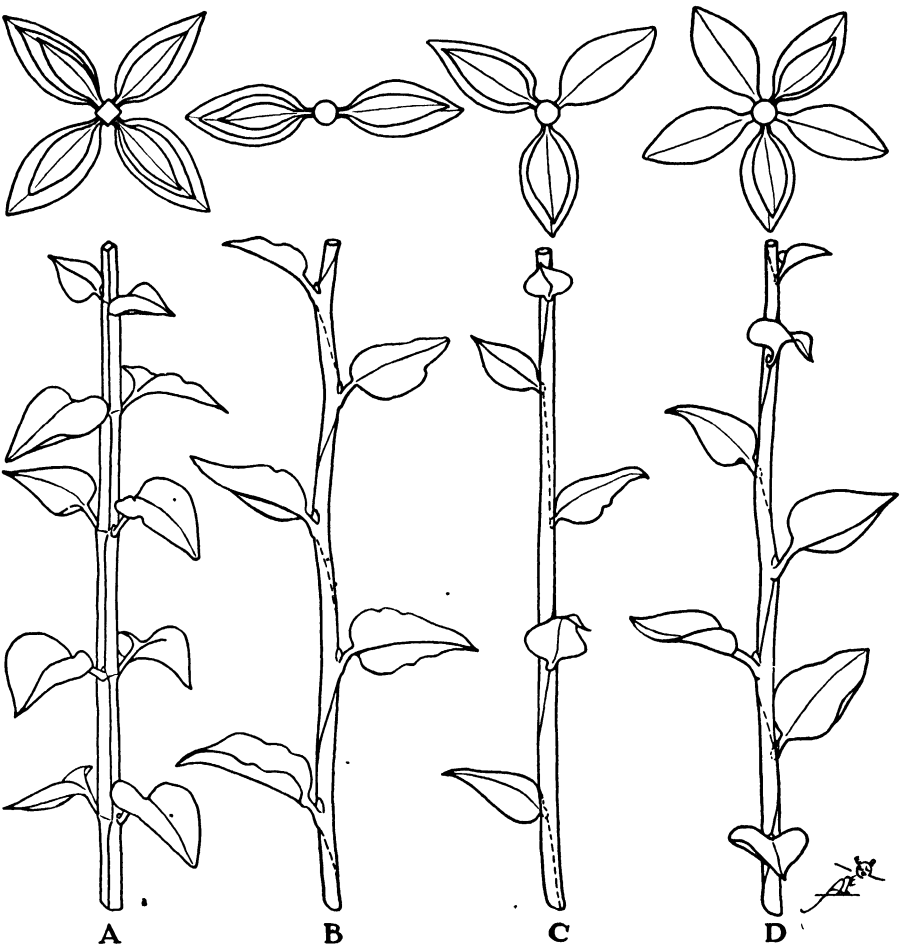

FIG. 18. Diagram of leaf arrangement on stems, as seen from above and from the side. A, oppositely arranged leaves; B-D, alternately arranged leaves. B, the one-half, or two-ranked, arrangement; C, the one-third, or three-ranked, arrangement; D, the two-fifths, or five-ranked, arrangement.

that is, the spiral passes through 3 nodes before completing a cycle and the fourth leaf-base is directly over the first—they are said to have the 1/3 alternate arrangement. These leaves occur in three ranks on the stem. This arrangement is best seen in the sedges.

Many trees have a more complicated leaf alignment. A spiral drawn around the stem from one bud to another directly below it passes through 5 nodes and twice around the stem; the sixth bud is directly below the first bud. This arrangement is called the 2/5 alternate type. Still other leaf and scale arrangements may be found, such as 3/8, 5/13, 8/21. The

numerator of any fraction in the series is equal to the sum of the two preceding numerators. The same relationship holds for the denominators.

These arrangements of leaves are not invariable. Owing to the influence of light on the growth of stems and leaves that are not equally illuminated on all sides, the stems become twisted and the arrangements are altered.

Other stem characters. Certain other stem characters are often used to identify trees and shrubs. Since a *bud* is present in the axil of each leaf of most deciduous trees and shrubs, bud arrangement is a useful character in the dormant season when there are no leaves on the stems. Buds differ in size and form in different species. Their outer *scales* may be smooth or hairy. *Leaf scars,* which are left when the leaves have fallen, also have rather definite shapes and patterns. The outer covering or bark of a twig may be green or gray or brown, and various other descriptive terms are applied to its surface, such as smooth or rough, ridged or warty. In a few instances the color and form of the *pith* may be distinctive.

Keys to plants based on vegetative characters. If we examine a maple tree we notice that its leaves are simple, lobed, palmately veined, and oppositely arranged on the stem. No other trees in North America have all four of these characters. The eastern hemlocks have short-petioled, needle-like flattened leaves with white lines on the under surface. When characters such as these are definitely assorted and grouped so that by careful reading and comparison with the specimen in hand we may find the name of the plant, we have what is known as a *key.*

Many keys have been published for the plants of local, state, and national regions. Local keys are usually more convenient because the number of plants included is smaller. For the beginner those based on such external characters of leaves and stems as are outlined above are most useful; moreover, they are quite adequate for the identification of most trees and shrubs.[1] Keys are often based on the forms and detailed structures of flowers, fruits, and seeds; such keys are necessary to identify many of the common herbs. Keys based on both vegetative and reproductive characters are more difficult to use since they imply considerable knowledge of structures and terminology.

Species and genus. No one expects anything but an oak tree to develop from an acorn, or anything but a hickory tree from a hickory nut. To go

[1] Every student should find the most convenient keys to the trees, shrubs, and herbs of his region. There are many keys available that cover limited areas. These have been published by agricultural experiment stations, museums, state academies of science, and various other institutions.

a step farther, when white-oak acorns are planted the individual trees that develop are normally all white oaks like the parent trees. These individual white oaks all belong to a single *species*. Similarly black oaks develop from the acorns of black-oak trees, and only yellow oaks grow from yellow-oak acorns.

Species that have many fundamental characters in common are grouped together as a *genus* (plural *genera*). We do this in common speech when we speak of the "oaks," and we identify the *species* when we say this is a white oak or a black oak. Botanists long ago began the use of Latin names in order to avoid the confusion arising from the fact that common names applied to the same plant in different localities differ widely, and the impossibility of learning these common names in several hundred languages. The Roman name of the oak is *Quercus* and the Latin word for white is *alba*; hence the name chosen for white oak is *Quercus alba*. All oaks belong to the genus *Quercus*, and for each species a second name is chosen by the author who first describes the species; by agreement subsequent authors use this same name. This is a great convenience, for students of all countries can use the same language when referring to the names of plants. These names have come into such general acceptance in all scientific writings that they are often spoken of as "scientific names" in contrast to the "common names" which may vary in every locality and country.

REFERENCE

Hitchcock, A. S. *Methods of Descriptive Systematic Botany.* John Wiley & Sons, Inc. 1925.

(Special references to plant floras adapted to particular regions are too numerous to list. See footnote, p. 24, of this chapter.)

CHAPTER IV

SEASONAL ASPECTS OF PLANTS

The succession of the seasons and the changes in plants and landscapes associated with them are familiar to everyone who has lived in the temperate zone. Even in the tropics there are but few localities in which seasonal changes in weather and in plants do not occur.

Changes in plants during the year have always attracted attention, even of primitive men. They have inspired much prose and poetry, as well as scientific study and description. Explanations for their occurrence were proposed so far back in the history of the human race that they became an important part of mythology and folklore. Even today newspapers and magazines frequently contain stories that are merely new versions of these ancient myths which ascribed supernatural and mysterious powers of foresight to plants and animals alike.

The changes that occur in the form and appearance and in the relative abundance of different species from season to season may be seen in the lawns, pastures, cultivated fields, and forests of your own community. An accurate account—a diary—of such observations over a period of a few years would include many valuable botanical data. This is another way in which the study of plants may be approached.

Many seasonal phenomena may be studied best as individual problems during appropriate seasons when the material is abundant and observations may be made over extended periods of time. As an aid to such preliminary observations, certain facts about seasonal aspects of plants have been brought together in this chapter. Data helpful in further observations and interpretations are included in many of the subsequent chapters.

There are such great differences in the behavior of individual species that few generalizations apply equally to all kinds of plants. Some of the questions and problems that are sure to arise from your own preliminary observations may be solved by further study or by well-planned simple experiments. Let us begin with plants in autumn when most courses in botany begin, and, by following the cycle of the seasons, con-

sider some of the most apparent changes that occur in plant processes and plant organs.

The autumnal aspect. The summer with its long days, high temperatures, and intense light is waning. The effects of cooler weather and of the shorter period of daylight upon certain chemical processes in plants soon become evident in the leaves of our deciduous trees and shrubs. The green color of chlorophyll gradually disappears, and the yellow pigments with which the green pigment had been associated in the cells of the leaves now become conspicuous. In many leaves there is an additional formation of other pigments which range in color from red to purple and which are called collectively the anthocyanins. As the season advances both the yellow pigments and the anthocyanins break down; and brown substances, especially tannins, increase and modify the leaf color. When the autumn is characterized by bright sunshine and moderately cool weather coloration is at its best. When frost occurs early or when the weather is wet and cloudy, the anthocyanins are formed to only a slight extent and the yellow and brown pigments are dominant in the landscape (Plate 2).

These autumn color changes in the leaves of many deciduous trees contrast sharply with the persistent green color of both the needle-leaved and broad-leaved evergreens. Many herbs likewise remain green through the winter months, at least in parts near the soil. Furthermore, the leaves of some trees and shrubs remain green until after they have fallen to the ground.

Colors and pigments. The color we ascribe to an object or substance depends upon the kinds of light rays that pass from it to the retinas of our eyes. When a beam of "white" light passes through a clear glass prism the rays of different wave length are separated by refraction and appear as bands of color (Plate II). Similarly we see a rainbow when the different rays of ordinary daylight are reflected to our eyes in separate bands by drops of water in the atmosphere. On the one side of the bow we perceive the longer waves of light as red, on the other side the short waves as violet. Between these extremes the bands of orange, yellow, green, blue, and indigo represent in order color perceptions resulting from the effects of rays of successively shorter wave lengths.

The colors of objects are also partly dependent upon the relative sensitiveness of our eyes to the different rays of light. They are especially sensitive to the rays we perceive as green and yellow.

The various chemical compounds in plants absorb certain light rays and reflect others. We receive our color impressions from the reflected rays. As a matter of convenience we call these compounds pigments and we ascribe to them the colors perceived through the eye when light is reflected from them. Thus we speak of green pigments, yellow pigments, and various others from red to violet. Among the most important pigments in plants are *chlorophylls* (leaf green); the *carotenoids* (including carotenes and xanthophylls), varying from pale yellow to orange-red; and the *anthocyanins,* varying from red through blue to violet.[1]

Pigments and the colors of leaves. The colors of certain leaves—for example, the purple-leaved coleus and canna—may result from a combination of all these pigments. The anthocyanins may occur in the outer cell layers of the leaf, the chlorophylls and carotenoids in the inner cell layers. When a red leaf is placed in hot water the anthocyanins disappear from the cells into the water and the green color of the chlorophyll within becomes evident. The chlorophylls and carotenoids may be dissolved from the leaves by alcohol, and then separated from each other by appropriate chemical means. Carotenoids are always present in green leaves, but their presence is obscured by the chlorophylls until the latter disintegrate. Surprising as it may seem, the carotenoids may be present in as large amounts in the leaves of midsummer as in the yellow autumn leaves.

In many common trees and shrubs the anthocyanins are formed mainly in the autumn; in others, such as certain varieties of maple, the young leaves also may be red. The anthocyanin in purple varieties of beech, plum, hazel, and barberry is evident throughout the growing season.

[1]

Pigments	Apparent Color	Chemical Composition
Chlorophyll a	Blue-green	$C_{55}H_{72}O_5N_4Mg$
Chlorophyll b	Yellow-green	$C_{55}H_{70}O_6N_4Mg$
Carotenes	Yellow to red	$C_{40}H_{56}$
Xanthophylls	Yellow	$C_{40}H_{56}O_2$
Anthocyanins	Red to blue	Various combinations of C, H, and O

The anthocyanins are very complex substances composed of a few fundamental compounds (anthocyanidins) combined with various sugars and sometimes with various organic acids also. They are soluble in water and occur in the solutions in the plant cells. Some of the anthocyanins, such as those in certain varieties of apples and peaches, are formed only in light especially of short wave length. Others, such as those in red beets and radishes, may be formed in darkness. Chlorophylls and carotenoids are not soluble in water and are formed in definite bodies in the protoplasm known as plastids. The carotenoids of plants when eaten by animals reappear in yellow cream, yellow body fat, egg yolks, and butter. Carotene has recently been shown to be the forerunner of vitamin A. The molecule of the vitamin is just one-half of the carotene molecule.

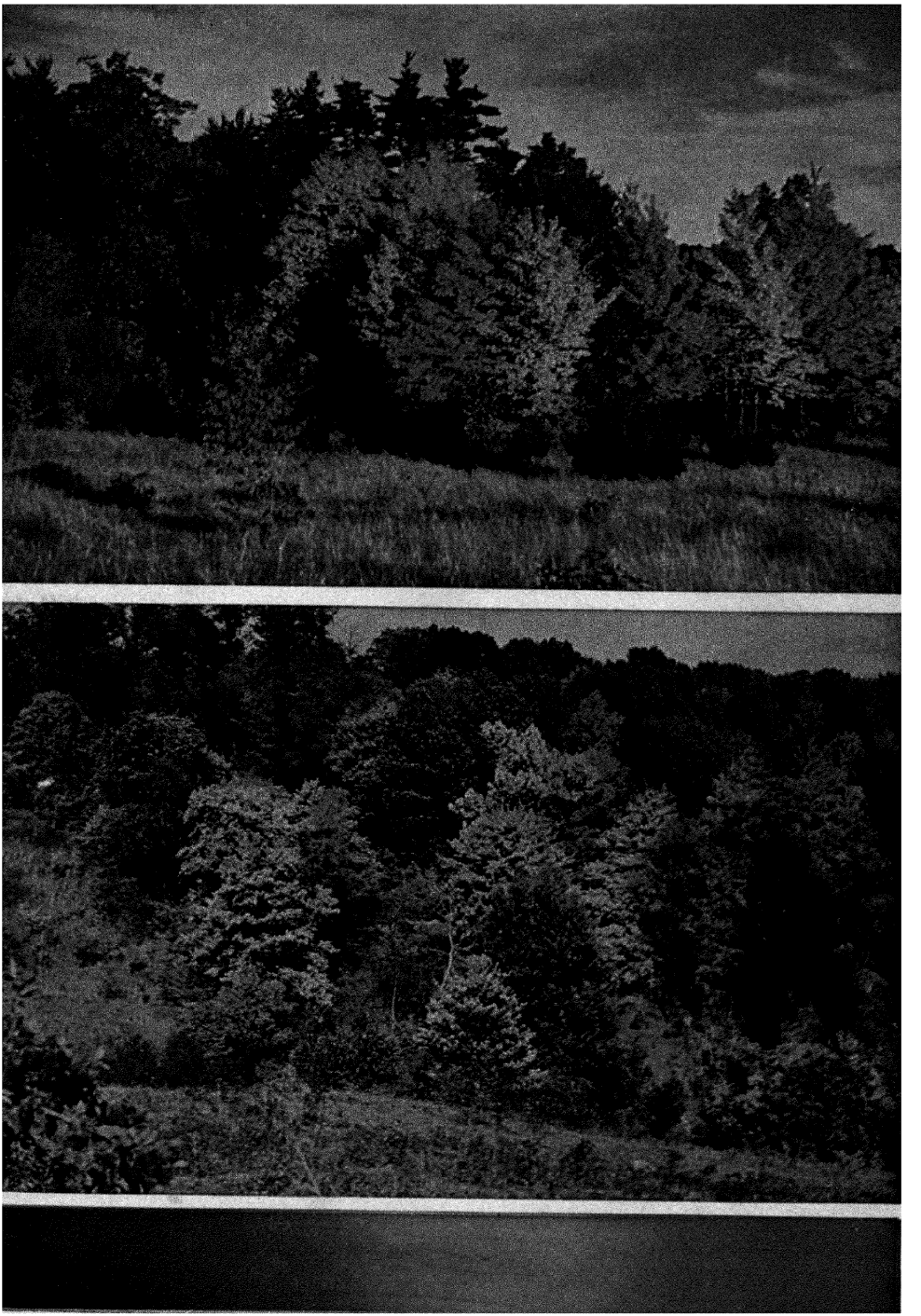

PLATE II

Above: Autumn coloration under cool moist conditions, Cook Forest, Pennsylvania. Photo by G. S. Crowl. *Middle:* Autumn coloration under warm drought conditions, central Ohio. The broad-leaved trees in both pictures are the same species. Photo by G. S. Crowl. *Below:* The spectrum of sunlight.

Many other examples of leaf pigmentation may be found in every community.

Pigments not limited to leaves. Of course these pigments are not limited to the leaves of plants. The presence of chlorophyll in most herbaceous stems and the young stems and twigs of woody species is familiar to all. Likewise, certain parts of flowers are usually green, and the term "green fruits" has come to be a synonym of young fruits in common speech. Many varieties of fruits remain green when ripe, while in others the chlorophyll disintegrates and the associated yellow pigments become more evident. In still others anthocyanins partially or wholly mask the yellow. Some seeds, such as those of certain varieties of peas and beans, are green. Chlorophyll is formed in the aerial roots of many orchids and in the roots of many other plants when they are exposed to light.

The carotenoids seem always to be present wherever chlorophyll occurs. They may also occur in the absence of chlorophyll. Carotenoids are the underlying cause of the yellow and orange colors of the flowers of zinnias, sunflowers, and goldenrods; of the fruits of oranges, lemons, and tomatoes; and of the seeds of corn, peas, and clover.

The anthocyanins are most conspicuous in red, purple, and blue flowers and fruits; but purple cabbage, potatoes, popcorn, and beets exemplify their common occurrence in other plant parts. Among the fungi (molds, lichens, mushrooms) other pigments may be as brilliant and varied as are those in our common green plants.

Pigment formation dependent upon both heredity and environment. Among the common plants one may find some species that lack anthocyanins, while others are without chlorophyll and carotenoids. The absence of a pigment from a plant, or a part of a plant, may be due to its heredity, its stage of development, or some condition in the environment of the plant. Chlorophyll is not formed in the cells of toadstools or in "Indian pipe" (Fig. 19) in any environment. Neither is it formed in some parts of variegated leaves under any circumstances. The other pigments also may be absent from certain plants regardless of the conditions under which they develop. The absence of pigments in these plants must be due to the hereditary constitution of the plant.

Environment and chlorophyll. Any condition that is necessary for the maintenance of the plant is indirectly essential to the formation of plant pigments. There are, however, certain conditions that are more directly related to it. In most plants light seems to be necessary for the making



FIG. 19. Indian pipe (left) and pinesap (right), two seed plants that lack chlorophyll. These plants are common in moist woods where there is a thick layer of leaf litter and humus on the soil.

of chlorophyll. We are all familiar with blanched celery in which the part deprived of light lacks chlorophyll, or with the white and yellow potato sprouts that develop in a dark cellar. During the warm nights of early spring bluegrass grows rapidly, and in the early morning the base of the blade that grew during the night is disclosed by its lack of chlorophyll. But in some plants light is not necessary for the formation of the green pigments. Green seedlings of spruce, pine, and other conifers may develop in the dark. Grapefruit and lemon seedlings, certain algae, and the sporelings of mosses and ferns may synthesize chlorophyll in darkness if they are supplied with sugar.

Sugar is one of the substances from which the chlorophylls are made, and from the formulas of chlorophyll (page 28) it is evident that compounds of nitrogen and magnesium are also utilized. Experiments have shown that manganese and iron are essential to the formation of chlorophyll, but they do not constitute a part of the chlorophyll molecule. The seedlings of some green plants growing at temperatures below

50° F. may fail to form chlorophyll, and unless the temperature is raised they ultimately die.

Environmental effects on carotenoids. The formation of the yellow pigments is also dependent upon certain environmental conditions. The seedlings of some varieties of corn and other plants are conspicuously yellow when growing in darkness; others, such as oats, are colorless under the same conditions and become yellow only when exposed to light. Perhaps there are certain factors that might be substituted for light in these cases, but they have not been discovered. Seedlings in which chlorophyll is made in the dark also contain carotenoids.

Anthocyanins and the environment. The roots of some plants, such as beets and radish, become red or purple in darkness; but light is necessary for the formation of anthocyanins in most leaves and fruits. In some instances the blue and violet rays are necessary. In both leaves and fruits intensity of color is increased by abundance of light, relatively low temperature, and a low supply of nitrates and certain other inorganic ions in the soil. Apparently these environmental conditions influence the formation of anthocyanins partly through their influence on the sugar content of the cells, but many other conditions within the cells are necessary for the formation of anthocyanins.

Leaves and fruits on the same tree or on the same variety of tree in different local situations may differ widely in the amount of anthocyanin they contain. Peaches in the top of the tree, and apples fully exposed to the sunlight are redder than those inside the crown and shaded by the outer foliage. The more intense coloring of fruits from the Northwestern States as compared with those from the Eastern States exemplifies this same principle. Low night temperatures also are very important in the accumulation of sugar and the formation of bright colors in apples.

At low temperatures anthocyanin formation increases in many evergreen plants; for example, the leaves of certain varieties of juniper and arbor vitae become copper-colored in autumn, and similar changes occur in many heaths, of which the cranberry is an example (Plate III).

The intensity of anthocyanin colors of flowers may vary with light intensity. The red color in some flowers is associated with an acid condition, and blue with an alkaline condition. If a red geranium petal is crushed on a blotter and held alternately near ammonia and acetic acid, one may see these color changes. Similar color changes may also be seen in the uncrushed petals. This change in color does not occur in all anthocyanins because of the presence of certain ions, such as potas-

sium. The flowers of the cobaea vine change from green to red, and finally to violet, as they fade. Some rose flowers are pink when the buds unfold and bluish when they fall. Flowers of the French hydrangea are blue when the plants grow in acid soils containing salts of aluminum. They are rose colored when the plants grow in alkaline limestone soils where the aluminum salts are insoluble. It must be remembered that the anthocyanins form a very large group of chemical compounds, and the behavior of the pigments of any particular plant may be explained only by the properties of the particular pigments present in that plant.

Deciduous and evergreen habits. Another striking autumn phenomenon is the falling of the leaves from many species of plants. This has been shown to be definitely related to the shortening daily period of light. During the summer a specialized layer of cells, called the *absciss layer*, forms at the base of petioles and leaflets. The subsequent disintegration of this layer may be started by conditions within the leaf brought about by a variety of external conditions such as drought, change in length of day, low temperatures, or leaf injuries. Hence any one, or all, of these conditions may bring about leaf fall. Trees and shrubs that lose all or nearly all of their full-grown leaves annually are said to be *deciduous*.

In contrast to deciduous plants are those in which the life of any one leaf extends through several years. These plants may have either broad or needle leaves and their appearance varies but little from season to season; the most familiar examples are the *evergreen* trees and shrubs. Many herbaceous plants also have green leaves during the winter, as for example, the common dandelion, evening primrose, teasel, and chickweed. These also might be classed as evergreens.

Dormancy and periodicity. The gradual lowering of the temperature and decrease in the length of the daily light period lead not only to pigment changes and leaf fall, but to the death of many plants that started from seed the preceding spring. Some part of the plant, however, remains alive and dormant throughout the late summer, autumn, or winter. The part or parts that remain alive and dormant vary greatly with the kind of plant. If the plants have completed one life cycle—including germination of the seed, vegetative development, flowering, fruiting, seed formation, and death—within a single warm season, they are called *annuals*. The dormant organ of such plants is the seed. The seeds of some annuals, however, may germinate in the autumn; the plants pass the winter in the vegetative condition and bear seed the following spring.

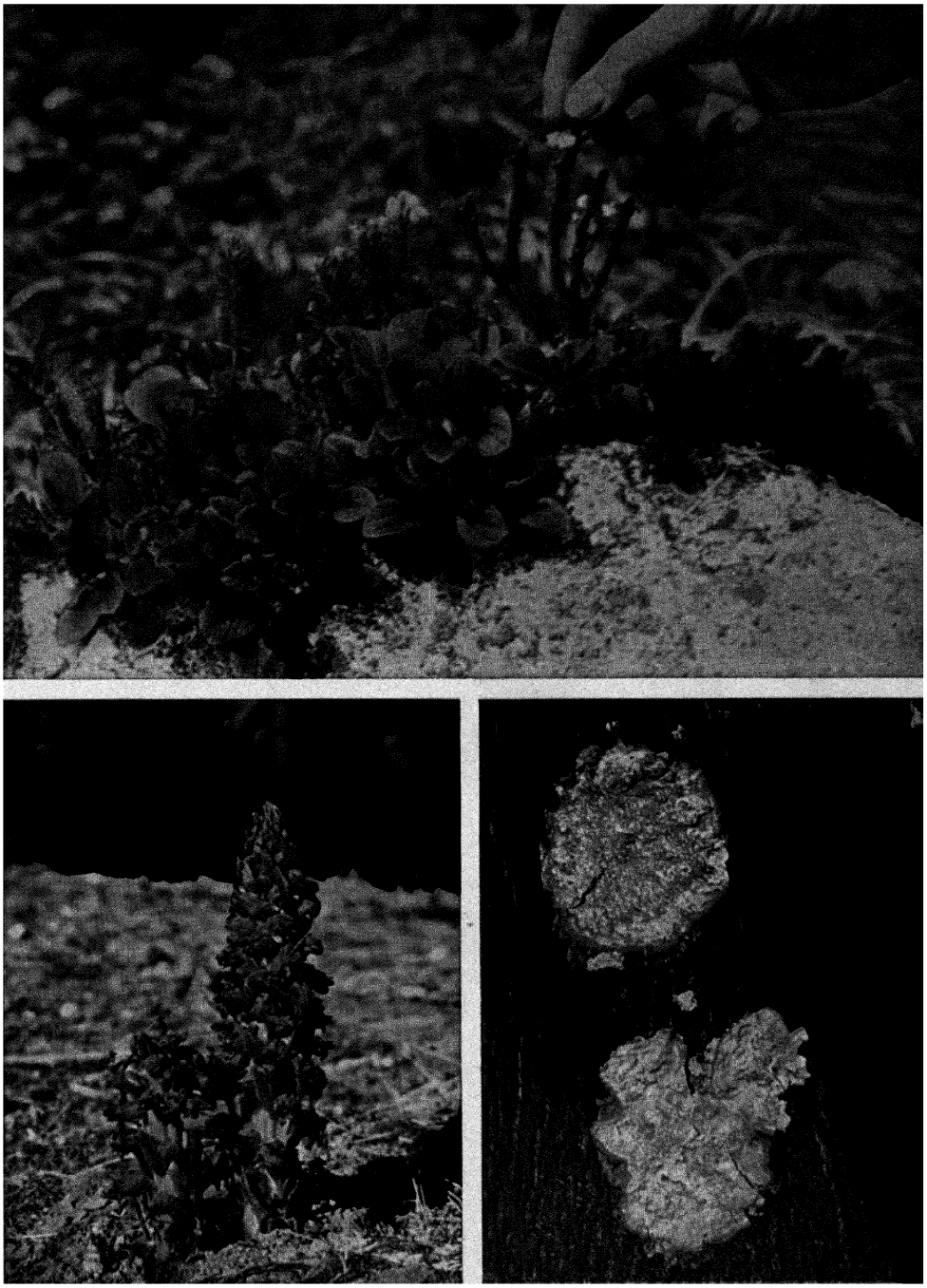

PLATE III

Above: Tundra plants, including a 40-year-old nearly prostrate willow, White Horse Pass, Alaska. Photo by W. H. Camp. *Below* (*left*): The snow plant (*Sarcodes*) parasitic on fungi in the pine forests of the Sierra Mountains, California. The plant develops soon after the snow melts. Photo by W. H. Camp. *Below* (*right*): A Florida lichen, in which the fungus is parasitic on purple bacteria. Photo by G. S. Crowl.

When the life cycle from seed germination to seed formation covers a part of two warm seasons the plant is called a *biennial.* Shepherd's-purse may grow as an annual or as a biennial in certain climates, and wheat is cultivated both as "winter wheat" and as "spring wheat." Varieties of wheat have been selected for each of these growth regimes.

During the life cycle of many biennials the first season of growth ends with the formation of a thickened root, a short stem, and a rosette of leaves near the soil surface. These young plants remain dormant during the winter and in the second growing season their life cycle is completed by the development of upright stems, flowers, fruits, and seeds. Then the plant dies. Whether certain plants grow as annuals, biennials, or perennials depends upon the temperature, length of day, and length of the growing season to which they are exposed.

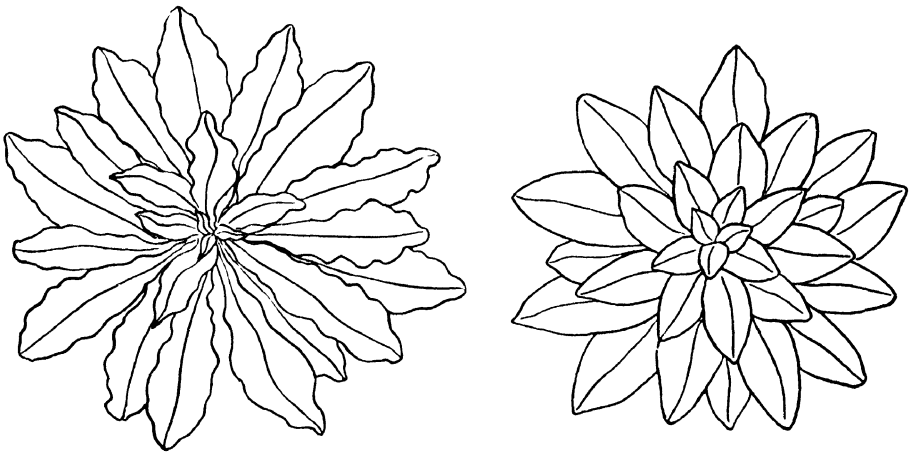

FIG. 20. Diagram of winter rosette of leaves of teasel (A), and of evening primrose (B).

The *perennial herbs* are like annuals and biennials in having a vegetative stage previous to the formation of flowers and fruits, but differ from them in having continuous vegetative growth and seed formation for many successive seasons. The annual active period of growth of perennial herbs is followed by a dormant one when most of the living plant is underground, with no parts extending much above the soil surface. Some of these plants have "winter rosettes" (Fig. 20) of leaves, others have very short lateral branches with small leaves, and still others have large buds above ground. Some of the perennial herbs may continue living indefinitely. Perhaps some have been living in their

present localities for centuries; but since a part of the underground roots, or stems, dies each year and new parts are added each year, the age of the oldest part of the plant body is rarely more than 3 to 10 years.

Trees and shrubs are *woody perennials*; they may live 5 to 10 years or longer before they begin to bear flowers, fruits, and seeds. Any horticulturist or forester will tell you that there is great variation in the abundance of reproductive structures in trees from year to year and that certain trees bear fruits and seeds only once in several years. This periodicity is dependent in part on weather and soil conditions, and in part on heredity.

Winter aspect. The most distinctive feature of plants in winter is the dormancy of most plant organs (Fig. 21). The internal causes of



FIG. 21. A forest in winter when all the aerial parts of plants are dormant. Photo by C. H. Jones.

dormancy characteristic of late summer and autumn usually disappear during the winter months, but owing to low temperatures no growth occurs. Many plants will start developing at this time if they are moved into a greenhouse.

Nevertheless, some processes continue within plants that have every

appearance of being dormant. Roots develop slowly in unfrozen soil, and there may be some movement of materials within the plant body. In plants with green parts (winter wheat, bluegrass, and evergreen trees and shrubs) food manufacture may occur when daytime temperatures are above the freezing point. Witch hazel and alders may flower during winter thaws, as well as during late autumn and early spring.

Winter and early spring are the best periods in which to study the characteristic buds, twigs, and bark of the woody perennials. By means of these characteristics one may readily learn to identify trees in winter.

The leaves of temperate evergreens vary in their endurance of freezing temperatures. A sudden exposure to low winter temperatures during midsummer kills them. Most of them, however, withstand temperatures well below the freezing point after they have become "hardened" by exposure to the gradual changes in temperature during autumn. But they do have limits below which injury or death results from low temperatures. In some species injury results only when the low temperatures continue for several days. Others are killed by exposure to temperatures below freezing for a few hours. Twigs and parts of larger stems also may be killed by low temperature. In any part of the temperate zone trees and shrubs may be "killed back" by extremely low temperatures.

The amount of "winter injury" varies from year to year, and many interesting problems occur to the careful observer. Winter injury may result from low temperature alone; but in many instances it results from a drying up of the plant during sudden thaws in late winter or in early spring while the soil is still frozen. The roots of winter wheat and other grasses are often broken or pulled from the soil as it is heaved by the formation of layers of ice beneath the surface of the soil. When subzero temperatures occur, the water in the buds, twigs, and smaller branches is frozen. Still lower temperatures may even freeze the water in the trunks of large trees. A sudden drop to a very low temperature may result in the splitting of the wood and bark.

There is another effect of winter that is quite beneficial, or even necessary, to many plants. Many seeds and buds do not germinate readily unless they have been exposed to temperatures near the freezing point for several weeks. Many plants, such as blueberries, unless exposed to a low temperature in the dormant period, do not grow well during the following season. Neither of these cases of "winter conditioning" depends upon actual freezing; indeed, many plants grow best after an exposure to a temperature of 5° to 10° above the freezing point for a

few months. Tulip, hyacinth, and narcissus bulbs that are to be "forced" into early blooming are planted out-of-doors; after several weeks of winter temperatures they are brought indoors. Without this low-temperature treatment of the bulbs, the new plants will develop poorly and bear malformed flowers or none. Inquiry among local nurserymen will probably disclose other practical problems connected with the winter season.



FIG. 22. Springtime: Winter dormancy is broken and the beech leaves are unfolding.

Spring aspect. The lengthening of the daylight period and increase in temperature bring to an end the dormant period of plants. Lawns and fields begin to green through renewed growth of dormant leaves and buds. Buds on many trees and shrubs enlarge and a new set of twigs and leaves develops (Fig. 22). This is the best time of year to see that the buds of woody plants are stem tips bearing either leaves or rudimentary flowers, or both, usually with an outer covering of scales. Examination of trees and shrubs at this time will disclose not only these three types of buds, but also several ways in which buds "open" and enlarge. This is the time of year when you can learn by your own observations:

which buds on different plants open first and from what buds the current year's branches develop, whether the extension of the main stem or branch always develops from the terminal bud, and if the branches from all lateral buds grow equally. You can also ascertain whether leaves and flowers develop on twigs from the same or from separate buds, which of our common trees blossom before the development of leaves, and whether these flowers are borne on twigs of the previous year or only on new twigs. These are but a few of the questions that may be answered by a study of woody plants in the field.

With the coming of spring countless millions of seedlings appear in every unoccupied plot of ground. New branches develop on perennials and biennials, and leaves are followed soon after by masses of flowers of every imaginable hue. Spring is the period of most rapid development in most plants, partly because the overwintering parts have been "conditioned" by the low temperature and partly because of increased light, increased length of day, and an abundance of available water in the soil. After growth has started it may be retarded either by drought or by low temperatures. On the other hand, elongation of the stems and expansion of the leaves of most trees and shrubs stop within a few weeks, even if temperature and moisture conditions continue unchanged. The growth of new stem segments is definitely limited by internal conditions and their elongation usually ceases by late May or June in northern latitudes. Sprouts from stumps and pollarded trees continue to elongate for several weeks more.

This is the period when many of the flowering plants of densely shaded woods have their annual development, flower, fruit and return to dormancy. In the open there are many plants in which the period of development continues into the summer and autumn before flower, fruit, and seed formation closes the annual cycle.

Spring, then, is the period of most active growth of roots and shoots of woody plants. It is the period of most active utilization of food, and the period of rapid respiration and food synthesis. The high rates of these processes stand in sharp contrast to their much lower rates during the winter season.

Summer aspect. With the coming of the longest days temperatures are high, and available soil water on the average begins to decline. Growth of plants, as a whole also declines, but many of the flowers of springtime are now being followed by fruits and seeds.

The development of branches and the enlargement of trunks of trees and shrubs are greatly reduced. Soil water declines to the point where many plants with shallow root systems wilt, and summer leaf fall may take place. Some plants or plant parts may become dormant as a result of high temperature and the long daylight period.

There are fewer plants in bloom in midsummer than in spring or autumn. The smaller grasses have attained maturity and completed their life cycles. The larger grasses, such as corn, continue development and bloom in summer. Summer is the period of greatest food accumulation in the stems and roots of biennials and perennials. It is also the period when fungi and bacteria cause numerous plant diseases and rapid decay of organic matter. Insects also have reached maximal abundance, and their injuries to leaves and stems and fruits become most apparent.

Some plants bloom only when the days are long and the nights are short. As a result the summer season is the time of flowering of corn, clover, mallows, cotton, and many other plants.

As the days become shorter at the close of summer and the temperatures decline, increased water is available in many parts of the United States because less of the rainfall is lost by evaporation. The water relations of plants are improved over those of the summer and the growth of many herbaceous plants increases. Not infrequently a second wave of flowering occurs in some plants, such as violets, that bloom abundantly during the spring months.

But the further decline in temperature brings the conditions of autumn, and we have completed our very brief view of the more noticeable seasonal phenomena. We have observed that certain vegetational aspects are characteristic of each season; that some phases of growth belong to one season rather than to another; and that dormancy, growth, maturity, and death of plants form a regularly recurring cycle.

The problems of plant science are all about us and each season brings its own challenges to investigation and understanding. We need not confine our outdoor study of botany to a single environment, to one season of the year, or to any one locality.

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CHAPTER V

LOCAL PLANT COMMUNITIES

Under natural conditions plants live in communities; no plant lives alone. A potted fern at a window appears to be alone in an environment consisting only of the physical factors of the soil, atmosphere, water, gravity, and radiant energy from the sun. Its roots, however, are surrounded by millions of microscopic plants and animals whose numerous activities may influence the development of the fern. As we shall see later, some of the activities of these minute organisms are beneficial to the larger plant, others are detrimental. Some of them are known to cause diseases of the roots or of the whole plant.

Plant communities. A lawn is a familiar plant community in which the development of each individual plant may be influenced by the plants that surround it. The intermingling of grasses and clover with dandelion, plantain, and several other weeds is an illustration of the fact that plant communities in nature are mixed populations composed of several kinds of plants. Only in pure cultures, carefully prepared in laboratories, may one expect to see plant communities composed of but a single species of plant. In the practical consideration of certain communities one may choose to disregard the microorganisms and look upon a field of corn, of wheat, or of any cultivated crop as a community of only one species if all visible weeds have been removed. The forester may even disregard all the plants in a forest community but the trees, and speak of a pure stand of beech or of hemlock. Usually in any mixed population of plants a few species are much more abundant or modify the habitat more than others; they are referred to as the *dominant species* of the community. Plant communities are named according to their dominant species; for example, a bluegrass lawn, a pigweed community, a tall-bluestem prairie, an oak forest, a beech-maple forest, an elm-ash-silver maple forest.

Mutual effects of plants within a community. In lawns, pastures, or golf courses in which Kentucky bluegrass is the most abundant and dominant plant, the presence of the grass in some way interferes with

the growth of clover and weeds. If the bluegrass is carefully removed, the weeds and clover rapidly increase in abundance. Similarly the presence of weeds interferes with the growth of bluegrass. When one removes the leaves of a single large dandelion plant from a lawn for the first time he is usually amazed by the area of soil from which bluegrass was excluded by their presence. Trees with low branches may interfere with the growth and dominance of bluegrass in a lawn unless the trees are very small. Many people plant grass seed beneath such trees every autumn. The grass grows well throughout autumn and during the follow-

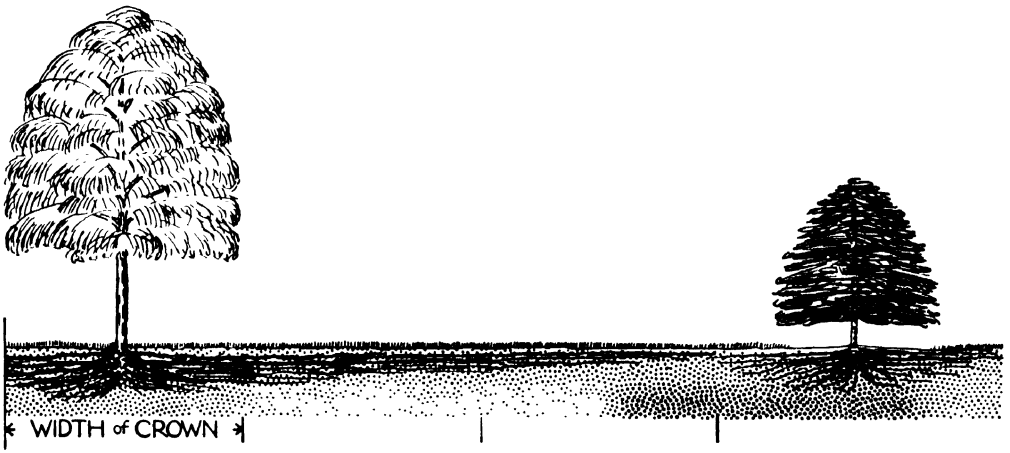

FIG. 23. Bluegrass may grow beneath a tree if all the branches of the tree are several feet above the ground. The diameter of the root system of a tree in a lawn may be as much as 5 times the diameter of the crown of the tree.

ing spring, but by late June or early July it becomes yellow and dies. If all the branches of a tree are high above the ground, bluegrass may continue to grow indefinitely beneath it (Fig. 23).

Succession. Since each plant in a lawn is influenced in some way by the presence of other plants, the relative abundance of bluegrass or of any other species of plant in the lawn may not remain the same from year to year. During one growing season some species may increase while others decrease in abundance. That is, the composition of a mixed population of plants is not constant; it changes in time as a result of the mutual effects of the plants upon each other and of increase and decrease in light, water, soil fertility, and other external factors. It is this instability of a mixed population of a community that concerns the owner of a beautiful lawn. Gradual changes in the relative abundance of the constituent species may in time result in a community that is very

unlike the original one. Some of the species of the first community may be entirely eliminated and other species may migrate into it from neighboring communities. Through such changes one plant community may be gradually replaced by another, a process that is referred to as the *succession* of plant communities.

The principles of dominance, changes in mixed populations, and succession referred to above are abundantly illustrated by local plant communities in lawns, parks, vacant lots, eroding slopes, abandoned farms, and forest remnants. All of these contain excellent field material that may be studied first-hand. Lawns are especially valuable materials for study because they may be observed conveniently and they probably attract the interest and add to the pleasure of more people than most other types of plant communities. Furthermore, they are similar to the communities of cultivated grasses in pastures, golf links, parks, and college campuses; consequently, many of the facts and principles discovered about one of these communities may apply equally well to the others. In this chapter we shall refer principally to the more evident facts about local plant communities that occur in the Central States. Explanations of many of the observations will appear in later chapters.

Changes in mixed populations of plants. The results of a very exact study of changes in the composition of a mixed population of plants in a pasture in New York during a five-year period are represented by the diagram in Fig. 24.

Note changes in relative abundance of the seven species of plants during the year in which the seeds were sown, and for each of the next five years. The change in composition of the plant population from year to year is merely the result of a relative increase in abundance of certain species and a relative decrease of others. Red clover is entirely eliminated at the end of the third year. Here then is an example of a change in a mixed population of plants over a period of years that is due neither to changes in the heredity of the plants nor to changes in climate or soil. It is due to the characteristic differences in the growth of the several species of plants and to their effects upon each other. One of the most important changes is the gradual increase and dominance of bluegrass.

One may ask why lawns, pastures, and parks everywhere do not in the course of time become dominated by Kentucky bluegrass. An analysis of the areas not dominated by bluegrass reveals that they are either very wet, very dry, very acid, sandy, shaded, or deficient in certain inorganic salts, especially of nitrogen, or that they are areas where the soil tem-

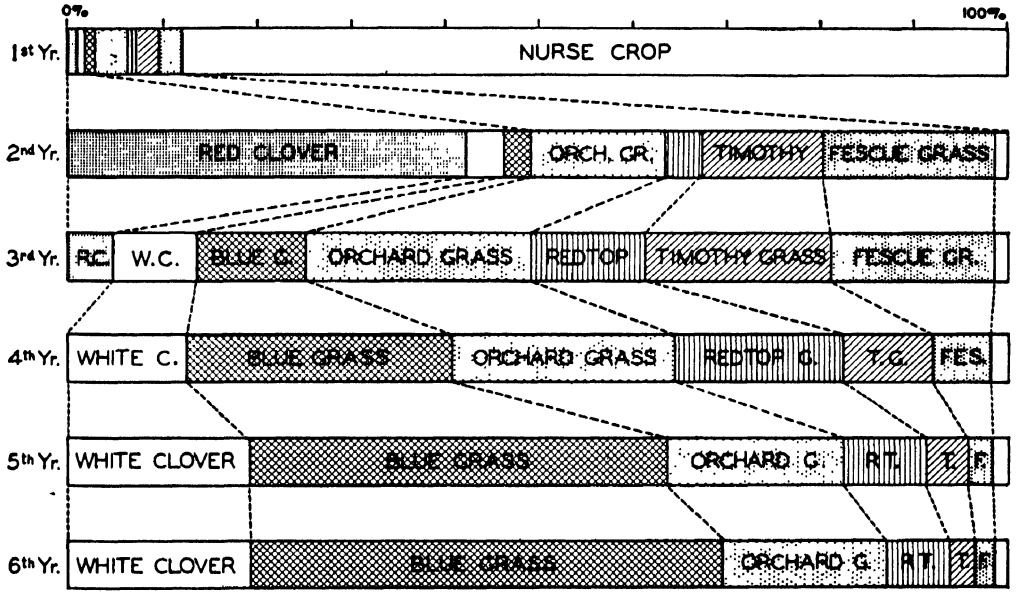

FIG. 24. Diagram of changes that occurred in a mixed population of plants in a pasture during a period of five years following the first year, when the seeds were sown with those of a nurse crop, such as oats or rye. The comparative yield of each kind of plant from year to year is given. Bluegrass is the only species that continued to increase in amount every season. Data from R. G. Wiggans.

peratures are high in summer. Evidently bluegrass can become the sole dominant only in those areas in which each of these several environmental factors does not exceed a certain intensity. Where one of these factors is exceedingly high or low, a bluegrass lawn may be obtained only if one is willing and able to adjust the environmental factors to an intensity that is more favorable to the growth of bluegrass. Kentucky bluegrass is most likely to become dominant in lawns with moderate moisture and temperature, abundant light, and loamy soils that are slightly acid but rich in salts of nitrogen, phosphorus, and potassium. With persistent effort one can adjust the relative amounts of most of these environmental factors.

Preference may be given, however, to another kind of grass that will grow better than Kentucky bluegrass under the local conditions. There are several varieties of bent and fescue grasses that grow well in soils of greater acidity. Consequently in the acid soils along the Pacific Coast and in the New England States bent grass lawns are more common than they are in the Central States. Where the light is insufficient for the growth of Kentucky bluegrass, certain varieties of bent and fescue

grasses may still grow well. In cool temperate climates other species of bluegrass (*Poa trivialis* and *Poa annua*) are frequently planted in shaded parts of lawns. These two species of bluegrass do not survive on hot dry soils during the summer months. Kentucky bluegrass is also limited in this respect. In the Southern States one may expect to find Kentucky bluegrass as a dominant plant in lawns only at high elevations or where the surface temperature of the soil is reduced by partial shade. The characteristic lawn grasses of these states are Bermuda grass during the summer months and Italian rye grass during the winter months. Near the Gulf borders carpet grass, centipede grass, and St. Augustine grass dominate the lawns.

The above facts about lawns and pastures sufficiently demonstrate how the composition of a plant community is influenced by the climatic and soil factors, and also by the effects of plants on each other. They also illustrate that certain biological facts and principles may be applicable in theory and practice in any part of the world. On the other hand, there are many facts and principles that cannot be generally applied because of local and regional diversity in soil, climate, and available species.

Owing to the great diversity in cultivated plants and in environments, at least one agricultural experiment station with several substations is maintained in every state of the Union, and the effects of local differences are continuously investigated. Anyone who wishes to supplement his own observations on lawns or other economic plant communities will find valuable assistance in the weed manuals and other publications of the nearest experiment station.

Bulletins on lawn-making frequently contain information about certain animals that destroy lawn plants or bring about changes in the composition of plant communities. Recent publications are the most desirable because some of the earlier recommendations for the care of lawns have been revised as new facts were discovered. For instance, field tests have shown that the traditional method of applying lime to all grasslands not only is unnecessary but may even bring about undesirable results in certain types of soils. Many owners enjoy making their own tests by applying various fertilizers to small strips in the lawn. Such tests are reliable, inexpensive, and a source of valuable information from year to year. Salts valuable as lawn fertilizers[1] are often mixed with

[1] In experiment station records the amounts and kinds of these salts that should be added to the soil are usually indicated by a brief statement such as 1 lb. of 10-6-4 fertilizer mixture per 100 sq. ft. The abbreviation 10-6-4 refers to the percentages of certain compounds of nitrogen, phosphorus, and potassium respectively in a fertilizer.

inert matter and sold on the market under the erroneous name of "plant foods." This misleading use of a name is one of many examples in which a scientific truth is ignored and denied for alleged commercial advantage. We shall learn later that the food used by plants is the same as that used by animals.

A change in the proportion of salts containing nitrogen, phosphorus. and potassium may affect the composition of a plant community. For example, soluble nitrogenous fertilizers may result in an increase in the amount of bluegrass and a decrease in the amount of clover, while phosphate fertilizers may result in a marked increase in the amount of clover. In the North Central States many pastures are dominated by poverty grass and weeds; bluegrass and clover are present but not abundant. Agronomists found, by means of hundreds of demonstration plots in these states, that the addition of 300-400 pounds of acid phosphate per acre results in a marked change in the composition of this pasture community. They also showed that this change will occur without the addition of lime except when the soils are very acid. At first there was a rapid increase in the amount of clover, followed later by an increase of bluegrass. Within two years these pastures had become dominated by clover and bluegrass, and by the close of the fourth year they were bluegrass pastures. For the farmer this procedure increases the value of the pasture from 200 to 300 per cent, and for others there is the pleasure of resting the eye on luxuriant green pastures.

There is also an interesting biological background to this sequence. The increase in clover followed the application of phosphate and resulted in conditions becoming favorable to bluegrass. The practice of using clover and other legumes as a means of enriching the soil is as old as the history of agriculture, but it was not known until near the close of the last century that the enrichment is due to the process of nitrogen fixation by bacteria that inhabit the nodules of the roots of legumes.

Animals, like plants, are dependent upon compounds containing certain kinds of mineral elements. They obtain nearly all of these compounds either directly or indirectly from plants. We, for instance, obtain them when we eat vegetables, meat, and dairy products. In this way some of the phosphate added to the pasture is gradually removed by the grazing animals. Some of it also disappears from the land by erosion and in drainage water. After several years the phosphate supply in the pasture gets so low that clover and bluegrass begin to decrease in

abundance, and poverty grass and weeds again increase. When clippings are continuously removed from lawns a similar loss in inorganic salts results and the growth of bluegrass and clover declines.

The succession of plant communities. One might refer to the demonstration cited above as an example of a poverty grass and weed community being succeeded by a bluegrass-clover community. The succession in this case, however, consists only of a change in the relative abundance of species already present. Succession in which there is also the added feature of species invading the community from neighboring communities may be observed locally by noting (1) the kinds of pioneer plants that first occupy an eroding soil slope or some other bare soil area, and (2) the kinds of plant communities that successively follow each other on this same area through the years. One may shorten his period of observation and obtain a similar story by noting the kinds of plant communities that now occupy artificially made slopes of different known ages. They may be found around any town where local construction work involves the movement of large quantities of soil.

The pioneer plants that occupy such bare areas must of course start from seeds that have been carried to the area by some means, and they consist of annuals, biennials, and perennials that can survive in the extreme environmental conditions that exist there. Most seedlings perish in such situations. The presence of the pioneer plants brings about changes in the habitat. They check erosion, increase the shade, and thus decrease the temperature of the soil surface on hot summer days. Certain kinds of plants that were unable to survive in the pioneer conditions may then develop on the area and increase in number. Their abundance may bring about conditions in which many of the pioneer species are unable to survive. One of the most striking changes that occur on such areas is the gradual disappearance of most of the pioneer annuals and biennials, and the final dominance of perennials. Perennials dominate the vegetation of the world, except in pioneer habitats.

This occupation of bare soil areas by a pioneer plant community, the subsequent elimination of the pioneers, and the succession of other plant communities exemplify some of the fundamental processes occurring in the revegetation of areas on which the original communities were destroyed by man, by fire, by wind, or by water.

As a nation we have recently become much concerned about the rapid run-off of water from our agricultural lands and the amount of soil car-

ried away from them (Fig. 25). Soil that has been thousands of years in forming under the influence of climate, larger plants, and microorganisms is being washed from the land to the sea in some places at the rate of more than 70 tons per acre annually. The subsoil that is exposed



FIG. 25. During the century and a quarter that the plants in this cemetery in Ohio have checked erosion, sheet erosion on the adjacent gently sloping farm land has removed the upper three feet of soil. Photo by C. H. Jones.

after a few years is a very poor habitat for most plants (Fig. 26). Where the soil is completely covered with vegetation the amount of erosion annually is so small that it can scarcely be measured; the run-off of water after rains is also reduced to a minimum. One of the important problems in any worth-while soil conservation program is to discover better methods of speeding up the natural processes of revegetation wherever practicable, and of preventing further unnecessary destruction of established vegetation.

A first-hand study of local plant communities that occur on lawns, campuses, eroding slopes, vacant lots, abandoned farms, or in forest remnants introduces one to many botanical facts and principles. It also raises numerous questions about the social behavior of plants, which in turn depends upon the effects of the environment on the physiological processes within these plants. These processes and their relations to environment and plant behavior are subjects of discussion in later chapters. The study of plant communities may lead not only to their biologi-

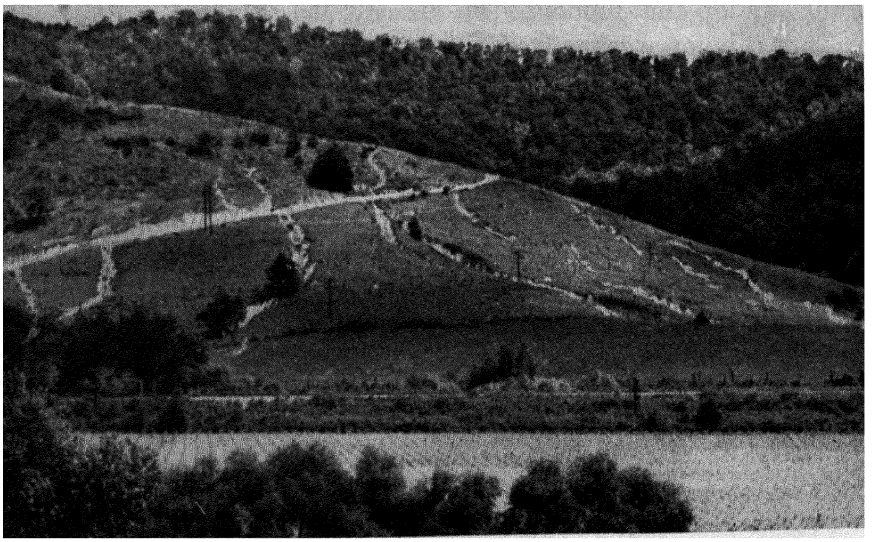

FIG. 26. One way of destroying a valuable heritage. The fertile top soil that was formed during thousands of years has been eroded from the hill in the center of the picture through bad farm practices. Photo by G. S. Crowl.

cal analysis, but also to an understanding of their economic, esthetic, and recreational possibilities. For the beginner those interests and appeals are most valuable which come to him through his own observations.

Summary. The vegetation of any soil area is a mixed population of several kinds of plants, some of which are readily visible, others microscopic in size. The relative abundance of the different kinds of plants in the mixed population, and also the kinds or species of plants present in it, vary from place to place. These variations in the composition of plant populations result in the formation of many different kinds of plant communities, which we may recognize and name on the basis of the more abundant or dominant species. The composition and distribution of these communities are dependent upon the influence of the plants upon each other, upon the animals that are present, and upon the factors of soil and climate. Owing to all these factors, the composition of a plant community on a given area changes in time. This change may be rather rapid or almost imperceptible, but it finally leads to one community being succeeded by another. The change in composition may consist only of changes in the relative abundance of the species already present in the community, or it may be due in part to the invasion of the com-

munity by species from neighboring communities. These changes are not due to an alteration in the heredity of the species involved. Changes in heredity, however, must not be overlooked, for they are known to occur at times, as we shall see in later chapters. The processes of revegetation of denuded lands are important in conserving soil.

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CHAPTER VI

POINTS OF VIEW IN THE INTERPRETATION OF PLANT BEHAVIOR

We have been concerned thus far mainly with the acquisition of easily observable facts and relations. We have seen how some of the resemblances and differences among plants may be used in distinguishing and naming trees, in observing seasonal changes in plants, and in studying the mixed plant populations of lawns and other local areas. There is a further use of facts and observations that leads to a clearer understanding and interpretation of the plant world.

The how and why of natural phenomena have always challenged thoughtful persons, and out of their observations and experiments have come a vast store of information and a great improvement in economic and social welfare, as well as more adequate explanations and more discriminating philosophies of life phenomena. Numerous individuals have directed their efforts toward the discovery of new facts and new relations among natural phenomena. Their discoveries have raised step by step the level of explanations and clarified our understanding of the sequence of natural processes. Still others have from time to time applied previous discoveries to the needs and betterment of society. Both types of contributions have given us a valuable social heritage which we should try to understand, perpetuate, and increase.

When we attempt to interpret natural phenomena that lie within the field of plant behavior we strive to use intelligently the contributions of others. Considerable as our progress as individuals may be, we cannot hope by our own observations to explain more than a small fraction of the problems of plant behavior even though we devote a lifetime to it. Our ability to utilize the discoveries of others, however, depends upon our efforts to observe at first hand and to comprehend what we see.

Older points of view. As far back as human records go, man has attempted to account for himself and his surroundings. Primitive man lived in most intimate contact with nature. Wishing to survive, he was compelled to give attention to other animals, to light and darkness, to

flood and drought, and to trees and herbs. He came to regard all these objects and processes of his environment as separate entities. Before he recognized their relation to one another, he had very definitely related them to himself as either benevolent or malevolent. Lacking the facts and the methods for testing the soundness of his ideas, he attempted to explain *why,* without knowing *how* natural phenomena take place. To him all natural objects appeared to be more or less human-like or god-like. Accordingly he attributed to other animals, to plants, to the moon and other inanimate objects the same abilities, motives, and emotions he recognized within himself or attributed to various deities. In other words, he *personified* and *deified* them.

The cruder of these explanations of physical phenomena have passed, but—if we may judge by the accounts of biological phenomena in popular literature—plants and animals are still looked upon as objects that can control their behavior and growth, read the future better than we can, and make plans accordingly. The authors of these accounts have not really progressed much beyond certain inhabitants of the West Indies who still fear the "duppy" that resides in the silk-cotton tree. To some of these authors there is a duppy or mystic directing spirit in every plant, while to others the will of the plant itself directs the behavior.

For example, who is not familiar with such alleged explanations as these: that trees in a forest grow tall and straight because they are trying to reach the light; that stems and petioles of plants growing at a window bend toward the window in order to get more light; that potato sprouts and stems of seedlings in a dark room grow longer in search of light; that plants produce seeds in order to propagate their kind, or to store food for future use or for the use of animals; that roots grow deep into the soil or toward a cistern in search of water; finally, that plants do this or that particular thing in order to adapt themselves to their environment?

Do not all these statements imply that the plant is conscious of its present and future needs and strives by various means to satisfy them? Whatever happens, according to this point of view, the plant is always forward-looking. In this type of explanation of natural phenomena every act is assumed to be purposeful.

Alternative point of view. An alternative point of view is taken by those who regard each event in a sequence of dependently related processes not as the *purpose* but as the *consequence* of the preceding events or processes. Working from this point of view, the student tries to rec-

ognize and understand the processes and conditions which bring about the phenomenon he wishes to explain. From this point of view natural events are assumed to follow each other in a cause and effect sequence, and explanations are obtained only through the discovery of the sequence of causes and effects.

All of us, therefore, are faced with deciding whether we shall accept, as explanations of natural phenomena, those that are based on needs and purposes or those that are based on consequences of preceding conditions and processes.

Interpretations exemplified. Everyone is familiar with the evaporation of water, with the formation of clouds, and with rain. Does water evaporate from the earth's surface in order to form clouds, or is this evaporation of water merely the consequence of a series of events that may be traced to molecular motion? Do clouds form to produce rain, or are clouds a consequence of a series of events that we may trace back to the evaporation of water? Does the rain fall in order to moisten the soil and keep the streams flowing, or because the force of gravity on larger drops forming in the atmosphere exceeds the forces of air movement and resistance? The origin of the large drops may be traced back through smaller and smaller particles to water vapor and its relation to the temperature of the atmosphere. In this brief outline we have merely suggested a few of the many facts and relations that must be apprehended before these phenomena can be seen as cause and effect sequences. Most persons, however, prefer to seek such data rather than accept as an explanation for rainfall the statement, "It is necessary to wet the soil and to make plants grow."

Explanations of physical and chemical phenomena have for the most part passed out of the stage of personification. It would be hard to find people who would consider the statement, "Sodium unites with chlorine in order to form sodium chloride or common salt," a satisfactory explanation of the union. No one would explain the flow of water downstream as a striving of the water to get to the sea. Feature writers would never dream of accounting for the movement of electrical energy from dynamos through wires to motors by saying, "The energy is needed to turn the motors." Most readers would not be satisfied with the substitution of purpose, necessity, or use, for cause in such examples.

But when biological phenomena are being described and explained many writers feel no need for securing the results of experimental study. On the contrary, they proceed with their discussion of natural processes

as if the processes were occurring to meet the needs and desires of the plants and animals.

During the last quarter-century great advance has been made in analyzing the chemical and physical phenomena that underlie plant behavior and plant processes. Much remains to be discovered in this field, but a broad foundation has certainly been built, mostly by those who have applied the principles of chemistry and physics to the study of biological processes and have approached problems from the point of view of causal sequences.

A little better understanding of this point of view may be obtained if we briefly sketch one of the examples of the effect of light on growth

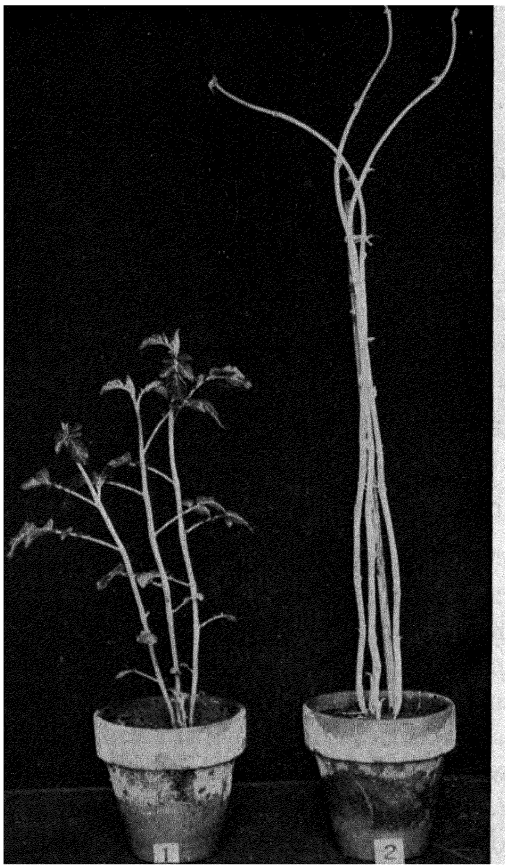

FIG. 27. Potato sprouts that have grown from tubers in different light intensities: 1, in a greenhouse; 2, in a darkroom. Photo by F. H. Norris.

in length of stems of sprouts and seedlings. Fig. 27 is an illustration of the familiar fact that stems of potato sprouts in a dark box in a home or a greenhouse grow in length more rapidly than those of sprouts exposed to bright light outside the dark box. How shall we account for this?

Evidently we cannot infer that the stem in the dark box is growing long in search of light without consciously or unconsciously assuming that it knows there is light outside the box and "by taking thought" can

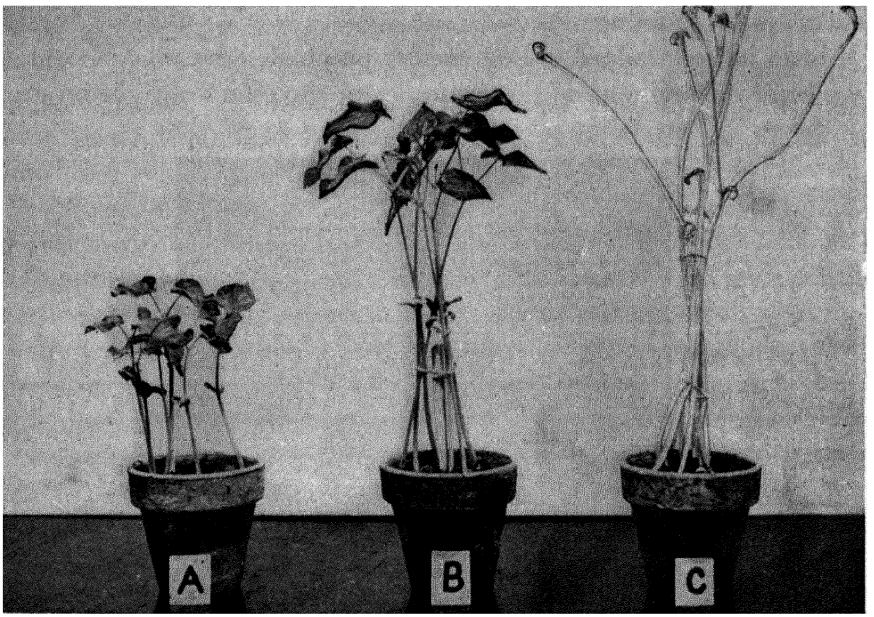

FIG. 28. Differences in stems and leaves of bean seedlings that grew in different light intensities: 100%, 50%, 0%. Photo by F. H. Norris.

increase its growth in length as it desires. In making these assumptions would we be personifying the stem, or deifying it? Need more be said about these assumptions?

Let us try another approach. The sprouts growing in the dark have comparatively small leaves and lack the familiar green color. Before inferring that these facts need to be considered in explaining the differences in the growth in length of the stems, note the photograph of bean seedlings in Fig. 28. The seedlings designated A grew in bright light, those designated B grew in shade, and those designated C grew in a nearby ventilated dark box. There were no appreciable differences in the other environmental factors. The stems of the seedlings that grew

in the shade and in darkness are longer than those that grew in bright light. The seedling from the dark box has small leaves and lacks chlorophyll, but the seedling in the shade is green and has larger leaves than the one in bright light. Hence, we may safely infer that the green color and the size of the leaves are not causes of the differences in growth in length of the stems. Again we have made the wrong approach.

Suppose we shift our attention from the more rapid rate of growth in length of stems in the dark to the slower rate of growth in length of the stems in the bright light. From physicists we learn that light does not affect plants unless it is absorbed by them. Hence the stems of the sprouts and seedlings in the dark are not affected by light, they are not attracted by light, nor is their growth in length affected by it. This is only another way of saying that a factor cannot do anything to a plant in its absence; to be the cause of something it must be present. Incidentally, the foregoing disposes of the notion that darkness accelerates the growth in length of stems, for darkness is merely the absence of light. Of all the suggestions we have made, the best inference, therefore, is that under certain conditions bright light checks the growth in length of stems of sprouts and seedlings. This inference has been sufficiently confirmed in many critically conducted experiments to be accepted as a principle we may use as a basis of explaining certain other growth phenomena.

For example, when a rapidly growing plant is placed in a room near a window or when it is in other locations in which the light intensity is greater on one side of its stem than on the opposite side, the stem visibly bends toward the brightly lighted side within an hour. Can a reasonable explanation of the bending of the stem be made on the basis of the principle cited above? Try it. Many chapters later you will be able to give a more detailed explanation.

From further observations you may learn (1) that the stem bends only near its tip, and (2) that it grows in length only near its tip (see also Fig. 32, page 69). Is the fact that these two processes occur in the same region of a stem merely a coincidence or is there a causal relationship? Here again you are supposed to be able to arrive at a reasonable answer and defend it.

All this time you have probably been wanting to know the answer to three other questions: (1) How does light retard the growth in length of stems? (2) Why do stems of plants in bright light sometimes grow in length faster than those in shade (Fig. 29)? (3) Why do stems often grow in length more during the day than at night?

You can understand the answer to the last question now, for you know that the temperature is often much lower at night than during the day. An increase in temperature from 55° F. at night to 90° F. during the middle of the day may result in a fourfold increase in the plant's rate of growth in height unless the supply of water is low. However, when the nights are warm or the supply of water is low, the rate of growth may be much less in the middle of the day than it is in late afternoon or early morning and during hours of darkness.

By the time you have completed Chapter XIX you will have enough facts to answer the second question without help, and after you have completed Chapter XXIV you can give a reasonable answer to the first one.

Interpretation of hereditary differences. The earlier paragraphs in this chapter have centered on differences in plant behavior which are due to a lack of uniformity in the environment. In Chapter I attention was called to other differences, such as the presence of leaves, roots, and seeds in some plants and their absence from others in all environments. Many writers seem to think that such structures developed to meet a need. The student of plant processes, however, is more likely to regard the origin of these structures as consequences of changes that occurred within the cells of remote ancestors without reference to the needs of the plants of today. To him they are the result of heritable alterations in the chemical and physical composition of the protoplasm. Purpose can scarcely be thought of as the cause of these minute changes in the composition of the protoplasm, or of the far more striking differences in structure and development that result from them. If these changes did not result in the death of the organism, the plant survived and the alterations were transmitted to the offspring. Such alterations in protoplasm and their transmission from one generation to another are discussed in the chapters on chromosomes, heredity, and variation.

Idea of best inference. Can one *know* by inference? Are all inferences equally valid? Suppose a friend who thinks the earth is flat challenges you to prove it is not flat. In reply you cite all the lines of evidence of the rotundity of the earth. But when you have done this have you done any more than show that the *best inference* is that the earth is sphere-like? Perhaps more important is the fact that you are as sure of this best inference concerning the shape of the earth as you are of the shape of a marble or tennis ball you have held in your hand. What, then, is a fact? As we proceed you will learn that much of our dependable knowledge

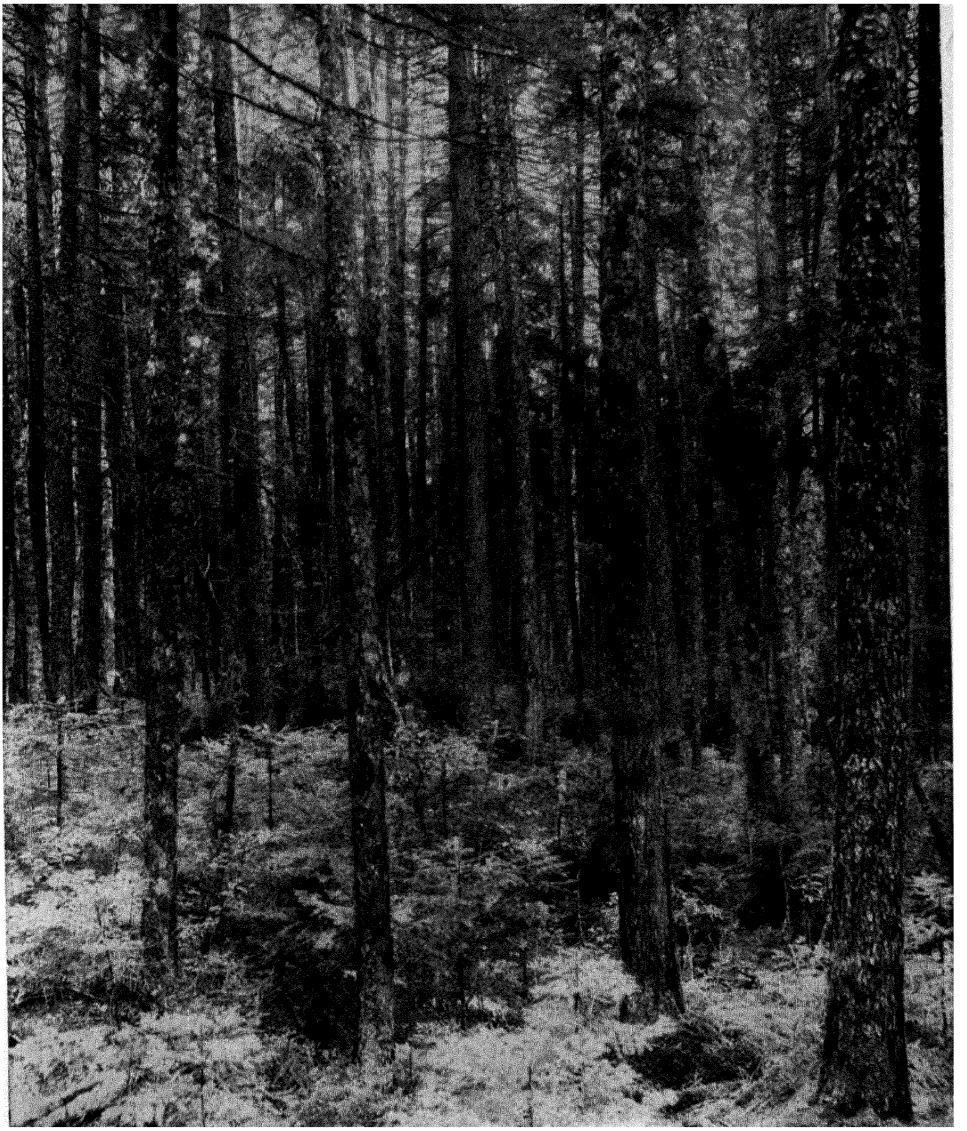

FIG. 29. The growth of young trees among the older trees in a forest is very slow. Spruce and fir forest in New Hampshire. Photo by U. S. Forest Service.

was gained by discovering enough facts to arrive at the best inference. Will plants bear leaves next year? Was Plato once a baby? Can you "prove" either of your answers? Are you sure they are the best that can be given? Why had your friend failed to draw the best inference about the shape of the earth?

Summary. Man seems always to have felt an urge to account for himself and for his surroundings. Perhaps this urge had its origin in the fear of the unknown rather than in the intelligent curiosity that incites the student of modern times. Until man began to apprehend the processes of nature and to perceive the consequences of one process in relation to another, there could be no scientific approach to interpretation. The myths that had grown up about the objects and processes of the physical world had to be replaced by facts and interpretations in accord with the general principle that what happens is a consequence of preceding events without reference to future needs or purposes. In interpreting the biological world on the basis of the principle of causality, progress has been comparatively slow. Personification of plants and animals is still chosen by many writers as the basis of interpreting biological phenomena. Only the more thoughtful ones are skeptical of interpretations that ascribe conscious effort to all sorts of living organisms. Slowly during the last century, and much more rapidly during the present one, biologists have paved the way for a more intelligent interpretation of biological phenomena. The work of all our biological research institutions is directed toward the discovery of the facts and interdependence of biological processes. Perhaps the greatest need today is that the average citizen should become as intelligently conscious of advances that have been made in the scientific interpretation of his biological environment as he is of those in his physical and chemical world. This chapter emphasizes the importance of clearly recognizing the different points of view from which interpretations of plant behavior are made.

CHAPTER VII

CELLS AS BIOLOGICAL UNITS

The development of every science is invigorated and its aims are redirected from time to time as the result of some important invention. A striking example in the field of biology is the invention of the microscope in the seventeenth century. Superficial observation and study of plants had been going on for untold centuries. The origin of many of our most important cultivated and medicinal plants antedates the oldest archeological discoveries. In Europe and Asia several thousand plants had been described by the time that the invention of the microscope made it possible to examine their more minute structure and to discover that many plants consist only of single cells.[1]

Cells. The early microscopists were so fascinated with the world of minute plants and animals previously unseen and unsuspected that they studied and described them in preference to the finer structures of the larger plants. Cells were seen and recognized as structural parts of plants, but for a hundred years observations were limited mainly to cell walls. In the latter part of the 18th century various microscopists began to study "cell contents." By the middle of the 19th century it became evident to a number of eminent biologists[2] that the properties which we associate with life are the properties of that part of the cell contents which had come to be called *protoplasm*. Moreover, its organization into *cytoplasm* and *nucleus*, and the enclosed *vacuole* had been recognized. Many biologists had by this time accepted three general principles: (1) that the bodies of all living organisms are composed of cells, or products of cells; (2) that in certain features the cells of plants and animals are essentially alike; and (3) that protoplasm is the physical basis of life phenomena. To these principles we may add (4) that when plants are

[1] One of the oldest books containing plant descriptions extant is Shêng-Nung's *Tree and Herb Book*, compiled before the Christian era. In it 252 species of plants are classified according to their alleged medicinal values.

[2] Attention may be called especially to Robert Brown, von Mohl, Schleiden, Schwann, Dujardin, Nägeli, Payen, Cohn, and Schultze, whose contributions are admirably discussed in L. W. Sharp's *Introduction to Cytology*, 3rd ed., McGraw-Hill Book Company, Inc., 1934, pp. 422-447.

similar it is because their protoplasms are similar, (5) that when plants develop or behave differently in the same environment it is because their protoplasms are unlike, and (6) that life is a recognized property of a very complex physical-chemical (colloidal) system.

Parts of the cell. As shown in Fig. 30, the essential parts of the usual enlarged plant cell may be outlined as follows:

1. The protoplasm, differentiated into cytoplasm, nucleus, and plastids.
2. The vacuole—a cavity within the cytoplasm filled with water containing sugars, salts, acids, and other substances largely in solution.
3. The cell wall—a more or less complete covering around the protoplasm. Fine strands of protoplasm sometimes extend through the wall from one cell to another.

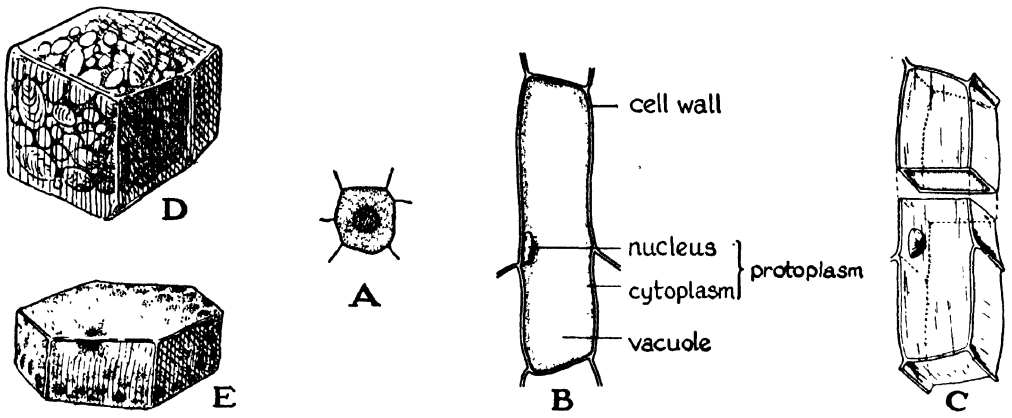

FIG. 30. Plant cells as seen through a microscope: A, a meristematic cell composed of a nucleus and cytoplasm surrounded by a cell wall; B, an older cell which has become enlarged by growth of the cell wall and the formation of a large central vacuole; C, cell B as seen in perspective; D, starch grains formed in plastids in a cell of a potato tuber; E, chloroplasts in a cell of a moss leaf.

In order to appreciate protoplasm as the medium in which the numerous chemical and physical processes of the cell occur, it will be necessary to digress for a moment and consider some of the properties of different states of matter. You have seen solid crystals of sugar and salt disappear as they dissolved in water. You are also familiar with gelatin and fruit jellies in which organic matter is dispersed in water without being dissolved. Protoplasm seen through the microscope resembles a jelly more than a solution.

The solid, liquid, and gaseous states of matter are familiar to every-

one. But when matter is dissolved in water or when, as in jelly, it is dispersed in water without dissolving, such strikingly new properties become evident that we must recognize two additional states of matter: *solutions* and *colloids.*

Solutions. When a substance dissolves in water its particles become subdivided and separated as molecules. The molecules of salts, acids, and bases are to some extent further separated into ions. The resulting solutions are either colorless or colored homogeneous liquids, and the particles remain equally dispersed throughout the solution because of their constant motion. For example, if a gram of table salt (sodium chloride) dissolves in a glass of water the solution remains colorless, but if a similar amount of copper sulfate dissolves in the water the solution is blue.

When salts, acids, and bases have dispersed in water as ions, each ion has a characteristic positive or negative electric charge. Many of the reactions which occur in solution are the result of these electric charges: particles with unlike charges attract each other and unite, and those with similar charges repel each other. For instance, if one pours the above solution of copper sulfate into the solution of sodium chloride, the resultant solution will contain temporary molecules, or compounds, of NaCl, Na_2SO_4, $CuCl_2$, and $CuSO_4$; and also the free ions: Na^+, Cl^-, Cu^{++}, SO_4^{--} . . ., etc. A solution is a stable system in which one or more substances become so finely divided in the form of molecules and ions that they become dispersed among the molecules of the water throughout the system.

Colloidal systems. When substances are almost completely insoluble in water it is possible by various means to subdivide them into very small particles which when dispersed in water continue to remain separated and distributed throughout the water for a long time. If grains of sand or pellets of clay are dropped into a beaker of water, they immediately fall through the water to the bottom of the beaker. If the pellets are crushed and the beaker is vigorously shaken for a moment, the smaller particles of clay are held in suspension in the water and it may remain turbid for an indefinite time. Streams and ponds that do not become clear on long standing are excellent examples of turbid suspensions. Some of the suspended particles in a drop of turbid water may be seen through a microscope.

Turbid water due to fine clay therefore illustrates a suspension in which solid particles are dispersed in water. Each particle is a cluster of

molecules and has a definite surface which is electrically charged. In very fine suspensions the particles may not settle out for months or years, because of the constant bombardment of the water molecules and because the particles have similar electric charges. Suspensions differ from solutions in that the water and the particles dispersed in it form a two-phase system. The one phase is the solid particle, the other is the water, and between each particle and the surrounding water is a definite surface of contact. When a mass is broken up into fine particles, the aggregate surface of the particles is enormous. For example, a one-centimeter cube has a surface of 6 sq. cm., but when disintegrated into particles of colloidal size the combined surfaces of all the resulting particles are equal to about 1.5 acres.

Another type of colloid is exemplified by milk, in which proteins and fat-like compounds (lipoids) are dispersed in water which contains other proteins, salts, and sugar in solution. Dispersed throughout this liquid phase of milk are numerous visible globules composed largely of fat. These globules slowly rise to the surface and form a layer of cream. In butter the phases are reversed; fine droplets of water are dispersed in fatty material. White of egg is a typical protein-in-water colloidal system; the yolk is a colloidal system of many phases, with fats, proteins, pigments, and other substances dispersed in water. When white of egg is heated or treated with alcohol, vinegar, or strong salt solutions it *coagulates*. When meat, which is largely protein, is boiled it also coagulates. Gelatin desserts and fruit jellies are familiar examples of colloids.

When a gram of gelatin is dispersed in 50 grams of hot water a highly fluid colloid, called a *sol*, is formed. When it cools and stands for a few hours it becomes a semi-solid jelly, or *gel*. The gelatin becomes finely divided and dispersed in the water but does not dissolve. Its particles are much larger than molecules. Owing to the elasticity and certain other properties of this type of colloid, the dispersed particles are thought to be fiber-like and arranged like twigs in a loose brush heap.

When a gelatin-water gel is heated it becomes highly fluid, but after it cools and stands for a time it again becomes organized into a more or less rigid gel. Thus the gel and sol states of a colloid may be reversible, and the change from the one to the other may be brought about by changes in temperature, water content, acidity, or any one of several other conditions. Drastic changes in the internal organization of a colloid may result in coagulation.

Protoplasm is a very complex colloidal system with protein, carbo-

hydrate, fat, and lipoid phases dispersed in water, in which are various salts, sugars, acids, and other soluble compounds. Many of these substances are chemically unstable and react with extreme readiness. All masses of protoplasm have a surface film rich in lipoids which prevents unlimited dispersion and keeps the mass intact.

The highly reactive character of the protoplasmic system at ordinary temperatures is one of its most important properties. Since it is a colloidal system there are very large surfaces between the water and the other phases, and here surface energy may bring about reactions not possible in a solution. These surfaces also accumulate electrical charges which may be significant in reactions. Because it is a many-phase system, a change of one phase may result in the alteration of other interlocking phases and the modification of the whole protoplasmic system. Like gelatin and jelly, protoplasm is more or less elastic, and some of its constituents may have a brush-heap structure.

Furthermore, protoplasm is a self-perpetuating system, in that it can combine foods (carbohydrates, fats, and proteins) into the system and enlarge its mass. It is evident, therefore, that the jelly-like part of the cell which was named protoplasm is not a single chemical substance. Life, like all the other distinctive properties of protoplasm, is a result of the chemical components and their complex organization in a colloidal system. When the system is disorganized the distinctive properties disappear, for the materials or compounds are not alive.

Cytoplasm. The protoplasm in most plant cells is organized into cytoplasm, plastids, and nucleus. In young cells these parts completely occupy the space within the cell wall (Fig. 31). As the cell enlarges, microscopic droplets of liquid become visible in the cytoplasm, the colloidal matrix is drawn together, and the droplets coalesce, forming larger water-filled cavities called vacuoles. In most plant cells the coalescence of small vacuoles results finally in the formation of a single vacuole, and the cytoplasm with its embedded plastids and nucleus becomes relegated to a thin layer lining the cell wall. In other cells the nucleus may retain its central position, supported by cytoplasmic strands which are the remnants of the cytoplasm separating the several vacuoles before they coalesced into the single large one.

Cytoplasm is usually granular in appearance because of the presence of particles of various foods and other substances. Cytoplasmic movements (streaming) may be seen in the cells of some plants.

Plastids are protoplasmic bodies in the cytoplasm. Special reactions

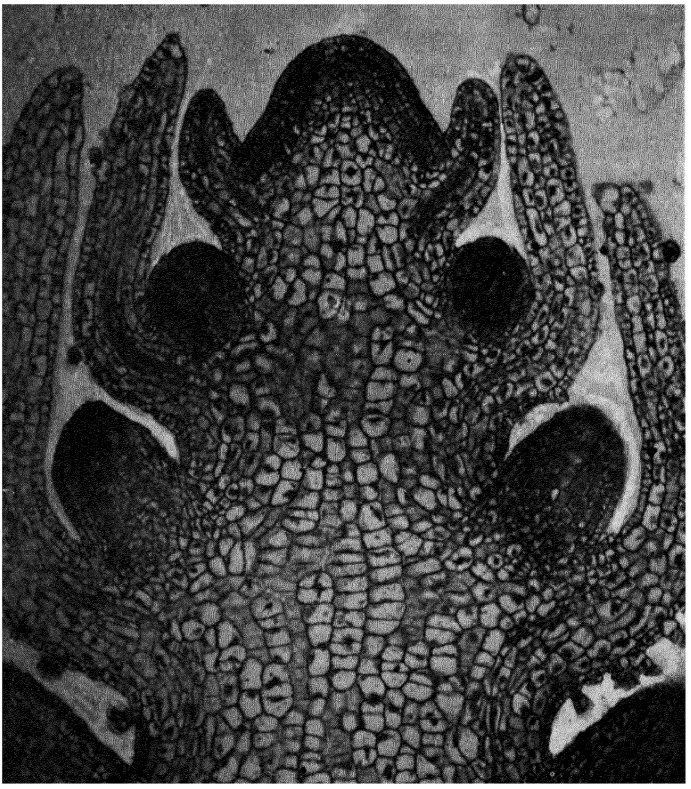

FIG. 31. Photomicrograph of a vertical section of a stem tip in a reproductive bud of coleus. The small meristematic cells nearest the apex are completely filled with protoplasm. The older cells which have become enlarged and vacuolate are similar in structure to B and C in Fig. 30. Photo by T. J. Johnson.

take place in them, often resulting in the accumulation of particular substances, such as starch and chlorophyll. There are usually several to many plastids in each cell; and as the cells multiply by division, the plastids also increase in number by division. They are named on the basis of certain substances that accumulate in them, as shown in Table 1.

In very young cells there are small colorless plastids (leucoplasts) that apparently may develop into these more specialized types, depending upon environmental conditions.

The nucleus. The nucleus is usually more refractive to light than the cytoplasm and under the microscope appears brighter. Often its proto-

TABLE 1. Names of Plastids and Their Characteristic Contents

Names of Plastids	Characteristic Contents
Green plastids or chloroplasts.	Chlorophylls, carotenes, and xanthophyll, sometimes minute starch grains.
Starch plastids or amyloplasts.	Starch grains.
Fat plastids or elaioplasts.	Oils and fats.
Color plastids or chromoplasts.	Pigments found in chloroplasts, also red, yellow, and other pigments.

plasm is denser and forms a more rigid gel, but sometimes it is a fluid sol surrounded by a membrane. Chemically it differs from the cytoplasm in that the proportion of proteins is less and its proteins are far more complex.[3] They are relatively high in phosphorus and possibly on this account more reactive. There seems to be good reason to regard the nucleus as the center of many cell activities; as we shall see in a later chapter, it contains certain very minute bodies (chromosomes) that are the carriers of many of the hereditary factors of the plant.

The vacuole. At maturity the vacuole occupies most of the space inside the cell walls; it is filled with "cell sap," a solution of sugars, salts, acids, and other soluble compounds. It may also contain colloidally dispersed proteins, carbohydrates, and other less soluble substances. Some of the substances in solution readily pass from the vacuole into the surrounding cytoplasm or from the cytoplasm to the vacuole; others do not. Sometimes crystals of salts accumulate in the vacuole, or the cell sap may become colored with pigments as in the cells of many flowers, fruits, and red autumn leaves.

The cell wall. The outermost part of a plant cell is the cell wall, formed at the surface of the enclosed protoplasm. During cell division the first wall between the daughter cells is composed of pectic material, and on the inside of this pectic wall (middle lamella) successive layers composed of cellulose or of cellulose and pectic compounds are deposited. Sometimes other substances, such as cutin and lignin, accumulate in cell walls and thereby change their properties. Most cells on the outer surface of plants contain cutin in the outer wall. The cells in wood

[3]

Nucleo-proteins { Nucleic acid + Protein base { Purine or adenine + Sugars + Phosphoric acid

exemplify walls that started as pectic compounds and cellulose and became lignified. Cell walls also possess colloidal properties and swell in water. They are composed of small submicroscopic particles between which molecules of water may penetrate and be held tenaciously.

The cell as a whole. From this description of the parts of the cell and the study of cells with a microscope, it should be possible to picture the cell as a structural unit, and at the same time as a dynamic unit, displaying those properties and processes commonly associated with living organisms. Some of these structures and processes may be briefly summarized.

1. All plants consist of one or more cells.
2. Cells are formed by the division of previously existing cells, and less frequently by the fusion of cells.
3. The properties associated with life reside in the protoplasm, which is a complex colloidal system of proteins, carbohydrates, fats, and lipoids permeated by a water solution of acids, bases, and salts, many of which are highly reactive. Owing to the enormous surfaces between the water and the colloidal particles the protoplasmic system contains surface energy and electrical energy not characteristic of solutions.
4. The protoplasm therefore is a chemical and physical system, no one constituent of which is living; the qualities that distinguish protoplasm from non-living systems result from the unique organization of atoms, ions, molecules, and colloidal particles with their associated chemical, electrical, and surface energies.
5. The protoplasmic system sustains itself in the presence of food, and can combine food substances into its own structure and thereby increase its mass. In other words, it *grows*.
6. In the development of the plant cell, vacuolation occurs and the cytoplasm at maturity becomes a sack-like layer surrounding a solution of sugars, salts, acids, and very dilute colloidal dispersions in the water of the vacuole.
7. During its development, the usual plant cell also becomes surrounded by a cell wall—at first primarily of pectic material, later of cellulose layers—which may be altered in several ways. The cell wall has a high water content during the active life of the cell.
8. The large proportion of water pervading all parts of the cell con-

stitutes a medium in which the movement of materials and the chemical and physical changes within the cell readily occur.

9. As a result of the chemical changes constantly going on in the cell, electrical energy is released as in a battery, and one end of the cell usually has a higher electric potential than the other. Consequently most cells are polarized, and their opposite ends may behave differently.
10. In cell masses of the larger plants electric potentials also develop, and the apex of a plant organ may become electrically negative or positive to the base.
11. Since the living part of the cell is protoplasm, it is the protoplasm that dies when a cell or any group of cells dies.

With these principles in mind, one has a basis necessary for interpreting the various extraordinary reactions of living plants. Today we know only a minor part of the energy and material relations within plant cells, but our present knowledge is certainly sufficient to lead us to doubt the necessity of assuming the presence of mysterious forces to account for the behavior of organisms.

CHAPTER VIII

THE TISSUE SYSTEM OF LEAVES

In the preceding chapter, cells are described as unit structures embodying several interrelated physical and chemical systems. Cells are considered as the physiological units of plants because they are the smallest bits of protoplasm known to be capable both of independent existence and of reproduction through division. In later chapters less highly organized cells of bacteria and certain algae are described. There are several thousand species of plants that live as single cells. In other thousands the cells are aggregated in colonies in which the individuals cells are more or less independent. In the larger and more familiar plants the millions and billions of cells of which they are composed remain not only firmly attached but are to some extent mutually dependent. During the development of these plants, systems of cells called *tissues* are formed by cell enlargement and differentiation.

Cells and tissues. The cells of a given tissue may have a common origin; all of them may be similar in position, shape, texture, or color; or several different kinds may form a distinct structural complex. Nevertheless, the tissues of many common plants may be distinguished readily. In this chapter we shall try to picture the tissues of a leaf, emphasizing the fact that the leaf, or foliage organ, like other organs of a plant, is a system of tissues, the cells of which are differentiated, but intimately related, structurally and physiologically.

Leaf bud development. Leaves develop from buds; they first become visible through the microscope as small protuberances (primordia) in the meristematic[1] region near the growing apex of the stem (Fig. 32). The cells of the primordium divide and continue to produce new cells—all very similar in size and shape. The uniform brick-like cells of the leaf

[1] A *primordium* (pl. *primordia*) is the beginning, original, or rudimentary state of an organ—in most cases, a minute mound of similar cells. The term *meristem* (Greek *meris* = a divider) refers to any part of a plant in which cell division, enlargement, and differentiation are possible or taking place; it often is a synonym of growing region. *Meristematic* cells, tissues, and regions are sometimes called *embryonic* cells, tissues, and regions. After cells and tissues are mature they may again become meristematic through changes in their immediate environment, and cell division begins again.

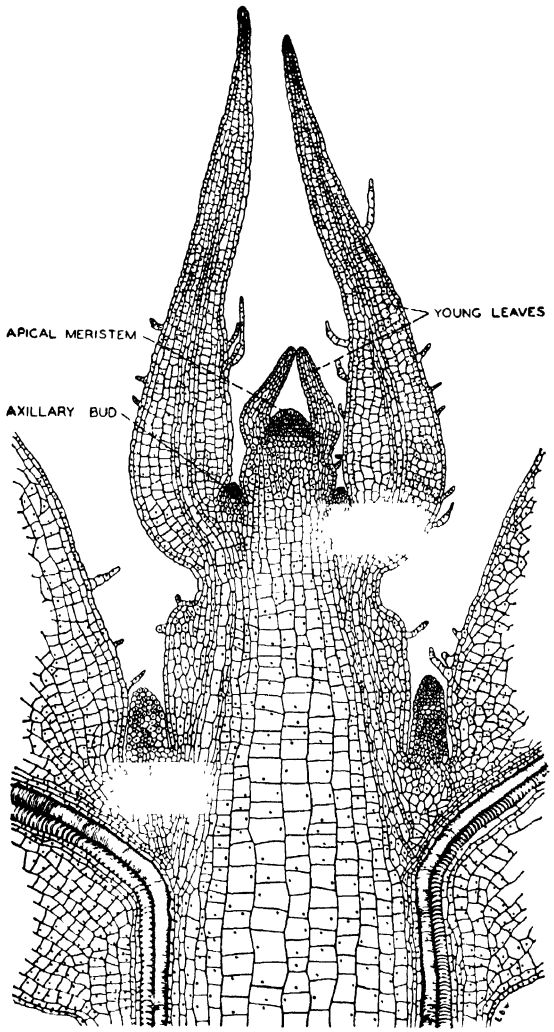

FIG. 32. Diagram of vertical section of a vegetative bud of coleus. Compare it with Figs. 31 and 83.

primordium are completely filled with protoplasm and become stratified in several (5-8) layers. As this protuberance expands farther—becoming more leaf-like, but still very small—cells in the middle layers divide irregularly and form groups of cells from which the vascular tissues of veins develop (Fig. 33).

In the leaves of many of our trees, to which the above description particularly applies, this entire development proceeds slowly through the spring, summer, and autumn months within the buds. By the end of

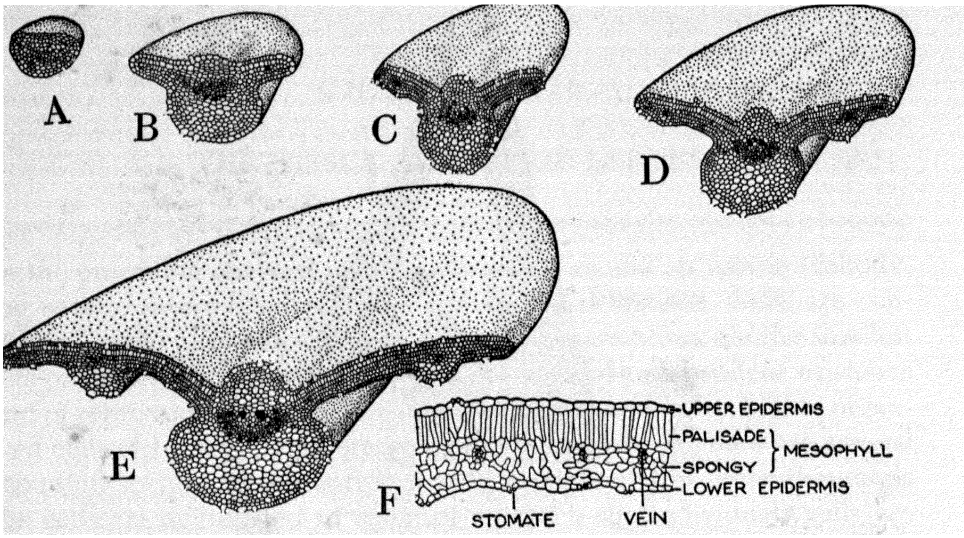

FIG. 33. Cross sections of leaves. A-E, sections of embryonic leaves from the terminal bud of a tobacco plant in the order of relative age. The oldest leaf (E) in the series was less than one centimeter in length. F, cross section of a small portion of a blade of a mature leaf of tobacco. Modified after G. S. Avery.

winter some of the leaves in the bud have attained their characteristic pattern in miniature. The cells of the prospective future veins are slightly differentiated, whereas the remaining ones are still similar. Thus far *cell division* has been the dominating process of development. All cells remain in complete contact and there are no intercellular spaces.

Leaf development. With the warmer weather of the following spring, growth is renewed. The stem tip and young leaves expand and press the bud scales apart. During the rapid increase in size, *cell enlargement* and *cell differentiation* dominate the growth process, leading to the formation of the distinctly different tissues as seen in microscopic sections. Cell division usually stops first in the *epidermis,* next in the *spongy mesophyll,* and last in the *palisade mesophyll.* Cell enlargement, however, continues longest in the epidermis; as a consequence, the cells of the spongy tissue are pulled into an open meshwork, and the palisade cells become separated laterally. Meanwhile the veins have increased in diameter. Expansion of the leaves follows rapidly after the opening of the buds; they often double their size within twelve hours. In some plants with small leaves the whole development from leaf primordium

to mature leaf may occur at a rather uniform rate during ten days to two weeks. In large-leaved plants, such as tobacco, the leaves grow for a month or more before becoming mature.

Leaf tissues. When we look at the surface of a magnified leaf we can see that the epidermis is composed of a layer of angular or interlocking cells (Fig. 34). The outer cell wall contains a deposit of cutin, a fat-

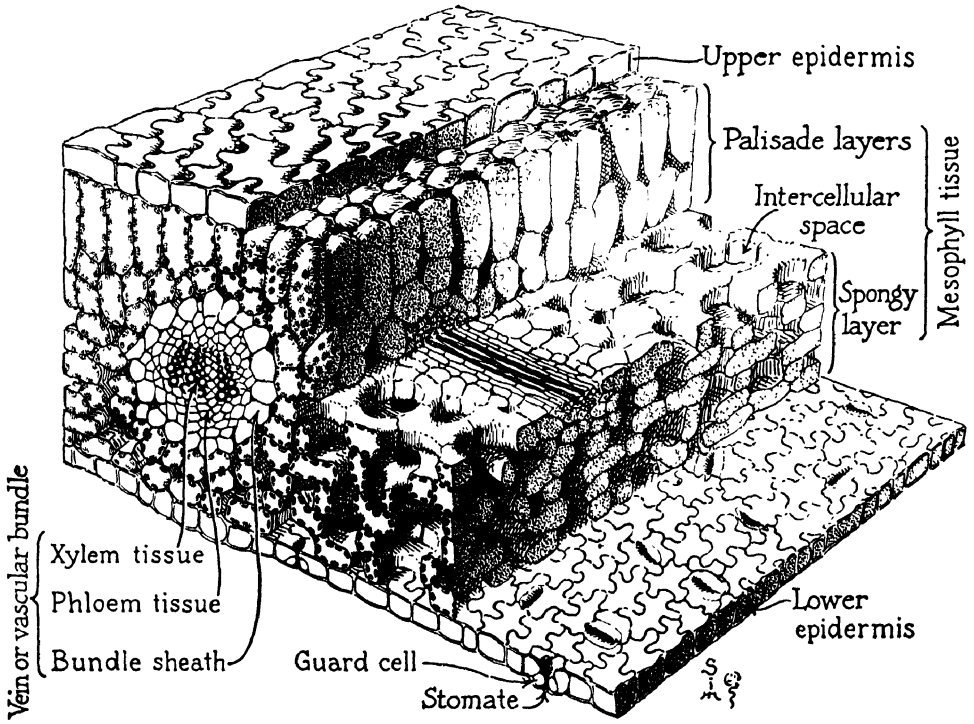

FIG. 34. Arrangement of tissues in a leaf of the common periwinkle (*Vinca*). Courtesy of World Book Co.

like substance. This cutinized layer is often called the cuticle. It may be very thin, or it may be so thick that the outer wall is the most conspicuous part of the epidermal cell.

In the lower epidermis, and sometimes among the upper epidermal cells, paired specialized guard cells partially separate and form a pore or stomate.[2] When open, the stomates are passages connecting the air within the intercellular spaces of the leaf with the external atmosphere.

Between the upper and lower epidermis there are several layers of cells constituting the *mesophyll.* The upper layers usually have elongated

[2] Some authors prefer *stoma* (Greek = mouth; pl. *stomata*); in either case the adjective is *stomatal.*

vertical cells, the *palisade layers*; and the lower have irregular cells more or less parallel to the leaf surface forming the *spongy layers*. Among these cells the *vascular bundles*—the veins—form a network extending to every part of the leaf. The midrib and larger veins increase in thickness and may become several times as thick as the rest of the blade. Each vascular bundle consists of *xylem* and *phloem* tissues surrounded by one or more cell layers of *bundle sheath*. In the larger veins and petioles of leaves the xylem and phloem may be surrounded by heavy-walled fibrous sclerenchyma,[3] or the sclerenchyma may be massed above and below the vascular tissues, as in many grasses. In the smaller veins the bundle sheath consists of thin-walled cells. So completely do the veins penetrate all parts of the mesophyll that any one mesophyll cell is rarely more than a few cells away from a vein (Fig. 52, page 111).

The *xylem* consists of elongated cells, and of tube-like vessels (*xylem tubes*) that originate by a disintegration of the cross walls in strands of several or many successive cells (Fig. 32). The xylem of a single vein usually contains several of these tubes—hence the name vascular bundle. The movement of water to the mesophyll occurs mostly in these tubes. The spiral thickening in xylem tubes in the leaves of many plants, such as nelumbo or geranium, is readily seen when segments of the blade or petiole are pulled apart. Because of thickening and lignification of their walls some of the xylem cells become wood cells.

The *phloem* tissue is composed of elongated small cells which differ from those of the xylem in that they retain their protoplasmic content at maturity. Foods move from the mesophyll cells through the phloem tissue to other parts of the plant.

The petiole. The petiole connecting the blade of the leaf with the stem consists essentially of one or more vascular bundles and associated fibers embedded in parenchyma tissues. The bundles are continuations of the vein system of the blade, and at the basal end connect with the

[3] The names of several common plant tissues are formed from the Greek word *enchyma* preceded by a descriptive prefix. Early plant anatomists held that all tissues are derived from a "fundamental" soft tissue, or *parenchyma*, a general term still used for thin-walled tissues such as occur in many edible fruits, pith, and the soft parts of leaves, stems, and roots. The term *sclerenchyma* is applied to hard tissues, such as the thick-walled fibers of wood, flax, and hemp; and to the rounded grit cells such as occur in pear fruits and in the bark of many trees. When mature, sclerenchyma cells die, and only the heavy walls persist. *Chlorenchyma* is any tissue containing chlorophyll, whether in leaf, stem, root, or other part of the plant. The term *collenchyma* is applied to soft tissue in which the cell walls are thickened irregularly, especially at the angles. These cells retain their protoplasm and may be rounded or elongated. They occur in thick veins of leaves, in petioles, and in herbaceous stems. *Mesophyll* (middle leaf) consists of parenchyma; it may be properly called *chlorenchyma* only when it is green.

bundles of the stem. Near the junction of the petiole and stem there is a short region in which the sclerenchyma is either less or absent, and in which parenchyma cells rich in cytoplasm form a disk-shaped layer several cells thick across the petiole, except in the bundles. This is the abscis layer (Fig. 35). It is formed during leaf development.

Later as the cell walls of this layer disintegrate many of the cells become separated. The middle lamella and sometimes other layers of the

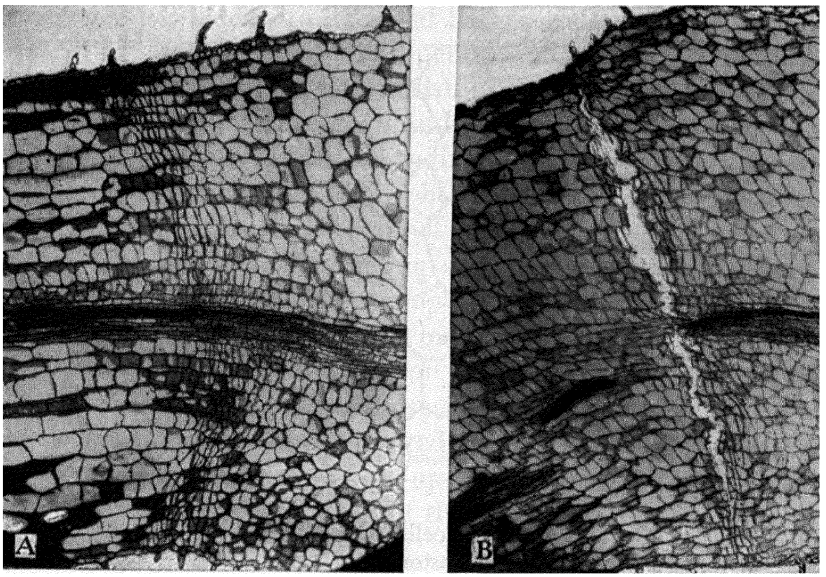

FIG. 35. Vertical sections of the bases of two petioles of coleus leaves: A, in which the abscis layer is almost fully developed, and B, in which abscission is nearly completed. Photomicrographs by R. M. Myers.

cell walls become jelly-like or are dissolved, and the petiole is separated from the stem. The leaves of deciduous trees may be supported for a time by the vascular strands, but these are ultimately broken. The breakdown of the abscis layer in the petiole of some herbaceous plants may take place and the leaf abscise within 48 hours. This process is retarded by hormones from the blade and hastened by such conditions as drought, injury to the blade, low and high temperatures. Abscission is usually preceded or followed by changes in the cells attached to the stem below the abscis layer. These changes result in the closure of the vessels and the development of scar tissue evident in the *leaf scar*. Abscission is not

The stomates. In describing the epidermis the paired guard cells which surround the stomate were mentioned. These are highly specialized cells formed by subdivision of epidermal cells; unlike the ordinary epidermal cells, they contain green plastids (Fig. 36). In tree leaves the guard cells do not separate until the leaf has attained a fourth or a third of its size. In many leaves they are found exclusively, or mostly, in the lower epidermis. Less frequently they are most abundant on the upper surface; they rarely occur in equal numbers on both sides

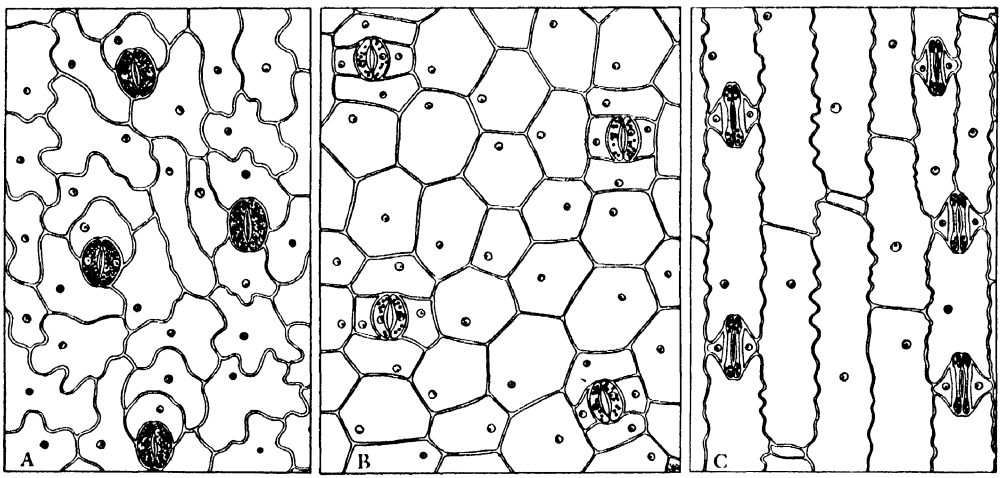

FIG. 36. Stomates in relation to guard cells, subsidiary cells, and ordinary epidermal cells. Lower epidermis of (A) Boston fern, (B) *Zebrina,* and (C) corn.

of the leaf. Stomatal openings are so minute that the area of an average pinhole may be equivalent to that of 2000 to 2500 stomates. On many common leaves, however, there are from 100 to 600 stomates per square millimeter of leaf surface, and when they are open their total area may be equal to nearly 1 per cent of the lower leaf surface.

The most remarkable thing about stomates is that they are opened by the swelling and arching of the guard cells, and closed by the shrinking and straightening of these cells. When a plant is moved from darkness to light, the guard cells are affected by light and their internal pressure increases, causing them to separate and open the stomate. On a warm day this opening may take place in about 15 to 30 minutes. Thus in the summertime stomates open after sunrise and remain open for two or more hours, depending on conditions discussed in Chapter XXIII. The closing of the stomates depends on a number of factors, mostly internal.

Here it need be emphasized only that external factors—light, water, and a warm temperature—are the most important prerequisites for their opening.

Summary. A leaf is a more or less flattened organ that develops from a leaf primordium, which originates in the meristematic tissue at the growing point of a stem. The blade may be sessile, or it may be supported at some distance from the stem by a petiole. The latter is essentially a structure containing vascular bundles surrounded by other tissues. The usual blade is a flattened body with an epidermis which is perforated by stomates that are opened and closed by guard cells. Within the blade, the mesophyll consists of several layers of parenchyma cells which are variously arranged and partly in contact with the intercellular air spaces that ramify throughout the leaf. The air spaces are continuous with the outside atmosphere when the stomates are open. Within and throughout the mesophyll there extends an ever-branching vascular system of water-conducting and food-conducting tissues that are in contact with most of the mesophyll cells, and never more than a few cells removed. Some or all of the mesophyll cells contain chloroplasts and chlorophyll. The larger veins of the leaves are often ensheathed with hard sclerenchyma fibers. These fibers increase the rigidity of the blade; but the collapsing of wilted leaves is evidence that they are not sufficient to hold the blade upright. Owing to the formation of layers of cutin, external cell walls of the epidermis may be more or less impervious to water.

The mesophyll is a system of living cells connected with the stem by water- and food-conducting tissues, distributed in a labyrinth of air passages through which water vapor, oxygen, carbon dioxide, and other gases can move freely. The whole is enclosed by a cutinized epidermis, in which are stomates that may be open in warm sunlight, thus connecting the internal with the external atmosphere.

CHAPTER IX

ENVIRONMENT AND LEAF DEVELOPMENT

Development of a leaf begins with the terminal growth of a primordium. This terminal growth in a fern leaf may continue long after the base of the leaf is mature. The tender, young coiled tip of a growing Boston fern leaf is familiar to all. In the broad leaves of common trees and shrubs all parts of the blade continue to grow and mature about the same time, though growth continues longest in the base. In the leaves of grasses, iris, aloe, and pine the basal region remains meristematic much

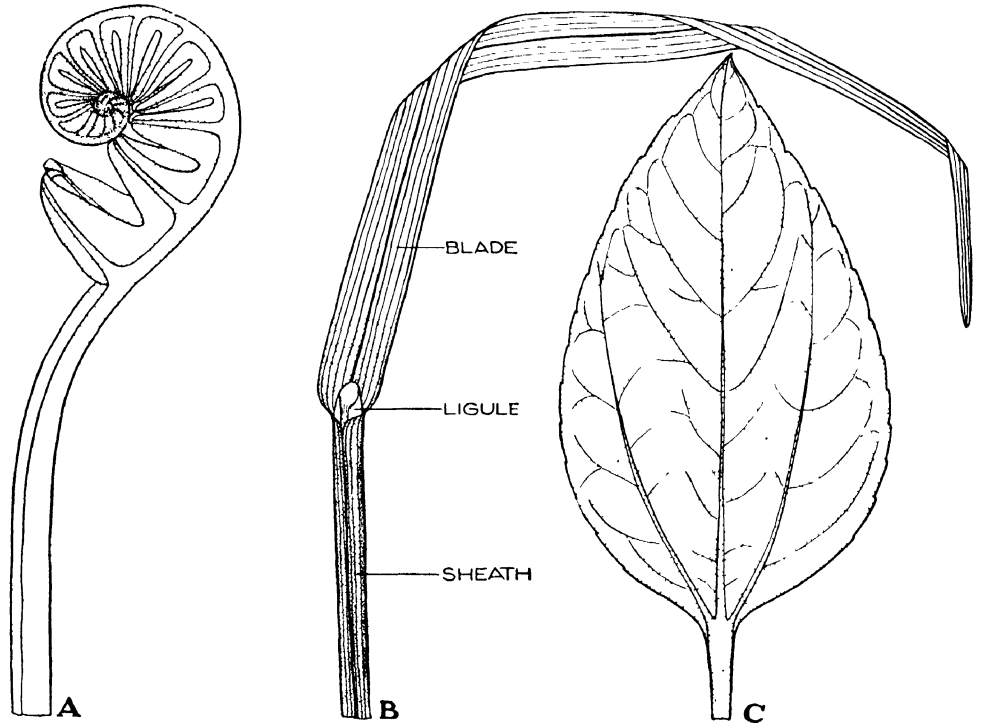

FIG. 37. Growing regions of leaf blades indicated by stippling. The fern leaf (A) continuous growth longest at the apex, and grass leaves (B) longest at the base. The growth of leaves similar to those of the sunflower (C) is much less localized.

longer than the apical portion. Hence these leaves continue to elongate from the base after the other portions are mature. When growing plants of grasses and aloe are placed in a dark box the leaves continue elongating; their white or yellow basal portions are the growing regions. In early spring one may often see the same thing in bluegrass lawns before sunrise. When bluegrass is clipped the clipped leaves continue their elongation. Cutting the tip of a fern leaf removes the growing region, and growth of the leaf stops. Appreciation of these three types of leaf development (Fig. 37) may aid in the interpretation of many leaf phenomena.

During development leaves may be subjected to drought, to intense light, shade, or darkness, to high and low temperatures, and to numer-

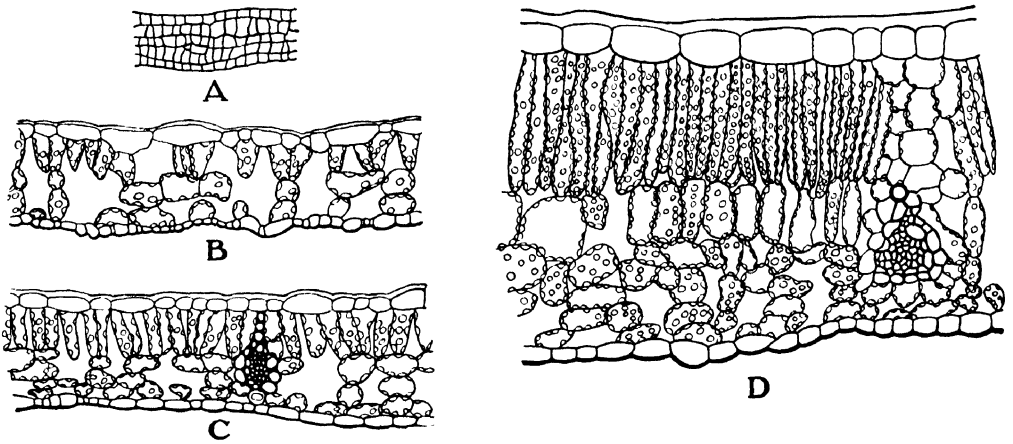

FIG. 38. Cross sections of leaves of sugar maple from different environments: A, section of a very young leaf with the usual three layers of mesophyll cells which do not increase in number in some environments; B, section of a leaf from the base of a tree in a forest; C, section of a leaf from the middle of the crown of an isolated tree; D, section of a leaf from the side of the crown exposed to the sun. Drawings redrawn from G. H. Smith (A) and from H. C. Hanson (B-D), *American Journal of Botany*.

ous other external conditions. The effects of these environmental factors on the growth processes within the cells may bring about an increase or decrease in the division, enlargement, and differentiation of cells. Consequently any change in the intensity of these factors during the growth period of a leaf may result in distinct differences in form and structure.

Light and leaf size. Leaves that have developed in full sunlight are usually smaller and thicker than the corresponding leaves that have developed in partial shade. The lobes of leaves, such as those of oak

and maple, are also thicker as well as narrower and longer when the leaf grows in bright light. The thickness of leaves in full sunlight may be as much as 2 or 3 times that of similar leaves that developed in shade. Studies of leaf development have shown that in moderate shade the number of cell layers of mesophyll is the same as in the embryonic leaf, while in full sunlight the number of these layers may be increased (Fig. 38). Moreover, there is increased elongation of cells at right angles to the leaf surface; that is, more of the mesophyll cells become palisade cells.

In dense shade the leaf blades of many plants mature at an early stage of development and remain smaller and thinner. In total darkness such blades develop little or not at all. Corn and other parallel-veined leaves are exceptions in that the blades of seedlings may enlarge in darkness even more than in light. Petioles generally lengthen more in shade and darkness than in light. Internally, the vascular tissues of the petiole and blade become differentiated more in full sunlight than in darkness.

Light and epidermal cells. From what evidence there is, it appears that in any one species the larger size of shade leaves is usually due more to the greater enlargement of the cells than to the increase in number of cells (Fig. 39). Likewise, the total number of stomates in these leaves may not increase, since the proportion of epidermal cells from which guard cells develop is about the same in both sun and shade.

The mean number of stomates per 100 original epidermal cells is as follows:[1]

European beech	Shade leaves 10.7	Sun leaves 10.4
Black elderberry	Shade leaves 15.5	Sun leaves 16.1
Myrtle blueberry	Shade leaves 12.2	Sun leaves 14.5

There are more epidermal cells and more stomates per square millimeter of surface in sun leaves than in shade leaves when the plants grow out-of-doors. Under these conditions the leaves are heated more than in shade, and evaporation of water from them reduces the water content of their cells. Since, in growth, enlargement of cells depends in part on water pressures inside them, sun leaves have smaller epidermal cells,

[1] Data from E. J. Salisbury, *Philos. Trans. Roy. Soc. London,* 216:1-65, 1927. The mean number of epidermal cells and pairs of guard cells, respectively, per square mm. in sun and in shade are given as follows:

European beech	Shade leaves 1157 and 145	Sun leaves 1905 and 222
Black elderberry	Shade leaves 268 and 47	Sun leaves 581 and 112
Blueberry	Shade leaves 545 and 90	Sun leaves 1049 and 132

and more per unit area; likewise their guard cells are smaller, and the pairs of guard cells per unit area are more numerous. When moisture

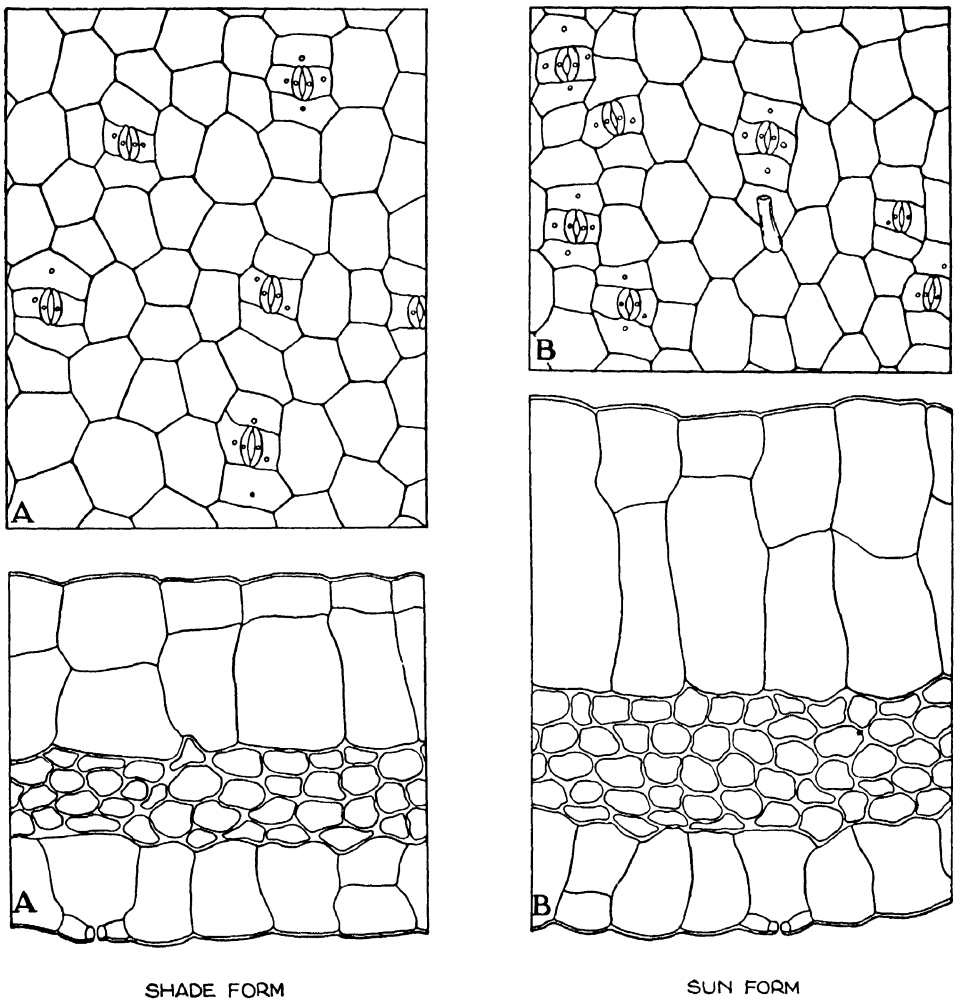

FIG. 39. Relation of growth of leaf tissues of wandering jew (*Tradescantia*) to light. Leaves (A) on plants shaded by two layers of cheesecloth are broader and thinner, and have shorter palisade cells, larger epidermal cells, and fewer stomates per square millimeter than leaves (B) on plants exposed to full sunlight. From F. H. Norris.

conditions are controlled so that evaporation from the leaves is about the same in sun and in shade, the numbers are approximately the same for equal surface areas. The effects of intense light upon leaf development are similar to those of drought.

Light and leaf structure. Following is a comparison of leaf structures[2] in a cross section of *Rhododendron catawbiense* from a spruce-fir forest (shade) and from a heath-bald (sun) on Mt. LeConte in the southern Appalachians, elevation 6600 ft. Evaporation of water from the Rhododendron plants in the heath-bald was about 3.5 times greater than from those in the forest.

	Shade	Sun	Ratio $\frac{\text{Sun}}{\text{Shade}}$
Average leaf dimensions	13.5 × 5.9 cm.	6.9 × 3 cm.	0.25
Mean thickness of leaves	0.358 mm.	0.525 mm.	1.5
Mean thickness, upper cuticle	6.0 microns	8.9 microns	1.5
Mean thickness, upper epidermis	11.0 "	13.5 "	1.2
Mean number layers of palisade	2.5 "	4.5 "	1.8
Mean thickness, palisade layers	70.0 "	144.0 "	2.1
Mean thickness, spongy parenchyma	253.0 "	321.0 "	1.6
Mean thickness, lower epidermis	10.5 "	16.2 "	1.5
Mean thickness, lower cuticle	2.9 "	6.7 "	2.3

The development of the finer veins of the leaf is similarly affected, and the meshes ("vein-islets") enclosed by the veins are smaller in sunlight than in shade. The area of vein-islets probably is determined not directly by sunlight, but indirectly by the increased evaporation and the decreased expansion of the leaf cells, as are leaf size, thickness, number of stomates, and epidermal cells per square millimeter. In all these phenomena hormones may play an appreciable part.

When an environmental factor is changed, all the tissues of the leaf may not be affected equally in their development. The enlargement or the differentiation of one tissue may be increased or decreased more than that of others. If the growth of the epidermis is checked sooner than that of the mesophyll, the mesophyll cells will be closer together and the air spaces smaller. If the growth of mesophyll cells is checked sooner

[2] Calculated from sections near the midrib. From S. A. Cain and J. D. Oliver Miller, *Amer. Midland Naturalist*, 14:69-82, 1933.

than that of the epidermis, the leaf will have larger air spaces. Air-space differences usually result in either an increase or a decrease in the area of mesophyll wall surface exposed to the air spaces. The area of this exposed mesophyll surface may become several times greater in leaves growing in full sunlight than in leaves growing in shade, although the epidermal surface is greater in the latter. The relation of the efficiency of a leaf to the area of mesophyll wall surface will become evident in later chapters.

If the edge of a blade matures before growth stops in the middle, stresses develop within the leaf and it may become convex or curled. The rigidity of many large leaves and the curving and twisting of petioles is due to such internal stresses and strains between tissues.

Light and leaf position. Plants placed at a window are exposed to only a fourth or a fifth as much light as plants out-of-doors; moreover, most of the light strikes only one side of the plant. This unequal illumination of opposite sides of the growing leaf blade results in an unequal growth in length of opposite sides of the petiole. Except in a very young leaf, in which the converse may occur, the cells on the shaded side lengthen more than those on the lighted side. The greater elongation of the petiole on the shaded side is evident in the bending of the petiole toward the window. Apparently the quantities of hormones in the lighted and shaded sides of the blade are unequal, and their consequent unequal distribution on opposite sides of the petiole results in a greater lengthening of the cells on the shaded side. Likewise there are unequal quantities of these hormones in the exposed and shaded blades in a

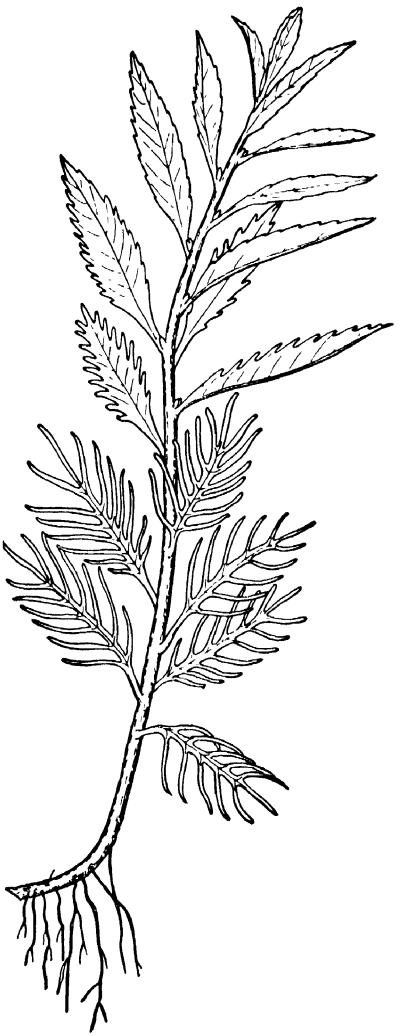

FIG. 40. When the growing stem tip of the mermaid weed is submerged, the leaves that develop are finely divided; when it is in air, the leaves that develop are not divided.

leaf mosaic; consequently there are differences in growth in length of their petioles.

The lengthening, bending, and twisting of petioles among adjacent leaves on inclined stems, and on vines growing on walls, often result in an arrangement and spacing of blades which when viewed from the direction of the most intense light appear as "leaf mosaics." The mosaic arrangement of leaves in rosettes is illustrated in Fig. 20, page 33.

The leaves of prickly lettuce and other "compass plants"[3] growing in

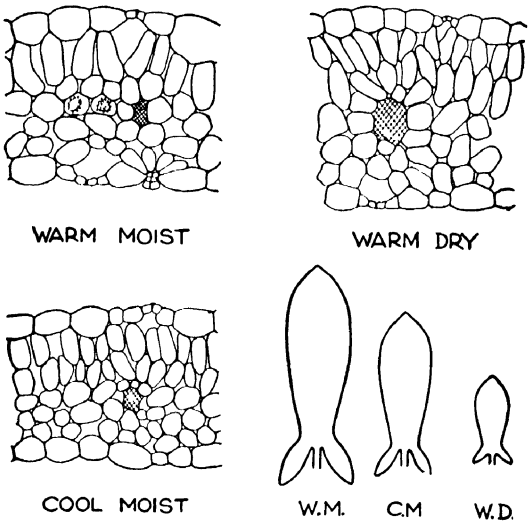

FIG. 41. Effects of temperature and drought on leaf size and structure of the sour dock. In the warm dry culture the plants wilted daily. The temperature of the substrate in the "cool moist" culture was on the average 10 degrees below that of the "warm moist" culture.

dry, intensely lighted habitats become twisted to a more or less vertical position in a north-south plane. In shade, these leaves have the usual oblique or horizontal position (Fig. 341).

Water and leaf structure. Some plants that grow partly submerged have finely divided leaves under water and nearly entire leaves above water. The mermaid weed (*Proserpinaca*), for example, grows well both on moist soil and in water. It is what may be called a highly *plastic* species since its leaf types are readily changed. As long as the leaf primordia are under water the leaves that develop are divided. If the leaf primordia are raised above the water, undivided serrate leaves result (Fig. 40). Moreover, if the stem tip is held alternately above and

[3] *Lactuca scariola, L. saligna, Silphium laciniatum,* and S. *terebinthinaceum.*

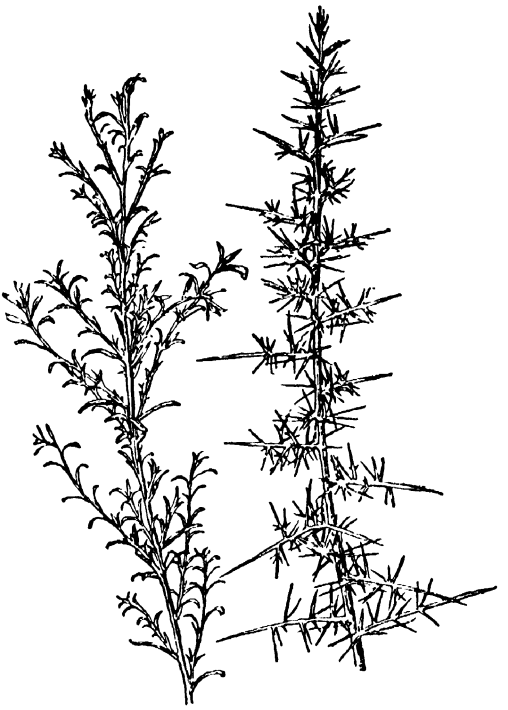

FIG. 42. The English gorse growing in moist places has leafy shoots; in dry situations the shoots are largely spines and thorns. After Lothelier.

below the water, successive tiers of divided and undivided leaves may develop on the same stem. The epidermis of submerged leaves may have paired guard cells which do not separate and form stomates. Internally the submerged leaves have considerably less differentiation of cells and tissues than do the aerial leaves.

In a preceding chapter attention was called to the chemical effects of light and temperature on the greening of leaves, on autumn coloration, and on abscission of leaves. Some of the effects of drought and temperature on the development of leaves are illustrated in Fig. 41 Drought often increases the spinescence of plants (Fig. 42).

Some of the variations observable in leaves that grow out-of-doors are the results of changes in such factors as light and water, similar to those discussed in this chapter. When individuals of the same species grow in very dissimilar habitats, environmental effects on leaf form often make it difficult to identify the plants. Keys to plant species are based on heritable characteristics as developed in a single natural habitat, preferably a favorable one.

CHAPTER X

HEREDITARY DIFFERENCES IN LEAVES

All leaves develop from a small mound of meristematic cells near the tip of a stem, and all these primordia look much alike. From the leaf primordia of elm trees simple pinnately veined leaves develop, but from the leaf primordia of the sugar maple five-lobed palmately veined leaves develop. The leaves of horse chestnut and buckeye become palmately compound, and those of the ash become pinnately compound. Since these characteristics regularly appear in any, or all, of the environments in which the trees grow, it is evident that these variations in leaf development, form, and structure are the result of hereditary differences.

Heritable variations in leaves have been occurring throughout the millions of years that leaf-bearing plants have existed upon the earth. If one were to begin studying these variations by noting all of the minute heritable differences in the form and size of teeth and lobes on leaf margins, or in the form, number, and arrangement of epidermal hairs on leaves, he would undoubtedly conclude that heritable variations in leaves are legion. He would probably conclude also that for every one of these variations that may be of some advantage to the plant there are hundreds of others that are of no particular value or harm to it. Regardless of their value or lack of value to the plant, all of them are the result of the same general changes in the composition and arrangement of molecules in the hereditary units of matter (genes) in plant cells. "Rain falls alike upon the just and the unjust" because the factors underlying the formation of clouds and rain bear no relation to justice. Similarly, the factors underlying the origin of heritable variations bear no relation to their value. Dissimilar variations occur in leaves of plants growing in similar habitats and, conversely, similar variations occur in leaves of plants growing in dissimilar habitats. A few kinds of variations have survived more abundantly in some habitats than in others. Many of the heritable variations in leaves are interesting as phenomena of nature. Man makes use of them also as a means of classifying plants, for various sorts of decoration, and as a source of certain economic products. We shall not at this

time consider how hereditary differences occur, but limit our attention to a few expressions of them in leaves. (See also Figs. 14-17.)

Size and form. The smallest flowering plant in North America is a little globular duckweed (*Wolffia*) about 2 millimeters in diameter, without distinct root, stem, or leaf (Fig. 11). The opposite extreme is represented by palms with leaves 20 feet long. The native fern from which the Boston fern was derived grows in the Everglades region of southern Florida and has been found with leaves over 20 feet in length. Pines have needle leaves which in some species may be more than a foot long; structurally they are quite different from the leaves thus far described (Fig. 324). Iris is readily recognized by its sword-like vertical blades and the tightly folded sheath enclosing the stem and younger leaf bases. The cactus (*Opuntia*) has small temporary succulent leaves (Fig. 43). *Victoria regia* of the Amazon River, the largest of the water lilies, may have floating blades 5 feet in diameter with petioles 2 inches thick and



FIG. 43. The cactus (*Opuntia*) in which the younger stem segments and fruits bear small, awl-shaped, succulent leaves. Photo by G. S. Crowl.

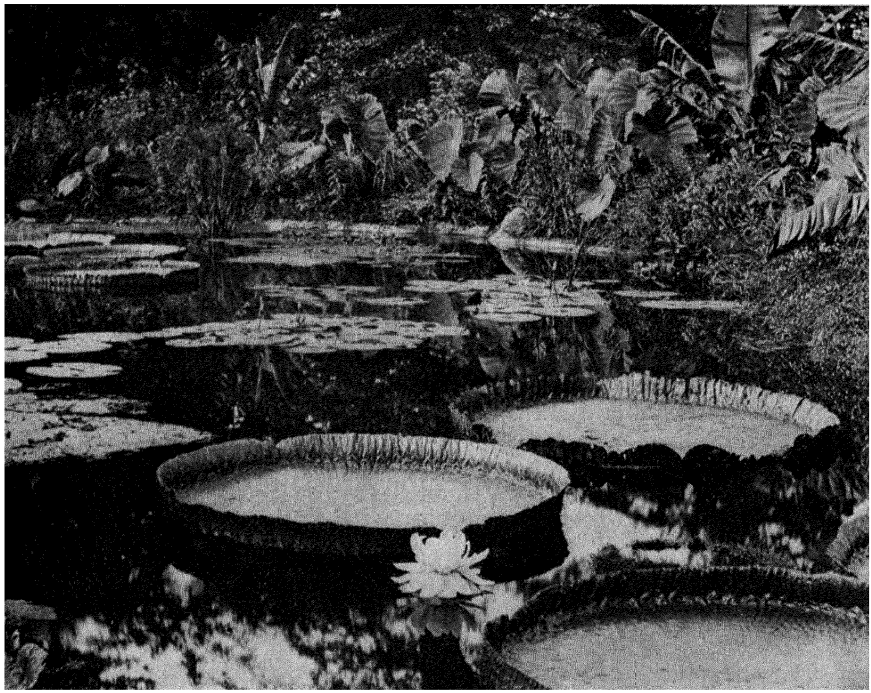

FIG. 44. The largest of water lilies, *Victoria regia*, in bloom. Photo from New York Botanical Garden.

20 feet long (Figs. 44 and 45). The century plant (*Agave*) has a type of hard leaf with a heavy base and thickened blade, often variously curved because of unequal growth (Fig. 46). At the time of flowering the upper leaves of poinsettia are bright red. The leaf (spathe) that subtends the flower cluster in the calla lily becomes white before the flowers mature.

Parts of leaves are sometimes so unusual that it is difficult to identify them as such. The stipules of the black locust tree develop as a pair of spines at the base of the leaf. The stipules of pea vine are leaf-like, and the terminal three or five "leaflets" are tendrils. On smartweeds the stipules form a sheath about the stem, whereas on rose leaves they are attached to the side of the petiole. The various species of asparagus have only very small scale leaves; the leaf-like organs are branches of the stem. All gradations between leaves and spines may be found on the common barberry. Near the stem tip bud scales develop from primordia similar to those of foliage leaves (Fig. 82, page 246).

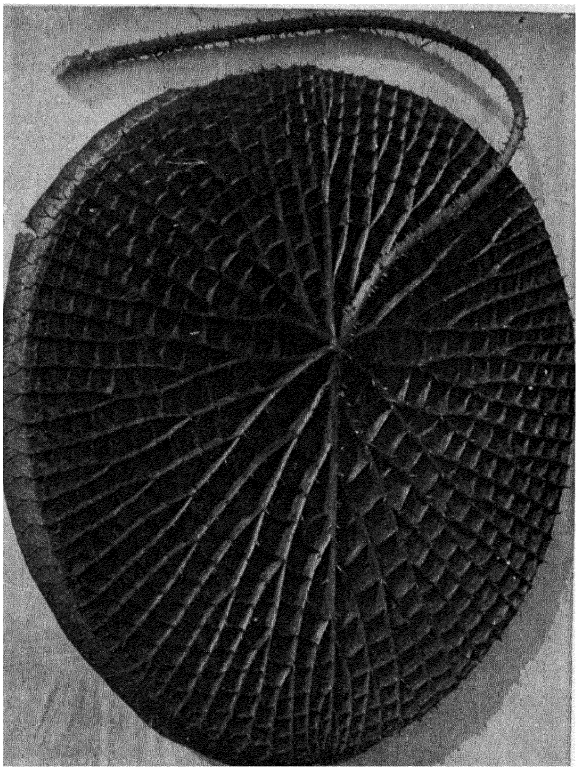

FIG. 45. Petiole and under side of leaf of *Victoria regia*. Photo from New York Botanical Garden.

Structures. Only a few of the striking differences in the structures of leaves are illustrated in this chapter. Simple one-celled hairs, or multicellular branched, stellate, and shield-like hairs are characteristic of certain leaves. The pine needle has peculiar chlorenchyma cells, and resin ducts. In the aloe leaf the chlorenchyma is a peripheral layer enclosing a mass of large, thin-walled gelatinous cells that have a high water-retaining capacity. The leaves of many aquatics that extend or develop above the water level are noted for the large proportion of air cavities extending not only throughout the leaf but downward into the stem and roots. The relative numbers of stomates and their occurrence on the two sides of a leaf are characteristic of a given species (Table 2, page 89). The number of stomates per square millimeter varies from place to place on a particular leaf, and the average of several counts must be taken when comparisons are made.

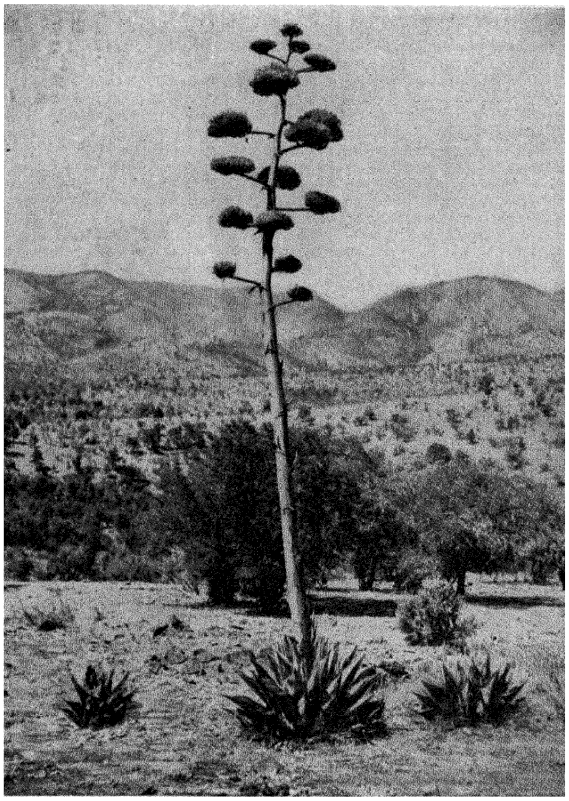

FIG. 46. Agave in bloom. From U. S. Biological Survey.

The pulvinus. At the base of the leaves and leaflets of certain plants, such as beans, clovers, honey locust, and red-bud, there is a thickened portion of the petiole, termed the *pulvinus*. It is composed primarily of parenchyma cells; the veins are more nearly central in it than they are in the rest of the petiole (Fig. 47). Water passes into or out of the cells more freely on one side of the pulvinus than on the other. This unequal movement of water causes unequal enlargement or shrinkage on opposite sides of the pulvinus, and a consequent movement of the attached petiole and blade. A more detailed account of the movement of water into and out of cells is included in Chapters XXII and XXIII.

In a pulvinus of the sensitive plant (*Mimosa pudica*) such changes in water content may be brought about on a warm day by simply touching the leaf. The observed effects are a lifting of the leaflets, a gradual closure of the branch "petioles," and a downward movement of the main

TABLE 2. Average Number of Stomates per Square Millimeter on the Upper and Lower Surfaces of a Variety of Leaves[1]

Tree Leaves			**Herb Leaves**		
American beech (*Fagus grandifolia*)	Up.	0	Giant ragweed (*Ambrosia trifida*)	Up.	100
	Lo.	100		Lo.	200
Yellow oak (*Quercus muhlenbergia*)	Up.	0	Hemp (*Cannabis indica*)	Up.	18
	Lo.	330		Lo.	230
Black walnut (*Juglans nigra*)	Up.	0	Prickly lettuce (*Lactuca scariola*)	Up.	85
	Lo.	460		Lo.	125
Tulip tree (*Liriodendron*)	Up.	0	Cattail (*Typha latifolia*)	Up.	225
	Lo.	240		Lo.	235
Cottonwood (*Populus deltoides*)	Up.	55	Jack-in-the-pulpit (*Arisaema triphyllum*)	Up.	0
	Lo.	85		Lo.	32
Scarlet oak (*Quercus coccinea*)	Up.	0	Willow herb (*Dianthera americana*)	Up.	80
	Lo.	1038		Lo.	80
			Water lily (*Castalia odorata*)	Up.	460
Shrub Leaves				Lo.	0
Sassafras (*Sassafras variifolium*)	Up.	0	Cow vetch (*Vicia cracca*)	Up.	130
	Lo.	35		Lo.	44
Grape (*Vitis bicolor*)	Up.	0	Corn (*Zea mays*)	Up.	70
	Lo.	72		Lo.	88
Cranberry (*Oxycoccus macrocarpus*)	Up.	0	Fescue grass (*Festuca sylvatica*)	Up.	200
	Lo.	632		Lo.	0
Hydrangea (*Hydrangea arborescens*)	Up.	0	Bluegrass (*Poa pratensis*)	Up.	160
	Lo.	25		Lo.	104
Maple-leaved viburnum (*Viburnum acerifolium*)	Up.	20	Water plantain (*Alisma plantago*)	Up.	50
	Lo.	30		Lo.	36

"petiole." This collapse of the whole leaf is in no way due to a mere relaxing of the leaf. The petiole is actually forced downward by the change in size of the cells of the pulvinus. Many of these leaves have characteristic positions with reference to the sun on bright days, and some "follow the sun" from morning to evening. These movements occur readily with changes in light intensity provided the temperature is high; if it is low, they are slow or do not occur at all.

[1] Data from papers by G. W. Blaydes, E. J. Salisbury, and L. E. Yocum.

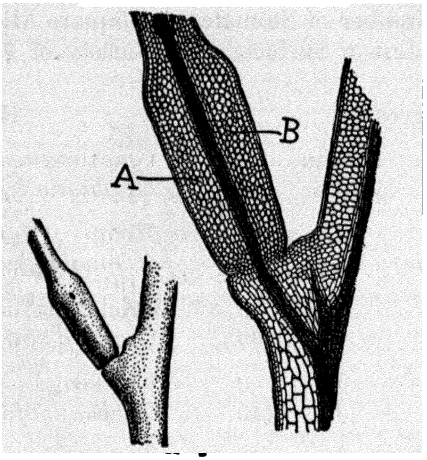

FIG. 47. Pulvinus and section of pulvinus from leaf of sensitive plant, both enlarged. When the leaf is touched, the water in the cells on side A passes outward into the intercellular spaces, causing the cells partially to collapse. The pressure of the cells on side B then forces the leaf downward. Courtesy World Book Co.

Rolling of leaves. Leaves of many grasses, especially those that live in dry regions, have chloroplasts in part of the mesophyll tissue only. There are other parenchyma cells, called reservoir cells, in which water noticeably accumulates. When the plants are subjected to drought these cells lose water and the leaves become folded, or rolled. Fig. 48 illustrates sections of leaves with reservoir cells. The inward rolling of leaves of corn and beach grass, and the folding of bluegrass leaves are common examples. These leaf movements have often been cited as examples of purposeful behavior, on the assumption that the leaves always roll so that the stomates will be on the inside. In nature, however, one may find leaves rolled in such a way that the stomates are on the outside and more exposed to light and dry winds than before the rolling. Bluegrass leaves which fold upward in drought have more of the stomates on the upper surface, whereas corn leaves which roll up have a greater number of stomates on the lower, exposed surface.

Aquatics. The leaves of submerged plants are noted for their thinness. They are usually ribbon-like as in pondweeds, or branched and dissected as in the water milfoil, water crowfoot, and water marigold. The leaf blades of many aquatic plants float on the surface of the water. The most striking features of floating leaves are the large air cavities and the restriction of stomates to the upper surface. However, paired guard cells often occur on the lower surfaces, and when the leaves develop above

flavoring confections and in medicine. Other chemicals characteristic of certain leaves are the nicotine of tobacco, cocaine of coca, theine of tea, and atropine of the deadly nightshade.

Economic uses of leaves. The use of leaves as food for grazing and browsing animals is of great economic importance. In connection with grazing animals it should be remembered that insects probably remove as much or more plant materials from a pasture than the larger animals.

The several products made from tobacco leaves are derived from distinct and selected varieties of the plant. The aroma, color, size, and texture of these leaves may be further modified both by the conditions under which the plants grow, and by the different methods of curing. Each variety attains its highest quality only under certain climatic conditions and on certain soils. For instance, the Mammoth variety cultivated in Connecticut, Maryland, and Florida has more leaves than others. The Cuban variety which is extensively used for cigar wrappers is sometimes shaded with cloth to increase leaf size and decrease leaf thickness. Burley, a coarse-textured variety, develops best on particular soils in Kentucky; it is much used in plug and smoking tobacco. Certain varieties cultivated on the sandy soils of Virginia and the Carolinas have been preferred for cigarettes.

Grass leaves, and fibers from the agave and from a Philippine banana, are extensively used for the manufacture of twine, ropes, and rugs.

A complete list of vegetables used as food would include a number of tender succulent leaves that form an important item of the human dietary in all parts of the world. Leafy vegetables are rich in vitamins; this is possibly their greatest value, aside from their contribution to flavors and odors.

A large and valuable literature deals with the effects of environmental factors on heritable qualities of economic plants. In this and the preceding chapter only a few examples have been cited. State and federal departments of agriculture have published many bulletins dealing with varieties of crop plants; with the particular temperature, light, moisture, and soil conditions most favorable for their development; and with the regions of the United States where they grow most successfully.

The references below contain additional information on hereditary differences in leaves, as well as in other plant organs, in respect to differences in cell substances synthesized in plants from foods. Further discussion of some of these plant products occurs in Chapter XIX.

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CHAPTER XI

A BIT OF USEFUL CHEMISTRY

Many gross features and properties of plants may be perceived by means of our unaided senses. With the help of a microscope, tissues and cells can be distinguished, and with the highest powers of this instrument many minute and important structures within the cells can be studied. These visible units of a plant are composed of invisible units, which may be investigated and mentally visualized by the methods devised by chemists and physicists for studying the composition and transformations of all matter. To understand the visible structures of a plant and the processes by which these structures are built and broken down, certain definite ideas about the invisible units of matter are essential. Consequently, it may be helpful to consider briefly here a few invisible units of matter and some of the usual chemical processes by which these units may be combined or changed. These general ideas and principles will be amplified and applied in subsequent discussions of physiological processes of plants.

Molecules and atoms. Like all other objects of our environment, plants are composed of molecules of definite chemical composition. The properties of the microscopically visible parts of a plant—the protoplasmic structures and cell walls—are determined in part by the kinds of molecules of which they are composed, and in part by the arrangement and organization of these molecules into aggregates. Each molecule of a particular compound such as water, sugar, or cellulose is made of still smaller units of matter that are definite in kind and in structural arrangement. The characteristic properties and reactions of molecules depend upon the presence and arrangement of these smaller units, the atoms and ions.

Water is a familiar compound, and in its simplest form its molecule consists of 2 atoms of hydrogen and 1 atom of oxygen—briefly designated as H_2O. Other designations are H—O—H and $\overset{+}{H}$—$\overset{-}{OH}$; the first of these indicates that both atoms of hydrogen are directly combined with

the atom of oxygen, and the second indicates the electrically charged ions into which the water molecule may be separated. A vessel of water always contains some free H^+ and OH^- ions. Likewise, every molecule is made up of atoms held together by electrical forces.

In stable molecules the positive and negative charges balance each other and the molecule is neutral; hence it is less active chemically than the free charged ions. Moreover, the electrical charges are important factors in determining the structural arrangement of the atoms and ions within a molecule, and also the stability and constancy of the molecules. Ions may separate under certain conditions and recombine under others without losing their identity.

Oxygen and hydrogen are gases with specific properties. As gases their molecules are widely dispersed. Each molecule of oxygen and of hydrogen is composed of two atoms, expressed as O_2 and H_2. In fact, every chemical element (hydrogen, oxygen, nitrogen, carbon, etc.) is characterized by a particular kind of atom.

In turn, the properties of atoms are determined by still smaller units of which they are composed. An atom is visualized no longer as a minute solid ball, but as a system of electrons, neutrons, and protons in which the negatively charged electrons are arranged about a central body composed mostly of neutrons and the positively charged protons. The arrangement and movement of these particles within the atom have been likened to the solar system, in which several planetary bodies (the planets) revolve about a central body, the sun. In an atomic system, however, the planetary electrons may not all lie in a single plane and their orbits of motion may not encircle the central body. Since the positive charges on the protons of an atom are balanced by the negative charges on its electrons, an atom is electrically neutral.[1]

Some chemical reactions are dependent upon the movement of an electron from one atomic system to another atomic system. Since the electron is negatively charged, the atom from which it departs becomes a positively charged ion and the atom to which it becomes attached becomes a negatively charged ion, both of which are chemically active and readily unite with other oppositely charged ions. Many of the common salts, such as Na^+Cl^-, are formed by the union of oppositely charged

[1] For further information about the constitution of atoms see a modern textbook of chemistry such as that by W. McPherson and W. E. Henderson, *Course in General Chemistry*, 4th ed., Ginn and Company, 1936, pp. 200-226; H. T. Briscoe, *Introduction to College Chemistry*, Houghton Mifflin Company; W. H. Hatcher, *Introduction to Chemical Science*, John Wiley & Sons, Inc.

ions. Chemical unions may also occur without a complete transfer of electrons from one atomic system to another. When two atomic systems approach each other, some of the outermost planetary electrons may be mutually held (shared) by both systems. Electrostatic forces hold the two atoms together as one molecule. Thousands of atoms may thus be held together in the largest molecules of plants and animals.

This incessant activity of electrically charged units within the atom makes its capacity for union with other atoms more easily understood. All of this internal activity within a molecule, say of water, may well cause us to wonder at its stability and uniformity of behavior. When we further attempt to picture the complex molecules and unceasing activities within every unit of a living cell, the regularity of development and the stability of living organisms composed of millions of cells are still more remarkable.

Our imagination is further taxed by fossil records which show that certain species of both plants and animals are so stable that they have

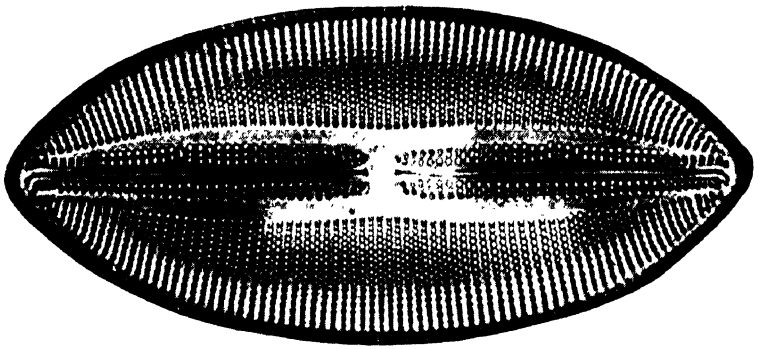


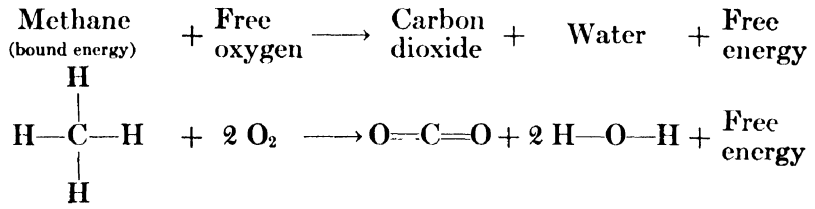
FIG. 50. *Navicula lyra*, a diatom present in marine deposits formed 25 to 30 million years ago. This species still lives today on sea coasts throughout the world. Photo by Spencer Lens Co.

remained apparently unchanged generation after generation through millions of years (Fig. 50). The stability of the cell, of the whole organism, and of the species is in the last analysis dependent upon the stability of physical-chemical units and upon the orderliness with which cycles of processes are repeated untold numbers of times. Cellular activity is far easier to comprehend than cellular stability; but this very stability is evidence of the inherent orderliness of natural processes.

Chemical processes in plants. An astounding number of different substances is formed in plants. Yet the formations and transformations of these substances involve only a few fundamental chemical processes.

An appreciation of four of these fundamental processes is an invaluable aid to an understanding of many of the material and energy transformations in plants.

Oxidation and reduction. Originally the term *oxidation* referred to the combining of oxygen with other elements and the consequent release of energy. For instance, when coal burns, free oxygen combines with the carbon in the coal, carbon dioxide (CO_2) is formed, and the chemically bound energy in the coal is liberated as heat and light. The same process occurs when wood or natural gas burns. The burning or oxidation of marsh gas (methane) may be indicated by a simple equation:[2]



Similar oxidations occur in living plants when the carbon of food substances combines with oxygen and the chemically bound energy in the foods is liberated.

When sugar is made from CO_2 and H_2O in the green tissues of plants the reverse of the burning process occurs. This reverse process is called *reduction*. Some of the chemically bound oxygen in the CO_2 or H_2O is liberated, and free energy is chemically bound in the sugar that is formed. In this particular process it is the energy of sunlight that becomes chemically bound in the sugar.

This early concept of oxidation and reduction is adequate for many of the problems we shall meet in general botany. When we recognize that free oxygen is being chemically bound in the plant and chemically bound energy is being liberated, we may infer that oxidation is occurring in the plant. When the converse occurs we may infer that reduction is occurring.

For certain problems, however, we may want to think of these processes in a more fundamental way. When an atom is oxidized it may lose one or more electrons to another atom; it thus gains in positive charges or valence. The atom to which the electron becomes attached gains in negative charges or valence; i.e., it is reduced. By this concept,

[2] In the equations in this book in which we wish to indicate energy transformations, the name of the compound containing chemically bound energy will be followed by the words "bound energy" in parentheses.

oxidation and reduction are seen to be complementary and simultaneous; this fact is indicated by the term *oxidation-reduction.*

This concept of oxidation and reduction is held to be true for many cases, such as the oxidation of iron and other metals. In the oxidation of methane, sugar, and similar carbon compounds, however, the electrons do not actually pass from one atom to another but are mutually shared by both atoms. Oxidation and reduction are involved in all physiological processes in which energy is chemically bound or liberated.

Hydrolysis and condensation. Some seeds contain starch but no sugar. When such seeds germinate, sugar appears in them and increases in abundance while the starch gradually disappears. When an animal eats a starchy food, the starch is converted to sugar in its alimentary tract. We are accustomed to say that the starch has been *digested* to sugar. The chemist refers to this process as *hydrolysis* because one molecule of water is added to the starch molecule for every molecule of sugar separated from it.

The converse process also takes place in plant cells, sugar being changed to starch. When several molecules of sugar are combined forming one large molecule of starch, a molecule of water is separated from each molecule of sugar added. Since several molecules are joined into one larger molecule with a loss of H_2O this process may be called *chemical condensation.* Many similar changes in the fat and protein compounds in living cells occur by hydrolysis and condensation. When these changes alone occur there is no gain or loss of chemically bound energy in the compounds involved.

Attention is called to these two contrasting pairs of fundamental chemical processes—*oxidation* versus *reduction*, and *hydrolysis* versus *condensation*—so that the discussion of food substances, their uses and transformations may be understood more readily.

In addition to these four chemical processes, there is another in which ions that have the same charge may replace each other in certain chemical compounds. For example, in a solution Na^+ and K^+ may replace each other. Likewise OH^- and NH_2^- may replace each other in certain organic compounds in living cells. This is called *chemical substitution.*

The number of atoms in a molecule may be small, as in water (H_2O), or it may be very large, as in proteins where each molecule is composed of more than a thousand atoms. Casein, one of the common proteins of milk, has the formula $C_{708}H_{1130}O_{224}N_{180}S_4P_4$. In nature, outside of living cells, such complicated molecules are rarely formed. One of the reasons

why discovery of the chemistry of living organisms has progressed so slowly is the presence of such large complex molecules. Another reason is that within the colloidal system of protoplasm with its surface energy and electrical energy there are many chemical transformations that are difficult or impossible to duplicate in the laboratory. Furthermore, hormones and other substances may affect processes in living cells in a most striking way when present in amounts too small to be detected by the ordinary methods of chemical analysis. Owing to the complexity of the problems of biochemistry, progress is slow; but students of this phase of biology may well be proud of the advances made during the last half-century.

Elements found in plants. About half of the known chemical elements have been found in plants through chemical analyses of a great variety of specimens. But this fact is of little significance. The roots of a plant are in contact with the water in the soil, and any soluble substance in the soil water is likely to pass into the water within the plant and thus be reported in a chemical analysis of the plant. On the other hand certain of these elements are known to be in the compounds of which the plant is made. First in abundance are carbon, hydrogen, and oxygen which occur in most plant compounds. Nitrogen and sulfur occur in all known plant proteins. Phosphorus occurs in some proteins and in various lipoids (phosphatides). Magnesium is one of the elements in the chlorophyll molecule. Calcium forms salts with the acid substances, such as pectic acid in the cell walls of plants. Any other basic ion may similarly form salts with acid substances in plants, but its presence may not be essential to the plant. Finally there are a few elements—namely, potassium, iron, manganese, boron, and sometimes copper and zinc—which are essential to the development of plants; but their definite relations to plant processes are still inadequately known. Some of them are toxic to the plant except when present in very minute amounts.

A list of the elements essential to the development of plants tells us little about the chemical composition of plants. They do not occur in plant tissues as free elements, but owe their importance to the part they play in the formation of compounds and the processes they affect. They enter plants and are utilized in plants, not as free elements, but as parts of molecules and compounds or as dissociated ions of compounds. Oxygen, for example, enters plants as free molecular oxygen and also in chemical combination, as in H_2O and CO_2.

CHAPTER XII

THE FOOD OF PLANTS

Three frequently used words will help us arrive at an understanding of the nature of food. They are: starvation, desiccation, and suffocation. Suffocation implies a lack of oxygen; desiccation, a deficient water content of the body; and starvation, a lack of food. More recently "mineral deficiency" has become a common expression among physicians to denote an inadequate supply of certain mineral salt ions. Botanists have found these four expressions of bodily needs—mineral deficiency, suffocation, desiccation, and starvation—equally pertinent in distinguishing the salt, oxygen, water, and food relations of plants.

Sources of foods. The fact that cattle, dogs, birds, insects, and other animals obtain food either by eating plants, by eating animals that feed on plants, or by eating commercial products obtained from plants, needs no further evidence. Equally commonplace is the admonition that to prevent the decay of food, the infection of wounds, and occurrence of certain diseases, it is necessary to avoid, to inactivate, or to destroy certain non-green plants known as bacteria and fungi. Most non-green plants, like all animals, must obtain food from other plants or from animals, or from plant and animal products. The green plants and a relatively few species of non-green plants therefore appear to be unique among living organisms in not being dependent upon any external source of food.

Aristotle's notions of food of plants. Twenty-three hundred years ago the philosopher Aristotle, speculating on the ways of nature, concluded that green plants obtain food from the soil. Reasoning by analogy from his observations of animals, he concluded that the source of food of any organism lies outside its own body. Since many green plants have parts of their bodies in the soil, he thought that they must procure food from that source. He had no basis for reaching a better conclusion regarding the food of green plants because very little was known about their physiology. The chemistry of the inorganic world also was largely a mystery at that time. Only a few of the metallic elements had been identified; and more than 20 centuries passed before oxygen, hydrogen,

nitrogen, carbon, and their simplest compounds were recognized and their nature was understood. Another century had nearly passed before the food of green plants was discovered.

Aristotle was further impressed by the absence of excretory organs in plants, but concluded that the soil in some way acted as the stomach of the plant and supplied it with only perfect food, from which no unused products would accumulate and have to be eliminated. For centuries these two notions of Aristotle prevailed and even now they have not entirely disappeared.

The food of green plants not in the soil. During the latter half of the last century students of plant physiology not only discarded the idea that green plants get their food from the soil, but they discovered how and where this food is made. In spite of all these well-publicized discoveries, the mistaken ideas of Aristotle are still current in conversation, advertising propaganda, public addresses, and modern literature three-fourths of a century after they were adequately disproved.

Even before the numerous discoveries of the 19th century, van Helmont (1577-1644), a Flemish physician and chemist, showed by a simple experiment that Aristotle's ideas about the food of green plants were erroneous. Van Helmont placed a willow branch in a tub of soil to which thereafter only rain water was added for a period of five years. At the conclusion of the experiment the willow branch had become a small tree and had gained 2627 ounces in weight, not including the leaves that had fallen each year. The weight of the soil in the tub decreased but two ounces.

In both animals and plants it is the protoplasm for which food is necessary. We have already seen that the protoplasm of all organisms is similar in its gross chemical composition. From these two facts alone it appears that the food of green plants must be similar to that of animals regardless of how it is obtained.

A part of man's food is obtained from seeds, bulbs, tubers, and roots. If these same plant organs are placed in a vessel containing only pure quartz sand and a little water, small plants presently grow from them. The same results are often attained by merely placing the seeds in moist air. Small plants will grow from detached bryophyllum leaves suspended near a window.

During the growth of these young plants millions of new cells are made, each composed of protoplasm and cell wall substances. For the making of these new cells the chemically bound energy and materials in food are necessary. One cannot avoid the conclusion that seeds, bulbs,

leaves, tubers, and roots already contain substances from which new protoplasm and new cell walls can be made, and from which chemical energy can be derived. What are these substances?

Foods in cells. Thin sections of seeds or tubers observed through a microscope are seen to be composed of numerous cell walls surrounding rather dense masses of granules and oil droplets (Fig. 51). Similar

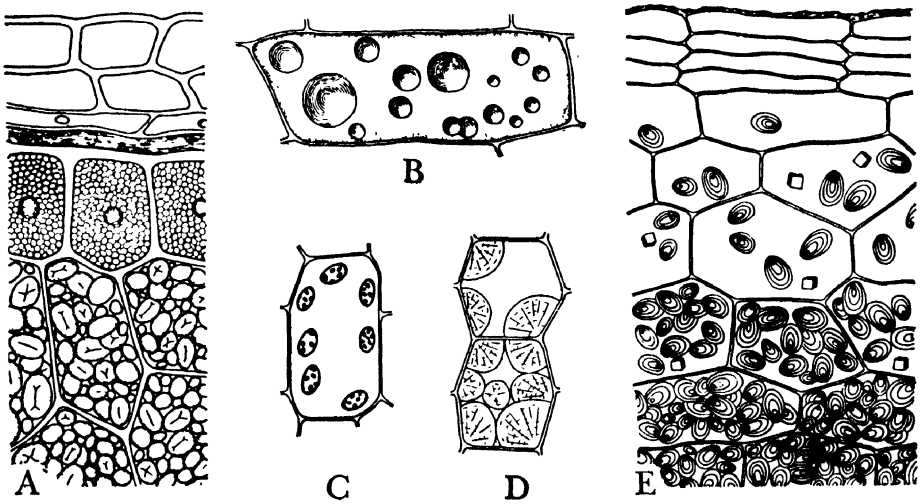


FIG. 51. Illustrations of various accumulated foods in plant cells: A, protein and starch in cells of a wheat grain; B, oil droplets in a cell from a coconut seed; C, small starch grains in chloroplasts; D, crystals of inulin in cells of salsify root; E, starch grains and protein crystals in cells of potato tuber. By S. S. Humphrey.

granules and oil droplets may be found in most living plant cells, but usually in much smaller quantities. The oil droplets may be distinguished by their appearance or by their bright red color in the presence of dilute solutions of certain dyes, such as Sudan III. The presence of fat-like substances in plant parts may also be detected by crushing a small piece of the tissue on paper and warming it. The fat-like substance melts and produces a translucent oil spot on the paper.

The remaining granules in the cells may be starch grains, protein granules, or granules and crystals composed of certain organic compounds combined with inorganic substances such as calcium and phosphorus. Organic substances when combined with phosphorus are frequently referred to as phosphatides. Starch grains may be detected by applying a drop of a dilute solution of iodine and potassium iodide to a section of the plant. When treated with this reagent, starch grains may be recognized by their various shades of blue and purple; the other substances in the cell remain colorless or are stained light brown.

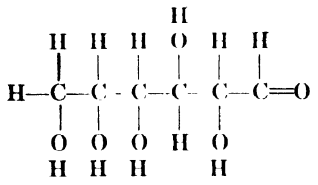
Protein granules may be distinguished from fat droplets and starch grains by a number of different stains; but perhaps a better concept of proteins may be obtained by kneading a small amount of wheat flour in water until all the starch grains have been washed from the dough. Sugars also are present in plant cells, but they are usually in solution in the cell and are invisible. Their presence may be detected by tasting the plant, or by placing a section of the plant organ in a drop of 20 per cent sodium hydroxide in which a few crystals of copper tartrate have dissolved. If a reddish-yellow precipitate of cuprous oxide is obtained, the presence of sugar is indicated. The reaction may be hastened by heat (40° C.). To detect cane sugar by this method the plant section should first be treated for several minutes with the enzyme invertase or with a dilute acid, for instance 5 per cent citric acid.

The cell walls are made principally of cellulose and pectic compounds, though some of them may also contain a substance (lignin) characteristic of wood, or a fat-like substance (suberin) characteristic of cork.

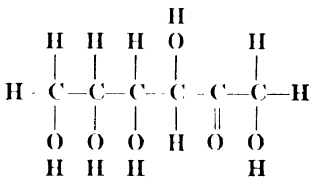
All the substances mentioned above have been extracted from plant cells by chemical methods, and most of them may be obtained on the market in a relatively pure state. Thus one may readily buy several kinds of sugar (especially sucrose, glucose, and fructose), starch, several kinds of plant oils, pectic compounds (Certo), and cellulose (filter paper); and then apply to them the tests that were proposed above for detecting the same substances in plant cells. Some of these substances we readily recognize as constituents of our daily diet.

Sugars. Each of the sugars mentioned above may be sold under any one of three names. Glucose ($C_6H_{12}O_6$), also known as grape sugar and dextrose, is not very sweet, but it is one of the principal sugars in plants and also in the blood stream of animals—in fact, it is sometimes called "blood sugar." Fructose ($C_6H_{12}O_6$), also called fruit sugar and levulose, is one of the sweetest of sugars and is common in plants.[1] Sucrose

[1] The apparent anomaly of two sugars having identical formulas ($C_6H_{12}O_6$), but differing in chemical properties, may be explained by the differences in the arrangement of the atoms. Following are diagrams of these differences in glucose and fructose molecules.



Glucose



Fructose

These diagrams of sugar molecules are introduced here merely to help visualize differences in the arrangement of atoms in the simple sugars, not to memorize.

($C_{12}H_{22}O_{11}$), otherwise known as cane sugar and saccharose, is the common household sugar. It is present in most plants and is especially abundant in sorghum, sugar cane, sugar beet, and sugar maple. Each molecule of sucrose is composed of a molecule of glucose chemically bound with a molecule of fructose minus one molecule of water. When treated with dilute acids, it is hydrolyzed to these two simple sugars.

Classification of foods. For convenience we may think of all these substances as belonging to a few large groups of chemical compounds: the carbohydrates, fats, and proteins. In a detailed consideration of foods this classification is incomplete unless numerous compounds that may be derived from carbohydrates, fats, and proteins by chemical alteration are assumed to be included. In any brief discussion of foods this assumption is usually made. The chemical alterations of the carbohydrates, fats, and proteins are brought about by such processes as partial oxidation, reduction, and hydrolysis. These processes result in the formation of alcohols, organic acids, organic bases, and other compounds which may still be usable by organisms as food. The total number of such derived compounds is undoubtedly very large, but aside from those formed in digestion and fermentation their relative bulk is exceedingly small. Since many of these derived compounds are acid or basic, they may form numerous chemical combinations with each other and with the mineral ions that pass from the soil into the plant.

Carbohydrates. The carbohydrates are composed of carbon, hydrogen, and oxygen. The hydrogen and oxygen occur in the proportion of 2 to 1 as in water (H_2O) and glucose ($C_6H_{12}O_6$). To this group belong all the sugars, starches, inulin, and cellulose. The pectic compounds are closely related to the carbohydrates. A molecule of pectic acid, for instance, is composed of molecules of certain sugars chemically combined with acids derived from sugars by partial oxidation. A molecule of starch, or of cellulose, is composed of many molecules of glucose in chemical combination, and a molecule of inulin is composed of many molecules of fructose similarly combined.[2] When acted upon by certain enzymes or acids these complex carbohydrates are hydrolyzed to the simple sugars out of which they were made. These complex carbohydrates are usually inert, insoluble compounds of no food value to the organism unless they are digested to the simple sugars which are soluble and chemically active.

[2] For a more detailed statement of the formation of complex carbohydrates, see p. 135, Chapter XV.

Fats. Fats and oils are likewise composed only of carbon, hydrogen, and oxygen, but they have comparatively little oxygen in proportion to carbon and hydrogen. There is no general chemical distinction between fats and oils. They are distinguished by their melting points. At ordinary room temperatures oils are liquids, while fats are solids. During digestion fats and oils are hydrolyzed to glycerin and fatty acids.

Proteins. The proteins are composed of carbon, hydrogen, oxygen, nitrogen, sulfur, and sometimes phosphorus also. During digestion the large complex molecules of proteins are hydrolyzed to simpler substances known as amino acids.

When we consider all the substances that we have seen in the cells of seeds and tubers, we readily recognize some of them as foods of man and other animals. Four questions may now be considered. Which of these substances are used as food in the animal body? When we buy a pound of potatoes do we buy a pound of food? Is the food of green plants and of animals identical? How does the green plant get food?

Foods used by man. For our own bodies we recognize as foods those compounds which can be transformed into the substances of which cells are composed and from which our body obtains kinetic energy by oxidation. These compounds, we have already seen, are carbohydrates, fats, and proteins, together with their partially oxidized, reduced, or hydrolyzed derivatives which may or may not be combined with certain ions of the mineral salts. But as foods these compounds are subject to one more limitation: they must be either in a soluble state, or capable of being digested by appropriate enzymes in the alimentary tract. The sugars and some of the derived compounds are already dissolved in water and may pass from the alimentary canal into the blood stream. Our bodies synthesize enzymes that digest starches, fats, and proteins, but not enzymes that digest cellulose, pectic compounds, wood, cork, and inulin. If we were entirely dependent upon our own enzymes even a pound of dried potatoes would not be a pound of food.

The non-green plants (bacteria and fungi) also synthesize enzymes that digest starch, fats, and proteins; and a few kinds of non-green plants synthesize enzymes that digest cellulose, pectic compounds, inulin, and wood. Thus the non-green plants as a group may utilize a wider range of compounds as food than is used by animals. It is interesting to note that some of the digestion that occurs in the alimentary tract of man and other animals is due to the non-green plants that live there.

The food of green plants. The food of the green plant may now be

considered. When a seed or a tuber is placed in a moist chamber and a young plant grows from it, what substances in the seed or tuber disappear as the cells of the new plant are made? They are exactly the same kinds of carbohydrates, fats, proteins, and derived compounds that the animal uses as food. Parts of the tuber, especially the cell walls, remain but may be digested and used as food by certain bacteria and fungi. From such facts as these, together with other facts that will be discussed in later chapters, botanists regard the food of green plants to be identical with that of animals.

The process by which the green plant obtains food, however, is unique. The food is not obtained from the soil, from the air, from water, or from other organisms. *It is made within the plant* from simple inorganic compounds obtained from the soil, air, and water. In the next few chapters we shall consider *material* and *energy transformations* essential to the food-making processes in green plants, the influence of the environment upon these processes, the consequent behavior of the plant in certain environments, and the vital importance of these transformations to the whole biological world and to industry.

Such substances as hormones, vitamins, and enzymes, which are essential to numerous processes in living organisms, are made from foods and will be discussed in Chapter XIX.

Summary. In the foregoing discussion we have considered two very different concepts of the food of living organisms, with special reference to green plants. The older view proposed by Aristotle is based upon the assumption that food is something that enters the organism from without. A more recent concept of food is based upon a knowledge of the physiology of organisms, that is, the ways in which substances are used within the organism regardless of whether they are obtained from the outer world or are made within the body. It limits food to such substances as carbohydrates, fats, proteins, and their derivatives which may be used in cell construction and as a source of energy within the organism.

Such a concept of food emphasizes the fundamental similarity in the nutritive processes of the protoplasm in all plants and animals. The older concept denies this fundamental similarity in organisms, and excludes all the modern concepts of the food of green plants.

CHAPTER XIII

FOOD SYNTHESIS

I. THE SYNTHESIS OF SUGAR—PHOTOSYNTHESIS

Some of the significant facts that finally enabled botanists to arrive at an understanding of the food of green plants, and a realization that this food is actually made within the plant were briefly mentioned in the preceding chapter. Much time and exact experimentation were required to discover the simpler material and energy transformations that occur in food synthesis, and the various conditions both inside and outside the plant that affect these transformations. It is now common knowledge among botanists that sugar is the first kind of food made in green plants, and that all other kinds of food are made by chemical alterations of this sugar. Furthermore, the facts discussed in the next few chapters will help us see that the material make-up of all living organisms is dependent upon chemical derivatives of the sugar made in plants; that the potential energy in sugar is the primary source of the chemically bound energy supply of all organisms; and that most of the energy that man transforms by various means into heat, light, electricity, and mechanical energy may be traced back through various transformations to the potential energy of sugar. In this chapter we are concerned primarily with the making of sugar in green plants.

Carbon dioxide and oxygen in relation to green plants. Toward the close of the 18th century oxygen and carbon dioxide were clearly recognized and named by the French chemist, Lavoisier. Following this advance in chemistry, a number of carefully conducted experiments by different investigators finally led to the discovery of certain fundamental relations between these two gases and living organisms. When the green parts of plants were exposed to light, the amount of oxygen in the surrounding air increased and the amount of carbon dioxide decreased. During the hours of darkness the converse occurred. When the roots or other non-green parts of a plant were substituted for the green tissues in the experiments, the amount of oxygen in the surrounding air de-

creased and the amount of carbon dioxide increased, both in light and in darkness. *The increase in oxygen and decrease in carbon dioxide in the surrounding air occurred only when some green tissue of the plant was exposed to light.* When animals and non-green plants were used in these experiments, the results were like those obtained with roots and other non-green parts of the plant. How was one to account for this unique effect of the green tissues of plants?

The phenomenon was not satisfactorily explained until after the middle of the 19th century. So little was known about the substances and processes within plants and about the factors in the environment of plants, that numerous facts had to be discovered by experimentation before any of the various hypotheses proposed could be eliminated or converted into a scientifically established conclusion. The facts finally established may be represented briefly by the following equation:[1]

$$\begin{array}{lllll} \text{Water} + \text{Carbon dioxide} & \xrightarrow{\text{Light energy}} & \text{Sugar (bound energy)} & + & \text{Oxygen} \\ 6\ H_2O + \quad 6\ CO_2 & \longrightarrow & C_6H_{12}O_6 & + & 6\ O_2 \end{array}$$

This equation is a summary of the overall energy transformation and of the initial substances used and the final products formed when sugar is being made in the green cells of plants. In every gram of sugar made, about 3.75 Calories of light energy become transformed to chemically bound energy. This is enough to raise the temperature of one liter of water 3.75° C., or to keep the reader alive for a few minutes. To show that the source of O_2 is in H_2O we would change 6 H_2O in the equation to 12 H_2O, add 6 H_2O on the right of the arrow, and follow through with a discussion much beyond our present aims.

Photosynthesis. This process of making sugar in the green parts of plants is called photosynthesis (Greek, *photos*, light; and *synthesis*, putting together), because light is necessary for this synthesis of large molecules ($C_6H_{12}O_6$) from smaller ones (CO_2 and H_2O).[2]

[1] One reservation to this statement should be made. The equation indicates that a hexose sugar (the molecule being composed of 6 atoms of carbon, 12 atoms of hydrogen, and 6 atoms of oxygen) is formed. This is generally considered to be glucose, though the known facts are not sufficient to exclude fructose entirely, at least in some cases. These two sugars are the only simple sugars found widely distributed in detectable amounts as free sugars in plants. Either of them may be formed from the other one in plants. See the structural formulas in the footnote on p. 104. Some investigators have suggested sucrose ($C_{12}H_{22}O_{11}$) as the first sugar made, but the evidence is not convincing.

[2] The older term, carbon assimilation, is still used by some writers; but, as we shall see later, the term assimilation is also used to designate the conversion of food into the substances of which cells are composed, a process that occurs in all plants and animals, whereas the process we are describing here occurs only in the green tissues of plants. Furthermore, the term carbon assimilation is a heritage of the early misconceptions of plant

Chemical reactions that are brought about by light are often referred to as photochemical reactions—reactions initiated by the collision of photons (units of radiant energy) with some part of a molecule. There are, of course, several kinds of photochemical reactions; but by tradition in botany the term photosynthesis usually refers to the making of sugar from CO_2 and H_2O in the chlorophyll-containing cells of plants.

By comparing the relative numbers of atoms in the molecules represented in the equation on page 109 we can see why free oxygen is one of the products of photosynthesis. For every molecule of CO_2 used, one molecule of O_2 is formed. From the principle first formulated by Avogadro—that equal volumes of gases under the same conditions of temperature and pressure contain the same number of molecules—we may infer that the volume of CO_2 consumed in photosynthesis is equal to the volume of O_2 liberated. This inference has been verified by experimentation. The comparative weights of the materials used and formed during photosynthesis may also be indicated:

$$264 \text{ gm. } CO_2 + 108 \text{ gm. } H_2O \longrightarrow 180 \text{ gm. } C_6H_{12}O_6 + 192 \text{ gm. } O_2$$

Obviously if one knows the amount of CO_2 used in photosynthesis, he can compute the amount of sugar made and the amount of oxygen set free. Similarly, if he knows the amount of oxygen set free or the amount of sugar made, he can calculate the amount of any one of the other substances involved in the process. How can one calculate the amount of energy that is chemically bound during photosynthesis?

It should be noted that the overall material and energy transformations that occur in the making of sugar are the converse of those that occur in the burning of sugar. If we regard the burning of sugar as an oxidation process, we may regard photosynthesis as a reduction process. It is the primary energy-storing process of the organic world.

Oxidation processes are often regarded as exothermic (heat-releasing), and reduction processes as endothermic (heat-storing). These terms are quite appropriate when transformations of heat energy only are involved. They are quite confusing, however, when these processes of living cells result in transformations to other kinds of energy, as, for instance, radiant energy to chemically bound energy, chemically bound energy to

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nutrition. In order to avoid confusion of terms we shall refer to the above process as photosynthesis. The term carbon fixation is of course entirely ruled out, because carbon is already "fixed" in CO_2 before the process begins. If we must substitute another term for photosynthesis in botany, it should be "sugar synthesis."

light, or to electrical energy. The first is exemplified by photosynthesis, the second by the production of light by fireflies and luminous fungi and bacteria, and the third by the electric discharge from an electric eel.

Before photosynthesis can occur in an illuminated green cell the initial materials, CO_2 and H_2O, must be available. Carbon dioxide is very soluble in water. Hence, all the green cells of the simpler algae that live submerged in water, and even those in the leaves of the common water weed (*Elodea*), are in direct contact with both water and CO_2. Both of these substances pass readily into the cells and then to the chlorophyll in the chloroplasts.

In land plants the water moves up from the soil through the roots, stems, and petioles into the veinlets of the leaf (Fig. 52), and then passes

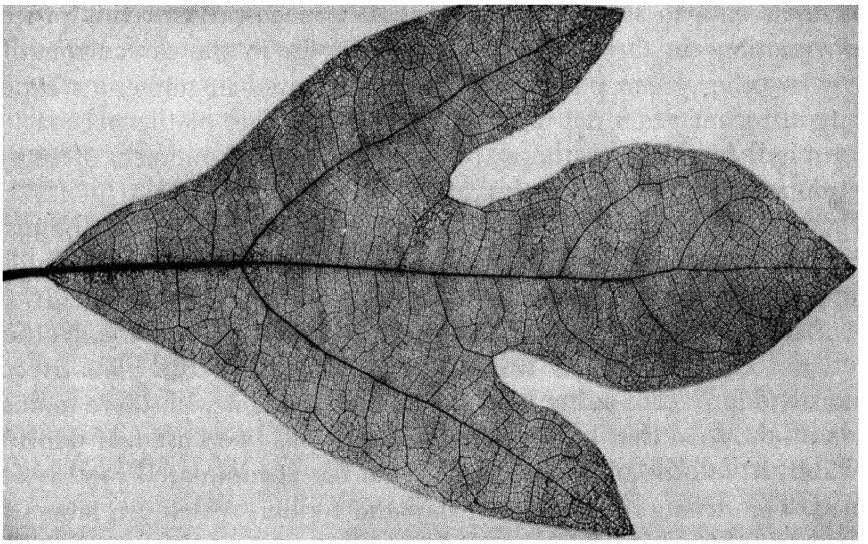

FIG. 52. The vein system of a skeletonized sassafras leaf. The leaf was kept in water until bacteria had digested the epidermis and mesophyll.

from cell to cell throughout the leaf. No appreciable amount of carbon dioxide gets to the leaves from the soil by way of the roots. It enters the leaf from the surrounding atmosphere above the soil. Some of it may pass directly through the epidermal cells to the chlorenchyma beneath. Most of it passes through the stomates into the intercellular spaces of the mesophyll, where it comes into contact with the wet walls of the mesophyll cells that are exposed to the internal atmosphere of the leaf.

It dissolves in the water of the cell and finally gets to the chlorophyll in the chloroplasts (Fig. 34).

Most of the oxygen liberated during photosynthesis passes from the cells into the intercellular spaces of the chlorenchyma, then through the stomates into the outer atmosphere. This passage of CO_2 into, and of O_2 out of, the chlorenchyma also occurs when photosynthesis takes place in green stems and fruits or in any other green part of the plant. The sugar that is not locally consumed or transformed within the chloroplasts passes from them to all other parts of the plant. The manner of its transfer will be discussed in later chapters.

Factors involved. Had the earlier investigators known that the increase of O_2 and the decrease of CO_2 in the air surrounding green plant organs exposed to light were the *result* of the synthesis of sugar, they could have used their data to show that chlorophyll is necessary for this process. The variations in the amount of CO_2 and O_2 in the air surrounding leaves or other green plant parts have been used in numerous experiments in recent years not only to establish the fact of the necessity of chlorophyll for photosynthesis, but also to study the effects of several environmental factors upon the rate of photosynthesis.

From the facts discussed thus far, one would expect sugar to be made in plants only when the following are present: chlorophyll-containing cells, water, carbon dioxide, light, and a suitable temperature. If any one of these factors is absent, no sugar will be made, and the synthesis of other foods from sugar cannot long continue. If the plant is continuously deprived of either light or carbon dioxide it will starve to death when all the food that has accumulated in it has been used. If deprived of water, it will die of desiccation before the accumulated food is consumed. The drying of freshly cut hay and fodder, which are later used as a source of food for animals, is a good illustration of the death of plant organs by desiccation before the food within them is consumed by the plant.

In experiments it is possible to expose a plant to a temperature in which it will consume sugar faster than it makes it. Plants in the field are frequently exposed to such temperatures for short periods of time. Various investigators have concluded that this condition may frequently limit the distribution of particular plants in certain geographic areas. As we shall see later, it greatly affects the amount of growth of certain plant organs. The death of plants exposed to extreme temperatures is more

often due to other causes, among which may be mentioned the coagulation of protoplasm.

Sugar synthesis in bacteria. One outstanding exception to the making of sugar by photosynthesis may be mentioned here, but it will be discussed in more detail in a later chapter. A few kinds of bacteria are known to make sugar from carbon dioxide and water in the absence of light. The energy necessary for this process is obtained by the oxidation of iron, sulfur, or nitrogen that has previously been reduced. A few other kinds of bacteria (purple bacteria) are unique in containing a pigment which, like chlorophyll, is effective in photosynthesis. The accompanying purple pigment ($C_{48}H_{66}O_3$) is similar to the carotenoids described in Chapter IV.

The amount of sugar made. The amount of sugar made in plants varies so greatly in different plants and under dissimilar conditions that it is difficult to make a general estimate of it. The results of many experiments show that under favorable conditions a square yard of leaf surface makes on the average about 0.5 gram of sugar per hour. At this rate about four months would be necessary for a square yard of leaf surface to make sugar equivalent to the *food* a man consumes in one day. In Chapter XVIII an acre of corn is compared with an acre of young apple trees with respect to several plant processes. This acre of corn has about two acres of leaf surface. During the growing season it makes about 10 tons of sugar, an average of about 2 pounds per plant. The acre of young apple trees (10,000 leaves per tree) makes about 8.7 tons of sugar, an average of about 44 pounds per tree. On the basis of data from many sources it is estimated that the plants of the United States make nearly three-fifths of a cubic mile of sugar each year. For the land plants of the world, 9 cubic miles of sugar annually seems to be a conservative estimate.

Now let us recall the fact that for every 180 grams (almost 0.4 lb.) of sugar made, 674 Calories of light energy are transformed to available potential energy in this sugar. The potential energy in the sugar made annually in the United States alone is estimated to be about 14×10^{15} Calories. Yet large as this figure is, it is far below the one that would represent the energy liberated annually on the earth today by plants, man, and all other living organisms. Through the burning of coal, oil, and gas alone man liberates about 14×10^{15} Calories of energy each year. The energy was transformed from radiant energy to potential energy by the plants of the distant past. The facts upon which these

statements are based will become clearer as we proceed with the study of other processes that occur in living organisms.

What becomes of the sugar made in plants? The answer to this question will become more evident as we proceed with the next six chapters. For the present we may be brief. Some of the sugar is transformed to other types of foods; some is transformed directly into substances of which cells are composed, particularly the substances in cell walls; some of it is oxidized in the plant; and some of it accumulates within the plant.

The accumulated sugar of course merely represents the part that has not been used within the plant or converted to other kinds of food within it. Animals and non-green plants get some of it. The amount of sugar that accumulates depends partly upon the rate of photosynthesis and partly upon a number of other processes and conditions. Some plants, such as sugar cane and the sugar beet, are noted for the large amounts of sugar that accumulate in them in a suitable environment. Under good growing conditions, sugar is usually present in varying amounts, as glucose, fructose, and sucrose, in the cells of all green plants.

In plant cells these three sugars are intraconvertible; i.e., one sugar may be formed from another by certain rearrangements and combinations of atoms:

$$\text{glucose} \rightleftharpoons \text{fructose}$$

$$\text{glucose} + \text{fructose} \rightleftharpoons \text{sucrose} + H_2O$$

The rearrangements of atoms involved in the transformation of glucose to fructose and vice versa may be inferred from the structural formulas represented in the footnote on page 104. The formation of glucose and fructose from sucrose is merely a process of hydrolysis; the converse is a process of condensation.

Summary. The primary food of all living organisms is sugar. It is the basis of all other food syntheses and is made in green plants by a process of photosynthesis. In this process sugar is made from carbon dioxide and water in the chloroplasts of green plants exposed to the radiant energy, light. An insignificant amount of sugar is also made photosynthetically in purple bacteria that contain a chlorophyll-like pigment, and chemosynthetically in the dark in certain colorless bacteria that obtain energy by oxidizing reduced iron, sulfur, and nitrogen. In every case the initial materials are carbon dioxide and water, and the end products are sugar and molecular oxygen. The intermediate steps in the process are not fully known.

CHAPTER XIV

FOOD SYNTHESIS

II. FACTORS INFLUENCING THE RATE OF PHOTOSYNTHESIS

The basic facts about photosynthesis discussed in the preceding chapter do not exhaust the subject; neither do they satisfy anyone who wants to understand the fundamental processes of his natural environment. The answers to many questions about plants involve facts concerning the chain of chemical reactions that occur in photosynthesis, and the influence of the various factors of the environment. The value of certain practices in the handling of plants and the interpretation of plant phenomena in nature depend also upon a knowledge of these relations. Many questions concerning these relations cannot be answered today, but additional facts that are helpful in answering some of them will now be discussed.

Light the energy of photosynthesis. Under natural conditions the energy of photosynthesis is sunlight. Heat cannot be substituted for light in this process. No sugar is made from CO_2 and H_2O in green plants deprived of light, regardless of the temperature to which they are exposed. Radiant energy that we perceive as light is referred to as the

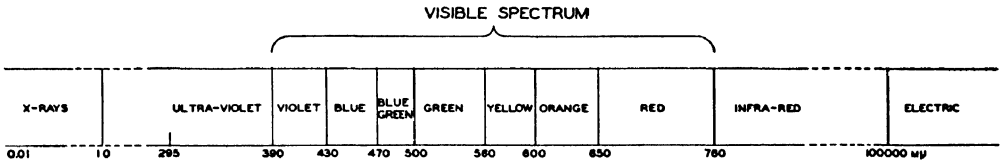

FIG. 53. The spectrum of radiant energy. One millimicron (mμ) = one-millionth of a millimeter. See also Plate II.

visible spectrum (Fig. 53). This is the radiant energy that is effective in photosynthesis. It can initiate chemical change by displacing or activating the outermost electrons of atoms. The effects of radiant energy of longer wave lengths, such as infra-red, are apparently limited to the movement of atoms and molecules. Photosynthesis is not known to occur when the plant is exposed only to infra-red radiation.

Within the visible spectrum the radiant energy that we call red, orange, yellow, and blue light is the most effective in photosynthesis. The color of leaves is evidence that relatively more of the radiant energy we see as green is reflected by chlorophyll. In land plants most of the photosynthesis is brought about by the radiant energy of the red end of the spectrum, but the radiant energy that penetrates the water to the depth of deep-sea algae is mainly the blue end. The effectiveness of the blue and the red rays is about equal when their intensities are equal (Fig. 54).

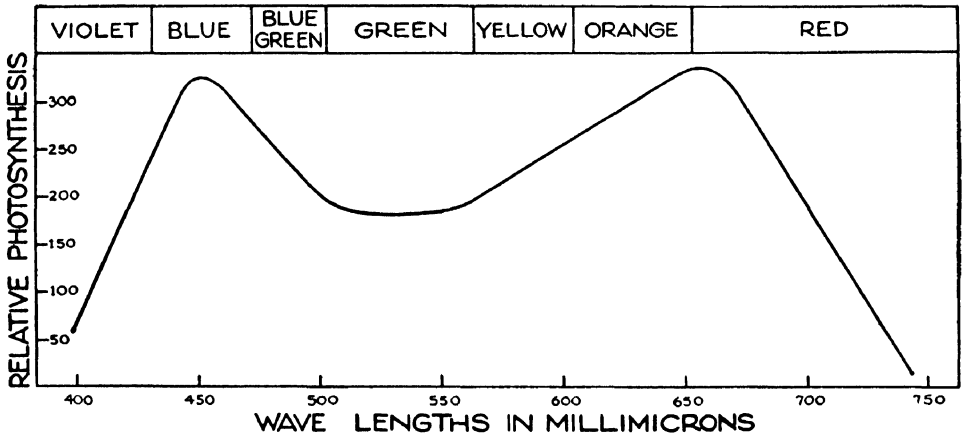

FIG. 54. Relative rates of photosynthesis in different rays of light of equal intensity. After B. S. Meyer and D. B. Anderson.

Apparently only the radiant energy that is absorbed (transformed) by chlorophyll is directly effective in photosynthesis. Any artificial light that emits these particular rays may induce photosynthesis. Some plants may start from seeds, grow to maturity, and bear flowers, fruits, and seeds when exposed only to electric light at an intensity about one-tenth that of full sunlight. Other plants will grow in this light intensity, but without bearing flowers and fruits.

The lowest intensity of light at which photosynthesis will occur has not been discovered. It has been reported to occur in deep-sea algae at light intensities lower than that of full moonlight.

A much more important fact to know is the light intensity from day to day in which the plant can survive on the sugar made. For convenience of reference we may call this the *critical light intensity*. This critical light intensity varies when other external factors, such as temperature, available moisture, and the concentration of carbon dioxide, are altered. This fact will be demonstrated later. Among different plants there is a

wide range of critical light intensity. Many fail to grow in the shade of buildings or of other plants—for instance, in certain forests or beneath some trees and shrubs on lawns—because the light intensity in such situations is below their critical light intensity. Many of the small trees one sees in the undergrowth of forests are merely surviving with a minimum of growth each year; most of them usually die while still small.

Plants that endure the most shade may be those in which maximum photosynthesis is attained at low light intensities. Many more measurements are needed to test this idea, but a few facts may be cited by way of illustration. The maximum rate of photosynthesis in certain deep-sea algae may occur at depths of 50 feet or more where the light intensity is very low. When these algae are brought nearer the surface where the light intensity is higher, the rate of photosynthesis is much lower.

Similar data were obtained by a study of one of the shield ferns that grows in the dense shade of forests. Photosynthesis increased in this fern with increase of light up to an intensity equal to one-fifth that of full sunlight, but when the intensity exceeded two-fifths that of full sunlight the rate of photosynthesis decreased. Photosynthesis in another extreme shade fern (*Trichomanes*) increased with increase of light up to one-eighth of full sunlight and then decreased to none at one-half full sunlight. In the wood sorrel (*Oxalis acetosella*), a small herbaceous plant that grows well in the shade of northern forests, maximum photosynthesis was attained when the light intensity was only one-tenth that of full sunlight, and this rate was maintained at higher intensities.

Such plants as corn, wheat, apple, and spinach do not survive in dense shade. In them photosynthesis is reported to increase with increasing light intensity, in some cases up to full sunlight. When the measurements are made on single leaves, however, maximum photosynthesis is usually found at intensities considerably below that of full sunlight. When the whole plant is tested the results are different, because many of its leaves are shaded by others and do not get the full effects of increased light. The greatest increase in photosynthesis with increase of light occurs when the original light intensity is very low. Measurements of photosynthesis in relation to light and other external factors are now being made by an increasing number of investigators. Many of the problems being investigated are too complicated to be mentioned here.

The owners of commercial greenhouses are most interested in the light intensity that results in the best yields of flowers, fruits, and vegetables in different species of plants. During the cloudy days of winter,

photosynthesis is often much too low for best results, for light intensity in greenhouses may range as low as 1/100 of full sunlight and be below the critical light intensity of many plants.

Many investigations designed to ascertain the value of supplementing natural light with electric light are in progress. This problem is further complicated—and also rendered much more interesting—by the fact that the length of day to which a plant is exposed greatly alters its vegetative and reproductive processes. These length-of-day effects may be brought about by light intensities much below those necessary for adequate photosynthesis. During the winter, exposure to light of an intensity somewhere between 1/100 and 1/100,000 that of full sunlight for a few additional hours each day greatly alters the behavior of certain plants. Lengthening the day by this means, however, is not a substitute for low light intensity during dark days. These relations are discussed in more detail in Chapter XXXI.

Water and photosynthesis. The degree of saturation of the tissues of a plant may modify the rate of photosynthesis in two ways: through the opening and closing of the stomates, and through its influence on the rate of chemical processes in the chlorenchyma cells. The effects are apparent in the daily periodicity of photosynthesis. In the morning hours the plant tissues are nearly saturated, the stomates are open, and photosynthesis soon attains a maximum rate. Later in the day the rate declines because of water loss from the mesophyll cells. Still later photosynthesis is further decreased by the gradual closing of the stomates. Of course, the temperature of the leaf is another factor which influences the daily increase and decrease in sugar manufacture. When plants begin to wilt, photosynthesis is sharply decreased, mainly because the water content of the cells is lower, and to some extent as a result of the closure of stomates.

Structures and photosynthesis. Plant structures are the result of certain plant processes. These processes in turn are conditioned by both heredity and environment. After a structure is formed it may in turn influence certain processes in the plant. We may therefore expect the rate of photosynthesis to be different in different kinds of plants, partly because their structure-building processes and resultant structures are different.

Even a cursory observation of plants in one's surroundings is sufficient to show that chlorenchyma is not restricted to leaves. Green stems, green fruits, green parts of flowers, and even certain green seeds (peas

and lima beans) are objects of common observation. Many tropical orchids and bromeliads have aerial roots that become green when exposed to light (Fig. 55). Roots of trees and many other plants are often exposed to light through soil erosion. An examination of these exposed

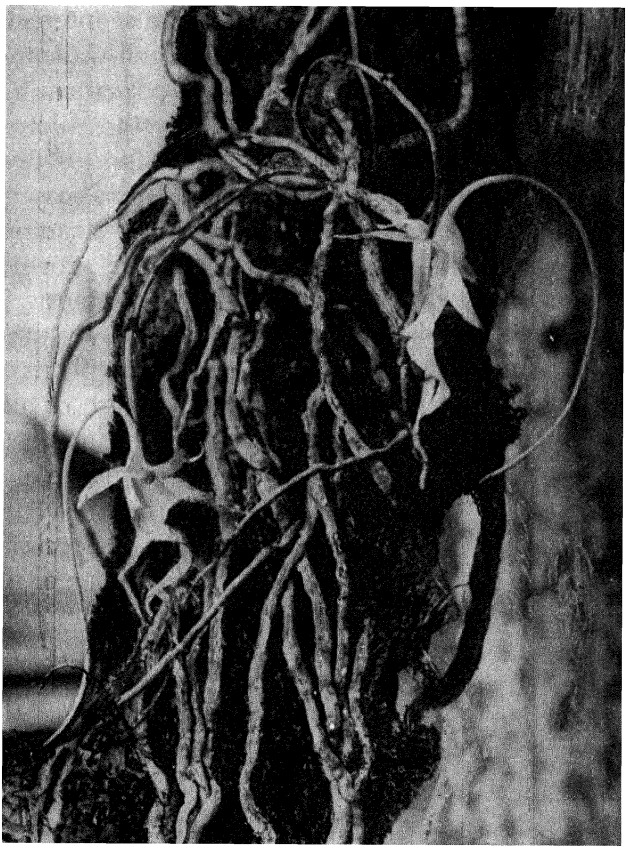

FIG. 55. The chlorenchyma of this Florida orchid is in the roots. The plant has no leaves and very small stems. Photo by W. M. Buswell.

roots is an easy way of discovering that chlorophyll may be formed in the roots of many kinds of plants. There are many microscopic green plants in which all cells of the plant body are green. Most of the body of a moss or liverwort is green. The green stem of a cactus is the conspicuous part of the plant; leaves are either temporary or entirely absent. Wherever chlorophyll is present in plants, photosynthesis will go on if other necessary conditions are suitable.

Leaves and photosynthesis. In the majority of land plants most of the photosynthesis occurs in the leaves. We have already seen that leaves of various species of plants may differ greatly in several ways, such as the amount of cutin on the epidermis, the number of stomates per square centimeter of surface, the thickness of the leaf, the compactness of the chlorenchyma in relation to the number and size of intercellular spaces, and the consequent exposure of the mesophyll cell walls to the internal atmosphere of the leaf (Chapter X). All these structures may influence the entrance of carbon dioxide into the cells of the chlorenchyma and thus indirectly influence the rate of photosynthesis.

Moreover, the environment in which a leaf grows may greatly affect the processes underlying the development of these structures (Chapter IX). Hence plants of the same species that have grown in different environments may have different rates of photosynthesis. Experiments have shown that certain plants growing in a relatively dry atmosphere may make more sugar during their lifetime than plants of the same species growing in a very humid atmosphere. A part, or all, of this difference may depend upon differences in the development of the leaf structure in dry and moist air, particularly the structure of the chlorenchyma and stomates.

The mesophyll. The amount of mesophyll wall surface exposed to the internal atmosphere of the leaf is considered to be one of the important factors in photosynthesis. Through it most of the CO_2 enters the cells of the chlorenchyma. Some CO_2 may enter the leaf directly through the epidermal cells, but entrance in this manner may be greatly impeded by the thickness of the outer walls of the epidermal cells and by the presence of cutin. Moreover, the area of the exposed mesophyll surface is usually many times greater than the total area of the epidermis. From measurements made on several different kinds of leaves it was found that the area of this inner exposed surface may be from 9 to 30 times greater than that of the epidermis. From the data of numerous tests it appears that in leaves of land plants the CO_2 enters the cells of the chlorenchyma largely from the internal atmosphere of the leaf.

The epidermis. The chief structures in the epidermis that influence the rate of photosynthesis are the guard cells enclosing the stomates through which CO_2 enters the intercellular spaces of the chlorenchyma (Chapter VIII). When one begins to consider stomates in relation to the entrance of CO_2, several complicated problems in physics soon arise. These problems will not be discussed here, but a few facts will be stated briefly.

If the stomates are closed, the entrance of CO_2 is diminished. But stomates that appear closed to the human eye may sometimes be open wide enough to admit the passage of molecules of CO_2, which are much too small to be seen through the best microscopes. The length of the shortest diameter of a fully opened stomate of average size is several million times the diameter of a molecule of CO_2.

When the stomates are open or partly open, the relative rates at which CO_2 passes through them are proportional not to the respective areas of the stomates, but to their respective perimeters (the distance around each pore). Because of this fact and certain related ones, the amount of CO_2 that passes through the stomates is about 50 times greater than would be expected on the basis of their total area. When the stomates are closely spaced, less CO_2 passes through each one than when they are farther apart. From such facts as these it is obvious that the stomatal mechanism of leaves may indirectly affect the rate of photosynthesis.

Stomatal behavior. The opening and closing of stomates are largely dependent upon alterations in the intensity of light, moisture, and temperature. As we shall see in more detail in Chapter XXIII, these external factors initiate a sequence of physical and chemical processes in the guard cells. These processes ultimately result in changes in the volume and shape of the guard cells, and consequently in the size of the stomate between them.

Under excellent growing conditions the stomates of many plants are closed at night and open during the greater part of the day. But during hot dry weather the stomates of many of these plants may be open mainly at night and closed during the day. In other plants they may be closed except for a few hours in the early morning. In certain cacti and other succulents they may remain open twenty-four hours each day.

The entrance of CO_2 into the intercellular spaces of the chlorenchyma of young stems, green fruits, flowers, and seeds may also occur through stomates in the epidermis of these organs. Chlorenchyma in the stems and exposed roots of woody plants, however, soon becomes covered by a layer of cork, the presence of which is a partial obstruction to both light and the entrance of CO_2. The chlorenchyma in the roots of orchids and also in the leaves of certain plants is separated from the epidermis by one to several layers of non-green cells. Stomates are absent in algae and the so-called green leaves of mosses. The submerged leaves of aquatic plants may have rudimentary stomates or none. Stomates may be present

in plants or parts of plants without chlorophyll. Rudimentary stomates have also been reported in all types of subterranean organs.

Although the presence and behavior of the stomatal mechanism may greatly influence the rate of photosynthesis, it is evident that one should be cautious about drawing inferences which imply that stomates behave as they do in order to facilitate photosynthesis.

Chloroplasts and photosynthesis. In almost all green plants chlorophyll is confined within the colloidal matrix of definite protoplasmic bodies, the *chloroplasts*, which also contain carotene and xanthophyll. Certain primitive algae do not have well-defined chloroplasts. In most of the green plants, therefore, photosynthesis occurs only within the chloroplasts. As a result of changes in the viscosity and streaming of the protoplasm in which these plastids are located, their arrangement within the cell may vary from time to time. The number, distribution, and surface area of chloroplasts constitute another structural mechanism that influences the relative rates of photosynthesis in different plants.

Many facts about plants are so variable that an exact determination of them is physically impossible and of no great consequence. On the other hand, a close approximation to the truth based upon a limited number of facts is often very helpful in checking one's concepts. As an example, a few estimates of the number and area of chloroplasts in plants may be cited.

In the castor bean leaf there are about 495,000 chloroplasts in the mesophyll beneath each square millimeter of leaf surface. About 82 per cent of them are in the palisade cells, and 18 per cent in the cells of the spongy mesophyll. In the sunflower, nasturtium, broad bean, and elm the corresponding numbers of chloroplasts per square millimeter of leaf surface are 465,000, 383,000, 283,000, and 400,000.

These figures may be used as a basis for further estimates. Beneath each square inch of elm leaf there are about 250,000,000 chloroplasts. The combined surface of these plastids is approximately 20 square inches, if we consider them as spheres 4 microns in diameter. An average elm leaf (5 square inches) has 100 square inches of chloroplast surface. A large elm tree with 1,000,000 leaves—estimates have been as high as 7,000,000—has a leaf surface of about 0.8 acre, and a chloroplast surface of about 16 acres, or 1/40 square mile. To appreciate the importance of this enormous plastid surface in photosynthesis, one must remember that most of the chlorophyll is concentrated near the surface of the chloroplast, and that CO_2 and H_2O enter the chloroplast through this surface.

This plastid surface is really the photosynthetic area of the leaf. Some allowance should be made for the area occupied by the larger veins.

Enzymes and photosynthesis. In addition to chlorophyll and other pigments, the chloroplasts also contain enzymes. Since enzymes are involved in photosynthesis and in other biological processes discussed in subsequent chapters, certain of their general features may be noted at this time.

Enzymes are organic catalyzers which accelerate chemical reactions that occur in physiological processes (photosynthesis, digestion, and the like) without becoming a permanent part of the final products of the process, and without being destroyed by the reaction. An enzyme may therefore continue to catalyze a particular chemical reaction until it is destroyed or made inactive by other conditions in the cell. Ultra-violet radiation and high temperatures may destroy enzymes. Synthesis of enzymes undoubtedly occurs in all growing parts of a plant. Without them the chemical changes in cells would be so slow that living organisms could not long survive. Furthermore, many processes in cells are not known to occur in the absence of certain enzymes.

In order to speed up chemical reactions in laboratory experiments and industrial processes, chemists often subject the materials to very high temperatures. Eventually they discovered that many of these processes could be made to occur just as rapidly at lower temperatures by the addition of a small amount of some inorganic substance, called a catalyst. A high temperature cannot be substituted for enzymes in living cells, but a temperature increase that is not detrimental to protoplasm does accelerate plant processes.

Some processes may be catalyzed by either organic or inorganic catalysts. For example, if we boil cane sugar (sucrose) in pure water, it hydrolyzes to glucose and fructose slowly.

$$\text{Sucrose} + \text{Water} \longrightarrow \text{Glucose} + \text{Fructose}$$

$$C_{12}H_{22}O_{11} + H_2O \longrightarrow C_6H_{12}O_6 + C_6H_{12}O_6$$

If a very small amount of acid is added, the reaction proceeds rapidly. During the process of boiling, some of the sugar is converted into mucic acid, which further accelerates the process. Even at much lower temperatures the reaction is fairly rapid, but for every increase of 10° C. the speed of the reaction increases from 2 to 3 times. Many other chemical processes have this same relation to increase in temperature.

In plant cells the hydrolysis of sucrose is catalyzed by a specific enzyme known as invertase (sucrase, or saccharase). The converse process, the synthesis of sucrose from glucose and fructose in a plant, is also accelerated by invertase or other enzymes. Many enzymes have the property of catalyzing a reaction in either direction, the direction being dependent upon other conditions in the cells.

Invertase that has been extracted from plants may be obtained from chemical supply companies. When sucrose is dissolved in water with a small amount of this extracted invertase, it is hydrolyzed as indicated above. If the solution is heated to 40-50° C. the reaction is most rapid; it decreases rapidly above this temperature. Temperatures of 60° C. or above completely inactivate many enzymes when they are wet. Most of them are destroyed at temperatures below the boiling point of water.

The activity of enzymes is influenced by many conditions within the cells. Among these may be mentioned various concentrations of acids, alkalies, salts, the substances acted upon, and the substances formed.

The potency of enzymes in accelerating chemical change in living cells is apparently due to the ease with which they unite with certain substances involved in the reaction and form unstable intermediate compounds. Through reactions of these unstable compounds the enzyme is again liberated, and only the stable products of the whole series of reactions accumulate. For instance, sugar and molecular oxygen are the stable end products of photosynthesis, but between them and the initial materials (CO_2 and H_2O) several temporary intermediate compounds are formed. Chemically trained students in increasing numbers have tried to discover what these intermediate compounds are and the order in which they are formed. Some of the problems will be mentioned briefly.

Intermediate compounds in photosynthesis. Formaldehyde has often been proposed as the first intermediate substance in photosynthesis, but always with inadequate proof. Recent investigators are giving more attention to enzymes and the part that chlorophyll may play in the process. For many years it has been known that chlorophyll absorbs certain rays of radiant energy. This is only another way of saying that chlorophyll transforms certain radiant energy to some other kind of energy—or better, that certain photons of light upon striking some part of the chlorophyll molecule impart their energy to it. The sequence of events that follows is not known well enough to be discussed here.

The difficulty of arriving at scientifically established answers to many

questions about biological processes lies partly in the complexity of the transformations that proceed as a chain of reactions, and partly in the complexity of the large molecules involved in the reactions. The empirical formulas of the two chlorophylls, a and b, are given on page 28. Merely to illustrate the complexity of these compounds, one of the recently proposed structural formulas for chlorophyll is reproduced here (Fig. 56).

Before we can know exactly how photosynthesis occurs, it will be necessary to find out how the atoms in CO_2 and H_2O become separated and subsequently united as in $C_6H_{12}O_6$, whether they unite with the

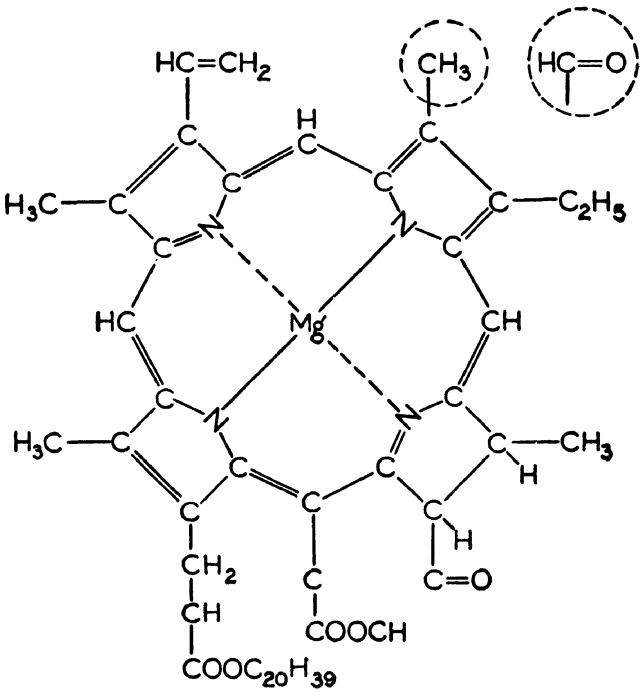

FIG. 56. Diagram representing the arrangement and complexity of the molecule of chlorophyll a. If the group, CHO, in the detached circle is substituted for the CH_3 group nearby, the diagram would represent the molecule of chlorophyll b. From B. S. Meyer and D. B. Anderson, 1939.

chlorophyll molecule, how the enzymes enter into the process, and what products are formed first as the chlorophyll and enzymes are again set free. It is impossible at present to say how many intermediate products there are, the order in which they are formed, and how many enzymes catalyze their formation.

Rate of photosynthesis. From the foregoing discussion it should be evident that the rate of photosynthesis is influenced by many conditions within the plant and by several environmental factors. Attention has been called to some of the influences of the stomates, intercellular spaces, distribution of chlorophyll, activity of enzymes, light, temperature, carbon dioxide, and water. Other conditions, such as the amount of chlorophyll and possibly the acidity of the cells, also influence the rate of photosynthesis. The effect of any one factor is probably always influenced to some extent by the relative amounts of the other factors involved. Some idea of this fact is best obtained by studying the results of experimental data such as those represented in the accompanying curves.

The curves in Fig. 57 represent the relative rates of photosynthesis in wheat seedlings in relation to light intensity and the concentration of carbon dioxide in the air, when the temperature is 22° C. and the relative humidity is 70 per cent. As shown in the lowest curve, where there was 0.01 of 1 per cent of CO_2 in the air an increase in the light intensity be-

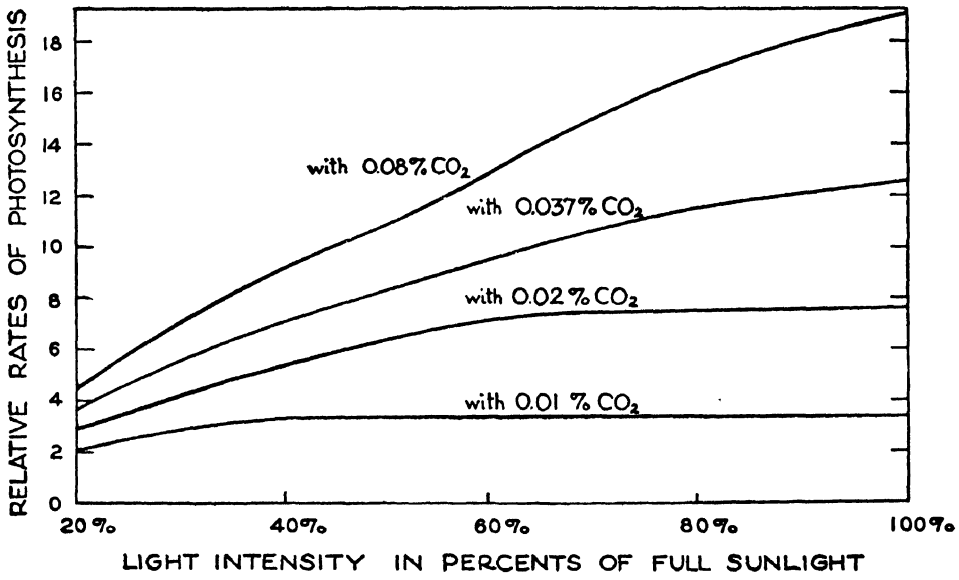

FIG. 57. Rates of photosynthesis in relation to light intensity and the concentration of carbon dioxide. Data from W. H. Hoover, E. S. Johnson and F. S. Brackett.

yond 40 per cent did not increase the rate of photosynthesis.

The percentage of CO_2 in the atmosphere near the earth's surface is usually given as about 0.03 (3 parts in 10,000 parts of air), though it may

vary considerably just above the surface of the soil, particularly if there is much decaying organic matter in the soil. From several measurements made in a field of sugar beets the percentage of CO_2 in the air at the tops of the plants was found to vary from 0.04 to 0.06, and at the ground level from 0.05 to 0.28.

From the curves in Fig. 57 we may see that the rate of photosynthesis at a given light intensity depends upon the available CO_2, and vice versa. In fields and gardens variations in light intensity are greater than variations in the concentrations of CO_2. Locally the concentration of CO_2 in the air surrounding plants is affected by photosynthesis, wind velocity, and several other factors.

The curves in Fig. 58 represent the relative rates of photosynthesis in leaves of a potato plant in relation to both temperature and the concentration of CO_2 in the air. The leaves were in full sunlight during each experiment, which lasted only ten minutes. Longer exposures would

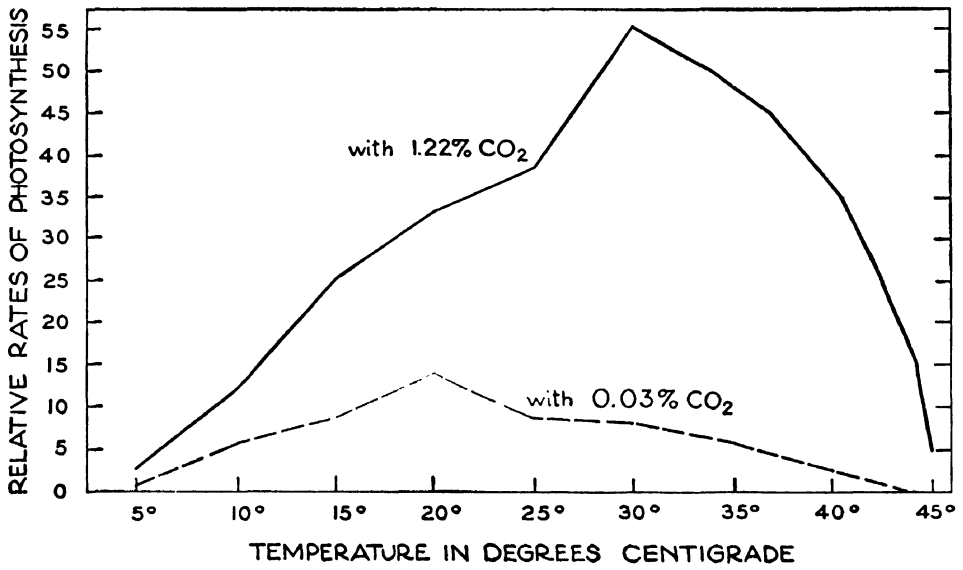

FIG. 58. Rates of photosynthesis in potato leaves in relation to temperature and the concentration of carbon dioxide. Calculated from data by H. G. Lundegardh.

result in some changes in the curves, but without annulling the principles represented. Here again certain interrelations between two different environmental factors and the rate of photosynthesis are evident.

Summary. The rate of photosynthesis is dependent upon the interrelations of several external factors and certain conditions and processes

within the plant cells. Some of these factors affect photosynthesis directly, others less directly through a series of other processes. The important external factors that most directly affect the rate of photosynthesis are the intensity and kind of light, the concentration of carbon dioxide in the air or water environment, the temperature, and water—though most of the effects of water on photosynthesis are indirect. Among the important internal conditions are the amount and distribution of chlorophyll and enzymes, and such structural features as stomates, intercellular spaces, and veins, which influence the movement of materials into and out of chlorenchyma.

The importance of photosynthesis to all living organisms will be appreciated better as it becomes more evident, from the facts in later chapters, that all the organic compounds in the bodies of plants and animals and all the commercial products obtained from them have their beginning in the synthesis of sugar. When it is clear that the chemically bound energy supply of the bodies of all living organisms, and most of the energy that we use in our homes and industries can be traced back to the radiant energy chemically bound in sugar, we can view photosynthesis in true perspective.

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CHAPTER XV

FOOD SYNTHESIS

III. SYNTHESIS OF STARCHES

Some of the sugar in plants may be changed chemically to insoluble starches and other carbohydrates, to fats and oils, and to proteins. In the body of animals sugar is changed to a starch-like compound called glycogen, and also to fats and oils. While studying such transformations we may also appropriately consider many facts about the accumulation and digestion of these foods. In this chapter we shall be interested mainly in the formation and digestion of starch and a few other carbohydrates.

Starches, fats, and oils are made from sugar alone. Proteins are made from sugar and certain salts of nitrogen, sulfur, and, in some cases, phosphorus also. These transformations of sugar to other kinds of food are either condensation processes or a combination of oxidation-reduction and condensation processes. The simplest transformations, such as the formation of starch from glucose or of inulin from fructose, involve only chemical condensation. We shall first consider the synthesis of starch from sugar.

Synthesis of starch from sugar. Starch is formed in plant cells from glucose by chemical condensation:

$$\text{Glucose} \longrightarrow \text{Water} + \text{Starch}$$

$$n\ C_6H_{12}O_6 \longrightarrow (n-1)H_2O + (C_6H_{10}O_5)_nH_2O$$

Special groups of enzymes catalyze the process of starch synthesis. Some of the plants in which starch is not formed may lack one of these several enzymes. The digestion of starch back to sugar in living cells, or in media in contact with living cells, is catalyzed by several complex groups of enzymes. The digestion of starch occurs readily in test tubes with enzymes extracted from plants. Recently it has been shown that some of the steps in starch synthesis may also occur in test tubes if

glucose-1-phosphate, boiled starch, and appropriate enzymes from plant cells are placed in the tubes.

A reaction that may proceed in either of two directions is said to be *reversible*, and is often represented by two arrows. A longer arrow is usually used to indicate the direction in which the process is proceeding more rapidly.

(A) Glucose $\rightleftharpoons$ H_2O + Starch

(B) Glucose $\rightleftharpoons$ H_2O + Starch

Statement (A) above indicates that the condensation of glucose to starch is proceeding more rapidly than the digestion of starch to glucose; statement (B) indicates that digestion is the more rapid process. Whether digestion will exceed condensation, or vice versa, at any particular time depends upon certain conditions in the plant cell, such as acidity, water content, and the concentration of glucose. External factors, such as temperature and light, affect these internal conditions and thus indirectly affect the digestion and condensation processes. For instance, when Irish potatoes are stored in bins at 10°-30° C. the sugar in them is mostly condensed to starch; but when they are stored at temperatures either above 30° C. or near freezing much of the starch is digested to sugar. Potato chips prepared from potatoes in which sugar has accumulated are dark in color.

When the chloroplasts are exposed to light more sugar is made in them and some of it condenses to starch. On the other hand, when the guard cells of leaves are exposed to light the conditions initiated in them by the light result in a change of starch to sugar.

These changes of sugar to starch and of starch to sugar may occur repeatedly in the same cell, and at any time during the day or night. Many efforts have been made to detect the amount of sugar that must accumulate in a cell before some of it begins to condense to starch. This amount of course is variable, depending both upon the kind of plant and upon the conditions to which it is exposed. The formation of starch is dependent upon the hereditary make-up of the plant. Closely related plants may differ greatly in this respect, and in some plants (onion, hyacinth, and many others) starch is formed only under exceptional environmental conditions, or not at all.

The number of species of plants in which starch never forms under any environmental condition is unknown. It is very simple to remove

leaves from a plant with a knife and place the cut ends of the petioles in beakers of water containing different concentrations of sugar and also different kinds of sugar. They can then be readily exposed to different environmental conditions. Even the leaves in which starch ordinarily does not form may synthesize it under these experimental conditions either in the light or in the dark. Best results are usually obtained with about a 10 per cent solution of sugar. Since starch is made from glucose, one might expect to find starch in the leaves only when glucose is placed in the beakers, unless he recalls that by the influence of the enzymes in plant cells certain kinds of sugars may be transformed to others. In such experiments starch is formed in the leaves whether the sugar in the beakers is glucose, fructose, mannose, galactose, sucrose, or maltose. Even certain alcohols may be converted to starch in the leaves of plants.

Starch accumulation. Sugar is involved directly or indirectly in all the major physiological processes in plants. Starch, on the contrary, merely accumulates. In time it may be digested back to glucose, either in the plant that makes it, or in some other organism that eats it. Starch is formed in plastids (leucoplasts and chloroplasts) and occurs in the cells as small grains that are insoluble in water; therefore it does not pass from cell to cell. When starch is found in a cell one may infer that it was made in that cell. It may be formed in all kinds of living plant tissues, in either light or darkness if sugar is present. The fact that it accumulates sooner or oftener in certain cells or tissues is evidence that the conditions affecting its formation are not uniform throughout the plant. There may be a lack of general uniformity in the types of plastids, the amounts and kinds of enzymes, the concentration of sugar, and the acidity of the cells.

This lack of uniformity among cells is easily demonstrated with green and white variegated leaves. Since sugar is made only in the chloroplasts, its concentration in the non-green parts of the leaves is comparatively low, and starch is usually formed only in the chlorenchyma of these leaves. This fact is demonstrated by the ordinary iodine test for starch in leaves after the chlorophyll has been removed with hot alcohol.

If these variegated leaves are first detached from the plant and placed for about one day in a beaker containing a sugar solution as described above, starch may then be found in the non-green parts of the leaf. Variegated leaves of geranium are excellent materials for these tests (Fig. 59). It has been reported that even with this special treatment

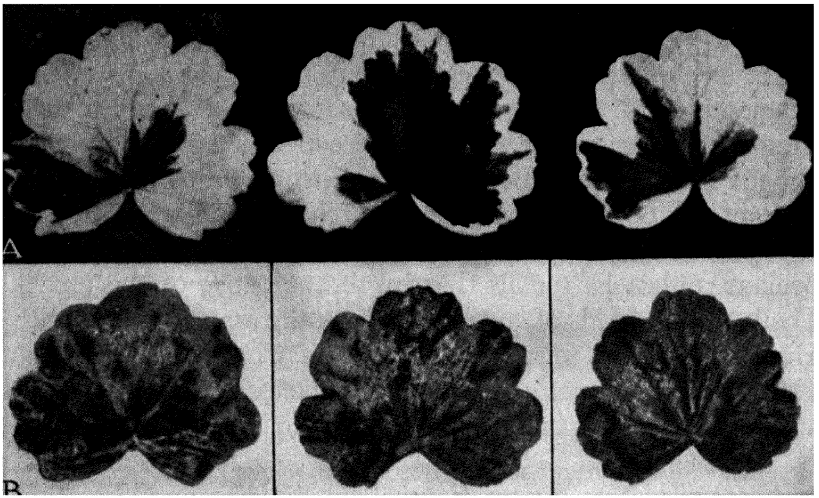


FIG. 59. Photographs of white and green variegated leaves of geranium after the leaves had been subjected to the iodine test for starch: A, leaves tested directly after removal from the plant; B, comparable severed leaves tested after the cut ends of their petioles had been immersed in a sugar solution for 15 hours. Photo by A. G. Chapman and W. H. Camp.

starch does not form in the non-green parts of such plants if plastids are absent.

Microscopic tests for starch are easily made, and the relations of starch accumulation to certain conditions and processes in the plant are fairly well known. As a consequence, starch synthesis, accumulation, and digestion are often studied as an index to other processes in which sugars are being made, consumed, or translocated.

Starch may accumulate temporarily in chloroplasts when sugar is being made, but in some plants, as in onions, oil accumulates in chloroplasts.

Commercial sources of starch. Conditions in certain tissues and organs are especially suitable to starch accumulation. Certain roots, stems, fruits, and seeds are of great commercial value, mainly because of the starch they contain. Besides being valuable as a food, millions of tons are extracted from plants annually and used in the industries for making various types of dusting powders, adhesives, pastes required in sizing cloth and paper, and as a source of dextrin and glucose. In the manufacture of alcohol a number of starch-rich cereals are used as a source of food for yeast plants.

Starch grains. Starch grains in different kinds of plants may differ in form, size, and internal structure (Fig. 60). This fact may be used as one means of identifying certain commercially prepared drugs and foods, and also certain impurities in them.

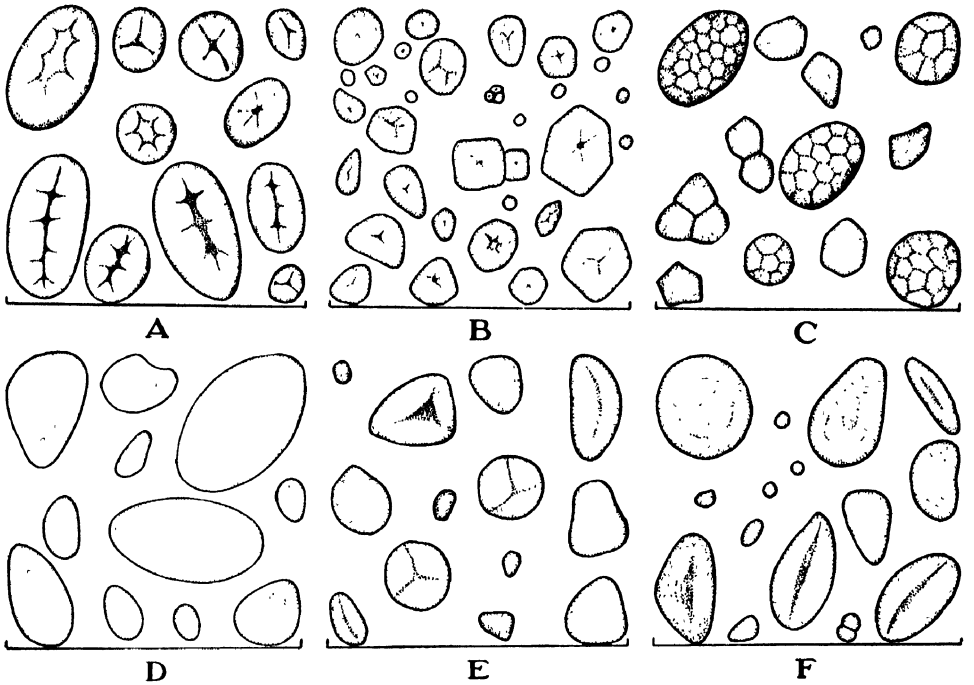


FIG. 60. Diagrams of starch grains from several kinds of plants: A, bean; B, corn; C, oats; D, potato; E, rice; F, wheat. Adapted in part from Leffmann and Beam.

Each grain is composed of at least two substances. The outer portion is composed of amylopectin, which becomes gelatinous in boiling water, but does not appear blue with iodine. The inner part of the grain is largely amylose. It is colloidally dispersed in boiling water and becomes blue with iodine.

Dextrins. When certain groups of enzymes are present, dextrins are synthesized from sugar in certain plastids in plant cells. Later, starch may be synthesized in other plastids in these cells. In young seeds of some plants, such as certain varieties of sweet corn, dextrin-forming plastids can be found in all stages of development. Since they become reddish in color when the iodine test is applied, they are easily distinguished from starch grains in microscopic mounts.

When starch grains are heated for a short time they are transformed to grains of dextrin. This is the procedure used in the preparation of commercial dextrin.

Dextrins are formed as intermediate products when digestion of starch to sugar in test-tube experiments is catalyzed by a group of enzymes known as diastase. The products appear to be formed in the following order: starch ⟶ dextrins ⟶ maltose ⟶ glucose

Glycogen and inulin. Glycogen, like starch, is a condensation product of glucose. It is common in the animal kingdom, but among plants it is known to occur only in certain fungi, bacteria and algae.

Inulin is a condensation product of fructose, and occurs in several kinds of plants. If roots of salsify or dandelion are placed in 70 per cent alcohol for a time, most of the inulin in them crystallizes; but the clusters of crystals, though they are large, are often difficult to see because of their transparency. The accumulated food in Jerusalem artichoke and oyster plant is largely inulin.

Sugars, starches, dextrins, glycogen, and inulin all belong to the general class of compounds known as carbohydrates, i.e., compounds of carbon, hydrogen, and oxygen in which the proportion of hydrogen to oxygen is 2:1, as it is in water.

The transformation of carbohydrates by condensation and digestion. The formation of starch from sugar by chemical condensation and the subsequent digestion of starch to sugar are common processes in plants. All complex carbohydrates, such as starches, glycogen, inulin, cellulose, and hemicelluloses, are formed from simple sugars by chemical condensation. Moreover, during the formation of fats, oils, proteins, and many other compounds in cells, chemical condensation usually occurs at one or more stages in the process. Chemical condensation occurs in every living cell of both plants and animals. It is the converse of all ordinary processes of digestion. Evidently a clear concept of its fundamental features is necessary to the understanding of many biological processes. A few examples will be given.

When 2 molecules of a simple sugar, like glucose, unite by condensation, the resultant sugar is called a disaccharide (double sugar):

$$\text{Simple sugar} \longrightarrow \text{Water} + \text{Disaccharide}$$

$$2\ C_6H_{12}O_6 \longrightarrow H_2O + C_{12}H_{22}O_{11}$$

When 3 molecules of simple sugars unite by condensation, the resultant sugar is called a trisaccharide:

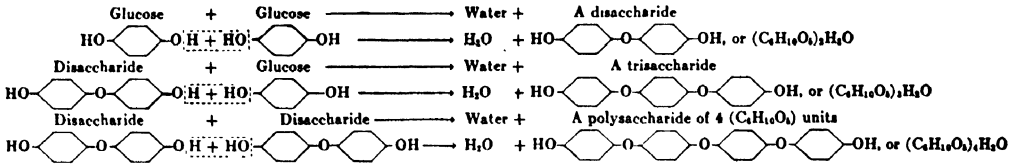
$$\text{Simple sugar} \longrightarrow \text{Water} + \text{Trisaccharide}$$
$$3\ C_6H_{12}O_6 \longrightarrow 2\ H_2O + C_{18}H_{32}O_{16}$$

The formula $C_{12}H_{22}O_{11}$ may also be written as $(C_6H_{10}O_5)_2H_2O$. Likewise, the formula of the trisaccharide, $C_{18}H_{32}O_{16}$, may be written as $(C_6H_{10}O_5)_3H_2O$ to indicate the number of molecules of sugar utilized in the formation of the larger molecule. When 2 molecules of sugar unite, 1 molecule of water is released. When 3 molecules of sugar unite, 2 molecules of water are released.

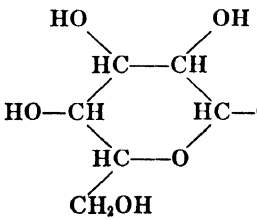
A general name for the product formed by the union of several molecules of simple sugars by condensation is *polysaccharide*. All these products are carbohydrates. We may now write a generalized equation that represents the formation of any polysaccharide from a simple hexose sugar, such as glucose or fructose.

$$n\ C_6H_{12}O_6 \longrightarrow (n-1)H_2O + (C_6H_{10}O_5)_nH_2O$$

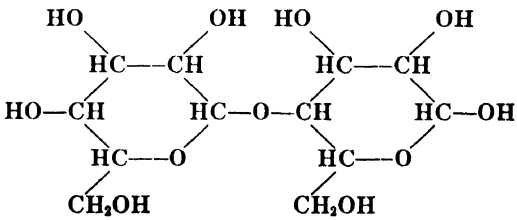
One important point to note is that for every molecule of sugar added, one molecule of water is liberated. This fact may be briefly represented in a diagram in which we let some symbol, such as ⬭, represent the main body of the glucose molecule.[1]



[1] The diagram in Chapter XVII indicating the arrangement of the atoms in a molecule of sugar (glucose) shows the carbon atoms in a straight chain. The following arrangement of the carbon and oxygen atoms is indicated by X-ray studies of polysaccharides.



Glucose



A disaccharide

If this process were to continue, a polysaccharide consisting of a long chain of many ($C_6H_{10}O_5$) units would be formed. From X-ray studies we know that the molecules of polysaccharides in plant cells do consist of long chains of these smaller sugar units. In some substances, such as starch and cellulose, the units are all ($C_6H_{10}O_5$) from glucose. In other substances these units may be formed from another kind of sugar, or the chain may be composed of units of different kinds of sugars, as in hemicelluloses. The chain may also consist of units of sugar and certain acids derived from it, as in pectic compounds.

One other important biological fact about condensation should be appreciated, namely, that the chemically bound energy in the sugar is still in the units of sugar in the new products formed. It is not liberated in the process of condensation.

Digestion, or hydrolysis, is the converse of condensation. As molecules of water replace those lost during the condensation of simpler molecules to more complex ones, the complex molecules are subdivided into the simpler ones from which they were formed.

A reversible process recently discovered and thought to be common in plants may be indicated briefly:

$$\text{Starch} + H_3PO_4 \leftrightharpoons \text{Glucose-1-phosphate}$$

It is referred to as phosphorolysis and the enzyme that catalyzes it is called phosphorylase.

Summary. Starch is formed in plastids (leucoplasts and chloroplasts) in plant cells from glucose by chemical condensation—a process that is just the converse of all ordinary processes of digestion. By condensation, many molecules of sugar become joined together by a loss of one molecule of water for every molecule of sugar added. Chemically bound energy is not liberated by this process and the starch therefore contains the potential energy that was in the sugar from which it was made. In the same way, many other complex carbohydrates (polysaccharides) are formed in plants.

Starch may be synthesized from sugar in both green and non-green tissues, and in either light or darkness. It is especially dependent upon the presence of plastids, certain enzymes, the concentration of sugar, and the acidity of the cells. It is a reversible process. External factors, particularly light and temperature, affect these internal conditions and thereby indirectly affect the accumulation of starch in plants. These internal conditions are not uniform throughout the plant, nor in different

probably act mainly as catalysts. Of the external factors, temperature, oxygen, and sometimes water occupy a place of first importance under natural conditions, and also in the cultivation and care of plants.[1] Under experimental conditions many factors are known either to increase or to decrease respiration in plants.

The relation of respiration to plant development and to certain practices in the care of plants and plant products. Plants often fail to survive, or their growth is retarded, merely because of a lack of sufficient oxygen. The aerial parts above ground are exposed to an abundance of oxygen in the surrounding atmosphere, but some parts are exposed only to the oxygen that is in the air of the soil. The parts of land plants that are underground (roots, underground stems, and also seeds and seedlings) may be deprived of sufficient oxygen when they are flooded by water, or when the ground water level rises too near the surface of the soil. The water *per se* is not harmful, but it excludes nearly all the free oxygen, and death by suffocation is the result. Less oxygen is likely to be available to the plant when the water is stagnant than when it is flowing.

Perhaps everyone is familiar with the fact that many common plants grow only where their roots are in well-drained soils, while others may grow where the soil is saturated or even submerged. This difference may be due to the fact that some plants, like some animals, can survive with less free oxygen than others. The roots of the black willow, for instance, will grow in soils almost wholly deprived of free oxygen, whereas the roots of sugar maple, scarlet oak, and many other trees will die of suffocation. However, the roots of most land plants grow well in water that is continuously aerated.

Some interesting ideas of the growth and distribution of plants in relation to free oxygen may be gained by observing the zones of plants on the wet shores of shallow lakes and in low places in fields and woods (Figs. 267, 268). Pondweeds, cattails, and bulrushes grow with their roots continuously submerged in water, and some have roots in muck where there is almost no free oxygen. In some of these plants large internal air passages extend from the leaves and stems all the way to the root tips. The submerged roots of such plants may not survive unless the oxygen that diffuses downward from the air-exposed leaves is adequate. The underwater parts of these plants drown, or suffocate, if the tops are cut off below the water level.

[1] Light should also be recalled in this connection because of its indirect effects on respiration through the amount of food made, the opening of stomates, and the raising of the internal temperatures.

There are other species, however, that survive without access to the atmosphere through large internal air passages. Willows, bitter pecan, and overcup oak are examples. Algae and other continuously submerged plants may grow where the amount of oxygen is very low. Of course, during the day, when photosynthesis is occurring, they have an abundance of oxygen.

The agricultural practice of draining soils is a common means of supplying the roots with an adequate amount of oxygen. Coarse soils are much better aerated than those of extremely fine texture. This fact is often exemplified by the differences in plants on such soils. The greater root growth in the small crevices of soils is undoubtedly related to the better aeration there. Soaking the soil of potted house plants about once each week not only assures more adequate watering but also results in a fresh supply of air to the roots as the water disappears from the soil.

The storage and shipping of fruits and bulbs introduce another situation in which a deficiency of oxygen may be detrimental. The cells in these plant organs are still alive, and their well-being depends upon a certain amount of respiration. If fruits are packed too closely, many of the cells die of suffocation and become brown; the color and flavor of the fruits that survive may become less desirable. Dark and hollow centers in potatoes are often the result of the death of cells by suffocation, because of high temperature and a lack of oxygen in storage bins. The need of further knowledge of the relation of respiration to the best preservation of fruits and other plant organs in storage and shipping accounts for some of the research that is being done on the best methods of refrigeration and ventilation in storage houses and shipping cars. Truckers commonly transport ripe fruits at night to avoid the suffocation of cells in the fruit that would result from the higher daytime temperatures.

When plant tissues are cut or otherwise injured, the cut or injured surfaces are exposed to an increased supply of oxygen. The exposed surface often becomes dark colored because of the oxidation of tannin or other substances in the cells. In the preparation of dried fruits this darkening is undesirable; either methods are used to prevent it, or the finished product is subjected to a bleaching process.

Water content effects. When the water content of cells is low the rate of respiration becomes low. This rate may continue low for several years in air-dry parts of plants, such as spores and seeds, then rise again as these structures becomes wet. For instance, respiration in wheat seeds

containing 16 per cent of water may be 2.5 times as rapid as it is when the seeds contain 15 per cent of water; and when they contain 17 per cent of water it may be 10 times as rapid. This fact illustrates the effect water may have on the rate of respiration in seeds during germination in soil and also when they are in storage, where an injurious amount of the released heat energy may accumulate.

Temperature effects. When no other factors are deficient, the rate of respiration is doubled for every increase of 10° C. up to a temperature that becomes detrimental to the further survival of the plant. This fact is recognized in refrigeration, which preserves the food value of fruits in two ways: (1) by decreasing the rate of oxidation of the food within the cells of the fruit, and (2) by decreasing the respiration and rate of growth of bacteria and fungi that may destroy the fruit.

The increase in rate of respiration with increase in temperature is often an important factor when the plant is growing, because the maximum rate of photosynthesis occurs at much lower temperatures than the maximum rate of respiration. During a period of hot days and nights in summer the rate of respiration may exceed the rate at which food is being made. This fact may be illustrated by curves representing the relative rates of photosynthesis and respiration in leaves of potato during a series of 10-minute exposures to different temperatures (Fig. 62).

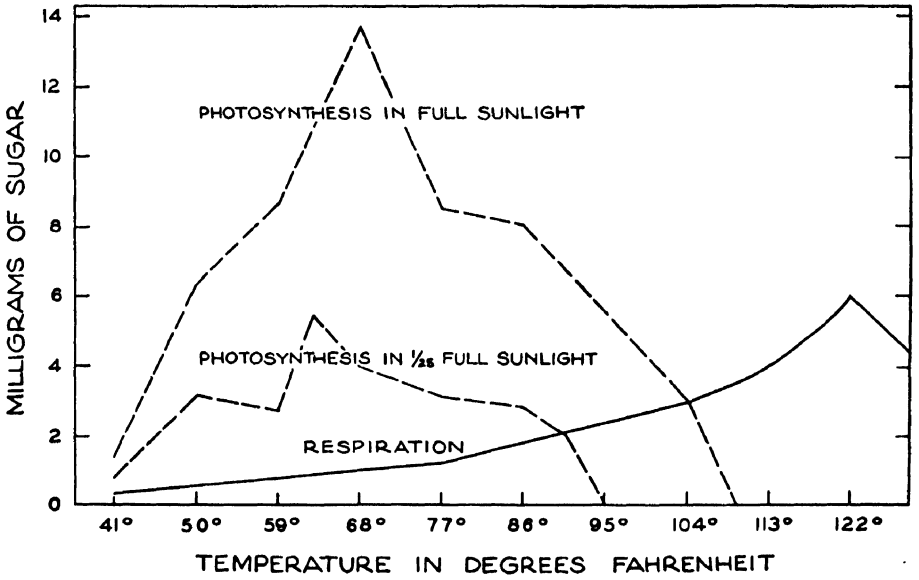


FIG. 62. Relative rates of photosynthesis and respiration in potato leaves during 10-minute exposures to different temperatures in shade and in full sunlight. Recalculated from data by H. G. Lundegardh.

The rate of respiration in this experiment increased with the increase of temperature until the heat became injurious. If the experiment had continued for a whole day instead of ten minutes, the first evidences of this injurious effect would have become visible somewhere between 100°-110° F. The maximum rate of photosynthesis, however, occurred at a much lower temperature, 68° F. In connection with these curves it is interesting to know that the maximum yield of potatoes is obtained in areas that have cool summers, where the mean temperature during the growing season is less than 65° F. Under experimental conditions where the temperature is kept constant both day and night throughout the period of growth, maximum yields of potatoes are obtained at about 62° F. If the plant is exposed continuously to a temperature of 85° F., no tubers are formed. The interrelations of the different organs of a plant with respect to environments will be discussed in Chapter XXI.

The compensation point. An interesting point in the upper curve is at 104° F. where the rate of respiration is equal to the rate of photosynthesis. For convenience of reference this point is often called the *compensation point.* In the curve which represents the rate of photosynthesis in potato at 1/25 of full sunlight, the compensation point occurs at 90° F. This fact is of interest even when the plant is in full sunlight, for many of its leaves are in the shade of others. These facts illustrate the general principle that the compensation point occurs at lower temperatures when the light intensity is low. It also occurs at lower temperatures when the concentration of carbon dioxide is decreased.

It is perhaps evident that a plant kept throughout the day at the compensation point would not gain in dry weight, except for the very small amount of mineral salts that may enter it from the soil; and that during each night there would be a loss in dry weight due to respiration in the absence of photosynthesis. A plant kept continuously under such conditions would soon starve to death. If the nights were cool, it would survive longer than it would if the nights were hot.

It must also be evident that the yield of plants depends upon the relative rates of photosynthesis and respiration. Under excellent growing conditions photosynthesis may exceed respiration in corn fourfold during the growing season. This would not occur unless photosynthesis exceeded respiration on the average about eightfold during the day. In plants that are merely surviving in the shade of others, growth is limited

because respiration consumes a much larger percentage of the food made in them in such situations.

The conditions under which the compensation point may occur differ greatly with the kind of plant. In Scotch pine it is reported to occur at 18°-20° C. when the intensity of light is 1/25 that of the full sunlight of summer. Comparing this report with the data obtained by several other investigators, we find that the compensation point occurs in some of our pines, arbor vitae, and tamarack at about this same light intensity. Corresponding figures for white pine and red oak are nearer 1/50 to 1/70, and for beech and sugar maple 1/100 to 1/200; for a few of the herbs, ferns, and mosses that grow in dense shade 1/200 to 1/300, and for some algae 1/10,000 or less. In general the compensation point occurs at lower light intensities in "shade plants" than in "sun plants." This difference is less pronounced at low than at high temperatures.

There can be little doubt that the differences in respiration and photosynthesis in plants indicated by the compensation point are an important factor in the survival and distribution of plants in different habitats in relation to temperature and light. Beech and sugar maple endure more shade than oaks, and many oaks endure more shade than most pines. One kind of forest therefore may gradually replace another by producing more shade than its seedlings can endure. On lawns and campuses many examples of differences in shade endurance by plants may be observed. For instance, during a period of excessively hot clear days bluegrass is favored by a small amount of shade, but it endures more shade in the cool days of early spring and late autumn than it does in the hot days of midsummer.

Comparative rates of respiration. The rate of respiration is greatest where there is rapid growth, as in germinating seeds and opening flowers. In some plant organs respiration may be more rapid on the basis of weight than in animals. The amount of food oxidized during a day ($\approx$ 1500 Cal.) in a man at rest is equal to about 4 per cent of his dry weight. The amount of food oxidized in a corn plant each day is equal to about 1 per cent of its dry weight. The corresponding figure for an opening cluster of flowers is about 8 per cent; and for some kinds of germinating seeds, about 20 per cent. The lowest rates of respiration occur in dry seeds and other dormant structures, and there is comparatively little respiration in woody stems and other hard parts in which there are only a few living cells.

The amount of carbon dioxide formed during respiration in all the

plants in the world each year is probably in the neighborhood of 8-10 times the amount liberated by the animals in the world during the same time. A corn plant, for instance, oxidizes about one-fourth of the food it makes. One-half of the food it makes is converted into fibers (cellulose, wood, cutin, etc.) which are indigestible by the enzymes of animals. They may, however, be digested and used as food by certain special groups of bacteria and fungi. The fibers that are not digested by these non-green plants become humus in the soil. Only about one-fourth of the food made in the corn plant accumulates, part of which becomes available to animals.[2]

Food per acre in terms of available energy. With a knowledge of respiration as a background we may compare the amount of food harvested per acre on the basis of Calories of energy. In Table 4 a summary is given of the average yield per acre, its food value calculated in Calories, and the number of men that can be fed for one day by the different crops harvested from one acre, assuming that each man requires 3000 Calories per day.

TABLE 4. Energy Content of Food Products from an Average Acre

Food Products	Yield per Acre		Millions of Calories Equivalent	Number of Men That Might Be Fed for One Day
	Bushels	Pounds		
Corn	35	1,960	3.1	1000
Sweet potatoes	110	5,940	2.8	900
Irish potatoes	100	6,000	1.9	600
Wheat	20	1,200	1.8	600
Rice	40	1,154	1.7	560
Soybeans	16	960	1.5	500
Beans	14	840	1.1	375

If the grain from an average acre of corn is fed to beef cattle, the dressed beef obtained amounts to only 125 pounds and yields energy equivalent to the food of 43 men for one day, a loss of 95.7 per cent of

[2] There is a possible error in this comparison, namely, there are many bacteria in the alimentary tracts of animals that may digest the cell walls of plants. Some of the products of these digestions pass into the cells of the animal. Some of the wood-boring beetles have fungi in their intestines that digest cellulose, and the beetle's food is the resulting sugars and other end products.

the energy in the corn. If fed to pigs, the yield of pork is 273 pounds, or sufficient food for 220 men for one day. Dairy cattle are second only to pigs as transformers of food in proportion to the energy lost. A great loss of energy always results when the food in plants is converted into meat before it reaches the human consumer. It is evident that as the population of a country increases beyond a certain point, unless it can afford to buy meat from foreign markets it must depend more and more directly upon the food in plants.

There are, however, certain animals that feed, either directly or indirectly, on plants in which the food is physically unavailable to man. All our sea-food animals, such as fish, clams, and oysters, convert large quantities of the food in aquatic plants into food that is available to man. The sheep and cattle grazing on the open range and forest reserves in the Western States and on similar areas in other countries may be looked upon as gatherers and converters of the food in plants that is not otherwise available to man.

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CHAPTER XIX

USES OF FOOD IN PLANTS

III. SUBSTANCES MADE FROM FOOD

All plants contain a variety of substances made from foods. Some of them are important constituents of cell structures; others, such as chlorophyll and enzymes, are essential in certain plant processes. Several others seem to be of no essential survival value or detriment to the plant. Foods are the source of building materials as well as the source of chemically bound energy. All the organic compounds of which cells are composed are constructed directly or indirectly from foods.

The manner in which cellulose may be formed from sugar by chemical condensation was described in Chapter XIV. It is briefly indicated as follows:

$$\begin{array}{ccccc} \text{Glucose} & \longrightarrow & \text{Cellulose} & + & \text{Water} \\ n\ C_6H_{12}O_6 & \longrightarrow & (C_6H_{10}O_5)n\ H_2O & + & (n-1)H_2O \end{array}$$

This is merely a condensation process in which n represents an unknown number. The value of n may vary in the same cell and also in different plants. It apparently represents a number having an average value near 2500. After condensation all the chemically bound energy that was in the sugar is in the cellulose.

Wax, cutin, and suberin are fat-like substances. In cell walls of plants they occur as solids. Their formation from sugar is similar to the synthesis of fats: oxidation-reduction processes precede condensation:

$$\begin{array}{l} \text{Sugar} \longrightarrow \text{Alcohols} \\ \text{Sugar} \longrightarrow \text{Fatty acids} \end{array} \Big\rangle \longrightarrow \text{Water} + \text{Waxes}$$

(oxidation-reduction) (condensation)

The fatty acids and alcohols combined in these substances are unlike those in ordinary fats. Substances referred to as cutin and suberin appear to be formed primarily by the union of fatty acids alone.

These two examples represent ways in which constituents of plant

cells are formed from soluble foods, though there are a greater number of intermediate steps of oxidation-reduction and perhaps also of condensation in some cases. We may generalize them as follows:

A. Soluble food ⟶ condensation ⟶ cell constituent

B. Soluble food ⟶ oxidation-reduction ⟶ intermediate products ⟶ condensation ⟶ cell constituent

The intermediate steps in the formation of all cell substances are not fully known, and very little is known about the formation of protoplasm. Several different enzymes catalyze the many processes that occur. By omitting the intermediate steps we may represent in tabular form many of the substances formed in cells and the basic foods from which they are made (Table 5).

Some of these substances were described in previous chapters. A few additional facts will be briefly summarized.

TABLE 5. Substances Made Within the Plant from Sugar

Food Used	Chemical Processes	Substances Made	Where Found in the Plant
Glucose	Condensation	Cellulose	Cell walls of all tissues
Sugars	Condensation	Hemicelluloses	Cell walls of many tissues
Sugars	Oxidation-reduction and condensation	Pectic compounds	Cell walls of all tissues
Sugars	"	Lignin	Cell walls of wood tissues
Sugars	"	Suberin	Cell walls of cork
Sugars	"	Cutin	Epidermal cell walls
Sugars	"	Wax	Epidermal cell walls
Sugars	"	Carotenoids	Green and yellow tissues
Sugars	"	Anthocyanins	Vacuoles of many tissues
Sugars	"	Essential oils	General or localized
Sugars	"	Mucilages	Many tissues
Sugars	"	Resins	General or localized
Sugars	"	Gums	General or localized
Sugar and proteins	"	Alkaloids	Generally distributed
Sugar and proteins	"	Enzymes	All living cells
Sugar and proteins	"	Hormones	Variously distributed
Sugar and proteins	"	Vitamins	All living cells
All foods	"	Protoplasm	All living cells

Cellulose. During the formation of new cells in all growing parts of plants, enormous quantities of food are annually converted into protoplasm, enzymes, pectic compounds, and cellulose. About one-half of the food made by a green plant is converted into these substances. More

than one-third of it is converted into cellulose alone. The youngest cell walls of nearly all plants are composed primarily of pectic compounds and cellulose. If thin sections of a plant are treated with a strong solution of chlorozinc iodide, or with a solution of iodine followed by 70 per cent sulfuric acid, and then observed through a microscope the location of cellulose in the cell walls is often disclosed by a blue color. If pectic compounds are abundant in the wall, a light brown color is evident. In some cell walls it is necessary first to remove lignin, cutin, or other substances that interfere with the test for cellulose.

Cellulose is formed in every cell of all plants, except in certain groups of algae (diatoms) and perhaps in certain bacteria. It is also found in the cell walls of a few species of animals. When formed it becomes a part of the permanent framework of the cell, for there are very few organisms that possess the enzyme *cellulase*, that digests cellulose. The digestion of cellulose in the alimentary tracts of animals is due to the presence of certain non-green plants and sometimes certain protozoa. In contrast to cellulose, hemicelluloses may be formed as secondary thickenings on the cell walls of a plant and later digested to sugar. They are most conspicuous in certain kinds of hard seeds, such as the seeds of dates, other palms, coffee, and iris. The manufacture of cloth, paper, celluloid, collodion, acetic acid, artificial rubber, charcoal, rayon, cellophane, and explosives is but a few of the hundreds of industrial uses made of cellulose.

Pectic compounds. Apparently pectic compounds are present in the walls of all plant cells. They consist of large molecules formed mainly by the condensation of certain sugars and an acid derived from sugar. Various amounts of pectic compounds are usually intermingled with cellulose in the walls of plants. The *middle lamella*, which holds the cells of plants together, is composed of pectose or of calcium pectate. The softening of fruits and vegetables when boiled in water or as they ripen under natural conditions or in storage, is due to the breaking down of this layer and the partial separation of the individual cells. A similar process occurs in the absciss layer at the bases of the petioles of leaves, pedicels of fruits, and at the bases of petals and stamens of flowers. The pistils of flowers often abscise in the same way, and no fruits are formed. In simple structures, such as algae and root hairs, the pectic compounds are mainly in the outermost exposed layer of the cell walls. Many plant mucilages and gums are also composed largely of pectic

compounds. Changes that occur in pectic compounds in plants may be represented briefly.

Pectose ⟶ Pectins ⟶ Pectic acid.

Pectic acid + Calcium salt ⟶ Calcium pectate.

Fungi that live parasitically within green plants are often found only in the layer of pectic compounds between the cells. There they digest and use these compounds as food. The isolated cells of the host die and disintegrate. A similar process may result in overripened fruits and vegetables wherever the enzymes that digest pectic compounds are present. The retting of flax fiber is merely a process of breaking down the pectic compounds that hold the fibers together.

Large quantities of pectin are extracted annually from plants and used in the preparation of jellies, salads, creams, and emulsions desired as foods and drugs. Most of the commercial pectin, such as Certo, is extracted from apple pomace or cull lemons. A smaller amount is obtained from the pulp of oranges, sugar beets, carrots, and algae.

Other cell wall constituents. Suberin, the substance that is characteristic of cork, apparently occurs in a definite layer in the cell walls of cork tissue. It may also become deposited on or within cellulose walls, a process called suberization. Several other substances, such as lignin, cutin, wax, resins, and tannins, may become intermingled with cellulose and pectic compounds as the walls increase in age. The cutinized layer of the exposed surfaces of epidermal cells is called the cuticle. Suberin, cutin, wax, and resin when present in or on cell walls make them less permeable to water and restrict the entrance of parasites. These substances often constitute a relatively large part of the vegetable material that ultimately becomes transformed to coal, for only a few kinds of organisms can digest them.

Lignin is characteristic of woody cells and of hard plant tissues in general. Its presence is easily demonstrated by treating plant tissue with a dilute solution of phloroglucin followed by strong hydrochloric acid; lignified walls become brilliantly red with this treatment. One of the problems of obtaining cellulose from wood is the difficulty of removing lignin and other substances that are associated with it in the cell walls of wood.

Pigments. In addition to the chlorophylls, carotenoids, and anthocyanins discussed in Chapter IV, many other pigments are formed from food in plants. Some of them are important as co-enzymes in oxidation-

reduction processes. Others appear to be of no particular value or detriment to the species in which they are formed. Before chemists learned how to make dyes in the laboratory man was dependent solely upon these natural dyes. Among the more important are annatto, camwood, fustic, henna, indigo, litmus, logwood (haematoxylin), madder, red sandalwood, saffron, and turmeric.

Resins, gums, and mucilages. Resins are insoluble in water and render cell walls impervious to it. They occur usually in definite glandular structures, or in tubes extending throughout the plant. Amber is a fossil resin. Resins are soluble in alcohol and certain oils. Commercially they are used in the preparation of a variety of varnishes, soaps, dyes and medicines. Resin is one of the important products of the pine forests of the southeastern United States (Fig. 63).



FIG. 63. Method of tapping southern long leaf pine to collect resin.

Gums and mucilages are much alike. They are insoluble in alcohol and become jelly-like in water. Upon drying, gums first become sticky and then hard. Mucilages swell greatly in water. They may be important in holding water in the plant tissues in which they occur. Commercially they are important bases of various mucilages and chewing gum.

Latex. Many plants, such as the milkweeds, euphorbias, figs, and rubber plants, have a milky colloidal "juice" called *latex*. This is a mix-

ture of rubber, resins, gums and foods. It is the source of commercial rubber (Fig. 64).



FIG. 64. Interior view of a forest on a rubber plantation in the East Indies. The trees have been tapped to collect the latex from which rubber is prepared for industrial uses. Photo from Chicago Natural History Museum.

Essential oils. The odors of flowers, and the odors and flavors of fruits and vegetables are due in part to minute quantities of essential oils. They are often associated with resins and gums and are very unlike the liquid fats (fatty oils). They are of no importance as food, but are highly prized as flavors and perfumes, and for a few medicinal and industrial uses. You are probably familiar with menthol, camphor, turpentine, the characteristic oils of mint, pine, juniper, wintergreen, geranium, lemon, orange, ginger, anise, cloves, sage, hops, wormwood, lavender, bergamot, bitter almonds, and vanilla. Some of the essential oils contain sulfur. These underlie the odor and flavor of onion, garlic, watercress, radishes, and many kinds of mustard.

The edible parts of many plants, such as sweet corn, turnips, peas, and others, when first harvested have a delicious flavor that is lost very rapidly. Some of this loss in flavor is due to the disappearance of essential oils, but a part of it is the result of the oxidation of sugar and of

the rapid change of sugar to starch in the harvested product. The higher the temperature the more quickly the change occurs.

Alkaloids. Under this general name may be grouped a large variety of chemical substances apparently of little or no value to the plant in which they are made, but which have been of great importance in medicine. They are nitrogen-containing organic compounds, derived from proteins, generally odorless but bitter to the taste. They have marked physiological effects upon animals, and are extensively used as stimulants and narcotics. The best known are nicotine, from tobacco; atropin, from nightshade; strychnine, from strychnos; cocaine, from coca leaves; quinine, from chinchona bark; morphine and codeine, from the poppy; and caffeine, from coffee and cacao seeds.

Tannins. The bark of many trees, the galls occurring on oaks, and certain unripe fruits, such as the persimmon, contain bitter astringent substances known as *tannins*. These substances coagulate proteins to insoluble compounds. The coagulation of proteins in raw hides is the basic process in the tanning of leather. With iron salts, tannins become black or green in color. Ink was formerly made in this way. The freshly exposed surfaces of many fruits and vegetables become dark because of the oxidation of tannic acid, especially in the presence of a trace of iron from a knife.

Enzymes. The importance of enzymes in all metabolic processes in plants has already been indicated. They are very complex, often consisting of a chemically bound aggregate of known molecules. They are recognized by their specific effects upon certain processes; and they are named on the basis of either the kind of substance on which they act or the kind of process which they accelerate. For instance, sucrase acts upon sucrose, and oxidases accelerate the process of oxidation. Many enzymes are very specific, acting only in one kind of process. In all, there must be several hundred, perhaps thousands, of them. They are primary factors in numerous biological processes. A few of the common digestive enzymes in plants, the substrate (substance acted upon), and the end product are presented in Table 6.

Vitamins. These organic substances, which are formed in plants in minute quantities, were first discovered through their influence on the health of man and other animals. The chemical composition of some of them has been discovered. Vitamins are like enzymes or parts of enzymes rather than food; that is, they are necessary not as building material or as a source of energy, but rather as catalysts of certain basic biological processes underlying health, growth, and reproduction.

TABLE 6. Enzymes, Substrates, and End Products of Enzyme Action

Enzyme	Substrate	End Products
Diastase	Starch	Glucose
Maltase	Maltose	Glucose
Sucrase	Sucrose	Glucose and fructose
Inulase	Inulin	Fructose
Hemicellulases	Hemicelluloses	Simple sugars
Pectosinase	Pectose	Pectin
Pectase	Pectin	Pectic acid
Pectinase	Pectic acid	Simple sugars and acids
Tannase	Tannin	Glucose and gallic acids
Lipase	Fats and oils	Glycerin and fatty acids
Peptase (pepsin)	Proteins	Soluble peptones
Ereptase (trypsin)	Proteins and peptones	Amino acids

Scurvy, beriberi, and rickets were the first symptoms of vitamin deficiency to be clearly demonstrated.

Vitamins, or their precursors, are synthesized mostly in plants. They accumulate in certain animal tissues and in milk from the plants eaten by the animals. Carotene is a precursor of vitamin A, and ergosterol of vitamin D. The bacteria in the alimentary tracts of animals probably synthesize many vitamins.

Perhaps we should not try to make a rigid distinction among enzymes, vitamins, and hormones. Thiamin in a drugstore is vitamin B_1; in a plant that makes it, it is a hormone; in both plants and animals it is part of a carboxylase enzyme. Similar relations are true of other vitamins.

Hormones. These substances constitute another group of organic compounds that promote profound physiological effects when present in extremely minute amounts. Like the enzymes and vitamins, they influence certain basic biological processes. Their presence or absence is recognized by certain symptoms of development. They were first definitely discovered in animals as secretions of certain glands. In 1928 the presence of similar substances in plants was definitely established. Some of them have been isolated from plants and their chemical constitution is known. Special names have been applied to different ones, but in a general textbook we shall refer to all of them as hormones.

Hormones influence the enlargement of cells, the formation of roots, and the dominance of certain parts of plants over others. There are probably very few, if any, developmental processes in plants that are not influenced by them, but many experiments will have to be performed

before summary statements can be made. They are soluble in water and may pass from cell to cell; hence they may be made in one part of the plant, such as leaves, and influence the development of cells in another part of the plant. General effects resembling those due to natural hormones may be brought about by closely related compounds sold by chemical supply companies.

Such substances as enzymes, vitamins, and hormones are the modern substitutes for the earlier assumptions of special vital forces and entelechies. Not only are development and health dependent upon the presence of these substances, but certain differences in species are dependent upon their systems of enzymes, vitamins, and hormones.

Assimilation. It is often convenient to have one word by which we may refer to the transformation of food into the substances of which cells are composed. The term *assimilation* has been used with that intent in biological sciences for a long time. But it has also been given different interpretations as the knowledge of plant and animal nutrition advanced. One therefore finds it used today as it might have been used a century ago, and also as it probably should be used on the basis of present knowledge. A number of other expressions likewise became associated with the concept of assimilation at different historical periods, and they have also survived to the present time. Other biological terms, such as food, respiration, osmosis, adaptation, natural selection, and many others have a similar history. All of them, as well as the associated expressions, need to be critically examined by each succeeding generation of students.

When protoplasm was first recognized it seemed so all-important, especially in the animal body, that the term assimilation was, and still is, sometimes restricted to the transformation of food into protoplasm alone. This is a definite use of the term; but to adopt it we must seek another term to refer to the transformations of food into cell walls and other essential constituents of cells. It seems most convenient to use one term to include all of these processes in both plant and animal bodies.

The greatest confusion arose before the discovery that the food of green plants and of man is essentially the same, regardless of the manner in which they obtain it. Assimilation is really one phase of growth that is common to all plants and animals. It is quite different from the formation of sugar from CO_2 and H_2O or of amino acids and proteins from sugar and certain inorganic salts. That is, food synthesis and the subsequent use of food in assimilation are two different groups of biological processes.

We have a sufficient background now to see that the food of green plants and man is the same; that food consists of organic substances that may be used as a source of chemically bound energy and as material that may be directly transformed into protoplasm, cell walls, or other essential constituents of cells. Accumulated insoluble food must of course first be digested in either case.

Water and inorganic salts (fertilizers) which are essential to plants in many ways are not a source of energy to green plants. They may become incorporated in cell structures more or less directly or through their use as materials in food synthesis. Nitrates and sulfates, for example, are utilized in the synthesis of amino acids and proteins which in turn are assimilated in the making of protoplasm. Attempts to include carbon dioxide, oxygen, water, and inorganic salts under the term food result only in rendering the term meaningless and useless. Some of the ways in which inorganic salts may affect plants have already been noted; others will become evident later.

Composition of a plant. All reports of the chemical composition of plants and of protoplasm have at least two defects: (1) no distinction is made between accumulated food and materials of which cells are composed, and (2) inorganic salts that have accumulated in crystals or are merely in solution in the water in the plant are not distinguished from those that have become an integral part of the cell structures.

With these defects in mind, the elemental composition of a corn plant that has attained full growth is presented.

Corn Plant	Water	79.7%			
	Organic matter	19.5%	Dry Matter 20.3%	Carbon	44.58%
	Mineral elements	0.8%		Oxygen	43.79%
				Hydrogen	6.26%
				Nitrogen	1.43%
				Potassium	1.62%
				Phosphorus	.25%
				Calcium	.59%
				Magnesium	.44%
				Iron	.10%
				Sulfur	.05%
				Chlorine	.20%
				Sodium	.15%
				Silicon	.54%

Organic matter as compounds:

Carbohydrates and fiber	17.2%
Fats	0.5%
Proteins	1.8%

From these figures and the facts in the last few chapters it is evident that 94.63 per cent of the dry matter in the corn plant had its origin in the sugar made from carbon dioxide and water. As the plant stood in the field, only 0.8 of 1 per cent of its weight was due to inorganic salts that had passed into it from the soil, and some of these were present in excess amounts. But one should not infer from this fact that these salts are not of much importance to the plant. It is merely another case in which a relatively small amount of something is essential to the development of the plant, and a deficiency soon results in slow growth or even death.

Such phenomena as the growth of seedlings rooted in pure sand, of a large plant with roots confined in a small pot of soil, or aerial epiphytes and free-floating algae, or, on the contrary, the failure of lawn grass to grow in dense shade even when fertilizers and water are added, may all be adequately explained on the basis of the facts in the last few chapters.

Summary. In these last four chapters we were concerned primarily with the synthesis and uses of food in plants. The ways in which man and other animals are dependent upon food synthesized in plants were also noted. Both plants and animals are dependent upon food as a source of chemically bound energy which is liberated by respiration, and as a source of building material in assimilation. Owing to the gross similarity of protoplasm in plants and animals their food is essentially the same. It consists of carbohydrates, fats, and proteins, and any of their derivatives that may be used in respiration or assimilation. The range of these substances that can be used by an organism as a source of food depends upon its system of enzymes. Some organisms, for instance, can digest substances that are indigestible to others.

Assimilation may be considered as the transformation of food into protoplasm, cell walls, and other essential constituents of cells, such as enzymes, chlorophyll, vitamins, and hormones. During this transformation certain inorganic salts are variously combined with the organic compounds. Some authors use the term to denote only the transformation of food into protoplasm, thus leaving no general term to designate the transformation of food into other essential parts of the cell. Assimilation should be strictly distinguished from food synthesis and also from digestion.

The substances in the cell walls of plants are constructed primarily from sugar. An enormous quantity of food is annually converted into cellulose. In the making of protoplasm all types of foods are assimilated, and in addition water and the ions of inorganic salts are incorporated

in the system. Chemically, assimilation of foods consists of condensation processes or of a combination of oxidation-reduction and condensation processes. Assimilation is one phase of growth. About one-half of the food made by a plant is converted into its own tissues. Perhaps the amount is often greater than one-half.

The known cases in which food, enzymes, vitamins, and hormones are essential to certain basic processes exemplify an extremely intricate phase of the chemistry of biological phenomena. Many of the substances that affect the reactions in living cells are known, but relatively few of the details of the many chains of reaction that occur are known. Enough facts have been discovered, however, for one to learn (1) to relate certain symptoms of development to the presence or deficiency of particular substances, and (2) to know many of the major links in numerous chains of reaction. As this kind of knowledge increases, the bases of certain types of superstitions and assumptions about living cells disappear.

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CHAPTER XX

SOME BIOLOGICAL RELATIONS OF GREEN PLANTS

In the previous chapters many facts about the dependence of animals and non-green plants upon green plants became evident from time to time. A consideration of several of these facts in one chapter will help us obtain a better perspective of their interrelations. Perhaps this can best be done by reference to two concrete examples. For one example we may choose the so-called balanced aquarium or microcosm; for the other we may consider man on some populated island, or in some specific country such as the United States.

To understand these examples we must be able to recall and relate the facts about the following processes:

The manner in which food is obtained by plants and animals.
The making of sugar by photosynthesis in green plants.
The synthesis of proteins, especially the synthesis of amino acids.
The synthesis of vitamins in plants.
The assimilation of food to cell constituents in both plants and animals.
The oxidation of foods in respiration in both plants and animals.
The transformations of energy in foods and products of assimilation.
The loss of material and energy when a man eats meat instead of eating the plants fed to animals he ate.
The ways in which man obtains and transforms energy.
The transformation of energy accompanying the changing of plants to peat, coal, oil, and gas.

A microcosm. To set up a microcosm all that is necessary is to obtain a 3- to 5-gallon bottle; fill it about one-fourth full of pond water; add a few ounces of soil, a goldfish, and a quantity of algae that are edible by fish; seal the bottle air-tight and set it in a well-lighted part of the room, but not in bright sunlight and not where its temperature will often exceed 70° F. The fish and algae will then continue to live and grow in the bottle for months or even years (Fig. 65).

With the pond water and soil we incidentally place numerous bac-

teria and small animals in the bottle. We might avoid many of these organisms by using sterilized water and pure chemical salts, but some of them are also in the gelatinous walls of the algae, upon the surface of the fish, and especially in its alimentary canal.

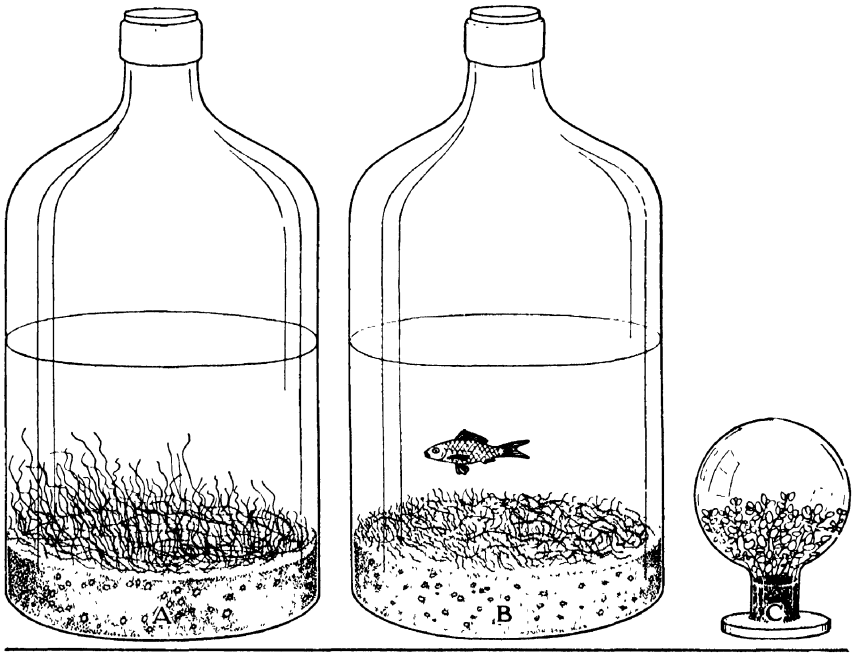


FIG. 65. Diagrams of microcosms in sealed containers in which the organisms indicated live for many months: A, algae; B, algae and a fish; C, Helxine (Paddy's wool).

We may ignore these small organisms for the moment and begin with the fish and algae. The statement that "the fish and algae each give off what the other needs," is both false and misleading. Of the many things necessary for the existence and growth of the algae in the bottle, only one of them comes in part from the fish, but the algae are not dependent upon the fish or any other animal for even that one. To explain the microcosm it is necessary to account for (1) the oxygen used by both the fish and the algae in the process of respiration, (2) the food used by both fish and algae in respiration and assimilation, (3) the carbon dioxide used by the algae in photosynthesis, (4) the energy used by the plant in photosynthesis, (5) the chemically bound energy used by both fish and algae, and (6) the conditions under which respiration and assimilation in both fish and algae are compensated by photosynthesis in

the algae. Without this compensation the fish would soon starve to death. It is assumed that the reader can account for all six of the conditions listed above. Perhaps vitamins should also be considered.

Since an adequate supply of inorganic salts was included in the soil, they may be ignored in this discussion. The presence of bacteria that cause decay undoubtedly prolongs the duration of the microcosm. They may digest and oxidize cell structures that are not acted upon by the enzymes of the fish and algae, and by this means delay the time at which the supply of carbon dioxide in the bottle becomes inadequate.

Perhaps it is evident that the algae and certain decay-producing bacteria could exist together in this bottle without any animal being present. The animals are dependent upon the plants, but the plants are not dependent upon the animals. They were placed in the bottle merely to imitate natural conditions. Even if all the animals in nature were destroyed, most of the plants would still survive indefinitely. Only those that are dependent upon the cross-pollination effected by animals, and those that are strictly parasitic upon animals would perish.

A human cosmos. Our second case, man in the United States, is somewhat more complicated because man uses plant products and the chemically bound energy of plants in many ways in which the fish does not. Food is used in the body of man in the same manner in which it is used in the body of a fish: as a source of chemically bound energy, and as a source of material that is transformed into the substances of which cells are composed. Moreover, food is used in this same manner in the bodies of the many domesticated animals which man employs in various ways. The dependence of man and his domesticated animals upon green plants for sugar, amino acids, vitamins, and a supply of chemically bound energy necessary to body processes probably does not need further emphasis.

Many of the uses which man makes of the material products of plants are also familiar to all of us. That plants are the main source of all the energy employed by man is not so well appreciated. The remainder of this chapter, therefore, will be devoted primarily to his dependence upon plants as a source of energy.

In addition to the energy that is transformed in the bodily processes of man and his domesticated animals, man employs energy as heat, light, electricity, and mechanical power in his home, in public buildings, on the street, on the farm, in the factory, and on the highways. Less than 2 per cent of all this energy is obtained from wind and water power.

More than 98 per cent of it may be traced back through various energy transformations to the light energy that was chemically bound in sugar during photosynthesis. Many questions relevant to these facts may be considered.

How efficient are plants as transformers of light energy? How rapidly is man releasing the chemically bound energy of plants? Is the present civilization releasing it more rapidly than it is being bound by plants today? Is all the energy bound by plants available to man? Has the replacement of the horse by the automobile and tractor—which use the energy bound by the plants of the past—altered the value of the energy bound by plants of the present? What of the future?

The answer to any one of these questions must be an approximate one; but an estimate based upon available data is so much better than a mere guess or no answer at all, that space will be given to a tabular summary of a few data and certain general statements based upon data too numerous to be presented here (Table 7).

The acre of corn referred to in the table was located in central Illinois. The yield of 100 bushels of grain on this acre is three times the average. The whole plant is considered in the calculations. The acre of apple trees was located at Ithaca, New York.

Most all of the chemically bound energy that accumulates in the corn plant and apple tree would ultimately be available to non-green plants, for as a group of organisms they may digest and oxidize most of the substances made in the green plants. Only about one-fourth of the energy that accumulates in a corn plant is available to man as a source of bound energy in food, and still less of the energy that accumulates in the young apple tree is similarly available. As a source of energy in fuel, however, the amount that is available to man depends upon how meticulously he harvests and uses the different parts of the plant. In one country the roots may be left in the soil and the smaller branches may be heaped in piles and burned, while in another where the supply of chemically bound energy is scarce and expensive the smaller twigs, roots, and even the leaves may be collected for fuel. In the early days pioneers on our own prairies and plains sometimes used the stems and leaves of native grasses as fuel. But regardless of how meticulously man harvests green plants, other animals and the non-green plants will take a certain toll. The insects in a pasture, for instance, may eat almost as much grass as do grazing animals.

TABLE 7. A Comparative Summary of Energy Transformations in an Annual Herb and in a Woody Perennial

	Acre of Corn (Illinois)	Acre of Apple Trees (New York)
Length of growing season	100 days	188 days
Number of plants per acre	10,000	400
Average leaf area is attained in	50 days	28 days
Total radiant energy available	2,043 million Cal.	2,718 million Cal.
Total energy bound in sugar	33 million Cal.	30 million Cal.
Percentage of light energy bound in photosynthesis	1.6%	1%
Photosynthetic efficiency based on part of spectrum that is effective in photosynthesis	8%	5.5%
Average amount of sugar made per day	200 pounds	93 pounds
Total sugar made per season	about 10 tons	about 8.7 tons
Chemically bound energy released by respiration in the plant	8 million Cal.	10 million Cal.
Percentage of energy bound by photosynthesis released within the plants by respiration	23.4%	33.3%
Of the sugar made each season there is oxidized by respiration in the plant	about ¼	about ⅓
The average rate of photosynthesis (12 hrs.) compared with respiration (24 hrs.)	about 8 times	about 6 times
Bound energy in the structures and accumulated food in the plants	25 million Cal.	20 million Cal.
Percentage of total energy of photosynthesis in accumulated foods	about 25%	...
Percentage of total energy of photosynthesis accumulated in structures	about 50%	...

Sources and amounts of energy. Several investigators have analyzed plants and calculated the amount of carbon and bound energy in them per acre. From all these data it seems that an average acre of corn accumulates a little more than 8 million Calories of energy, or about one-third as much as the acre of corn described above; and that in all kinds of crops the average annual accumulation of energy per acre is about 6 million Calories. In an acre of forest it is about 10 million

Calories.[1] By using these figures for the country as a whole and adding a little extra for range and desert vegetation, we find that the green plants of the United States accumulate about 10×10^{15} Calories of energy annually. This is approximately 70 per cent of the energy chemically bound by them in photosynthesis.

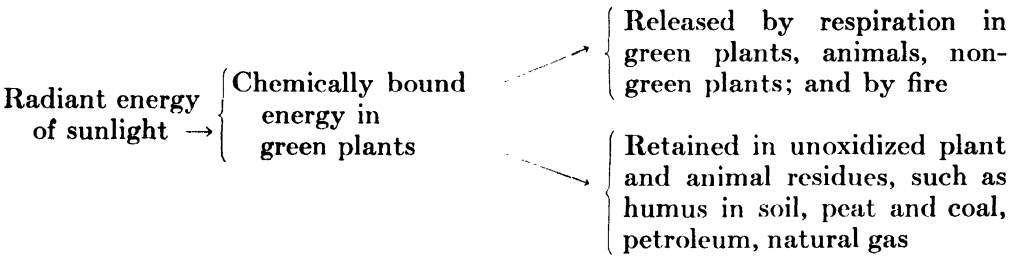
Through the use of plants as food for himself and his domesticated animals, and in several other ways, man in the United States annually destroys plants containing about 6×10^{15} Calories of bound energy. In addition to this the coal, oil, and gas removed from the earth each year in this country have an energy value of more than 5.5×10^{15} Calories. From these calculations we seem to be responsible directly or indirectly for the dissipation of chemically bound energy about as rapidly as it accumulates in the green land plants of today. To this we must add the amount released by undomesticated animals and the enormous amount released by non-green plants.[2] What of the future?

Energy transformations and conservation. In the early years of the present century the chief energy transformers in industry and transportation were the steam engine and the horse. Coal was often used for the supply of chemically bound energy in the steam engine, but the use of wood obtained from nearby living forests was not uncommon. All the chemically bound energy transformed into mechanical energy in the horse came each year from the living plants of the farm. Horses were used for practically all transportation except that upon railways and water. The farmer not only harvested the chemically bound energy which he used on his own farm, but in addition he sold enormous quantities of it for horses employed in various ways in the city. Since the horses also came from the farm, the farmer furnished both the energy and the transformer. With the coming of the automobile and tractor, conditions were reversed. The farmer now buys from industry not only the transformer (motor) but also the chemically bound energy (gas and oil) that was stored in plants millions of years ago. Such drastic changes in the sources of energy have been reflected in economic relations for many years. Moreover, there is a limit to the natural deposits of chemically bound energy in coal and related products.

[1] If the reader wishes to calculate the equivalent of Calories of energy in terms of grams of sugar, he can do so by multiplying by 180/674 or by dividing by 3.75. Grams of sugar may be stated in terms of CO_2 used in photosynthesis by multiplying by 264/180. See the equation of relative weights in Chapter XIII.

[2] One may also consider this problem on the basis of whether plant residue (humus in the soil, peat, coal, etc.) is accumulating today as rapidly as it is being destroyed. It did accumulate more rapidly than it was destroyed before man came upon the scene.

The major transformations of chemically bound energy among living organisms may be summarized diagrammatically.



All animals eat large quantities of food in proportion to their gain in weight. Evidently much more food is used in the animal body as a source of energy than as a source of body material. Usually when one animal eats another it obtains less than 10 per cent of the energy the first animal obtained directly from plants. If a third animal eats the second one, it derives less than 1 per cent of the energy in the plants eaten by the first one. The animal population of a region cannot exceed the supply of the chemically bound energy in the plants of that region except in those instances where man is able to obtain food from a foreign market.

In the United States there are today about 2.5 acres of cropland per capita. This figure could be raised to 3.2 if 109 million acres of plowable pastures were converted to cultivated land. Cropland acreage per capita in many countries is less than 1 and in several less than 0.5. Obviously human diets cannot be the same in all parts of the world.

Through such procedures as plant breeding, conservation of the soil and water, the use of fertilizers, and improved methods of forestry, the annual accumulation of chemically bound energy in plants may be greatly increased, perhaps doubled or even more. But these procedures require intelligent effort and foresight, and the elimination of wasteful exploitation of natural resources. For example, the world's annual growth of wood is estimated at 38 billion cubic feet. Under good forest management it might be 350 billion cubic feet.

Summary. In the world of living organisms green plants have a unique position. Except for their dependence upon certain groups of bacteria,[3] and those seed plants for which pollination by animals is essential, they are independent of other organisms. From one point of view all animals are parasitic on plants. Animals are not essential to most plants. But animals and non-green plants are dependent upon the green plants

[3] The importance of certain bacteria to green plants will become evident in the chapters on non-green plants.

for chemically bound energy and certain synthesized products. Man in particular is dependent upon green plants for sugar, amino acids, vitamins, precursors of vitamins, and, up to the present, for more than 98 per cent of the energy he utilizes. In addition, there are thousands of uses made of plants and plant products for convenience, recreation, and art.

Furthermore the facts recorded in Chapter LII are ample evidence that the chemically bound energy utilized as a source of energy in lighting, heating, and turning machinery in our industries is being mined as "fossil fuel" from unrenewable sources. We are passing through a stage of development in this country in which ignorant, indifferent, uninformed, and ruthless exploitation of plants and plant environments should speedily be replaced by intelligent efforts at conservation based upon a knowledge of plants and of their biological relations.

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CHAPTER XXI

INTERRELATIONS OF THE PARTS OF A PLANT

One part of a plant may be dependent upon processes that occur in another part. Roots and leaves are mutually dependent. Consequently the effects of an environmental factor upon the processes in one part of a plant may influence the development of other parts. We now have a sufficient background of facts to understand some of these interrelations; others will be postponed to later chapters.

Interrelations involving movement of materials. Several of these interrelations are known to be dependent upon the movement of materials from one part of the plant to another. Many of them depend upon the movement of sugar from the green to the non-green parts of a plant. The growth of seeds, roots, and underground stems depends upon sugar made primarily in the leaves. Even green fruits and green stems, except in such plants as cacti, are dependent in part upon sugar from the leaves. The influence of any factor upon the making of sugar in the leaves may be reflected in the growth of all these organs. The processes in the leaves, in turn, are dependent upon the movement of water and inorganic salts from the roots. The relative growth of the aerial stems, leaves, and fruits also depends in part upon which ones get the major supply of these substances from the roots, especially when the supply is low or inadequate.

We may begin the analysis of interrelations by citing a number of growth phenomena which are dependent in large part (1) upon the synthesis of sugar in the chlorenchyma and its movement to other parts of the plant, and (2) upon the synthesis of proteins from this sugar and certain inorganic salts. The correct interpretation of some of these examples may be evident as rapidly as they are read; others will be correctly interpreted only if the reader pauses long enough to analyze the problems in considerable detail.

Specific examples of interrelations. Under good growing conditions the largest Jonathan apples are not obtained if there are fewer than 30 leaves per apple. The largest Delicious apples are not obtained if there

are fewer than 50 leaves per apple. For the largest Elberta peaches about 30 leaves per peach are necessary. For the best cluster of grapes there should be not less than 12 to 15 leaves per cluster.

The roots and underground stems of troublesome weeds, such as dandelion and thistle, will die of starvation if the green tops are removed frequently and immediately after they begin to develop, or if they are densely shaded by another plant such as alfalfa. In interpreting this fact it should be remembered that the synthesis of starch, fats, and proteins may occur in roots and underground stems, and that any of these three substances may be transformed to sugar in the cells of these organs. An adequate interpretation of this fact and of several of those that follow involves, therefore, an explanation of why the roots and underground stems cannot make starch, fats, or proteins and survive upon them as food when the tops of the plants have been removed or when the rate of photosynthesis is continuously low.

A good yield of Irish potato tubers is not obtained if the potato plants are continuously exposed to high temperatures (Fig. 66) or dense

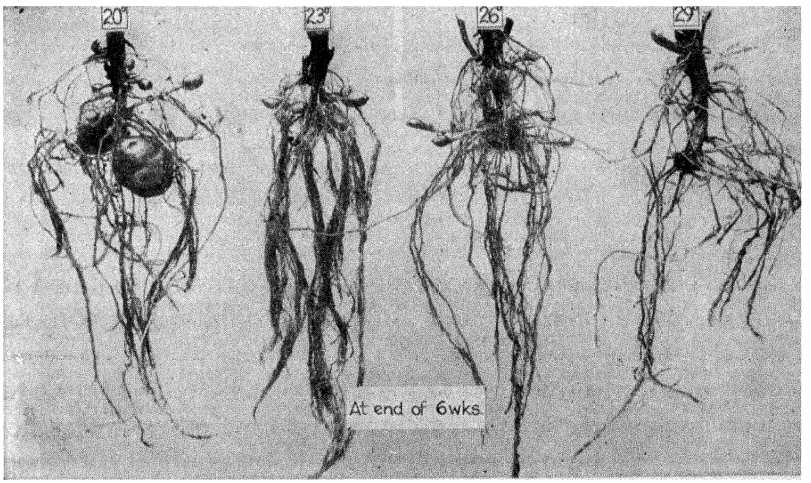

FIG. 66. Effects of different temperatures on the formation of potato tubers. Photo by John Bushnell.

shade, or if the soil contains an abundance of nitrates. Under any of these conditions the tops (aerial stems and leaves) may grow fairly well; with a high nitrate supply there is usually a luxuriant growth of tops. Under experimental conditions a low yield of tubers also results

when the potato plant is exposed to a very low concentration of carbon dioxide.

As a rule there is a much greater growth of tops in proportion to the growth of roots when plants in a moist climate are exposed to a high temperature, dense shade, high nitrate supply in the soil, or to a low concentration of carbon dioxide in the air. On the contrary, there is a relatively greater growth of roots in proportion to tops when the supply of water or of salts of nitrogen in the soil is moderately low (Fig. 67).

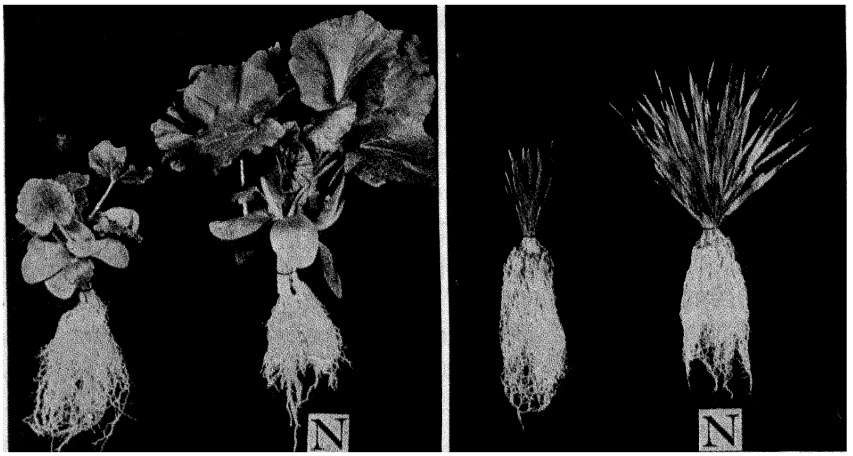

FIG. 67. Relative growth of tops and roots of squash and wheat seedlings that grew in culture solutions without and with added nitrogen (N). Photos from Mary E. Reid, Boyce Thompson Institute.

The amount of food that accumulates in roots and underground stems is influenced by the environmental conditions to which the tops of the plants are exposed.

Bluegrass in the shade of trees in a lawn that is frequently watered, treated with ammonium sulfate, and mowed during the warmest months of summer may not survive as well under this treatment as bluegrass that is neither watered nor fertilized during this part of the season.

The practice of pruning and pollarding trees checks the growth of both tops and roots, but the growth of the roots is checked more than that of the tops.

In dry climates alfalfa is mowed 3 to 5 times in a season, but if it is mowed as frequently as this in moist climates most of the plants die within a year or two.

Sassafras may grow as a weed in pastures in certain parts of the country, but not when sheep are present in abundance. Almost pure forests of hemlock, of pine, or of hickory have been known to develop in pastures in which seeds of many other trees were present. In a forest the kinds of seedling trees that grow to maturity may depend in part on the presence of browsing animals, such as deer.

On the roots of the plants of the clover family there are nodules resulting from the presence and activities of nitrogen-fixing bacteria. When the clover plant is exposed to dense shade, or when its roots are in soils containing an abundance of salts of nitrogen, there are fewer nitrogen-fixing bacteria and nodules than there are when the clover tops are exposed to an abundance of light, or when the roots are in soils in which the supply of nitrogen salts is low.

Many plants propagate vegetatively if one merely cuts off the leafy tip of a stem (a cutting) and inserts its basal end into moist soil. In a short time roots will grow from the base of the stem and the cutting will continue to grow and become a complete individual plant. Many persons remove the leaves from cuttings, but the new roots will appear sooner, be more abundant, and grow more rapidly if some of the leaves are not removed. Exact observations may be made more readily if the cuttings are placed in water in a beaker instead of in soil (Fig. 68).



FIG. 68. The initiation and the growth of roots from cuttings are dependent upon leaves. Photo by F. H. Norris.

Interpretations exemplified. The reader may be satisfied with the inferences he drew and the interpretations he made as he read each of the above paragraphs; or he may wish some means of checking them. Only one example will be discussed here, namely, the relative amount of growth of roots and shoots of plants supplied with different amounts of nitrates in the soil. If the supply of nitrates is very low the root system is large in proportion to the tops. If it is very high the root system is small in proportion to the tops. One might speedily dismiss the whole matter by saying that in the first instance the roots grew long in search of more nitrates for the tops, and in the second instance the tops had plenty of nitrates and the roots did not have to grow long in search for more. But would one be content to ascribe to roots either the intelligence necessary to diagnose the needs of the tops, or the superhuman ability to grow, or not to grow, at will?

Now, if we try to explain these growth phenomena on the basis of the manufacture and uses of food in plants, it is necessary only to recall and relate those groups of facts which showed that (1) foods are used in the building of cells and that growth does not occur without them; (2) the amount of sugar that enters the non-green parts of a plant depends upon the extent to which photosynthesis exceeds respiration and other uses of sugar in the chlorenchyma; (3) no part of the plant can grow well unless it is adequately supplied with both sugar and proteins, or with the conditions necessary for making them; (4) although rapid growth depends upon a plentiful supply of proteins from which the new protoplasm is largely made, considerably more sugar than protein is consumed in the building of new cells; (5) particular parts of the plant are dependent upon the movement of certain materials from other parts; and (6) a definite set of conditions is necessary for the synthesis of sugar and proteins in plants. Fats were omitted from this summary because they seem to be made readily enough in the cells when sugar is present.

Since all the sugar is made in the tops of the plant, the roots will get an ample supply of it only when it is made in the shoots much more rapidly than it is used there. On the other hand, the shoots will have a good supply of the nitrates needed in protein synthesis only when the amount that passes into the roots from the soil greatly exceeds the use of nitrates in protein synthesis in the roots.

Chemical analyses of plants show that if the supply of nitrates in the soil is low the tops have larger amounts of carbohydrates in proportion

to proteins. The tops do not grow well because there is a deficiency of protein in them. Sugar and starch accumulate in them. The sugar moves downward and the roots become well supplied with it. The nitrates that enter the roots are used there in protein synthesis, and as a consequence the roots grow relatively large in proportion to the tops.

Chemical analyses also show that the tops have a larger proportion of protein when the supply of nitrates in the soil is high. Under these conditions the tops grow well. A relatively greater amount of the sugar made in the chlorenchyma is used directly in the growth of tops, and consequently the roots are less well supplied with sugar and their relative growth is less.[1]

Hormones and interrelations. Having seen how this one example of growth can be interpreted upon the basis of foods without assuming any purposeful acts by a part of the plant, we may now ask whether the growth of roots is dependent upon the tops only for sugar. It is possible that their growth may be dependent upon the tops also for minute amounts of certain hormones (or auxins), vitamins, and amino acids, or for certain precursors of these substances. This question was asked many years ago, and it has been answered in the affirmative and the negative many times. Recently, however, there has been a concerted effort by many workers to decide it on the basis of critical experiments.

A brief account of one type of these experiments will indicate some interesting features of the general problem. Several attempts have been made to place small pieces of roots in solutions of certain materials in which they would continue to grow entirely isolated from the rest of the plant. These efforts were finally successful. One investigator put a small piece (1 cm. long) of the tip of a tomato root in 50 cc. of water in a sealed flask which also contained:

1,000.000 mg. of sucrose
17.300 mg. of essential inorganic salts
0.005 mg. of brewer's yeast extract.

The pieces of root grew in this culture. At the end of one week a small tip of this root was transferred to a fresh solution, and so on week after week. These pieces of roots continued to grow after each transfer without any decline in the rate of growth with time. But if the brewer's yeast was omitted the root ceased to grow after two or three weeks.

What is there in this minute amount of brewer's yeast that is so im-

[1] The other examples listed are left for class discussion.

portant to the growth of roots? It is not in the ash (inorganic salts) of the yeast. It is organic. Is it one substance or more than one? Can anything else be substituted for it? Are some substances necessary for the starting of roots, and others for root growth? Are the same substances necessary for the roots of all plants? Are the formation and growth of tubers also dependent upon such substances? These are some of the questions being investigated at the present time. It has been found that vitamin B_1 (thiamin) is at least a partial substitute for yeast extract.

From the results of numerous experiments we know now that the formation and growth of roots and tubers are dependent upon the translocation of hormones as well as sugar from the top of the plant. These discoveries are the basis of the attempts being made to discover what substances may be used to hasten root formation in numerous plant cuttings. Certain substances are now being advertised for this purpose.

Such synthetic auxin-like compounds as 2,4-dichlorophenoxyacetic acid (2,4-D) are important in weed eradication. They upset necessary interrelationships within the plant, often resulting in the death of the entire plant. Their toxic effects vary with the plant, with the concentration of the herbicide, and with many other factors.

Summary. The organs of a plant are mutually dependent because of substances made in, or absorbed by, one part of the plant that are necessary in the growth of other parts. Many common interrelations in plant organs are dependent upon the synthesis and transfer of sugar and of the substances used in protein synthesis. As a result of these interrelations environmental factors may influence the development of one part of a plant through their influence upon the processes in another part of it. Similarly one plant organ may affect another as a result of hormone synthesis and distribution. Other interrelations between the parts of plants will be noted in later chapters.

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CHAPTER XXII

PHYSICAL PROCESSES INVOLVED IN THE MOVEMENT OF MATERIALS IN PLANTS

The movement of materials into and out of plants, and from place to place within the plant, was often mentioned in previous chapters without reference to the manner of movement or to the energy necessary for it.

The reason for this omission will soon be apparent. Energy is always necessary for the movement of material from one position to another. The immediate source of this energy may be in the moving object, or it may be in the environment of the object. For a clear concept of the movement of materials into, out of, and within a plant it is necessary, therefore, that one distinguish whether the source of the energy which causes the movement is within the moving material, within the plant, or in some other external agency. It will be much easier to attempt this distinction now by viewing in retrospect some of the processes already discussed and considering some additional ones. It is sometimes difficult, even impossible today, to make this distinction; but the major source of energy in many plant processes is not difficult to recognize.

Intrinsic and extrinsic sources of energy. Perhaps a crude analogy may clarify this problem of recognizing different sources of energy. The movement of a floating log in a river is dependent upon a source of energy obviously outside the log. The movement of a man swimming in the river results from a combination of the energy that moves the log plus a source of energy within the man. By utilizing this second source of energy the man may move upstream. The movement of a boat in the river may be traced to the same source of energy we think of when explaining the movement of the log, plus another external source of energy that may be traced to the motor attached to it, or to the man rowing it.

The movement of materials into, out of, and within plants, like that of the objects in the river, depends upon several diverse sources of energy. The plant may have no active part in the movement. We must not be misled into thinking that the plant, being alive, can take in sub-

stances, move them where they are needed, and throw off those that are not needed. The active agent may be the moving substance itself, and the energy that impels it may be external to the plant. Obviously such movements should be described not by terms implying that the plant "takes up," "takes in," and "gives off" the materials, but by terms implying that the materials are moving into, or out of, the plant. The latter terms focus one's attention upon the really active agent, while the former imply that the passive medium (the plant) is the active agent. By common agreement the term absorption is used merely to indicate that a substance enters the plant, without reference to the manner of its entrance or the energy that moves it.

Movements of materials and the water medium within plants. In addition to recognizing the energy relations of moving substances, it is also important to visualize the water within the plant, since this water is the medium in which substances move. We have already seen that leaves are composed of cells. In each living cell of the leaf a central vacuole filled with water and dissolved substances is surrounded by a thin film of protoplasm, which is in turn enclosed by a cell wall composed of cellulose and pectic compounds and sometimes of other substances also. Similarly, all other organs of a plant are composed of cells. Water not only fills the vacuoles of the cells, but it also surrounds and is between most of the minute particles of which the protoplasm and cell walls are composed. Cell walls become much thinner when the water in them disappears by evaporation, just as a wet cardboard becomes thinner as it dries.

By weight, about 80 per cent of a growing corn plant in midsummer consists of water. We may therefore think of a corn plant as a branched column of water held in place by exceedingly thin films of protoplasm and cell walls. Substances that move into and within the plant are moving mainly in solution in this water. Substances that move out of the plant are moving out of this water. The water also moves.

These movements may be inhibited or retarded by layers of cork and by cell walls that are highly cutinized because the fat-like particles in these walls may not be embedded in water. Movement of materials into and out of cells may be impeded also by the film of protoplasm in each cell. This fact may seem strange because of the large amount of water in protoplasm, but it is probably due in part to a greater accumulation of fat-like substances in the outer surface layer of the protoplasm. For the present, however, we may accept and use the fact without account-

ing for all the intricate physico-chemical conditions of which it is a consequence.

For many years students of plants have been trying to explain the movement of materials into, out of, and within plants. Not all the questions raised have been satisfactorily answered, but enough has been learned for botanists to conclude that these movements are dependent upon the same physical processes that occur in non-living systems. Most of them have already been imitated in experiments by means of laboratory apparatus. These movements will now be considered in more detail in relation to some of the physical processes involved.

Mass movements. The flow of water in a stream and the movement of a current of air (wind) along the street are familiar examples of what is meant by mass movement. Frequently it is a flowing movement or current. Mass movements of materials may occur in plants. If you put your finger in water and then withdraw it, a film of water adheres to it because of the cohesion of the molecules of water, and the adhesion of the molecules of the water and those of the skin. These cohesive and adhesive forces between molecules at the surfaces of objects may result in tensions, called *surface tension.* Surface tension may cause the movement of water for short distances, and any substances dissolved or dispersed therein move with the water. For instance, if two microscope slides are held closely together and one end is placed in a shallow dish containing a dye dissolved in water, a small mass of the solution quickly moves up between the two slides. This is a familiar phenomenon to anyone who has frequently washed slides or dishes. Similarly, water may move into the small spaces between the fibers of a blotter, a piece of wood, or a plant, or into the pores of the soil. This movement of water into small spaces as a result of surface tension is often referred to as *capillarity.*

We have already seen that protoplasm may move about within a cell by flowing movements (protoplasmic streaming). Substances, such as food and salts, that are in the protoplasm are of course carried along in the same manner that a log is carried in a stream. There may even be some movement of materials in this way between cells when strands of protoplasm extend from cell to cell through minute pores in the cell walls. Surface tension is one of the forces which cause protoplasmic streaming.

There is also a streaming, or mass movement, of water up the con-

ductive tissues of a plant from the roots to the leaves. This movement is discussed in a later chapter.

In Chapter VII we mentioned the fact that one of the results of oxidation-reduction processes in living cells is a small electrical difference between the parts of a cell and between the tip and base of a plant organ. These electrical differences are mentioned here merely because they may affect the mass movements mentioned above and also some of the diffusion phenomena described below. For example, electrical polarity is thought to be an important factor in axial as well as lateral movement of certain substances in plants.

Diffusion. All soluble materials that move into, out of, or within plants move wholly or in part by diffusion. Plants may wither and become dry. Water placed in an open dish slowly disappears. We cannot see the water moving from the dish or from the plant, because it is moving in the form of free molecules that have separated from the liquid mass. It is diffusing from them into the air, and what we see is the result of this diffusion. Later we shall see some of the results of the diffusion of water into a plant, and from cell to cell within it.

Instead of water we may place some aromatic liquid, such as peppermint oil, in the open dish. In a short time the presence of this oil in all parts of the room may be detected by its odor. Neither the oil nor the water has been destroyed, but the molecules of each have become widely dispersed in the air of the room. That is, they are now scattered among the molecules of oxygen, nitrogen, and other gases in the air. Similarly, the odor of flowers and fruits is the result of the diffusion of some substance from them that we detect by our sense of smell. From these examples it is perhaps clear that we are using the term *diffusion* to refer to the *dispersion of material by molecular movement.* Although we can neither see nor smell oxygen and carbon dioxide, there are ways of proving that they also move into, within, and out of plants by diffusion.

If a water-soluble colored salt, such as potassium permanganate, is placed at the base of a column of water in a glass J-tube, changes in depth of color become apparent as molecules of the salt move among the molecules of the water. These color changes accompany the slow diffusion of the salt upward in the column of water. Even the force of gravity does not prevent the upward movement of the molecules of a salt in the water. Similarly, any substance that is soluble in the water of the plant may move into the plant and from cell to cell within the plant by

diffusion. As we shall see later, some substances do not pass through the layer of protoplasm in the cells as readily as others.

The accumulation of water in the vacuole by the process of *osmosis* and the swelling of cell walls or of a piece of wood by the process of *imbibition*, are merely processes of diffusion under special conditions with special results. Even the mass movement of a stream of water up the conductive tissues of a plant is indirectly dependent upon the energy of diffusion.

An understanding of all these processes evidently depends upon a fairly clear concept of the process of diffusion. One may begin by thinking of all solids, colloids, solutions, liquids, and gases as composed of molecules always in motion. Anyone who has used a microscope has probably observed that the smallest visible particles mounted in a drop of water—for example, chalk dust—are constantly in motion as the result of being bombarded from all sides by the molecules of the water. This is called *Brownian movement* after Robert Brown, an English botanist who first described it. The smaller the particles of a given substance the more rapidly they move. While watching them one needs only to imagine more and more rapid movement of smaller and still smaller particles to form a mental image of molecular motion.

Diffusion is the result of molecular motion. Consequently the energy involved in all diffusion processes can be traced to the energy of molecular motion of the diffusing substances themselves. Each substance diffuses independently of the diffusion of other substances, except for the interference caused by one molecule colliding with another. A substance will diffuse more rapidly into a vacuum than into air because of the fewer collisions with other molecules. Likewise, a gas, such as oxygen or carbon dioxide, will diffuse more rapidly in air than in water.

The energy of molecular motion is correlated with heat and is directly proportional to the absolute temperature. Apparently at minus 273° C. there would be no molecular motion and no diffusion. One may therefore think of the heat energy of the environment as being the source of energy of the movement of materials into, within, and out of plants by diffusion. The heat energy liberated in the plant by respiration would be an additional source of energy in this process, but a rather insignificant one. The radiation of energy from the sun is the principal source of the heat energy of the earth's surface, and this in turn becomes the source of the energy of molecular motion in plants and all other objects on the surface of the earth.

When a soluble dye is placed in the bottom of a slender glass tube filled with water, the greater concentration of the dye in the bottom of the tube at the beginning of the demonstration is evident by the deeper color there. Gradually, however, the color of the dye becomes evident farther and farther up the tube, and after many months the color is uniform throughout the tube. The dye is now equally concentrated throughout the entire column of water. That is, the number of molecules of dye in comparison to the number of molecules of water would be the same in a cubic centimeter of the solution taken from any part of the tube.

Evidently for several months before the concentration of the dye became uniform a greater number of molecules of dye moved upward than downward in the tube. Since more molecules of dye are moving in any direction in the region where its concentration is greatest, the dye will diffuse from regions where it is more concentrated toward regions where it is less concentrated. When the concentration of the dye becomes uniform, as many of its molecules will be moving in any direction in any part of the tube as in any other.

When the above facts are fully appreciated it will be easy to see why carbon dioxide and oxygen diffuse into the green parts of a plant at one time and out of them at another time. Each gas diffuses independently of the other, and solely in relation to *its* own concentration inside and outside the plant. The same principle holds for the diffusion of water, of a salt, or of any other substance dissolved in the water. For instance, if carbon dioxide is used in photosynthesis in a particular cell, its concentration within that cell becomes lower than it is outside the cell. Then, according to the laws of diffusion, a greater number of molecules of carbon dioxide will move into that cell than out of it, until its effective concentration is again equalized.

If we gauge our language by our knowledge, we will no longer say that the plant "takes in" and "gives off" carbon dioxide; we will use expressions that imply that the carbon dioxide passes into and out of the plant. To be specific, we may say that it diffuses into and out of the plant. The movement of other materials should be similarly analyzed.

As our knowledge increases, it becomes more and more evident that a plant is a complex system of materials and processes surrounded by another system of materials and processes that we call the environment; and that the same natural laws are operating in both systems. Processes follow one another as a consequence of their dependent relations in these

systems. To explain why a particular process occurs we must be able to show that it is a consequence of preceding processes.

Diffusion under special conditions. When the basic facts of diffusion are clearly understood they may be used in interpreting complicated processes in which diffusion plays a part. Among these processes are imbibition, osmosis, and transpiration.

Imbibition. We have already seen that a piece of wood is composed of cell walls. Even more familiar is the fact that when a piece of dry wood is placed in water or in a moist atmosphere it swells, or increases in volume and weight. Before the discovery of explosives stone was quarried by pouring water upon pieces of dry wood that had been wedged into holes drilled in the rock. Even at the present time this method is used in quarrying marble and granite for special purposes. The swelling of wood is the result of the entrance of water between the particles of which the *cell walls* are composed. The entering water pushes these particles farther apart and increases the size of each cell wall. This fact is easily demonstrated by placing a flat piece of dry gelatin, or agar, in water for a few minutes. Any of the solid or colloidal parts of a plant may increase in size in the same manner, but the swelling of cell walls, protoplasm, and mucilages are the most conspicuous examples. The entrance of water into solids or colloids and the resultant swelling have long been referred to as *imbibition.*

Evidently the energy of diffusion is involved in imbibition. The concentration of water is greater outside than inside the piece of dry gelatin or the dry cell walls of the piece of wood. But the water also adheres to the smaller particles of the wall and forms thin films around them. The cohesion of the wall particles is overcome by the pressure of diffusion and by the adhesion of the water to them. They are forced farther apart by the entering water and the walls swell. When a piece of dry wood is placed in water the water first enters the intercellular spaces, pores, and open vessels, forcing out the contained air. This movement is the result of surface tension (capillarity). It rapidly distributes the water into some of the xylem tubes and intercellular spaces in the wood block, but it does not result in increasing (swelling) the volume of the block.

Osmosis. The term osmosis is sometimes used synonymously with diffusion. It has been used also to refer to the diffusion of anything through any membrane. These uses are not acceptable, because there is no need for the word if it is a synonym of diffusion, and because the

term is needed to designate diffusion through a particular kind of membrane under special conditions with special results.

There are certain conditions in plant cells under which the number of molecules of water moving from outside the cell through the film of protoplasm into the vacuole is greater than the number moving outward from the vacuole. As a result, the water in the vacuole increases in volume and thereby presses against the protoplasm and cell wall. These structures become stretched and extended, and the whole cell becomes larger and firmer, or turgid. When the enlarging cells occur in masses as in plant organs and press against each other, the mutual pressure among all the cells causes the whole plant to become rigid or turgid. When these processes and conditions become reversed, the plant wilts. If there is any advantage in adding the word osmosis to our consideration of diffusion in plants, it lies in limiting its use to the diffusion of water through certain kinds of membranes, such as protoplasm, when certain other conditions exist. What are these conditions, and what is peculiar about these membranes?

The concentration of water in the vacuole is a factor in osmosis. When the diffusion of water is inward through protoplasm into the vacuole, one may infer from the general laws of diffusion that the *water* inside the vacuole is less concentrated than the *water* outside the cell. This condition actually occurs when the concentration of dissolved substances (sugars, salts, organic acids) in the water enclosed in the vacuole exceeds the concentration of dissolved substances in the water surrounding the cell.

At room temperature (20° C.) there is a definite number of molecules of water in each cubic centimeter of pure water. If some sugar is added, the water then appears to occupy more than a cubic centimeter of space. The reader will undoubtedly explain this increase in volume by visualizing the molecules of sugar as diffusing or moving among the molecules of water and jostling them farther apart. Molecules of sugar now occupy spaces formerly occupied by some of the molecules of water, and there are fewer molecules of water in a cubic centimeter of this solution than there are in a cubic centimeter of pure water. The presence of the sugar molecules decreases the concentration of the water. Obviously the more sugar present the more dilute the water will be. In solutions of this sort the water is said to be the *solvent*, and the sugar the *solute*.

Many other conditions related in one way or another to the concentration of water sometimes appreciably affect osmosis in plant cells, but

seldom need be considered in problems discussed in general botany. Four of these conditions will be mentioned briefly. In a solution of water and sugar several molecules of water become chemically attached to each molecule of sugar; this is equivalent in effect to decreasing the concentration of freely moving molecules of water in the solution. Furthermore there is a well-known law in physical chemistry from which we may infer that the concentration of molecules of sugar in the surface of the drop of water in a vacuole is relatively greater than it is in the interior of the drop, thus further decreasing the relative number of freely moving molecules of water in contact with the protoplasmic membrane. In certain problems it is necessary also to realize that an increase in molecular motion of molecules of water in the vacuole caused by a rise of temperature in the cell beyond that of the external medium is equivalent in effect to increasing the concentration of water in the vacuole. Likewise an increase in turgor pressure in the cell is equivalent in effect to an increase in the concentration of water in the vacuole.

Differentially permeable membranes are factors in osmosis. The nature of the membrane, however, is as important in osmosis in plant cells as is the concentration of water. This fact may be demonstrated with a simple physical apparatus and also with living plant cells. Membranes such as filter paper and cellulose cell walls are very permeable to both water and the solutes in water. This is only another way of saying that water and solutes can diffuse readily through these membranes. Such membranes are of no importance in osmosis in plant cells.

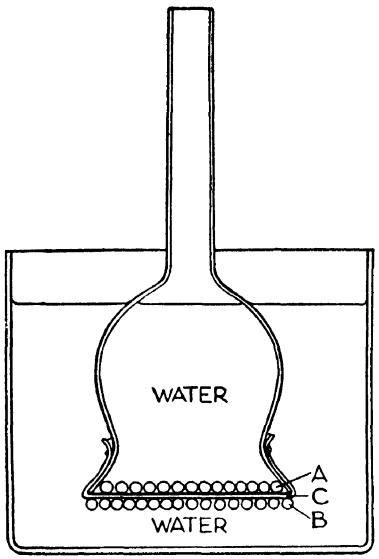
There are, however, certain kinds of membranes through which water can diffuse readily, but through which certain solutes in the water do not diffuse so readily. These are the membranes that are important in osmosis in plant cells. Protoplasm is an excellent example of this type of membrane. It differs in its permeability to different substances. It is very permeable to water but under most conditions it is practically impermeable to the anthocyanin and some of the other substances in solution in the water in the vacuole. Membranes of this type are said to be *differentially permeable.*[1]

There is a second type of differentially permeable membrane which is more permeable to certain solutes than to water. Sheets of rubber and cutinized cell walls are more permeable to carbon dioxide than they are to water. Such membranes are of no importance in osmosis in plant cells,

[1] The less appropriate terms, semipermeable and selectively permeable, are sometimes used to indicate this type of membrane.

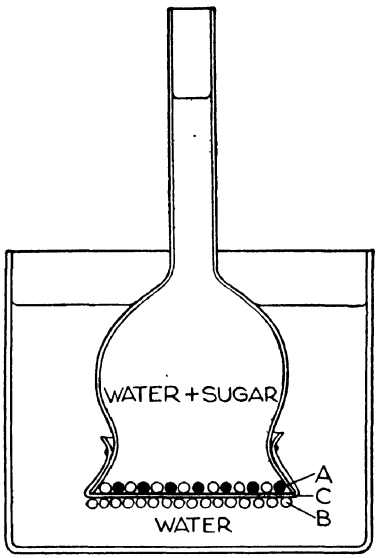
but they are useful in demonstrating certain principles of osmosis and permeability.

Molecules of oxygen and nitrogen are smaller than those of carbon dioxide, but sheets of rubber are much more permeable to carbon



A

FIG. 69A. Diagram to illustrate the passage of water through a membrane: A, represents a molecule of inside water; B, a molecule of outside water; and C, the membrane. Equal numbers of water molecules are in contact with the inside and outside of the membrane, and the movement of water molecules through the membrane in both directions is the same. Hence the level of the water in the tube remains unchanged.



B

FIG. 69B. Diagram to illustrate osmosis: A, represents a sugar molecule; B, a water molecule; and C, a differentially permeable membrane. The sugar in solution dilutes the water so that fewer water molecules are in contact with the inside than with the outside of the membrane. Hence water passes in more rapidly than it passes out, and the level of the water in the tube rises.

dioxide than to the other two gases. Consequently, if one ties a knot in the neck of a rubber balloon filled with ordinary air and then places it in a bottle of carbon dioxide,[2] the balloon will gradually increase in size. Outside the balloon there is pure carbon dioxide. In the air inside the balloon there are about 3 parts of carbon dioxide in 10,000. At the be-

[2] Place the balloon in a bottle of water. After inverting the bottle replace the water with carbon dioxide.

ginning of the demonstration, therefore, there must be about 3000 molecules of carbon dioxide entering the balloon for every one that leaves it. Obviously both the swelling of the balloon and the pressure inside that stretches it result from the entrance of carbon dioxide. The entrance of carbon dioxide and the pressure on the walls of the balloon are consequences of the energy of molecular motion.

For a demonstration of the osmosis of water in a non-living system one may use the apparatus represented in Figs. 69A and 69B. Various kinds of membranes and solutes may be tested by this means. The thistle tube with attached membrane is first placed in a vessel of water as in Fig. 69A to see if the membrane is permeable to water. The solute may then be added to the water in the thistle tube. If there is a definite continued rise of water in the thistle tube the membrane is more permeable to water than to the solute. A temporary rise that soon subsides, such as one obtains with a membrane of filter paper, is due merely to the fact that the molecular motion of water molecules is more rapid than that of the molecules of the solute. One may also tie the membrane across the mouth of a bottle filled with a solution and then immerse the bottle in water; or one may convert the membrane into a small bag.

Demonstrations that are even more instructive may be made directly with living plant cells. In a series of small glass dishes or hollow ground-glass slides we may place distilled water containing different amounts of sugar varying all the way from none at all on one end of the series to as much as 20 per cent on the opposite end. We may now place living plant cells in these different solutions and with a microscope watch what happens. At one end of the series where there is little or no sugar in the external water, the plant cells may become larger; a little farther along in the series the cells appear to remain unchanged in size and shape; still farther along they will decrease slightly in size. Toward the end of the series the protoplasm is partly separated from the cell wall, and in the last of the series the protoplasm has become a small mass in the cell, since the vacuole has entirely disappeared. That is, the water that was formerly in the vacuole has diffused out of it.

All these observations may be interpreted on the basis of the laws of diffusion and the differential permeability of membranes. Perhaps it is sufficient to add here that where the protoplasm just began to separate from the wall the concentration of the water in the vacuole was practically the same as that of the water in the dish if the temperature was the same; where the cells became larger the concentration of the water in

the vacuoles was originally lower than that in the dish; and where the protoplasm was separated from the wall the concentration of the water in the vacuole was originally higher than that of the water in the dish. Since the protoplasm separated from the cell wall, it is the differentially permeable membrane of the cell. The bounding surfaces of plastids and nuclei within the protoplasm are also differentially permeable. Instead of single cells, pieces of plant tissue may be placed in the series of solutions and the relative changes in turgidity and size of the tissue may be observed.

When fresh-water plants are placed in salt lakes, water diffuses out of them into the lake because the concentration of the water in the lake is less than it is inside the plant cells. Such conditions are sometimes referred to as *physiological drought*. There is an abundance of water outside the plant but its concentration is too low. A whole lake full of salt water may be as dry as a desert to a plant.

Plasmolysis and turgor. When the protoplasm of a cell separates from the wall because water is diffusing out of the vacuole, the cell is said to be *plasmolyzed*, and the process is referred to as *plasmolysis*. The shrunken cell is *flaccid*, and conversely the swollen cell is *turgid*. Cell turgor may result from the entrance of water by imbibition or osmosis, or both. Other conditions being equivalent, turgor becomes greatest in the cells with the least extensible walls and in which the volume changes least.

Permeability. Permeability is a property of membranes that affects the movement of materials into and through them. At the present time it appears to be due to a number of qualities; we shall mention only the simplest ones here. A differentially permeable membrane should not always be visualized as a crude sort of sieve through which particles can or cannot pass according to their size. This fact is illustrated by the differential permeability of rubber membranes, through which the larger molecules of carbon dioxide pass more readily than the smaller molecules of water, oxygen, and nitrogen.

One of the features of premeability appears to be illustrated by a simple demonstration in which the membrane consists only of water (Fig. 70). Ether diffuses through a water membrane more rapidly than chloroform. Since ether is much more soluble in water than chloroform, this demonstration is cited to indicate that the solubility of the diffusing substance in the membrane is one of the factors of permeability. Solubility in turn seems to depend upon the relative attraction between the

molecules of the substances involved. If the membrane were equally permeable to these two substances, ether would still diffuse through it the more rapidly because its diffusion rate is about 1.6 times that of chloroform.

The most interesting features about the permeability of protoplasm are (1) its variability, and (2) the fact that the continuation of life depends upon its variation remaining within certain limits. A great number of conditions and substances increase or decrease the permeability of protoplasm to water and solutes. Among them are variations of temperature and light, or the presence of chloroform, ether, alcohol, saponin, and the ions of various salts.

The influence of external factors upon the permeability of protoplasm may be demonstrated easily by placing small pieces of the red garden beet in water and exposing them to any one of a number of factors. The anthocyanin is in solution in the vacuoles of the cells. If some factor increases the permeability of protoplasm beyond a certain point, this red pigment diffuses out of the cells. The influence of a factor that increases the permeability of protoplasm may be counteracted by another factor that decreases it. For instance, if sodium chloride is added, the red pigment begins to diffuse out of the cells; but if a little calcium chloride is also added the influence of sodium chloride is annulled. The permeability of protoplasm at any instant in a living cell is apparently an equilibrium dependent upon the interaction of many factors.

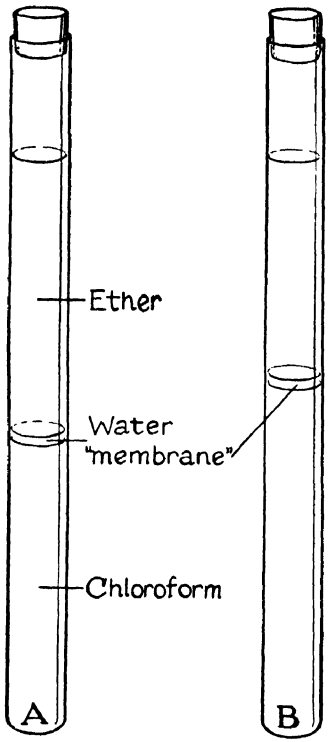


FIG. 70. Diagram of apparatus used to demonstrate the differential permeability of water to ether and chloroform: A, when first set up; B, several days later.

Summary. The movement of materials into, out of, and within plants occurs by various combinations of physical processes. All investigations indicate that these processes occur, not because plants exert some peculiar vital force, but because these processes are universal properties of matter. Their interactions in simple physical systems may be accurately measured, but the plant is such a complex system of structures

and processes that it is difficult to detect these interactions in all their details. We begin by recognizing the forces involved and then try to relate them to our present knowledge of plants. Among these forces we must recognize the mutual attractions among molecules of gases, liquids, and solids; surface tension; molecular motion and diffusion; and electrical forces. Certainly we shall no longer think that substances move into and out of plants because they are good or bad for the plant, or because the plant needs or does not need them. Also we shall be less inclined to think and say that the plant "takes in" and "gives off" these substances.

The movement of materials into, out of, and within plants by diffusion is much easier to perceive and is better understood than movement by other means. Moreover, several of the common observable results of this diffusion are not difficult to analyze. We have therefore given most attention to diffusion. A substance diffuses from regions where it is more concentrated toward regions where it is less concentrated, regardless of the concentration or the diffusion of any other substance with which it may be mixed. This is the result merely of the relative number of moving molecules. There are many more molecules of a substance moving in all directions where the substance is most concentrated. Water may be diffusing out of a cell, while the solutes in the water are diffusing into the cell or vice versa. The factors that influence diffusion most are temperature in relation to the rate of molecular motion, the concentration of the diffusing substance, and the nature of the medium into which it is diffusing. Diffusion under certain special conditions may be distinguished as imbibition and osmosis. Imbibition results in the swelling of colloidal membranes and cell walls. Osmosis results in the enlargement of vacuoles. In the following chapter we shall note how diffusion that is called osmosis underlies certain plant behavior familiar to all of us. In later chapters we shall see how energy of diffusion is the force underlying some of the mass movement of materials within a plant.

CHAPTER XXIII

PLANT BEHAVIOR RELATED TO OSMOSIS

Osmosis and the turgidity of cells are primary causal factors in certain kinds of plant behavior that have attracted the attention of almost everyone. We have already seen that when the concentration of *water* surrounding a plant cell is higher than its concentration within the vacuole, the water diffuses into the cell, thus causing an increase in cell turgor and also in cell size if the cell wall is extensible. The converse occurs when the higher concentration of water is within the vacuole: water diffuses out of the cell, cell turgor decreases, the cell may become smaller, and in extreme cases plasmolysis, wilting, and death may result. When all the cells of some part of a plant (leaf, flower, stem, etc.) increase in size they press against each other, with the result that the whole plant structure becomes firm and rigid. On the contrary, when all the cells of a plant shrink in size their pressure against each other diminishes and the plant becomes flaccid, or wilts. If the cells on one side of an organ shrink or swell more than those on the opposite side, curvatures or movements result.

Movements and growth curvatures. In growing regions increase in cell size is dependent both upon the entrance of water and upon an accompanying growth in area of cell walls. Increase in area of a cell wall, therefore, may be the result of stretching or of growth. The former may be reversible, the latter is non-reversible. Likewise, movements and curvatures that are dependent solely upon turgor and the elasticity of cell walls may be reversible. Growth curvatures may be permanent or temporary. For example, the growth curvature of a stem toward the more intense light during the day may be annulled by the greater growth of the cells on the concave side of the stem tip during the night.

Superficially these movements and curvatures of plant organs may appear to be intelligent acts of the plant. Speculations as to their advantages or disadvantages are not uncommon. Perhaps the reader will discover that they are all consequences of similar fundamental conditions and processes, regardless of whether they have "survival value."

By means of the facts and inferences already encountered and the brief summary of several examples in this chapter, the reader is offered an opportunity (1) to check his own observations of the kinds of plant behavior that are consequences of the conditions underlying osmosis and cell turgor, and (2) to evaluate conflicting interpretations of the observed behavior. Movements in some plants differ from those in other plants because the plant structures are different. A consideration of how these differences in structure originated must of course be postponed to the chapters on heritable variations and evolution. They are, however, the consequences of processes to which no one would ascribe intelligence and purpose unless he is accustomed to ascribe these human attributes to all physical and chemical processes in the universe.

Rigidity of plants. The rigidity of all herbaceous parts of a plant is dependent upon the turgidity and mutual pressure of cells described above. During dry weather leaves, young stems, flowers, and even fruits may wilt during the day and become firm at night or following rains, as the result of changes in the turgor of the individual cells. Spray systems are now commonly installed over market stands to prevent the loss of turgor in the cells of leafy vegetables on display. The rigidity of woody tissues is dependent not upon osmosis and turgor but upon the size of the cells and upon the composition and thickness of their walls.

Physiological drought. Owing to the relatively high concentration of water in the vacuoles of their cells, many fresh-water plants cannot grow in the ocean or in salt lakes and salt marshes where the concentration of water is relatively low. The fact that water plants may wilt in such habitats can be demonstrated by placing a plant in a vessel of salt water. Similarly, most land plants do not grow on salt plains (Fig. 71). Man sometimes makes miniature salt plains by adding salt to the soil to kill weeds. One of the difficult problems encountered in applying irrigation water to soils of arid regions is the necessity of preventing the accumulation of inorganic salts in the soil surface as the added water evaporates. The preservation of food in water of low concentration (brine) is a very old custom. Sugar and salt are used as the means of diluting the water to the point of physiological drought for the bacteria and molds that are agents in the spoilage of food.

Vinegar is also used to prevent the growth of these organisms. It is primarily a solution of acetic acid in water. This acid lowers the concentration of water in vinegar and also coagulates the protoplasm of

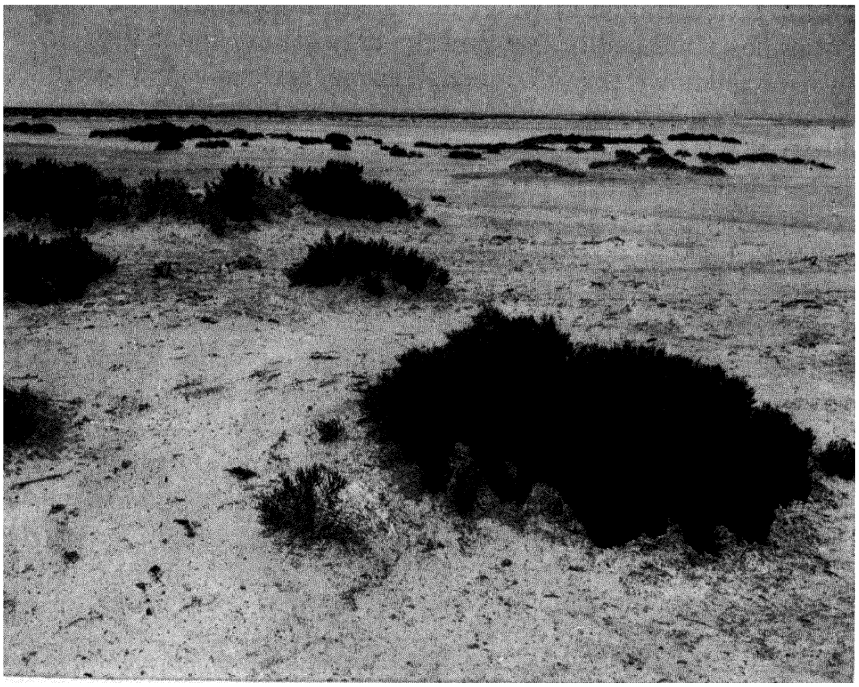


FIG. 71. Hummocks of pickleweed (*Allenrolfea*) on salt-flats in Utah. Photo by H. L. Shantz.

living cells. This coagulative effect of acetic acid may be demonstrated by pouring a little vinegar on the "white" of an uncooked egg, or by examining living cells mounted in vinegar. The killing effect of many kinds of acids and salts should be attributed not to physiological drought, but to some other condition such as the coagulation of protoplasm, alterations in permeability, or inactivation of enzymes. For example, the small amount of copper sulfate or mercuric chloride necessary to kill plant cells has little influence on the concentration of the water in which these salts are dissolved.

Enlargement of cells during growth. In all growing regions of a plant cell division is usually followed by an increase in size of the young cells. The volume of these newly formed cells may increase many times (Fig. 31, page 64).

Some new protoplasm is made, but the total enlargement is primarily the result of the entrance of water into the cell under the conditions of imbibition and osmosis. The enlargement of the cell depends, therefore,

upon the concentration of water inside and outside the cell, the consequent osmosis and cell turgor, and the extension of the cell wall.

In some unknown way a hormone (auxin) formed in the young leaves seems to be necessary to some process involved in the extension of cell walls. If the hormone is absent little or no cell wall extension occurs. If it varies in amount in different parts of the plant, the cells do not enlarge uniformly. It is perhaps evident that turgor pressure will not become so high in the cells with walls that are growing or are easily extended. We may therefore have the anomalous condition of the entrance of water as a cause of increase in cell volume, and at the same time the lowest turgor pressure in the enlarging cells. If the cell walls are not growing or do not stretch readily, the entering water may result in a high pressure within the cells.

Turgor and growth pressure. Similarly, if the enlargement of a plant organ is restricted by mechanical means, the diffusion of water into each



FIG. 72. Fern leaves pushing upward through a cement sidewalk. Growth pressure may amount to hundreds of pounds to the square inch. After G. E. Stone.

of its cells exerts tremendous force against the obstruction (Fig. 72). The combined pressure in all the cells of a root may lift stones weighing several tons, displace stone curbings, or rupture concrete pavements. Turgor pressure may be just as great in the cells of stems and other plant organs. It is the force underlying the pushing of young stems of seedlings upward through the soil and of roots into the soil.

Since turgor pressure in cells is the result of the diffusion of water into them, the energy of molecular motion is evidently the force back of all these "marvelous powers" of plant growth. While the pressure exerted by the plant organ as a whole may be equivalent to several hundred pounds per square inch, a little calculation will show that the pressure on a single cell wall is but a small fraction of an ounce. This pressure is usually great enough to cause the walls of cells to bulge outward and become convex except where they press against adjacent cells and the surfaces become flattened or plane. The same phenomena may

be seen in a mass of soap bubbles. The walls of many cells are not uniformly thick and equally extensible in all parts, and some of the curious shapes of cells may be attributed to this fact.

It is important to remember that increase in size of a plant organ is the result of the enlargement of its component cells. The mere division of cells results only in increasing the number of cells that may enlarge. A cell may become larger only by the entrance of material from an external source. The great bulk of this material is water.

Plant movements and curvatures. Some of the smallest plants are motile and can swim about in water just as freely as small animals. But the movements of larger plants are limited to the bending, twisting, or elongating of certain organs or restricted parts of organs.

Tropisms. Tropic movements, or tropisms, are exemplified by the familiar curving of plant organs toward, or away from, different intensities of external factors, or the direction of the force of gravity or of an electric current. For example, one-sided illumination subjects the cells on opposite sides of a plant organ to different intensities of light. Similarly the force of gravity or an electric current may induce curvatures. If a plant organ curves toward the most intense light to which it is exposed, its curvature is said to be positively phototropic. If it bends away from intense light it is negatively phototropic. Similarly compounded names are applied to curvatures related to other external factors, namely, positively or negatively geotropic, hydrotropic, chemotropic, electrotropic, etc.; but the names are the least important features of the processes.

Tropic curvatures may occur in any plant organ. They occur primarily and are most prominent in growing regions, such as the tips of stems and roots and the petioles of young leaves. Moreover, they are primarily restricted to that part of the growing region in which the cells are enlarging. They are the result of unequal enlargement of the cells on opposite sides of the plant organ. Instead of personifying them, therefore, we may base our interpretations upon our knowledge of the dependent relations of the energy of molecular motion and diffusion, permeability of protoplasm, osmosis, cell turgor, and the extension of cell walls. If the initial influence of some external factor results in a decrease of turgor or of cell wall extension, the plant organ will bend toward that side to which the factor is applied, and vice versa.

Hormones and cell enlargement. During the last decade the influence of hormones upon cell enlargement and tropisms has become an inter-

esting subject of research. In spite of the fact that some of the conclusions of today may have to be modified as additional facts are discovered, some of them are too interesting to be omitted even from a general textbook of botany.

Cell enlargement in stems appears to be dependent upon hormones formed in young leaves exposed to light, though an excessive amount of these hormones inhibits cell enlargement. In contrast to the cells of stems, the enlargement of cells in the growing tips of roots is inhibited

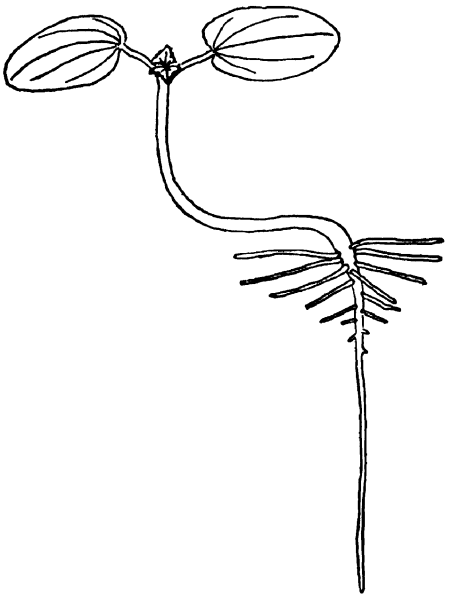


FIG. 73. Geotropic growth in a seedling after it was clamped in a horizontal position.

by these hormones except when only the merest trace of them is present. They seem to affect some process involved in the extension of cell walls. Their movement down the stem or up the root may be deflected by such external factors as light and gravity. In horizontal stems and roots they are deflected toward the force of gravity. Consequently, if a seedling is placed horizontally they accumulate in the cells in the lower side in amounts that are favorable to the enlargement of cells of the stems but inhibiting to the enlargement of cells of the roots. The stem tip therefore curves upward and the root tip curves downward (Fig. 73).

These hormones are complex organic acids that move toward the positive pole in an electric current. It is inferred, therefore, that the slight electrical difference on the two sides of a stem or root may be the cause

of their deflection toward the lower side. Similarly, in many plants they accumulate more abundantly on the shaded side of stems than on the side exposed to the more intense light. As a result, the cells on the shaded side enlarge more readily; this side of the stem becomes longer than the lighted side and actually pushes the tip of the stem toward the light.

These hormones may be extracted from plants and dissolved in wool fat, called lanolin. If a little of this lanolin containing the extracted hormones is placed on one side of a root or stem tip, the expected curvatures are obtained. Similar curvatures may be obtained by placing any of several closely related chemical compounds in the lanolin instead of the naturally occurring hormones (Fig. 74).

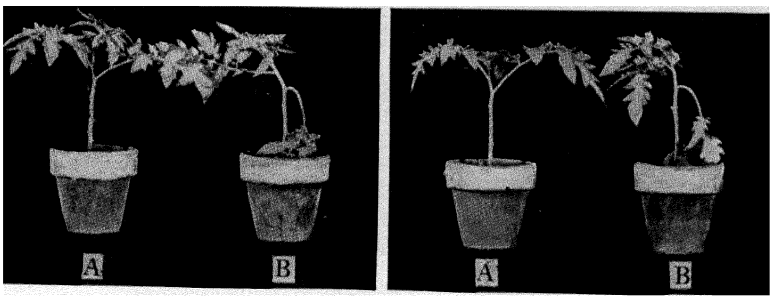


FIG. 74. Curvatures of stems and petioles resulting from the effects of chemical compounds similar to naturally occurring hormones: A, untreated plants; B, treated plants. The compounds in low concentration (0.01 mg. in 100 mg. of lanolin) were placed on the right side of the stems and on the upper surface of the two petioles that have curved downward. Photos from P. W. Zimmerman and A. E. Hitchcock.

Leaf mosaics. The formation of leaf mosaics (Fig. 75) as a result of differences in elongation, bending, and twisting of petioles and stems is a consequence partly of unequal illumination of petioles and stems and partly of unequal illumination of the blades of the leaves. Bending and twisting of petioles are the results of differences in cell enlargement in opposite sides of the petiole. This cell enlargement is dependent in part upon hormones that are formed in young leaf blades exposed to light and pass down the veins to the petiole and stem. If the right and left halves of a blade are unequally illuminated, the amounts of hormones that are formed and get to the right and left halves of the petiole will be unequal. Consequently, there will be a difference in the amount of cell enlargement on the two sides of the petiole and a curvature will result.

The petioles of leaves which develop in the shade of other leaves may continue to elongate for a longer period and the blade finally reaches the plane of the leaves above. Both cell division and elongation are affected. Many of the details of these processes are still unknown.

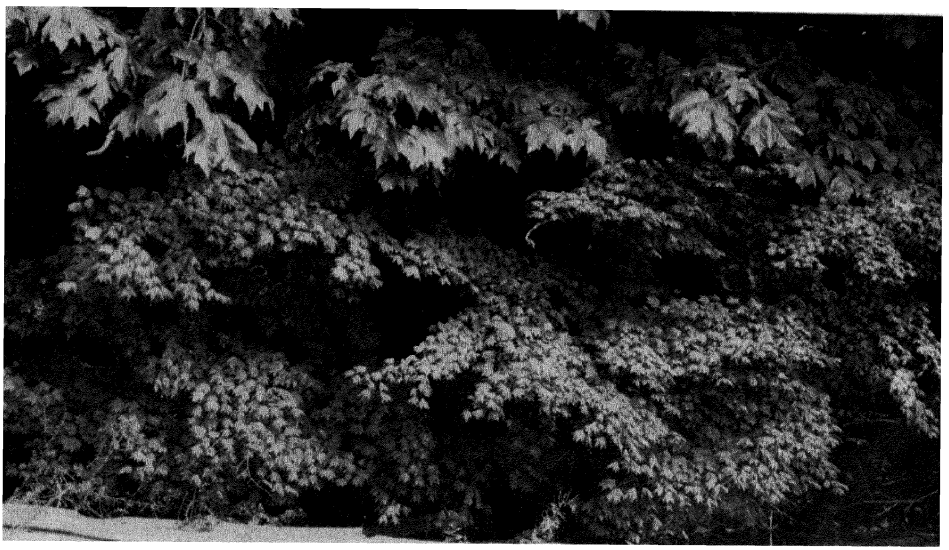


FIG. 75. Mosaics formed by the leaves of two species of maple (*Acer macrophyllum* and *Acer circinatum*), Olympic Mountains, Washington. Photo by W. S. Cooper.

Turgor movements and growth movements. Distinctions between these two kinds of movements are sometimes attempted. The difficulty in making a distinction lies in the fact that all growth movements involve turgor effects. The distinction becomes clear only when movements occur in those tissues in which all growth has ceased. Movements that are due entirely to changes in turgor are reversible. Those that are due to differences in growth may become permanent.

There are also curvatures and movements in which the cell structure determines the direction in which the plant organ curves or moves. These curvatures occur in such plant organs as leaves and petals of flowers in which the cells in the upper side differ from those in the lower. Such plant organs are said to be bilateral, in contrast to organs that are radially symmetrical. The movements may be purely turgor movements, or a combination of turgor and growth. Among the more familiar examples are the daily opening and closing of certain flowers in relation to

changes in temperature or light intensity; the opening of buds; the rolling and folding of leaves; and pulvinal movements, such as the movement of leaves of clover and of "sensitive" plants (Fig. 76).



FIG. 76. Sensitive plants (*Mimosa pudica*). The one on the left was mildly jarred just before the picture was taken. Photo by G. S. Crowl.

If young flowers of tulip are exposed alternately to low and high temperatures they may open and close several times in one hour. When the temperature is lowered the rate of growth of the outer side of the sepals and petals is greater than that of the inner side. As the temperature is raised the greater rate of growth of the inner side results in opening the flower. White water lily flowers open in light and close in weak light and darkness. A commonly cultivated purple water lily has flowers that close in bright sunlight and are open only in dense shade or at night.

The opening of buds is the result of growth of the bud scales and young leaves. In many buds there is increased growth on the inner side of the bud scales which results in spreading of the scales.

The folding and rolling of leaf blades of some species of plants are dependent upon the relative turgidity in rows of special cells in the upper

epidermis (Fig. 48, page 91). Turgor pressure in these cells is opposed to turgor pressure in the cells in the lower side of the leaf. When turgor pressure is high in these special cells the leaf is expanded. Leaves of many kinds of plants without such special cells also exhibit various degrees of rolling during periods of drought.

The folding of leaves of clover, honey locust, and sensitive plant in late afternoon or early evening is probably the result of unequal changes in permeability or in digestion of starch to sugar accompanied by changes in turgor and swelling of cells on opposite sides of the pulvinus (Fig. 47). These movements take place rapidly at higher temperatures, and very slowly or not at all at lower temperatures or when the plant is anaesthetized.

Changes in permeability, turgor, and growth accompanied by consequent curvatures and movements may occur in some plants as the result o' mechanical contact. The folding of leaves of the sensitive plant and the twining of tendrils are familiar examples. Somewhat less familiar are similar movements of the stigmas and stamens of certain plants, the closing of the leaves of the Venus's fly-trap *Dionaea*, and the bending of the tentacles on the leaves of sundew, *Drosera* (Fig. 77).

Some of the proteins in the insects that are entrapped by such plants are digested by enzymes from the plant or from bacteria. The resulting compounds diffuse into the cells of the plant. The insectivorous plant, however, is not necessarily dependent upon this external source of nitrogen compounds.

Stomates. The opening and closing of stomates are dependent upon the turgor and relative wall extensibility of the two guard cells. When they are expanded by increased turgor, unlike ordinary cells, they do not become spherical. The inner wall that bounds the pore is thicker and less stretchable than the outer wall away from the pore. Hence when turgid, the outer walls stretch and the guard cells become curved or bean-shaped. Since the concave sides of the two guard cells are adjacent, an opening appears between them. When these cells contract with decreased turgor the concave walls straighten and come together; the stomate is closed. This straightening of the concave walls may be due to the contraction of the walls, but the pressure of the surrounding epidermal cells also pushes the non-turgid guard cells together. If these epidermal cells were to shrink excessively they might also pull the guard cells away from each other.

As a guard cell expands with increased turgor evidently the wall on

CHAPTER XXIV

THE LOSS OF WATER VAPOR FROM PLANTS: TRANSPIRATION

Transpiration is essentially the evaporation of water from within plants. It includes both the vaporization of water at all cell surfaces exposed to the air and the subsequent diffusion of the vapor into the atmosphere surrounding the plant. In the chapters immediately preceding it was apparent that the diffusion of water molecules is a primary process in imbibition and osmosis. It is also a primary process in transpiration.

Transpiration is the most generally recognized of all processes in plants. Among the common practices based on this recognition are the daily watering of house plants; the elaborate systems of overhead and underground irrigation of gardens; the wrapping of cut flowers and freshly dug plants in waxed paper or other waterproof containers; the packing of nursery stock in moist sphagnum moss for long shipments; the enclosing of fruit and vegetables in oiled cloth or covered dishes in electric refrigerators; the periodic sprinkling of the floor and crates in the low-temperature storage of apples; and the placing of glass or paper covers over newly transplanted seedlings in the garden. These and many other practices are attempts to reduce the more harmful effects of evaporation of water from plants or isolated parts of plants.

Transpiration not limited to leaves. Transpiration may occur from the surface of any plant organ. Even the bark of trees does not prevent it entirely. "Sun-scald" of trees that have been transplanted from nurseries where their stems were shaded is the result of heating and drying by direct sunlight. Mature potato tubers, in spite of a cork covering, lose noticeable amounts of water and shrivel in the course of time. The evaporation of water from roots in dry soil, or from roots during the process of transplanting may result in serious injury or death. Transpiration from fruits in drought periods may result in shrinkage. The tips of tomato fruits may die as a result of excessive transpiration. The subsequent decay of these dead portions of the fruit is referred to as "blossom-end rot." After removal from the plant such fruits as prunes and grapes are often artificially exposed to warm dry air to hasten the loss of water

vapor from them, so that they may be safely stored for future use. The harvesting of many seeds, grains, and hay involves the drying, or the acceleration of transpiration, under natural or artificial conditions. High transpiration may result in the death of young flowers and in the cessation of sexual reproduction.

Of the various plant organs the thin blades of the leaves of most plants have the largest evaporation surface exposed to the atmosphere, and it is in them that the greatest amount of transpiration occurs in the growing plant. Cactuses are notable exceptions.

The bulk of the growing parts of plants is water. As we learned earlier, all the living cells of a plant contain protoplasm and a vacuole filled with water in which various substances are dissolved. Young tissues of plants may contain as much as 95 per cent water by weight, and older parts 60 to 75 per cent. When the water content of the active cells of plants is gradually decreased they become less and less active until a point is reached where injury or death results.

The leaves of most plants, therefore, with their high water content (60-85 per cent), their relatively large areas, and their exposure to an atmosphere that is usually only 10 to 75 per cent saturated, constitute the most important surface of water loss from plants. Discussion in this chapter, therefore, will be confined largely to the processes and factors that influence transpiration as it occurs in leaves.

Circumstances of water loss from leaves. In Chapter VIII the organization of water-conducting tissues and their distribution among the mesophyll cells are described. Attention was called to the air spaces among these myriad cells and also to the epidermis which encloses the mesophyll cells, air spaces, and veins.

The upper epidermis of the leaves in many species of plants is an unbroken layer of cells. Its outer cellulose walls may be thick and have a cutinized outer layer which is commonly called the cuticle. The lower epidermis, and frequently the upper, have stomates distributed among the epidermal cells. Hence when the stomates are open the epidermis of the leaf contains many thousands of minute passages through which gases may diffuse into the labyrinth of air passages among the mesophyll cells, or diffuse out of them. Any gas may do this, and its diffusion is quite independent of the diffusion of other gases or vapors.

Molecular motion and consequently evaporation are accelerated by a rise in temperature. When the surface molecules of the water acquire sufficient momentum to overcome the cohesion by which they are held in the liquid state, they diffuse into the surrounding air. The same is

true of the evaporation of water that is dispersed among the particles of a cell wall.

In the diagram (Fig. 78) of the diffusion of water from the vessels of the stem to the veins and cells of the leaf, and finally into the atmos-

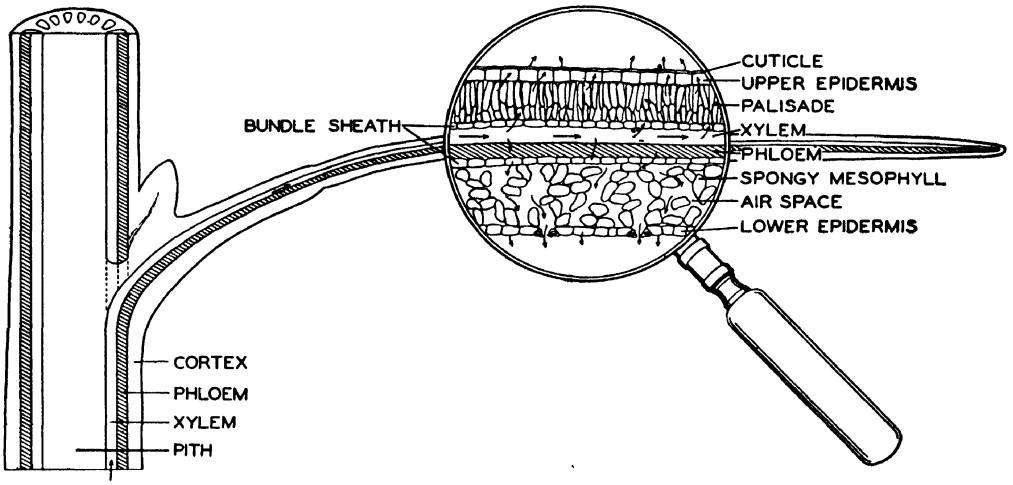


FIG. 78. Diagrammatic section of a stem and leaf. Arrows indicate paths of movement of water molecules.

phere, the paths of the diffusion of liquid water and of water vapor are indicated by arrows. From this diagram it should be clear that there are two surfaces where evaporation of water occurs: first, the outer surface of the epidermis, and, second, the cell wall surfaces of the mesophyll. The diffusion of water vapor from the outer surface is comparatively simple and is discussed under "cuticular transpiration"; that from the internal surfaces of the leaf is complicated by certain structural and physical factors and will be discussed under "stomatal transpiration."

Cuticular transpiration. Let us now have another look at a leaf—first the outside. The epidermis of the leaf is composed of living cells all containing water and having more or less saturated cell walls. Some of the water molecules continually acquire sufficient energy to break the mutual bonds of cohesion and also of adhesion of the water to the wall molecules, and pass into the atmosphere. The cuticle, which is the outer layer of the epidermal walls, reduces this evaporation to an extent which depends upon its thickness and its fat or wax content. The cutin simply decreases the number of water molecules that reach the epidermal surface since water molecules do not pass readily into fat-like and wax-like substances. Nevertheless the cuticle is not wholly impervious and

some water reaches the surface, vaporizes, and diffuses into the air. This water-vapor loss from the surface of the epidermis is termed *cuticular transpiration*. It occurs at all times, but less rapidly from leaves coated with cutin and wax than from leaves with little or no cutin. Cuticular transpiration amounts to only 5 to 15 per cent of the total water-vapor loss from the leaves of most plants.

The epidermis of many plants has small unicellular or multicellular outgrowths known as hairs and glands. Some of these remain alive as long as the leaf or stem on which they grow; others die early and become filled with air. All living hairs and glandular outgrowths increase the cuticular surface of the leaf and also increase the cuticular transpiration. Leaves of pumpkin and squash, nettles, tobacco, cultivated geraniums, and petunias have long-lived hair-like epidermal appendages.

Dead hairs are common on leaves and stems of most plants. The mullein has a dense covering of much-branched dead hairs on all exposed surfaces, and on the leaves the felt-like layer on either side may be thicker than the blade itself. Other examples of plants with hairy leaves are velvet grass, silky willow, Labrador tea, Shepherdia, Spanish moss, some species of sage, goldenrod, and aster.

When the rates of transpiration in plants of equal leaf area were measured it was discovered that the rate of water-vapor loss from mullein is about the same as that from tobacco, which has very similar leaves but lacks the dense hairy coverings. Mullein leaves are often mentioned as examples of leaves that conserve water allegedly because "the hairs cut down sunlight and wind." Further experiments with mullein show that these effects are quite unimportant and that the hairs do not reduce stomatal transpiration at all. They may decrease cuticular transpiration slightly in the dark and in still air. Mullein plants with hairs removed from the upper leaf surfaces, mullein plants with hairs removed from both surfaces, and mullein plants with hairs intact, under the same conditions lost water at nearly identical rates.

Whether the shield-shaped hairs of such plants as Shepherdia are effective in reducing transpiration is unknown. But it is a safe assumption that hairy coverings are of no importance in "protecting" the plant from excessive transpiration in dry situations and in enabling them to survive in dry habitats.

Anyone who digs down to the very end of the taproot of mullein will be able to explain why this plant survives in dry habitats as well as in moist ones. This is deeper than many care to dig.

Of the numerous differences among leaves, such as those mentioned

in Chapters IX and X, a few may influence the rate of transpiration one way or the other, but a casual inspection of leaf differences is not a reliable means of discovering their influence on transpiration rates. Very thick cuticles, waxy layers, and resinous layers on leaves and stems undoubtedly decrease cuticular transpiration; but their effectiveness in curbing stomatal transpiration of any plant cannot be judged by appearances. It can be ascertained only by carefully planned experiments.

Stomatal transpiration. Transpiration from mesophyll cells is similar to that from epidermal cells, but there are a few important differences. Let us first consider conditions on a spring morning when the soil is moist and the whole plant is turgid with water. The sun is up and the air is clear. Under these conditions the stomates are fully open.

The water-conducting tissues of the veins are filled with water slightly diluted by inorganic salts or other substances. The vacuoles, the cytoplasm, and the walls of the mesophyll cells are nearly saturated with water, and likewise the walls on the inner side of the epidermal cells. This internal moist surface is 6 to 30 times that of the cuticular surface and bounds the labyrinthine intercellular air passages. The energy from the sun increases the molecular energy of the water molecules and their rate of movement is speeded up. They leave the cell surfaces more rapidly and diffuse in all directions in the intercellular spaces, from which they diffuse through the stomates into the atmosphere.

Outside the leaf, the atmosphere has a lower humidity and a lower concentration of water molecules. Consequently the diffusion of water vapor will be outward through the stomates. This loss of water vapor from the mesophyll cells is far greater than the evaporation of water from the epidermal cells. Quantitatively it amounts to 85 to 95 per cent of the water that passes into the atmosphere from plants. Evaporation of water from cell walls inside the leaf and the subsequent diffusion of water vapor through the stomates is called *stomatal transpiration.* When the leaf only is considered, it might also be called mesophyll transpiration.

The number of stomates is so great, they are so evenly spaced among the epidermal cells, and the individual pores are so small that diffusion of gases and vapor molecules from the interior of the leaf may be almost as great when the pores are open as if there were no epidermis on the leaf. Later in the day as the stomates gradually close, the stomatal transpiration is also reduced, but not much until the stomates are nearly closed, because the rate of diffusion through the stomates is dependent not upon their area, but upon the perimeter of the pore.

During the daylight period both stomatal and cuticular transpiration occur. At night there is usually only cuticular transpiration. This difference plus the effects of the higher day temperatures are shown in the following table in which the relative amounts of the total transpiration from certain plants during daylight and darkness under field conditions are stated in percentages.

Plant	Daylight	Darkness
Wheat	96%	4%
Oats	94%	6%
Alfalfa	97%	3%
Pigweed	97%	3%

Opening and closing of stomates. The opening and closing of stomates are obviously matters of first importance in modifying transpiration. The relation of stomates to the movement of guard cells was discussed in Chapter XXIII. The stomates on a plant are not opened or closed simultaneously, because conditions are not identical in all parts of a leaf or in the different leaves on the same stem. Consequently, when we say that the stomates are gradually closed, we mean that some are closed quickly, some are closed slowly, and others scarcely at all. When we say that the stomates are closed, we mean that almost all are closed and the remainder nearly so.

We learned earlier that oxygen and carbon dioxide, gases important in respiration and photosynthesis, diffuse into and out of the leaf largely through the stomates. Here we are emphasizing water-vapor loss through stomates. In this connection it is well to remember that stomates do not open to promote photosynthesis and do not close to conserve water. During droughts they may open most inopportunely and allow further water losses. In late summer they may close early in the daytime and restrict photosynthesis when all other conditions appear to be favorable. The turgor movements of guard cells are conditioned neither by photosynthesis nor by transpiration, but by a series of changes in these cells. These are slight changes in acidity which influence the activity of enzymes and also the change from starch to sugar, or sugar to starch. Increase in sugar content leads to diffusion of water into the guard cells, and greater turgor. The stomates are opened. Change of sugar to starch in the guard cells results in closing the stomates.

Movement of water from veins to mesophyll cells. Let us, however, again turn our attention to the mesophyll cells. During the morning the sugar content of these cells increases. They also contain salts, acids, and

other soluble compounds that dilute the water. As water molecules leave the walls and diffuse into the intercellular spaces, other water molecules are pulled into their places by the forces of cohesion and surface tension. This cohesion of the molecules of water in closed tubes is so great that the pull extends all the way down the veins and vessels of the leaves and stems. For example, when the cut ends of stems in a bouquet are placed in a vase of water, transpiration from the leaves results in a movement of water from the vase and up the veins of the stems to the leaves and flowers exposed to the air.

The removal of water from the cells of the leaf increases the concentration of the sugar and other solutes and decreases the concentration of the water. The water becomes less concentrated in the mesophyll cells than it is in the xylem of the veins. Water molecules, therefore, diffuse osmotically from the vessels into the adjoining mesophyll cells, and finally into the epidermal cells, in both of which the concentration of water has been lowered by transpiration.

The lifting power of evaporation may be demonstrated by evaporation from a porous porcelain cup suitably mounted on a long glass tube, both of which have been *completely* filled with freshly boiled water (Fig. 79). The lower end of the tube dips into a vessel of water and mercury.[1] When the porous cup is exposed to the air, evaporation occurs at the surface of the cup. This develops a tension which is trans-

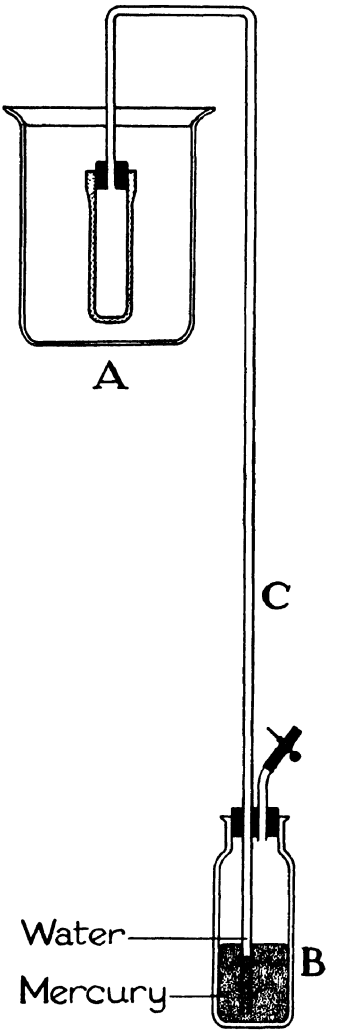


FIG. 79. Diagram of apparatus used to demonstrate the lifting power of evaporation. Tube C is a meter or more in length. This tube and the porous cup, which is immersed in water in beaker A, are filled with air-free water. The beaker is removed only when the apparatus is being used. The short tube in bottle B is closed with a stopcock when the apparatus is not in use to prevent the water from being siphoned from the beaker.

[1] Full details for setting up these experiments may be obtained from papers by H. Thut, *Ohio Jour. Science*, 28:292, 298, 1928; *Amer. Jour. Bot.*, 19:358-364, 1932.

mitted through the water column in the tube to the mercury, and the mercury is pulled upward.

If the apparatus is carefully constructed and all air removed from the water, the mercury column may be readily pulled to a height of 120 to 130 cm. When the cups were coated with gelatin and the size of the pores was thus reduced, a height of 226.6 cm. was attained. Mercury is 13.6 times as heavy as water, and when evaporation of water lifts mercury 226.6 centimeters it is equivalent to lifting water 100 feet. The height to which the mercury is lifted in such experiments is limited by the entrance of air into the cup or tube through minute pores. The tensile strength of water enclosed in tubes is equivalent to at least 150 atmospheres, and the energy of molecular motion is sufficient to lift columns of water many times the height of the tallest trees.

When twigs of arbor vitae, red cedar, or box elder are used in place of the porous cup, transpiration may raise mercury columns 90 to 101 cm. in height before enough air enters the tube to terminate the demonstration. This is equivalent to a column of water 40 to 50 feet in height. During the experiments from which the above figures were obtained the height of the barometer varied from 73 to 75 cm. of mercury. Is barometric pressure the cause of the rise of water in these experiments?

Water-vapor gradient. Next to the opening and closing of the stomates, the most important factor influencing transpiration is the condition of the water vapor inside and outside the leaf. If the concentration of water vapor inside the intercellular spaces of the mesophyll is greater than it is outside the leaf, there will be a gradient in the diffusion of vapor from the cells of the leaf to the outer atmosphere. This gradient is augmented by the relative rates of molecular motion whenever the temperature of the leaf is higher than that of the atmosphere. The gradient may be steep if the air outside is very dry and the air inside nearly saturated, and the temperatures of the leaf and the air are the same. Under these conditions the concentration of water molecules is much greater in the air spaces of the leaf than in the atmosphere. If the temperature of the leaf becomes higher than that of the atmosphere the gradient will be increased because within the air spaces the number of free molecules is increased as well as their rate of movement. If the temperature of the leaf becomes lower than that of the atmosphere the gradient will be reduced because the number of free molecules within the air spaces and their rate of movement are decreased.

Let us assume that during the course of a clear warm morning in

summer the temperatures of both the atmosphere and the leaf are gradually raised from 68° F. to 86° F. The concentration of water vapor in the atmosphere changes very little, because the volume of air is so enormous and the air is continually moved by currents. Inside the leaf the same rise in temperature results in rapid increase in water-vapor content, because the volume of the intercellular spaces is very small compared with the evaporation surface. Calculations indicate that the vapor diffusion gradient between the inside of the leaf and the atmosphere has increased 2.5 times. If now the internal temperature of the leaf rises an additional 9° *above* that of the air, the gradient is increased to 4 times what it was in the early morning. Assuming that there is an abundant supply of water within the plant and the stomates are open, the rate of transpiration would be about 4 times as great. Guard cells may open and close stomates and thus accelerate or stop stomatal transpiration. But when the stomates are even partially open the most important factor is the water-vapor gradient from inside the leaf to the air outside.

Intensity of sunlight and transpiration. Under good growing conditions light intensities naturally occurring in daytime are sufficient to result in the opening of the stomates, except on extremely cloudy days and when the plants are densely shaded. Sunlight thus indirectly accelerates transpiration. Furthermore, the radiant energy of sunlight directly increases transpiration in humid climates, because it raises the internal temperatures of exposed leaves above that of the air, sometimes as much as 5° to 10° F. This in midsummer is enough to double or treble the vapor diffusion gradient between the inside of the leaf and the atmosphere.

In the shade, leaf temperatures are about the same as those of the air, or lower. When the atmosphere is very dry, leaf temperatures in the shade may be several degrees cooler than air temperature.

Soil water and transpiration. Another factor that greatly influences transpiration is the water content of the soil. Even though the stomates are open and other conditions favor high transpiration, if the water supply in the soil becomes low, transpiration may be markedly decreased. If the soil water in immediate contact with the roots is soon exhausted, water in the xylem vessels of the stem and roots fails to diffuse into the leaf cells as rapidly as it evaporates from them. There is an increase of tension in the water in the veins and vessels of the leaf, the stem, and finally of the root; the mesophyll cell walls become less and less saturated —hence fewer water molecules leave the cell surfaces.

The percentage of water in leaves during dry periods has been found to be 5 to 10 per cent less in early afternoon than in similar leaves at night. Under moist conditions the daily fluctuations may be only 1 to 5 per cent. Obviously even if the stomates are open the rate of transpiration is reduced, since the mesophyll walls are drier by midday than they were in the early morning.

A dandelion plant rooted in a shaded ravine bottom may lose 5 to 10 times as much water as a similar plant living near the top of the south-facing slope of the same ravine. The lower plant has a constant soil-water supply; the upper plant has a very limited supply. A corn plant in a moist region may lose more water in a season than a similar plant in a dry region, simply because there is more water available. If the corn plants in the dry region were growing in irrigated fields, they would lose more water than the plants in moist regions.

If the soil is dry and little water passes into the plant, transpiration from the leaf and stem surfaces may lead to wilting and finally to the death of the cells of the leaves, the stem, and the roots. This is death by desiccation. The lower or older leaves usually dry out first and the younger leaves last.

Water-holding substances. Another effective factor that may retard transpiration is the presence within the plant tissues of colloidal gels such as pectic compounds, mucilages, and gums. When saturated, these compounds, like saturated jelly, have little effect on the rate of evaporation of water from them; but as their water content decreases, the force by which the remaining water is held increases. Many succulents contain these compounds. Cacti, which contain mucilages and are highly cutinized, may retain sufficient water for life and renewal of growth for a year or more. Even such thin leaves as those of tobacco, when removed from the plant, may retain sufficient water to keep them pliable for weeks in a room where most other leaves become desiccated and brittle.

Wind. Moderate air currents may accelerate transpiration by the removal of more or less saturated layers of air from the immediate surfaces of the plant. When these layers have been removed further increase in wind velocity has little or no effect on the rate of transpiration.

The pull of transpiration. One of the consequences of transpiration that extends throughout the plant is the movement of water to the leaves from other organs. The net result of all the diffusions of water molecules in leaves from vessels to mesophyll and epidermal cells is that

water, because of the cohesion of its molecules when confined in small tubes, is pulled forward in the veins of the leaf and the vessels of the stem. It is this pull upon the continuous water columns in the xylem vessels of stems that accelerates the movement of water to the leaves at the tops of trees.

If during rapid transpiration the upward movement of water is stopped by compressing the stem or by severing the stem from the roots, the water in the veins of the leaf and in the vessels of the stem is soon depleted. No more water passes to the mesophyll cells and the epidermis. Transpiration continues and leads to the loss of turgor of the mesophyll and epidermal cells. The stomates are closed by the loss of turgor of the guard cells, and the rigidity of the leaf declines—the leaf is "wilting."

On a clear warm day in midsummer the same sort of thing happens in an intact plant, but it does not always proceed so far. If the rate of transpiration is more rapid than the rate at which water enters from the soil and is drawn up the stem into the leaf, turgor decreases and stomates gradually close. Cuticular transpiration alone continues, and the transpiration rate is greatly reduced. Water continues to move up from the roots through the stem and into the leaf cells; and after a time the water content of all cells is restored, and the cells become turgid. Under the conditions assumed in this paragraph the leaves may not regain their customary rigidity before evening. The stomates, however, may remain closed until after sunrise the following morning.

During dry periods in summer, water may move to the leaves from nearby fleshy fruits on a tree, and as a result the fruits become shriveled. The water is kept from the fruits by the pull of transpiration from the leaves (Fig. 80).

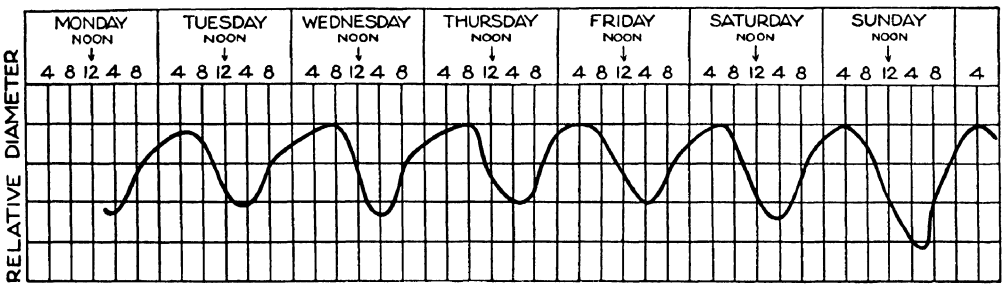


FIG. 80. Diagram of daily increase and decrease in diameter of lemon fruits attached to the tree. Transpiration from these fruits is negligible. The daily shrinkage was due to movement of water from the fruit to adjoining stems and leaves. During the night the water content of the fruit was restored. After E. T. Bartholomew, 1926.

Summary. The principal internal factors that influence the rates of evaporation and diffusion of water vapor from plants are: (1) the opening and closing of the stomates; (2) the concentration of water vapor in the internal air spaces of the leaf in comparison with that of the atmosphere; (3) the temperature of the leaf; (4) the water content of the plant tissues, as affected by the rate of movement of water from the soil; (5) the occurrence in the cells of colloidal gels which have a high water-holding capacity, such as pectic compounds, mucilages, and gums; and (6) the cutinized epidermal walls in some plants.

Wax and resinous coatings on the epidermis may reduce cuticular transpiration, but their effect on stomatal transpiration is slight. Dead hairs, even when forming felt-like coverings, decrease transpiration very slightly or not at all; living hairs increase it to some extent. The value of any superficial structures in conserving water cannot be estimated by examining the plants. Their effects can be determined only by careful experimentation.

The most important external factors that affect the rate of transpiration are: (1) the energy of sunlight as it affects the internal temperatures of leaves in relation to external temperature, and the opening and closing of the stomates; (2) the temperature of the atmosphere and the soil; (3) the concentration of water vapor in the atmosphere; (4) the water conditions in the soil; and (5) the movement of air. Wind prevents the accumulation of moist air about the plant surfaces; but when the velocity is increased beyond that necessary to remove the layer of moist air, there is little further increase in transpiration.

The evaporation and diffusion of water from the mesophyll cells are followed by the osmotic movement of water from the veins into the mesophyll cells. This movement in turn exerts a pull on the water columns in the veins of the leaf, stem, and roots, and probably on the water in all the other cells of the stems and roots. This is commonly called the pull of transpiration.

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CHAPTER XXV

TRANSPIRATION AFFECTS PLANT DEVELOPMENT AND DISTRIBUTION

Environmental factors that affect the rates of transpiration, photosynthesis, or respiration often limit the development and distribution of plants. In green plants both photosynthesis and respiration are essential processes. Without them these plants neither grow nor survive very long. When respiration continuously exceeds photosynthesis green plants die of starvation.

Although transpiration, unlike respiration and photosynthesis, is not known to be essential to plants, its harmful effects become apparent when water loss exceeds absorption and results in wilting, desiccation, and even death. Excessive transpiration may profoundly affect food synthesis, growth, and the formation of flowers, fruits, and seeds. It is often an effective factor in limiting the geographic distribution of individual plants and of plant communities. Because of its effects on the qualities and yields of crop plants, transpiration has been an ever-present influence in the regional allocation of crops in the United States. Throughout human history it has been one of the primary factors that limited the population of various geographic regions.

Tissue development in the growing regions of plants depends upon an adequate water content in the cells. The enlargement of cells and tissues ceases when transpiration exceeds the water supply. During hot dry weather in summer a plant exposed to full sunlight may be actually smaller in the evening that it was in the early morning. Tree trunks may be measurably smaller in diameter in late afternoon than they were in early morning (Fig. 136, page 324).

Each spring we may observe the opening of buds and the growth of new leaves on trees and shrubs. There is little cell division after the leaves are one-fourth grown, and further expansion is the result of the growth of cell walls and the osmotic absorption of water in the cells of the leaf. During warm moist weather the volume of a young growing leaf may become doubled during one night. When transpiration exceeds

absorption there will be no further enlargement. Likewise, any increase in size of other parts of a plant occurs by cell division and enlargement or by the enlargement of cells previously formed. Consequently, the growth of all plant organs may be affected by transpiration. Furthermore, the rates of chemical processes (oxidation-reduction, hydrolysis, and condensation) may vary as the water content of the cells fluctuates, and result in changing the chemical compounds formed in these cells. Some of the effects of drought upon the growth of the epidermis and mesophyll of leaves are illustrated in Chapter IX.

The effects of low water content in plants are most pronounced during those occasional short or prolonged periods of drought, of high temperature, or of low humidity, when transpiration greatly exceeds water absorption in many species of plants. If a number of different species are exposed to these extreme environmental conditions, the effects on their individual rates of transpiration, their photosynthesis, their growth, and their survival are usually different. The vegetative tissues of certain fungi, mosses, ferns, and a few seed plants may become dry and brittle without being killed. They may survive in this condition for days or weeks, and resume growth when water becomes available. The vegetative tissues of most plants, however, die from the effects of excessive water loss long before they become air dry. A deficiency of water within the cells of plants is sometimes referred to as "internal drought."

Transpiration from seeds, bulbs, tubers, and other dormant organs is slow, and these are the only organs of many plants that survive prolonged periods of drought.

The very slow-growing and succulent species of desert regions and other extremely dry habitats may survive, grow, and reproduce in surroundings in which other species wither and die in a short time. Experiments have shown that some of these succulents, when detached from the soil and placed on a window ledge or table, not only survive for months, but may even bloom and bear fruit several months later. The extremely slow rate of transpiration from these plants in a hot desert climate is almost incredible.

Some of the differences in rates of transpiration among a variety of species of plants growing in diverse environments, are summarized in Tables 8, 9, and 10.

On an average day in the growing season a mature corn plant may

TABLE 8. Rates of Water Loss *per Day in Midsummer*:

A single plant of corn may lose 3 to 4 quarts
A single plant of giant ragweed 6 to 7 quarts
A single young 10-foot apple tree 10 to 20 quarts
A 12-foot columnar cactus 0.02 quart
A coconut palm in the moist tropics 70 to 80 quarts
A date palm in a Sahara desert oasis 400–500 quarts

lose the equivalent of 100 per cent of the water contained in it. On the same basis a date palm may lose 90 per cent and a columnar cactus .04 per cent.

TABLE 9. The Water Losses from Single Plants during a *Growing Season* Estimated from Experimental Data

Plant	Length of Season in Days	Water Loss
Tomato	100	30 gallons
Corn	100	50 gallons
Sunflower	90	125 gallons
Giant ragweed	90	140 gallons
Mature apple tree	188	1,800 gallons
Coconut palm, Philippines, moist tropics	365	4,200 gallons
Date palm, Sahara desert oasis	365	35,000 gallons

Effects of excessive water loss. When rains are frequent and well spaced throughout the growing season and the soil contains a favorable supply of water, the enormous losses of water vapor by individual plants, or by plant communities, are of little importance in the survival of the plants. However, if transpiration in excess of water absorption leads to a reduced water content in tissues, photosynthesis is decreased and growth is retarded or stopped. If this retardation of processes takes place during the early life of many species of plants, the plants may not fully recover from these effects when subsequently supplied with an abundance of water.

Irrigation and dry farming are methods of balancing transpiration with soil water. The former is a method of conveying water to fields, and the latter of conserving water that enters the soil from natural sources during the years crops are not planted.

TABLE 10. Estimates of the Water Losses by Transpiration from Crops and Plant Communities Growing Under a Variety of Conditions

Kind of Plant	Amount of Water Loss per Acre	
	in Gallons	in Acre-inches
Corn in eastern Kansas, 6,000 plants per acre, 100 days	325,000	11
Corn in central Illinois, 10,000 plants per acre, 100 days	400,000	15
Young apple orchard in central New York, 400 trees per acre, 188 days	240,000	9
An acre of irrigated date palms in a southern California desert, 400 trees per acre, per year	2,500,000	90
An acre of 12-ft. columnar cacti in a southern Arizona desert, 400 plants per acre, per year	275	0.01

Irrigation. Long before the earliest historical records man cultivated plants in deserts and semi-deserts by irrigating gardens and fields with water from streams, lakes, and artesian springs. Egypt, for example, has practically no rainfall, but the government had organized irrigation projects along the Nile River as early as 4000 B.C. Later it became the granary of the Roman Empire. The high transpiration rates of most crop plants can be sustained if the soil water is renewed at all times. Today more than 7 million acres in Egypt are irrigated and 2 or 3 crops of cotton, cereals, beans, sugar cane, and vegetables grow and mature each year.

At the present time more than 25 per cent of the land surface of the earth is too deficient in rainfall for crop plants without irrigation, and only a very small fraction of this land can be irrigated. The half-buried cities discovered in some of the deserts of Asia are evidences of the former existence there of large human populations. As a result of shifts in rainfall patterns in these regions irrigation long ago become impossible and the inhabitants migrated elsewhere.

When the Aztecs established their capital in 1325 A.D. where Mexico City now stands, they built floating gardens in the nearby lake in which

maize, beans, tomatoes, and vegetables were raised for the community. Seeds were planted in soil on large mats of interwoven branches which were moored in shallow water. This scheme of irrigation brought the plants to the water instead of the water to the plants.

Irrigation has long been practiced in our southwestern deserts, first by the Indians and more recently by the white settlers. These irrigation projects made possible the cultivation of tropical and subtropical fruits and vegetables wherever irrigation water was available. At first these gardens were mostly of local importance; but with the introduction of better methods of harvesting, better refrigeration, and more rapid transportation, the desert gardens became big business, and the fruits and vegetables now enrich the markets of the eastern states.

Irrigation and Crop Yields. How directly crop yields are correlated with the available water in regions of high evaporation may be seen in the following results of experiments with corn at the Utah Experiment Station:

Acre-inches Water Added	Yield in Bushels per Acre
0.00	26.00
15.00	53.00
20.00	63.00
37.00	76.00

Similar results were obtained in experiments with wheat:

Acre-inches of Water Added	Yield in Bushels per Acre
4.60	4.50
8.90	11.30
17.50	15.30
30.00	26.60

Even in the eastern states where irrigation is usually considered unnecessary, market gardeners and orchardists have found it quite profitable to supplement the water in the soil from rains. During drought periods this practice has often led to profitable yields when nearby unirrigated crops were a total failure.

Geographic allocation of crops. During the early migration of settlers westward from the eastern seaboard into the great central valley, the selection of crop plants suitable for cultivation was gradually altered by trial and error. Temperature effects led to the early separation of crops

profitable in the southern, middle, and northern states. When new generations of pioneers invaded the grasslands beyond the forest border a new group of factors set limits to crop production. Not only does the rainfall gradually decrease westward to about one-half that at the forest border, but the rains usually occur in the spring and early summer. Moreover both the amount of rainfall and its distribution are very irregular in successive years. The atmosphere is drier, and in late summer hot winds move in from the southwest and cause wilting, arrest of growth, or desiccation of immature crop plants which mature regularly in the same latitudes eastward.

To stabilize agriculture in the grasslands new crops or varieties were needed that could withstand high temperatures, that mature earlier, and that have smaller tops in proportion to the root system. Sorghums were introduced by the Department of Agriculture from the dry regions of Asia and Africa that met the above specifications. Sweet sorghums were widely planted in the southern and mid-western states as a source of syrup and fodder. The shorter grain sorghums, especially Milo and Kaffir, are more dependable than corn. Still another sorghum called Sudan grass was proved to be a better source of forage in the southern half of the plains region. Short-lived millets were likewise introduced from the Old World.

South of Nebraska the yield of hard winter wheats was found to be more consistent than that of soft red winter wheats from the eastern states. Northward hard spring wheats and durum wheats are profitable even as far west as the mountains of Montana.

As a result of hybridization and selection at the experiment stations, many new varieties of all these plants have been made available. They are higher yielding, less susceptible to injury by certain fungi and insects, and better fitted to the various local temperature, moisture, and soil conditions in the plains country.

Distribution of local plant communities. The differences among the native plant communities that develop in ponds, marshes, shrub swamps, swamp forests, and the adjoining upland are so marked that almost everyone can recall the distinctive appearance of both the plants and the communities.

In the pond are wholly submerged "pond weeds," some rooted and others not. On the surface may be floating algae or duckweeds, and extending above the water surface are water plantain, arrowhead, water smartweed, and many others. The marshes are characterized by bul-

rushes, cattails, sedges, and grasses; the shrub swamps by certain dogwoods, buttonbush, alders, and shrubby willows. The swamp forest is dominated by species of sycamore, elm, ash, maple, hickory, and oak. There are also scattered small trees and shrubs beneath the forest canopy, and certain characteristic herbaceous plants form a ground cover. An undisturbed upland forest in the same region consists of another group of tree species such as the upland oaks, hickories, maples, beech,

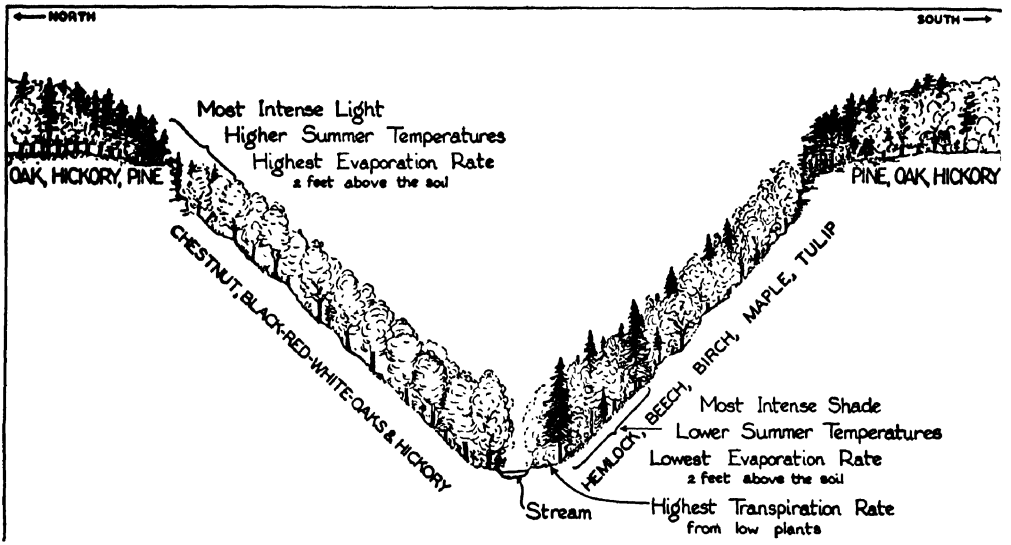

FIG. 81. Diagram of contrast in vegetation on north- and south-facing slopes of a gorge in Pennsylvania.

walnut, and linden. It also has several layers of undergrowth—small trees, shrubs, and herbs.

In the chapters on photosynthesis attention was called to the manner by which certain kinds of plants may exclude others in a forest by overshading them. Likewise the discussion of respiration included the fact that only certain species of plants can grow submerged in water, or where the soil is saturated with water and deficient in free oxygen.

Transpiration is a third factor in the elimination of species, and is most effective in upland forests. Here high transpiration rates may cause wilting and death during periods of drought. Again the plants most affected are the seedlings with their limited root systems. But in very prolonged droughts certain species of trees in the swamp forest may be injured to a greater extent than the upland trees because they have shallow root systems. In the complex forest communities the largest

plants, while shading and reducing the transpiration of the plants beneath them, also have far more extensive root systems. Consequently transpiration of the larger plants may decrease the water content of the soil so much during certain seasons that the herbaceous and woody plants beneath with small or shallow root systems die.

Another example of the effectiveness of transpiration may be illustrated by the vegetation in gorges (Fig. 81). On the sides of the gorge are rock cliffs above long talus slopes. A narrow flood plain borders the stream. To picture the extreme conditions we may consider a section of a valley extending in an east and west direction.

On top of the cliffs the upland hard pines are the only trees that have survived. On the south-facing talus slope the mixed oak forest predominates, with scattered pines and hickories. On the steep north-facing talus, hemlock, beech, birch, maple, and tulip are dominant. In the upland surrounding this gorge the vegetation is oak, hickory, and pine. Beech, hemlock, and birch have not survived above or on the south-facing slope. Evaporation is several times as great there as on the shaded, humid side of the gorge, and the water supply in the upper layers of the soil is exhausted much sooner. Similar gorges where the upland climate is too dry for trees such as beech, hemlock, tulip, and birch may be found in many parts of the eastern United States. The trees in the gorges are living in a humid "microclimate" where drought rarely becomes sufficiently excessive to inhibit their development. The undergrowth in such situations is just as different from that on the south slope and the upland as are the dominant tree species.

Transpiration in relation to available soil water will be discussed further in Chapter XXX.

Major vegetation types and transpiration. Transpiration when studied in the laboratory and greenhouse is often compared with evaporation from a wet surface. Under the experimental conditions the curves representing the rates of evaporation and transpiration are frequently very similar. One may therefore be led to the conclusion that where the rate of evaporation of water is high in nature, the transpiration will also be high. This reasoning overlooks the matter of water supply upon which all transpiration is dependent. Forests, prairies, steppes, semi-deserts, and deserts occur in regions of successively increasing drought and increasing evaporation from water surfaces. The annual evaporation may be 50 times as great from an open pan of water in the desert as from a similar pan in some wet forest region. The annual transpiration from

desert plants, however, is very slight when compared with that of plants in a wet forested region.

Transpiration in nature decreases as one goes from forest to prairie, to steppe, to semi-desert, and to desert for the obvious reason that the plants in these formations have successively decreasing amounts of water available. Their periods of greatest loss of water are more and more limited to moist periods instead of throughout the year. The date palm mentioned earlier in this chapter illustrates how great transpiration may become in some plants when there is an unlimited water supply. The cactus exemplifies how low it may be when the water supply is reduced to a minimum. An acre of forest may lose 10 to 25 acre-inches of water in moist temperate regions, while an acre of prairie grass in Nebraska loses about 2 acre-inches. If transpiration of trees were as effectively checked as in certain cacti without interfering with photosynthesis and respiration, the whole landscape east of the Rockies would be dominated by forests.

Is transpiration an essential process? Transpiration is an inescapable physical process in most species of plants. Is it merely neutral, or harmful, or is it an essential process comparable to photosynthesis and respiration? This question has often been discussed pro and con in botanical literature, and it is frequently answered without a clear analysis of the problem. In the case of a green alga or a flowering plant growing submerged in water, transpiration certainly is not an essential process. If the plant is removed from the water and placed in the air, transpiration occurs only as an unavoidable process and its effects soon cause death. Transpiration goes on whether its effects are harmful or beneficial, just as water evaporates from a wet towel or any other saturated object exposed to the air. Consequently if transpiration is an essential process in plants, it must be limited to those in which some part or the whole plant is exposed to the atmosphere.

One should be clear whether the term "essential" is applied to the survival of the plant, or merely to some particular quantitative difference in its development. We have already seen that leaves are thicker, have a thicker cuticle, more layers of palisade cells, and a greater amount of woody cells when they develop in dry air where transpiration is high than when they develop in moist air where transpiration is low. Transpiration may be essential to many such quantitative differences among plants, without being essential to the survival of the plant. These differences are merely the ultimate effects of transpiration on development.

Among the claims that transpiration is an essential process are: (1) that it is necessary to cool the plant on hot summer days, (2) that it is necessary in the absorption and conduction of salts from the soil to the leaves, (3) that it increases the water supply of the plant, (4) that it regulates the water content of the plant, (5) that it maintains the water supply of leaf cells, and (6) that it would not occur in plants if it were not of some value to them.

The fallacies implied in the last four statements should be so obvious from data discussed in previous chapters as to make further discussion unnecessary here. Some additional data may help to evaluate the first two statements.

The cooling effect of transpiration is most frequently cited as its essential feature. It is claimed that if transpiration did not occur, the temperature of leaves in full sunshine on a hot summer day would rise to 150° F. or more; this rise is sufficient to kill protoplasm. The well-known fact that the evaporation of water lowers the temperature of the mass from which it is evaporating is sufficient evidence that transpiration has a cooling effect on the plant, but it is not sufficient evidence that it is essential, or that it prevents the temperature of a leaf from rising to 150° F. every day in summer.

When one compares the enormous differences in the rate of transpiration in the date palm, coconut palm, and cactus in the tropics he might expect them to differ greatly in their internal temperature. It is known, however, that the temperature of all plants corresponds fairly closely to that of the atmosphere in which they are growing. The daily evaporation of water from the columnar cactus mentioned earlier in this chapter would lower its temperature less than $\frac{1}{1000}$ of a degree, yet it daily absorbs sufficient radiant energy from the sun to raise the temperature and kill the protoplasm if there were no other way by which heat passed from the plant to the surrounding air. A hot stove loses heat by radiation and convection. A plant warmer than the surrounding air also loses heat by radiation and convection.

When the temperature of a plant is more than a few degrees above that of the surrounding air the loss of heat from the plant by radiation and convection usually exceeds the amount lost by transpiration. The greater the difference between the temperature of the plant and that of the surrounding air, the less important is the loss of heat by transpiration in comparison to that lost by radiation and convection.

The relation of transpiration to salt absorption and conduction is an indirect one. The date palm mentioned earlier absorbs and loses

40,000 times as much water as the cactus plant cited in the same table. The roots of the coconut palm grow in both brackish and fresh water. If the absorption of salts depended upon the absorption and transpiration of water, one would expect to find corresponding differences in the salt content of these plants. No such differences occur. Salts enter the roots of plants as molecules and ions by diffusion. This diffusion of salts is undoubtedly influenced by electrical charges, but, as we have already seen, it is independent of the diffusion of water into the cells. After the salts have entered the plant, their movement within the plant is brought about by further diffusion accompanied by flow in the xylem tubes and by protoplasmic streaming.

Transpiration may indirectly influence the total amount of salts absorbed by plants through its effects upon several other processes. Two plots of bean plants were placed under experimental conditions so that the plants in one plot grew in a saturated atmosphere, the others in an atmosphere having only 25 per cent humidity. Transpiration was much greater in the plants exposed to the drier atmosphere. These plants were not as tall as those that grew in the saturated atmosphere. Their root systems were larger in proportion to the leaves and stems above ground, and both their dry weight and salt content were greater. That is, there was a greater amount of photosynthesis in the plants in the drier air, a greater amount of assimilation of foods, and a greater amount of salts absorbed. Here again is evidence of quantitative variations in plant development due in part to differences in transpiration, but such facts are not evidence that transpiration is essential to the plant. One may say, however, that it is essential to certain differences in development, provided that these same differences cannot be obtained by changing some other process.

From the experimental data available it appears that the most efficient leaves are those that develop when the roots of land plants are well supplied with water and transpiration rates are moderately high during the periods when the leaves are growing. The number of layers of mesophyll cells is greater and the mesophyll surface exposed to the air in the intercellular spaces per leaf area is at a maximum (Fig. 32, page 77). As a result a greater amount of sugar may be made throughout the life of the leaves. All these favorable effects of transpiration may be partially annulled by such conditions as an overabundance of nitrates, or by a deficiency of light or of certain ions of inorganic salts—for example, a deficiency of magnesium ions.

Most plant physiologists have come to the conclusion that wet cell

walls, exposed directly either to the atmosphere or to the intercellular spaces, necessarily lose water to the surrounding air by evaporation. Through a long process of evolution stomates have become an hereditary structure in all the larger land plants. The opening and closing of these structures have a marked effect upon the inward and outward diffusion of CO_2, O_2, and water vapor. When stomates are closed there is nothing to prevent the slow diffusion of water through all plant surface walls even though the walls contain cutin and suberin. When stomates are open there is nothing to prevent the rapid diffusion of water vapor from the mesophyll cell walls through the intercellular spaces and the stomates to the atmosphere. This rate is greatly increased in full sunlight when leaf temperatures rise above that of the atmosphere.

If in the course of plant history a cell wall substance permeable to oxygen and carbon dioxide but impermeable to water vapor had developed, the present daily waste of water in transpiration from plants might have been eliminated.

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CHAPTER XXVI

FORMS AND EXTERNAL FEATURES OF STEMS

Several facts about stems have already been considered. We have seen that leaves and axillary buds appear on the nodes of stems in a definite arrangement, and that stems of shrubs branch at or near the surface of the ground, in contrast to stems of trees. Foods may accumulate in any stem, but a greater amount accumulates in some stems than in others. The green stems of cacti and many herbs and the numerous young twigs of both shrubs and trees contain chlorophyll, and hence photosynthesis may occur in them. In many processes previously discussed it was evident that sugar made in the leaves moves through the stems to the roots; that water and inorganic salts after diffusing into the roots move to the leaves through the stems, and that processes characteristic of all living cells occur in living cells of stems. Some stems are short-lived; others remain alive and increase in both height and diameter for centuries. We have already seen that the direction and rate of stem growth are affected by gravity, light, moisture, and other environmental factors. In many sections of the country where deciduous forests prevail, the principal features of the forested landscape from late autumn until the early spring are stems.

What is a stem? The cylindrical, erect, aerial stems of most plants are readily distinguishable from leaves and roots. Many stems, however, are flattened leaf-like organs; others are succulent, and still others are so short that they are nearly obscured by leafy scales or rosettes of leaves. Many stems are entirely underground. What, then, are the distinguishing characteristics of stems? A stem develops from the plumule (bud) of the embryo, usually bears leaves and flowers, and has certain other characteristic features, both external and internal. Examination of several kinds of stems will help us recognize these features.

Woody stems. Stems 1 to 2 feet long of such plants as hickory, horse-chestnut, or maple (Fig. 82) consist of several yearly increments of growth. The most prominent features of woody stems in winter are the dormant buds, leaf scars, terminal bud scars, and lenticels. Leaves and

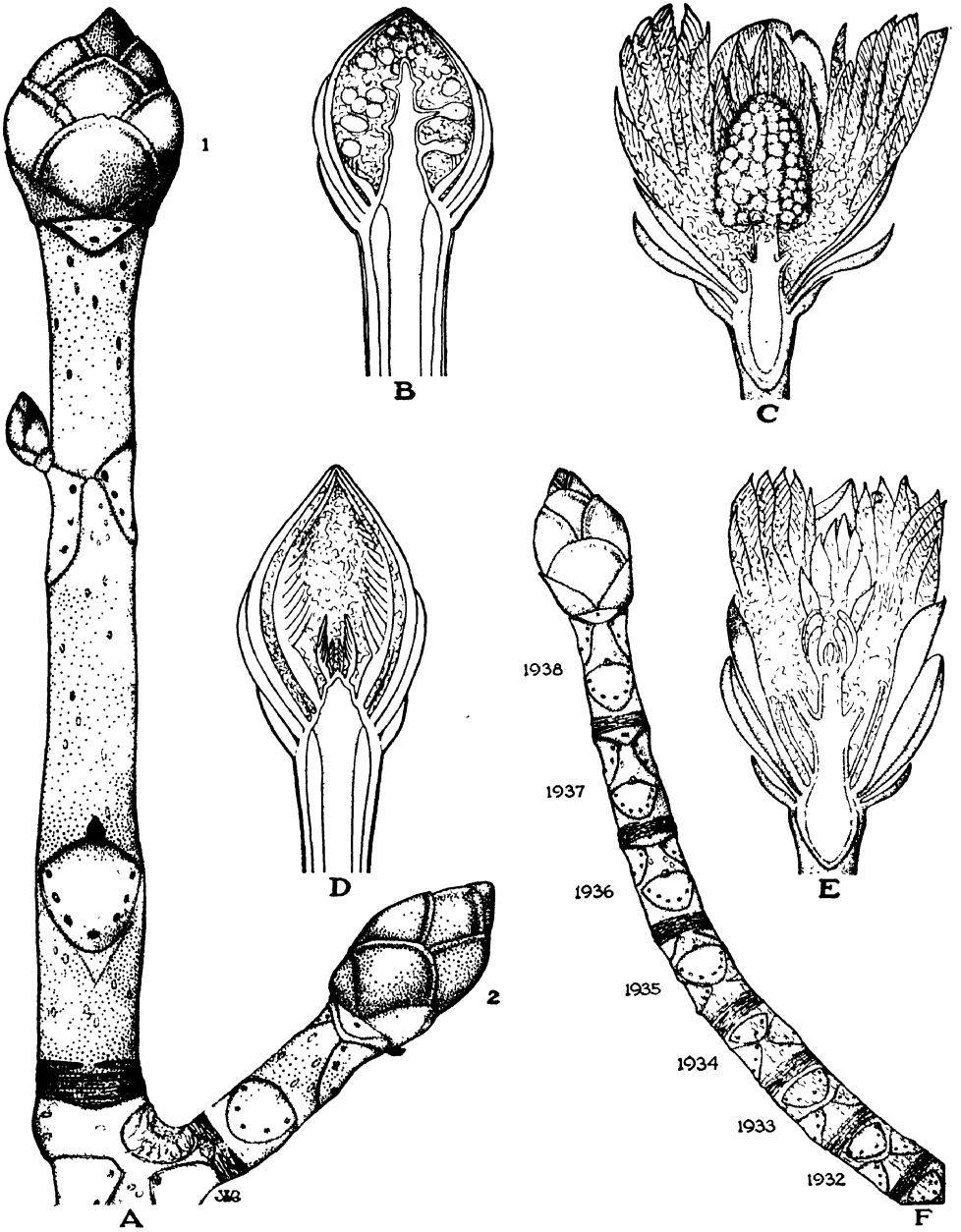

FIG. 82. External features of stems and composition of buds of horse chestnut (*Aesculus hippocastanum*). A, twig bearing a terminal reproductive bud (1), and a lateral branch bearing a terminal vegetative bud (2); nodes, internodes, leaf scars, vascular bundle scars, terminal bud scale scars, lenticels, and the lateral axillary buds are also represented. B-C, longitudinal sections of reproductive buds: B, dormant in winter; C, unfolding in spring. D-E, longitudinal sections of vegetative buds: D, dormant in winter; E, unfolding in spring. F, terminal bud scale scars and other external features on a 7-year-old branch in which there was comparatively little elongation of internodes each season.

branches usually occur only at certain places on the stem called *nodes*. The part of the stem segment between two nodes is the *internode*. The length of a twig or branch and the height of the plant depend upon the amount of elongation of the internodes.

We noted in an earlier chapter that deciduous trees lose their leaves annually and that the scar on the stem left by the abscised leaf is called the *leaf scar*. Within the leaf scar are smaller scars. These small scars are the severed ends of vascular bundles that extended from the leaf into the stem, and are known as *bundle scars* or *vein scars*. The age of the twig may often be ascertained by counting the ring-like markings, the *terminal bud scale scars*, found at intervals along the stem. These rings may be used as a means of locating the position of a dormant terminal bud of some previous year. The distance between two successive terminal bud scale scars is a measure of the growth in length of the stem during one year. This length may be used to compare the annual growth of stems of different plants, as well as the variations in growth from year to year on the same plant.

Scattered over the surface of the internodes are numerous small, roundish or elongated structures, the *lenticels*. When young, these are made up of loosely arranged cells through which gases pass into or out of the bark of the twig. Stomates are often present in very young stems, and the formation of a lenticel may be initiated by the division of cells immediately beneath a stomate. Later cork develops beneath the lenticel. Owing to the peculiar growth of the bark of such trees as birch and cherry, the lenticels become greatly elongated and partly encircle the stem.

Conspicuous external features of stems during dormant periods are the *buds*. There may be only one bud at a node, as on most stems with alternate leaves. Where the leaves are opposite there are two buds at each node. On the stems of other species of plants there may be several buds at each node either arranged in a whorl about the node or grouped about the primary axillary bud. In species of soft maple and forsythia these *accessory* buds are usually flower buds. The bud at the apical end of the stem is the *terminal bud*; all others are *lateral buds*. The terminal buds of some plants, such as willow, elm, hackberry, linden, and ailanthus, die and drop off in the spring of the year before the elongation of the internodes of the new stem segment is completed. The last lateral bud formed on twigs of these plants appears to be terminal in position, if only a casual observation is made.

Bud scales. The buds of most trees and shrubs of the temperate zones have external leaf-like scales, which are usually hard and fibrous as are those in the buds of oak, elm, maple, and buckeye. Less frequently, the buds are enclosed by stipules as are those of the tulip tree, magnolia, and some viburnums. The scales are often hairy or sometimes covered with wax and resins. These scales decrease transpiration from the tissues in the bud but do not "protect" them from freezing. In some plants there is a gradual transition from the bud scales on the outside to true leaves on the inside of the bud.

Nearly everyone has witnessed the opening of buds on shrubs and trees in spring. Sometimes the hard scales on the outside of the bud are pushed off by the enlargement of the inner scales and young leaves (Fig. 82). In other buds the scales may elongate somewhat, but in a short time abscise and fall off.

Composition of scaly buds. The composition of a scaly bud may be recognized easily by removing the scales and other structures, or by examining longitudinal sections of the bud, or, better still, by studying unfolding buds in spring. Each bud contains a *stem tip;* in most buds leaves have begun to develop on the stem tips. Such buds are *vegetative buds* (also called *branch buds* and *leaf buds*) and from them develop the leaf-bearing segments of the stems of the current season. From a careful examination of perennial woody stems one may learn that the number of young leaves in the bud corresponds with the number of leaf scars on each annual segment of stem growth. What inference may be drawn? What exceptions have you seen? Are all the leaves of a herbaceous plant, such as coleus, present in the terminal bud at a given time?

A similar examination of some buds of elm, forsythia, cherry, peach, or soft maple will reveal a stem tip bearing young flowers, but no leaves. These are the *reproductive buds*, which are also called *flower buds* and *fruit buds*. Subsequent growth of these structures results in flowers and fruits. In other buds, such as those of horse-chestnut, lilac, apple, and catalpa, both flower clusters and leaves are present. Such buds may be termed *mixed buds*.

Composition of non-scaly buds. If we examine actively growing herbaceous plants, we find that the buds are less conspicuous because of their small size and the usual absence of bud scales. The leaves near the growing stem tip are small; the youngest ones are folded about the stem tip just as they are in scaly buds. A longitudinal section of a coleus

stem tip under the microscope is seen to have all the structures found in scaly buds except the scales (Fig. 32). In addition to the stem tip there are young leaves, with additional buds in their axils. These small axillary buds within the larger bud may consist either of stem tips bearing

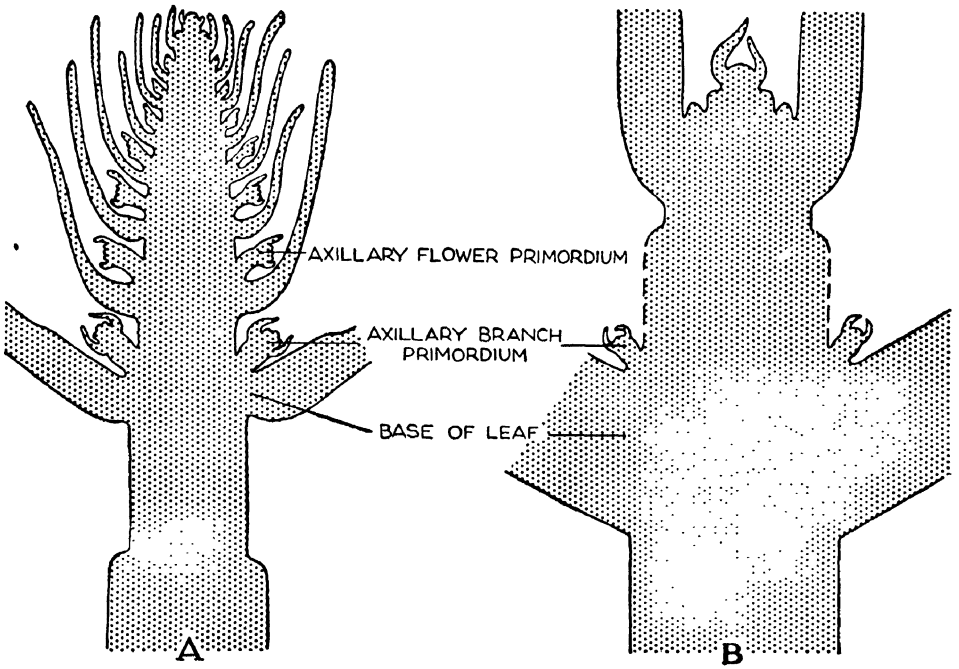

FIG. 83. Diagrams of longitudinal sections of terminal buds of coleus plants. In A the axillary buds, except the lowest pair, consist of stem tips bearing flower primordia of various ages. In B the axillary buds consist of stem tips or of stem tips bearing leaf primordia. Compare with Figs. 31 and 32, pages 64 and 69.

leaf primordia or of stem tips bearing flower primordia, depending on whether the plant is continuing vegetative growth or is changing to flower formation (Fig. 83). This change to a reproductive state in coleus is accompanied by a change in the shape of the terminal bud and the upper pair of leaves.

The youngest bud primordia consist only of stem tips. Buds of many embryos and those in the "eyes" of potato tubers often consist only of stem tips. Apical growth is particularly characteristic of stems and roots.

A bud then may be defined as a stem tip having extremely short internodes and bearing young leaves or flowers, or both. It may or may not be enclosed by bud scales. Stem segments bear leaves but once,

and all the leaves of a tree or shrub may have been present in some stage of development within the dormant buds of the preceding season

Adventitious buds. Branches usually develop from buds in the axils of leaves and may be referred to as axillary branches. Branch buds may, however, develop from internodes of young stems, from roots, and even from leaves. These are *adventitious buds*. Their occurrence on the internodes of stems is often a result of some interference with the growth of the tissues, as injury or disease. New branches from trunks of trees

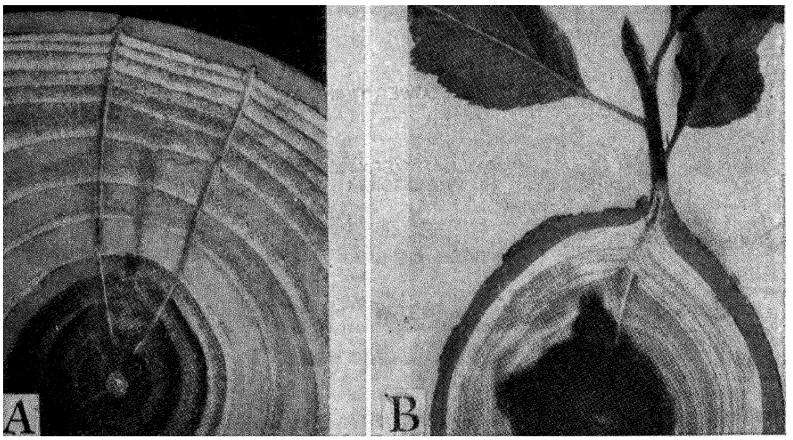

FIG. 84. Cross sections of stems of Virginia crab apple. A, two latent buds, the traces of which extend inward to the first cylinder of xylem. They began as axillary buds on the one-year-old stem and have survived for 13 years. B, a water-sprout has developed from a latent lateral bud. Photo by V. T. Stoutemyer.

several years old, and sprouts from the base of stumps were formerly thought to develop solely from adventitious buds, but recent investigations have shown that some of them develop from lateral buds that survive in the bark of the tree for many years (Fig. 84). Others start from adventitious buds. Pollarding (Fig. 85) results in the growth of many new lateral branches from the decapitated stumps of former branches. Perhaps all or nearly all of these new branches in pollarded trees start from latent lateral buds similar to those illustrated in Fig. 84.

Apical dominance. When the terminal bud of a twig is cut off, branches develop from lateral buds that would otherwise have remained dormant or died. Moreover, such branches usually grow from the uppermost lateral buds. This inhibiting influence of the buds nearest the apex over



FIG. 85. Pollarding of trees is followed by the growth of numerous branches from latent lateral buds in the decapitated stems. Such new shoots of willow are used in the manufacture of baskets and furniture. Photo from R. B. Gordon.

the buds lower down the stem is known as *apical dominance*. From present experimental data it appears to be the effect of one or more hormones, one of which is made in the young leaves. If this hormone is artificially applied to the cut ends of decapitated stems it checks the growth of the lateral buds. Apical dominance, through its influence on the relative growth of different parts of the plant, is one of the primary factors determining the form of a plant.

Buds and stem types. Many trees and shrubs may be recognized at considerable distances by the form of the plant and the type of branching. Such features are often obscured by the effects of environmental factors or by repeated pruning. Plants of the same species may be far from identical in appearance when growing in dense forests and in the open, or along water courses and on dry uplands. The appearance of ornamental shrubs may be changed markedly by the removal of certain dominant buds, thus allowing for the growth of other buds as noted in the paragraph above.

By comparing a palm, a spruce, and an elm, three types of tree crowns may be distinguished with reference to the mode of branching.

Branches usually do not grow from the lateral buds of the palm, and the growth of the terminal bud alone results in an unbranched stem or trunk with a crown of leaves at its summit. Such a stem is said to be *columnar* (Fig. 86).

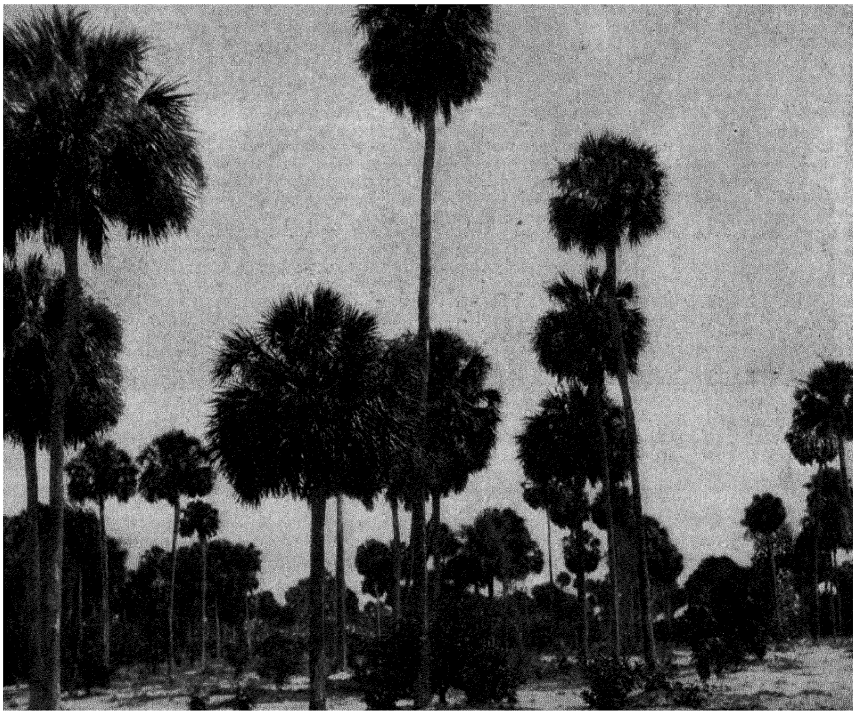

FIG. 86. Columnar stems of the cabbage palmetto. Photo from U. S. Forest Service.

A dominant terminal bud is present in spruce. Each year the main stem increases in length, and from the lateral buds branches grow outward, forming a whorl at the apex of the previous year's growth. The type of branching which results in a prominent main stem that extends beyond the smaller lateral branches is referred to as *excurrent* branching (Fig. 87).

In contrast to the spruce, the terminal buds of the elm are temporary. Since all branches of an elm develop from lateral buds, the main stem appears to be repeatedly divided and subdivided until it is lost in the crown of the tree. The tree trunk is ultimately terminated by innumerable branchlets, and from this fact the name, *deliquescent* branch-



FIG. 87. Excurrent branching of the alpine fir, black hemlock, and lodgepole pine; Bitter Root Mountains of Idaho. Photo from U. S. Forest Service.



FIG. 88. Deliquescent branching of post oak in an open field. Diameter of crown, 60 feet. Photo by C. H. Jones.

ing was proposed (Fig. 88). Although these types of branching are readily distinguishable, all gradations among them occur.

The form of a plant is thus seen to depend on the relative development of terminal and lateral buds. As indicated above, advantage is taken of this knowledge by florists, gardeners, and orchardists. Various ornamental effects in lawn trees and shrubs may be obtained by removing the terminal buds that inhibit the growth of the lateral buds. Fruit trees and grape vines are "pruned" to regulate the shape of crowns as well as the number and spacing of the branches.

Fruit spurs. It was indicated earlier that the age of a twig could be discovered by counting the number of scars left in successive years by the terminal bud scales. The distance between two such scars may be indicative of the favorable or unfavorable conditions under which the plant grew in a particular year, or it may be indicative of local internal conditions resulting from the growth of flowers and fruits.

On fruit trees such as apple and pear, the flower buds often occur at the ends of short stems known as "spurs." When the terminal bud is a

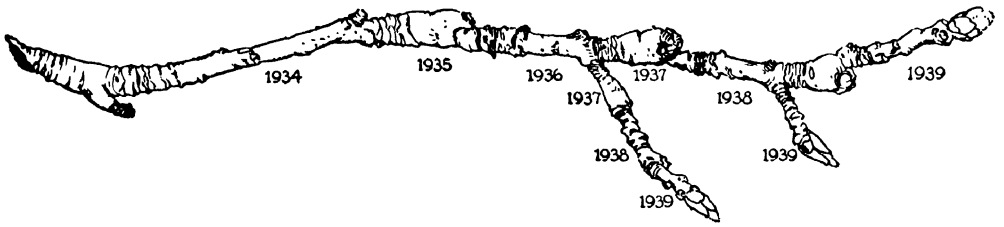

FIG. 89. Drawing of fruit spur of apple. Fruits were borne every other year. The fruit scars are present only on the annual stem segments formed during odd-numbered years. Courtesy of J. H. Gourley.

flower bud, subsequent elongation of the spur is dependent on a lateral bud. Frequently the spurs bear flowers only in alternate years, and the fruit scars are found only on alternate annual segments of the spur (Fig. 89). The spurs usually continue to bear flowers and fruits for many years and grow much more slowly than the vegetative branches. Successive development of lateral buds results in a crooked spur. The interval between successive terminal bud scale scars is exceedingly short during the years that fruits are borne.

Saint John's shoots. Some trees, such as elms, hackberry, and certain oaks, have two periods of stem elongation each growing season: one in early spring and another in early summer. The twigs of citrus trees in

California have three such intra-seasonal cycles of growth. The twigs on young trees of the rubber plant (*Hevea*) in Brazil may have as many as eight cycles of growth in one year. In the latitude of Ohio, a second elongation of shoots on elms is usually evident during the latter half of June, and frequently a third extension appears in August. In Europe these shoots have been called "St. John's shoots" and "Lammas shoots" because of their coincidence with the festivals of St. John's Day and Lammas Day.

Recognition of trees by twig characters. To those of us who are in the habit of recognizing common trees by leaf characters, it is at first surprising to find that identification can be just as certain with twig charac-

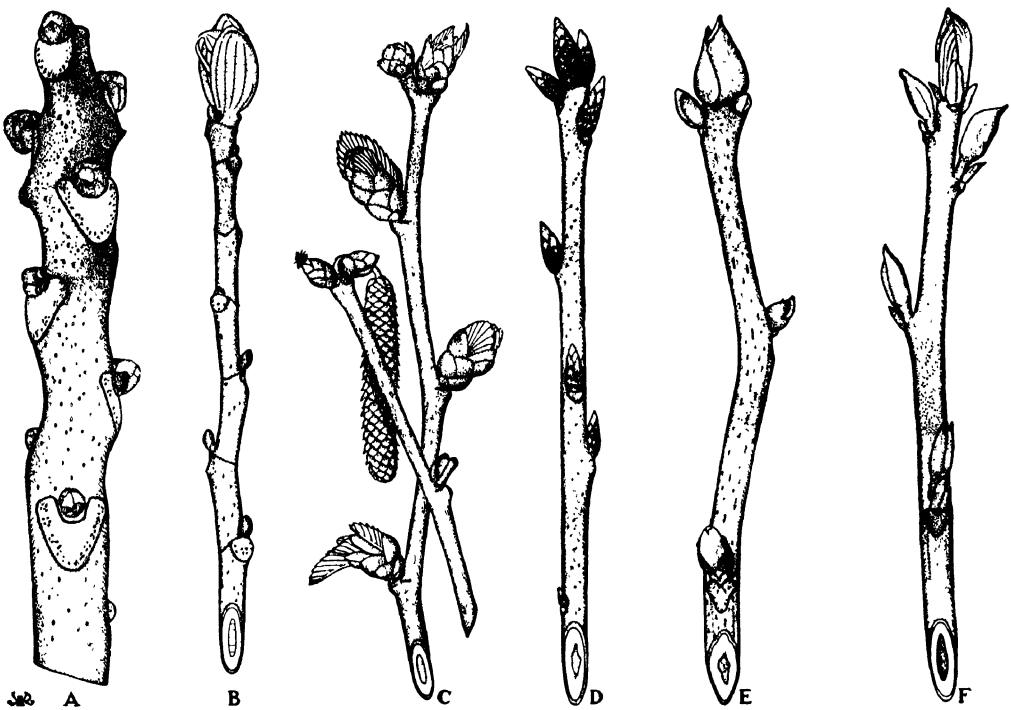

FIG. 90. Bud and twig characters of a few woody plants: A, tree of heaven (*Ailanthus*); B, tulip tree (*Liriodendron*); C, hazel (*Corylus*); D, red oak (*Quercus*); E, white heart hickory (*Carya alba*); F, bitternut hickory (*Carya cordiformis*).

ters (Fig. 90). Trees may be recognized by types of branching, which are usually more obvious in the absence of leaves. A critical comparison of the bark, buds, lenticels, and pith of our common trees soon enables one to select a few simple distinctive characters by which these trees may be readily identified during the winter. The prevailingly opposite

branching of the younger twigs of ash, maple, and buckeye; the innumerable and slender ultimate branches of the elm; the papery bark and elongated lenticels of some birches and cherries; the resinous buds of horse-chestnut; the star-shaped pith visible in cross sections of oak twigs; and the chambered pith of walnut and hackberry are a few examples of distinguishing characters that may be selected. Such characters may be used as a basis for making a key for the ready identification of woody plants.

Herbaceous aerial stems. Stems of herbs are usually readily distinguished from those of trees and shrubs by the comparatively smaller amounts of woody tissues. Some annual stems, such as those of sunflower, giant ragweed, and a few asters, become woody at maturity in certain habitats, but they are classed with herbaceous plants. It is really a matter of opinion whether certain semi-woody plants should be called herbs. Many herbs are annuals or biennials, in contrast to trees and shrubs which are generally perennials. Many herbaceous plants have perennial underground stems some of which are very hard and woody; but the annual aerial shoots that develop from these stems are herbaceous. Herbaceous stems are frequently green and have stomates.

Although many external features common to woody stems are absent, herbaceous plants are nevertheless often identified by certain features of their stems, such as shape, color, amount of hairy covering, and the presence of certain types of prickles, thorns, and tendrils.

Rhizomes and runners. A common type of underground stem is represented by the *rhizome* of bluegrass, Johnson grass, cord grass, Canada thistle, and Solomon's seal. Rhizomes grow horizontally at some depth below the surface of the soil, have scale-like, non-green leaves, and axillary lateral buds from which aerial branches develop at certain seasons of the year. Roots generally appear on the ventral sides of a rhizome at the nodes. The rhizome may be thick and fleshy (Solomon's seal, Fig. 91), or slender and woody as in many grasses.

Slender, prostrate stems, such as occur in strawberry and some ferns, are often termed *runners* or *stolons*. These prostrate stems and all underground stems are excellent means of vegetative propagation. They are distinguished from roots by the presence of nodes and internodes. The "turf" of lawns and meadows is a shallow layer of soil held together by an interwoven mass of rhizomes and the accompanying roots. Many of these structures are illustrated in Chapter XXXV.

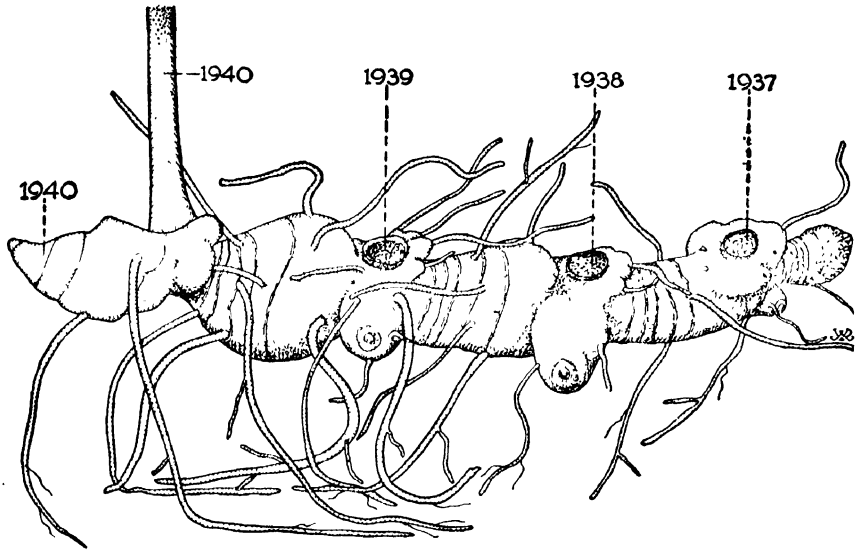

FIG. 91. Rhizome, roots, and base of an aerial stem of Solomon's seal collected early in July. An erect aerial shoot develops each year from the growing apex of the rhizome. The round scar formed at the end of the season when the aerial stem abscises is the so-called seal. Following the growth of the aerial shoot a new rhizome segment develops annually. The older segments at the opposite end of the rhizome gradually die and decay.

Tubers, corms, and bulbs. An underground stem familiar to everyone is that of the Irish potato. The slender rhizomes of the potato enlarge terminally into thickened structures known as *tubers*. In each eye of the tuber there is a cluster of rudimentary buds. When the tuber is planted, an aerial branch develops from a bud in one or more of the eyes, depending upon the degree of apical dominance. Large quantities of starch accumulate in the potato tuber, and it has become an important source of food, even replacing bread made from cereals in some countries. Tuber-like thickening may occur also in aerial stems as in kohlrabi. Some of the so-called short thick roots such as globe radish and turnip, are mostly enlarged hypocotyls (Fig. 114, page 296).

Another distinctive type of stem resembling the tuber is the *corm*, characteristic of jack-in-the-pulpit, dasheen, and gladiolus (Fig. 92). It is a short, upright, thick stem commonly covered by thin membranous scale-like leaves. It bears both lateral and terminal buds.

A *bulb* consists of a short, upright stem bearing thick leaf bases, axillary buds, and a prominent terminal bud. The underground bulbs of hyacinth, tulip, onion, and garlic are familiar to all. A few bulbs are aerial, such as the sets (Fig. 186B) on the flower stalks of onion and

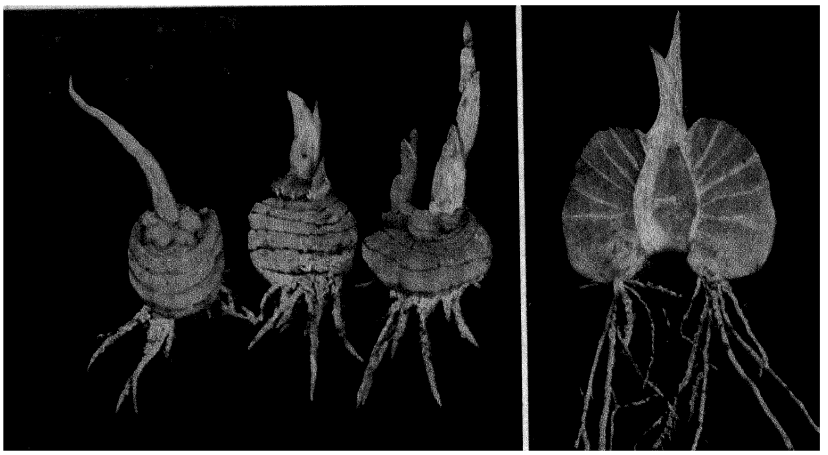

FIG. 92. Pictures of corms of gladiolus shortly after germination; at the right is a vertical section cut from the center of a corm. Photos from P. W. Zimmerman and A. E. Hitchcock, Boyce Thompson Institute.

the axillary structures of some lilies. Young bulbs which grow from the axillary buds of the main bulb are sometimes termed *bulblets*.

Failure of the internodes of the stem to elongate may also result in a *head*, as in cabbage; or a *rosette*, as in dandelion, evening primrose, and mullein. Ultimately elongated stems bearing leaves and flowers develop from the terminal bud in the center of the rosette (Fig. 141, page 340).

Thorns, spines, and prickles. *Thorns* are small, sharp-pointed stems; they may bear buds and leaves. Common examples are the thorns of hawthorn and honey locust (Fig. 93). The term *spine* should probably be used for leaf structures alone, such as the spines of barberry and the stipular spines of black locust, in spite of the fact that spines and thorns in common language often refer to the same structures. Pointed structures common on the stems of blackberry, rose, and smilax are *prickles*, which are merely outgrowths of the epidermis and cortex.

Climbing and twining stems. Many plants, such as grape, Virginia creeper, Boston ivy, and wild cucumber, may extend vertically sometimes for great distances by growing on or about other plants or objects. Some stems have *tendrils*[1] which encircle the support and anchor the growing vine. The Virginia creeper and Boston ivy have branching tendrils the ends of which are flattened disks or *holdfasts*. Tiny outgrowths from these holdfasts penetrate the crevices of the surface on

[1] These should not be confused with the *leaf tendrils* of the garden pea or the nasturtium.



FIG. 93. Thorns on honey locust.

which the plants are growing. In this way the vines can "climb" vertical walls. In the morning glory, the hop, and some beans the stem itself winds about the support and may be called a *twiner*. It is interesting to note that some plants twine clockwise and others counterclockwise, when viewed from above. No explanation of this difference in twining has been established.

Cladodia. This type of stem is found among the cacti and some other desert plants. Leaves are usually absent or ephemeral, and spines often develop on the green stems. Such stems are referred to as *cladodia* (singular *cladodium*).

Dormancy in buds. It is a well-known fact that mature buds of most woody plants, those in the "eyes" of potatoes and in bulbs pass through a dormant period after maturity. During this time there is no external evidence of growth, regardless of the environment in which the buds are placed. Such dormancy is the result of physiological conditions within the buds, and does not disappear until these inner conditions have changed. In temperate climates it may persist for several months. It is often commercially important for this dormant period to be shortened as much as possible.

Most dormant buds will grow much sooner than usual if they are subjected to various artificial treatments that accelerate certain physiological changes in them. These treatments are referred to as methods of "breaking dormancy." In temperate climates the internal conditions that cause dormancy in buds disappear under the influence of the low

temperature of the winter months. These conditions disappear much more slowly in some species than in others. As soon as they have disappeared, both flower and leaf buds of many woody plants will grow if the plant or stem cuttings are placed in a warm room and supplied with water. Often root formation occurs at the base of the cuttings. If the conditions causing dormancy have not disappeared, the plant may slowly die.

In recent years the vapor of certain chemical compounds[2] has been used to shorten the period of dormancy in the buds of many plants. The dormant period of buds of Irish potato has been experimentally shortened from one to four months, depending upon the variety tested. In the latitude of New York some of the common shrubs, such as lilac, flowering plums, crabs, and quinces, if exposed to vapor of ethylene chlorhydrin in December will bloom within a month. The plants or twigs should be placed within a tight box containing 1 ounce of ethylene chlorhydrin for each 8 cubic feet of space. After two days they should be transferred to a warm room or greenhouse. If these artificial treatments are applied early in autumn the results are unsuccessful. Treatment with temperatures near freezing for three or four weeks in early autumn before ethylene chlorhydrin is applied shortens the dormant period still more. Methods for breaking dormancy in buds are at present in an experimental stage of development but anyone may try them on some particular plant. Storage at low and high temperatures, drying, wounding, and treatment with special chemicals have all been used to shorten the dormant period of buds. Diverse results have been obtained with different plants.

In temperate climates dormant buds as well as the latent lateral buds in stems of shrubs and trees (Fig. 84) survive exposure to low temperatures that would quickly kill actively growing buds. Many dormant buds, however, are killed during unusual winters. In certain locations wind-blown sand may destroy the buds and all growing regions on the windward side of a tree (Fig. 93A).

This chapter contains a brief account of external similarities in stems and of some of the usual differences in form and habit of growth that may be found. Ordinarily stems may be recognized by the presence of one or more characteristic external features, such as nodes, leaves, and leaf scars. They may be herbaceous or woody, aerial or underground.

[2] Ethylene chlorhydrin, ethylene dichloride, ether, carbon bisulfide and many others.

They may vary in form from the cylindrical stems of trees, shrubs, herbs, and vines to tendrils, thorns, and the short thick stems characteristic of succulents, tubers, corms, and bulbs. Most stems bear leaves, flowers, and branches. Under certain conditions roots may also grow as lateral

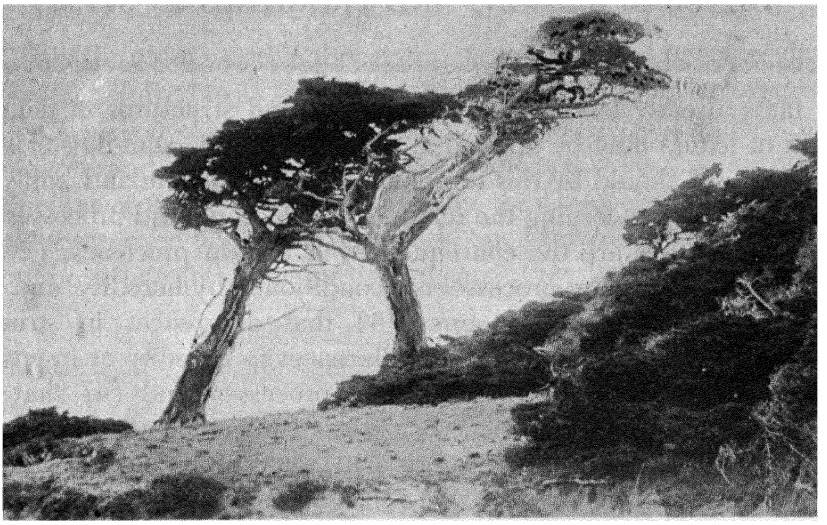

FIG. 93A. Effects of wind and wind-blown sand upon growth and form of stems—"the ostrich trees," formerly on Monterey peninsula, California. A cross section of the trunk of the tree on the right 20 feet above the soil was 6 feet wide and 10 inches thick. The pith was 4 inches from the windward side. The wood on this side consisted of 50 annual rings—on the opposite side, of over 400 rings. For more than 350 years the cambium persisted on the leeward side. Photo and data from W. S. Cooper.

organs on many kinds of stems. The form of the plant and its type of branching are dependent on the relative development of branches from terminal and lateral buds. Dormancy during summer and autumn is common in buds of most trees and shrubs in temperate climates. The period of this type of dormancy may often be shortened by artificial changes in temperature and by the application of certain chemical compounds. Numerous buds on each plant are kept dormant by apical dominance.

CHAPTER XXVII

GENERAL REGIONS AND PROCESSES IN STEMS

The facts already learned about processes and structures in cells and tissues of leaves may be applied at once to an understanding of stems. Moreover, we should by this time more fully appreciate and apply four generalizations concerning the relations of structures and processes: (1) that all structures are the consequences of certain processes; (2) that these structure-forming processes are conditioned by heredity, and influenced by environmental factors; (3) that differences in structure, whether they are dependent upon differences in heredity or in environment, were preceded by differences in processes; and (4) that after the structures are once formed they in turn influence all the processes that continue to occur in them. In the light of these generalizations, reference to any structure as having a "function" leads to a misinterpretation of all plant phenomena.

The more minute differences in stem structure, like those of leaves, are so numerous that one might study them for a lifetime without learning all about them. Much useful and interesting information about processes and structures in stems may be obtained, however, in a short time, and much of it without even a microscope. All one needs at first is a sharp knife and the stems of several kinds of plants. The familiar trees, shrubs, and herbs of any locality are suitable material. In some of them certain stem structures are more prominent than in others, and there are particular structures that are not present in the stems of all kinds of plants. A hand lens will be useful in these preliminary observations, and a microscope will be needed to obtain answers to some of the problems that arise.

Woody stems. If small pieces of woody stems, such as those of apple, ash, and grape, are cut crosswise and split lengthwise, the *bark*, the *wood* (xylem), and the *pith* are at once evident. The relatively greater hardness of the *wood cylinder* may be detected by pressing on each tissue with the edge of the thumb nail. These three regions are characteristic of all woody stems.

If blocks of older and larger woody stems are examined, it is evident that the wood cylinder has increased in diameter, that the bark is somewhat thicker than in younger stems, and that the diameter of the pith has remained unchanged. Evidently growth in diameter of stems consists of the formation of new xylem and, to a less extent, of new bark tissues.

When the older wood in the central part of the stem becomes darker in color it is referred to as *heartwood.* The younger, lighter-colored wood is called *sapwood.* Almost all the older wood is dead; and when fungi that can digest and oxidize the substances in the cell walls gain entrance into the center of the stem through wounds, they may destroy all but a thin shell of sapwood adjacent to the bark. Such hollow trees, however, may continue to live and grow for many years (Figs. 94 and 101).

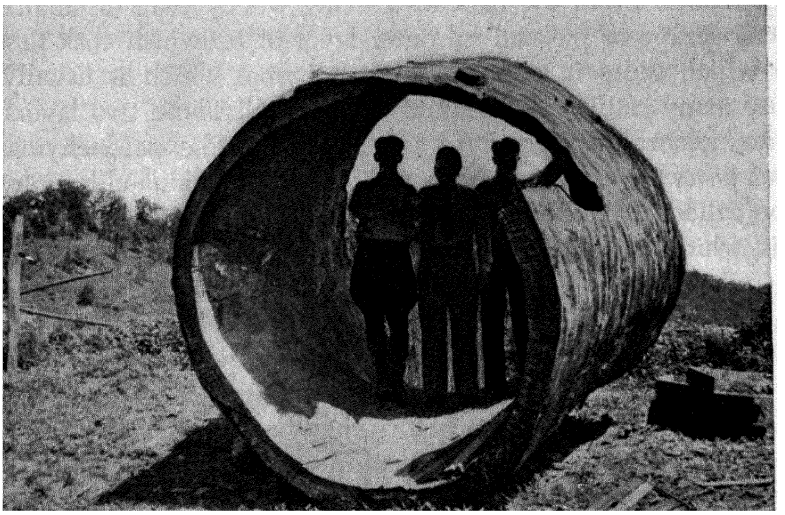

FIG. 94. Photograph of a hollow log from a sycamore tree which lived and grew for many years after the heartwood had been destroyed by fungi. See also Fig. 101.

It is evident from the differences in color and texture that the bark is composed of several kinds of tissues and that the cells of the wood cylinder are not all alike. The annual growth rings (ends of annual cylinders of xylem) may usually be counted in the wood cylinder, though sometimes a hand lens or even a microscope is necessary to distinguish them clearly. A careful examination of the ends of the

xylem tubes (*vessels*), which are visible through a hand lens, will disclose one of the two ways we can distinguish each annual ring of wood. Wood cells must be seen through a microscope for one to discover the second way. Annual rings are clearly evident in stems of pine and other conifers that have no xylem tubes.

Usually radially arranged rays, the *vascular rays*, can be seen in the split surfaces and ends of blocks of wood. The vascular rays in the xylem may be called *xylem rays*. On the split surfaces they appear as smooth, narrow, thin ribbons of different lengths extending crosswise to the "grain" of the wood. The xylem rays may also be seen on pieces of polished lumber one side of which was cut in a plane parallel to them. We shall see presently, however, that much of the conspicuous grain of polished wood is dependent upon differences in the wood cells in each annual cylinder of xylem.

Bark tissues. From the bark of a living woody twig or small branch one may scrape or pick off an outer layer of brownish cork tissue, beneath which there is a layer of parenchyma, which is usually green because many of the cells contain chlorophyll. These two layers of the bark are generally referred to as the *cortex*. The parenchyma is the *cortical parenchyma*, and any part of it that contains chlorophyll may also be called *cortical chlorenchyma*. The cortex is just within the epidermis, which, being only one cell thick, may be difficult to detect without a microscope. If one carefully scrapes the cortical chlorenchyma away with the edge of a knife, a number of hard fibers extending lengthwise in the bark become visible. These are *pericycle fibers*. If the point of the knife is slipped under these fibers, they may be lifted a slight distance from the stem before they break. Beneath the pericycle fibers is a layer of soft, usually colorless, tissue. When this layer is scraped off, the outer surface of the wood cylinder is visible. This innermost soft tissue of the bark is the *phloem*, containing the food-conducting cells. In the stems of some species, such as basswood and pawpaw, the phloem also contains fibers, *phloem fibers*, comparable to the pericycle fibers already noted. The term bast fibers is sometimes used commercially to refer to any of the fibers in the bark, whether in the cortex, pericycle, or phloem. In some twigs the radially arranged vascular rays in the phloem, *phloem rays*, are visible, but they can usually be seen only through a microscope.

The phloem and wood cylinder together constitute the vascular cylinder, or *stele*, of the stem. Its outer boundary is the pericycle. The

adjacent innermost layer of cells in the cortex is sometimes referred to as an *endodermis*, but in numerous stems it does not differ in structure from cortical cells immediately external to it. One may therefore visualize a woody twig as consisting of the *pith*, the *vascular cylinder* (*stele*), the *cortex*, and the *epidermis* if it is still present. The vascular cylinder in the youngest parts of stems is not completely closed but consists of several separate *vascular bundles* with parenchyma between.

Between the bark and the wood cylinder is a cylinder of meristematic cells, the *vascular cambium*. Since this cambium is but one cell, or at most only a few cells, in thickness, it is too thin to be seen without a microscope. Although in cross section it appears as a ring of very small, thin-walled cells, it should be visualized as a cylinder of meristematic cells immediately surrounding the wood cylinder and lining the innermost layer of the bark. As the cambium cells divide, new xylem cells develop at the outer surface of the wood cylinder, and new phloem cells develop at the inner surface of the bark. It is the formation of new cells in the cambium that results in the annual increase in diameter of perennial stems. In spring, when the cambium cells are dividing, the bark is easily separated from the wood cylinder. Those who have made whistles out of twigs or helped peel spruce logs for pulp milling are fully aware of this fact.

One should continue to whittle and observe until the relative arrangement of all these general regions is distinctly visualized. With the exception of the pith, each general region of woody stems should be visualized as a cylinder surrounding other cylinders of the stem. The wood cylinder surrounds the pith, and in turn is surrounded by a cylinder of cambium; the cylinder of bark surrounds both the cambium and the wood cylinder. Within the bark next to the cambium is a cylinder of phloem, followed in order by cylinders of pericycle, cortical chlorenchyma, cork, and epidermis, provided one is examining a twig or small branch. Within a few years the epidermis, cortex (cortical cork and chlorenchyma), pericycle, and other outer layers of the bark die and slough off. Consequently, the bark of the trunk of a large tree consists only of the phloem and layers of cork that develop annually from *cork cambiums*, which in turn develop each year from living phloem cells. Most of these features of a woody stem are represented in Fig. 95.

It is well known that the age of any part of a branch may be ascertained by noting its location in reference to the terminal bud scale scars.

Since an annual cylinder of wood is formed each year and the ends of these cylinders seen in cross section appear as distinct rings of wood,

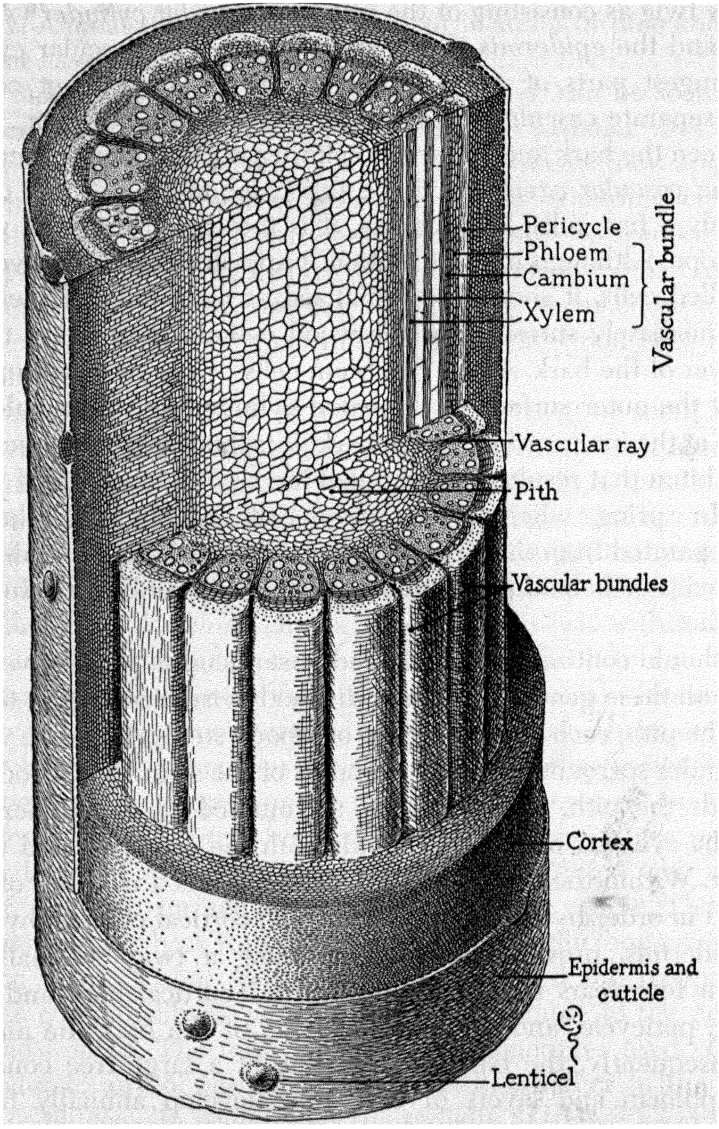

FIG. 95. Arrangement of general regions and tissues in a stem of moonseed vine. Courtesy of World Book Co.

the age of the stem may also be ascertained by counting the rings. An annual cylinder of phloem is also formed each year, but the rings of

phloem in cross section are not so evident. They may be seen in the ends of a twig of basswood with the aid of a hand lens.

The terminal stem segment contains one cylinder of wood and one of phloem. In the next stem segment below the first terminal bud scale scars there are two cylinders of wood and two of phloem. The cylinder of wood adjacent to the cambium is the one that extends through both annual stem segments. Likewise, the cylinder of phloem adjacent to the cambium is the one that extends through both stem segments.

In the stem segment below the second terminal bud scale scar there are three cylinders of wood and three of phloem. Only the cylinder of the wood and the cylinder of phloem adjacent to the cambium extend through all three stem segments. Can you visualize the positions of these cylinders all the way down the branch and trunk of a tree to its base near the soil?

If the tree is a century old there should be 100 annual rings of wood at its base. The innermost cylinder of wood adjacent to the pith is as high as the tree was when it was one year old. The next cylinder is as high as the tree was when it was two years old, and so on to the 100th and youngest cylinder of wood adjacent to the cambium. This cylinder extends all the way from the base of the tree to the tip of the terminal twig. Each lateral branch also has a similar arrangement of annual cylinders of wood.

Likewise, the innermost cylinder of phloem extends all the way from the tip of the terminal twig to the base of the tree. Each branch contains a cylinder of youngest phloem external to the cambium. The cylinders of xylem and phloem in any stem are continuous with those of the same age in each of its lateral branches.

Furthermore, these youngest cylinders of wood and phloem also extend all the way down the root to near its tip. The older cylinders of wood and phloem in the root, like those in the stem, are successively shorter and shorter until we come to the shortest ones, which were formed during the first season of growth. The pith in the stem, on the other hand, develops from the apical meristem and merely elongates each year and is therefore continuous from the tips of the branches to the base of the trunk (Fig. 96).

Since annual stem segments bear leaves but once, the youngest cylinder of wood is the only one that is continuous with the xylem in the veins of the leaves of deciduous trees and shrubs. Likewise, the youngest cylinder of phloem in the stem is the only one that is continuous with

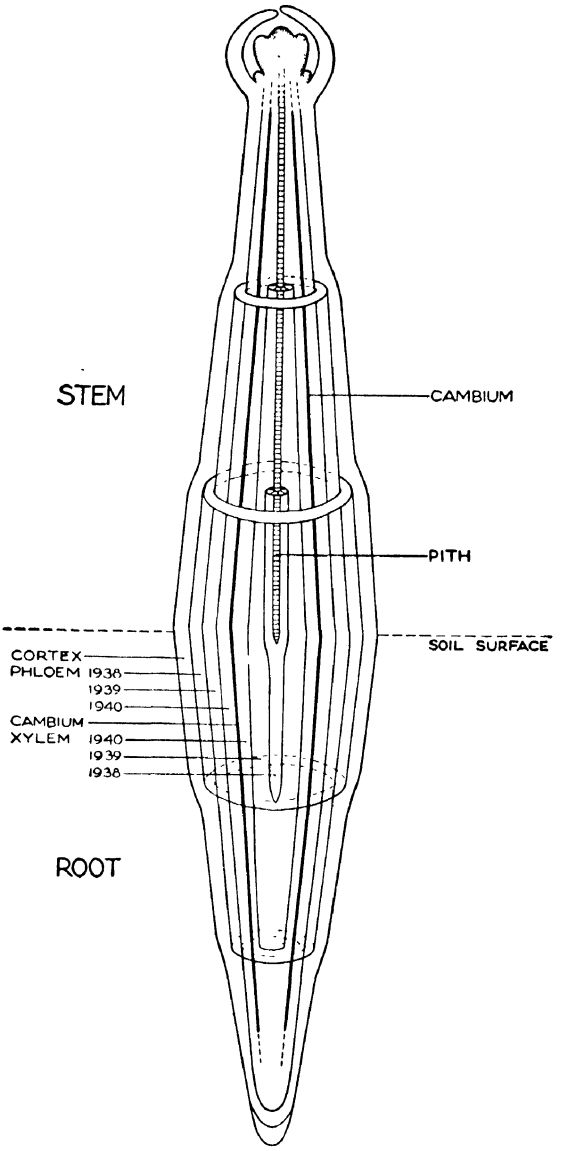

FIG. 96. Diagram of relative positions of xylem and phloem in a 3-year-old stem and root.

the phloem in the veins of these leaves. It is in this youngest cylinder of wood each year that most of the water is pulled up the stem by transpiration. Food translocation occurs mostly in the youngest phloem.

Girdling. As the term is used by botanists, girdling consists in completely removing a band of bark and cambium all the way around the stem. If the girdle is made on the trunk of the tree within a few feet of

the ground and below all lateral branches, an adequate translocation of sugar from leaves to roots no longer occurs in most species of plants, but movement of water in the xylem from roots to leaves still continues. In trees the roots and base of the trunk below the girdle may contain enough food to survive for a year or two after the girdle is made. Death and decay of the roots are ultimately followed by the death of the plant above the girdle as a result of desiccation.

In most species of plants apical dominance of the tops is sufficient to inhibit the growth of sprouts from the base of the trunk even in girdled trees. When excessive girdling annuls this apical dominance sprouts may grow from the roots or base of the trunk, as they usually do when a live tree is suddenly cut down. Likewise, if there are lateral branches below the girdle, or if apical dominance fails to inhibit the growth of sprouts from the base of the tree, the tree may survive for many years.

If the bark is not completely removed, or if the girdle is very narrow, new phloem may develop from the cambium before accumulated food in the roots is exhausted, and the tree may survive. When the girdled area does not become dry and is otherwise protected by grafting wax, a new cambium and phloem may develop across the girdle while the roots are still alive. Advantage is sometimes taken of this fact in horticultural practice. Branches, or even the main trunk, of fruit trees are girdled to bring about internal conditions favorable to the formation of flowers and fruits without killing the tree. Girdling prevents not only the downward translocation of sugar, but also the upward translocation of the amino acids and proteins made in the roots.

Girdling is often incorrectly done in that so much of the younger xylem is cut away with the bark that the movement of water to the leaves is greatly diminished. In such cases the leaves wilt within a few days, and the top above the girdle dies of desiccation before the roots starve to death. With the death of the top its apical dominance disappears, and sprouts may grow from the roots or from the base of the trunk. Apparent exceptions to these statements of course need further analysis than given here.

Herbaceous stems. If stems of herbaceous plants, such as those of common weeds, garden plants, and crop plants, are cut and dissected, as directed above for woody stems, soft tissues and vascular bundles are readily discernible, and in some species a hard outer rind is evident. Here again differences in color and texture are indicative of different kinds of tissues definitely arranged. In stems of dicots the cortex and

circle of bundles surround a relatively large pith (Fig. 97). Ridges of the pith that extend between the bundles may be visible in cross sections as pith rays. In old herbaceous stems, as those of sunflower, there may be a conspicuous ring of xylem with narrow xylem rays. Chlorenchyma is usually present in the cortex of herbaceous stems and sometimes in the phloem and pith. In a monocot like corn, the bundles are scattered

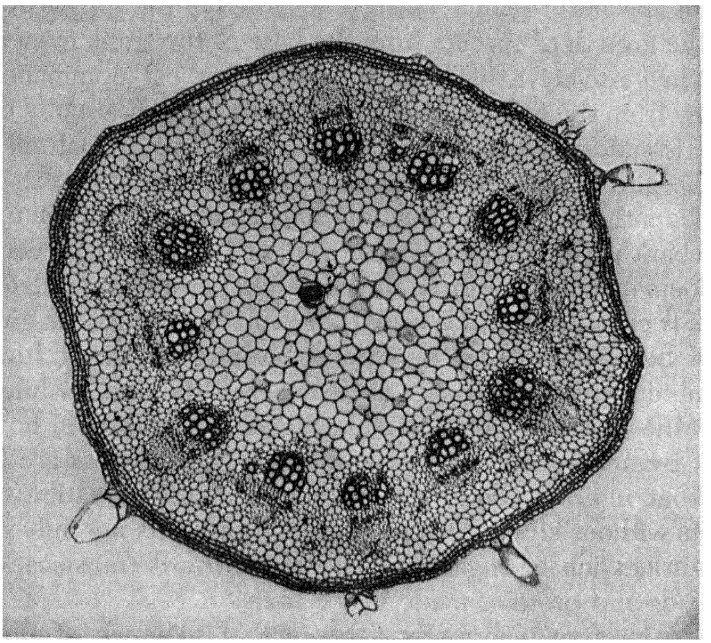

FIG. 97. Photomicrograph of a cross section of a young sunflower stem.

throughout the stem (Fig. 98). In many species of both monocots and dicots the cells of the pith disintegrate at an early stage of development, with the result that the stem is hollow. If an herbaceous stem bearing leaves is cut off near the surface of the soil and the cut end of the stem is placed in a weak solution of eosin or other dye that stains the xylem, the dye is pulled up the stem with the water, and the stained bundles in both stems and leaves may be seen more readily.

The stems of most monocots differ from those of dicots also in the absence of a vascular cambium. Hence, stems of most monocot plants, even though they are perennial, do not increase in diameter from year to year. For example, no slender bamboo stem ever becomes a big

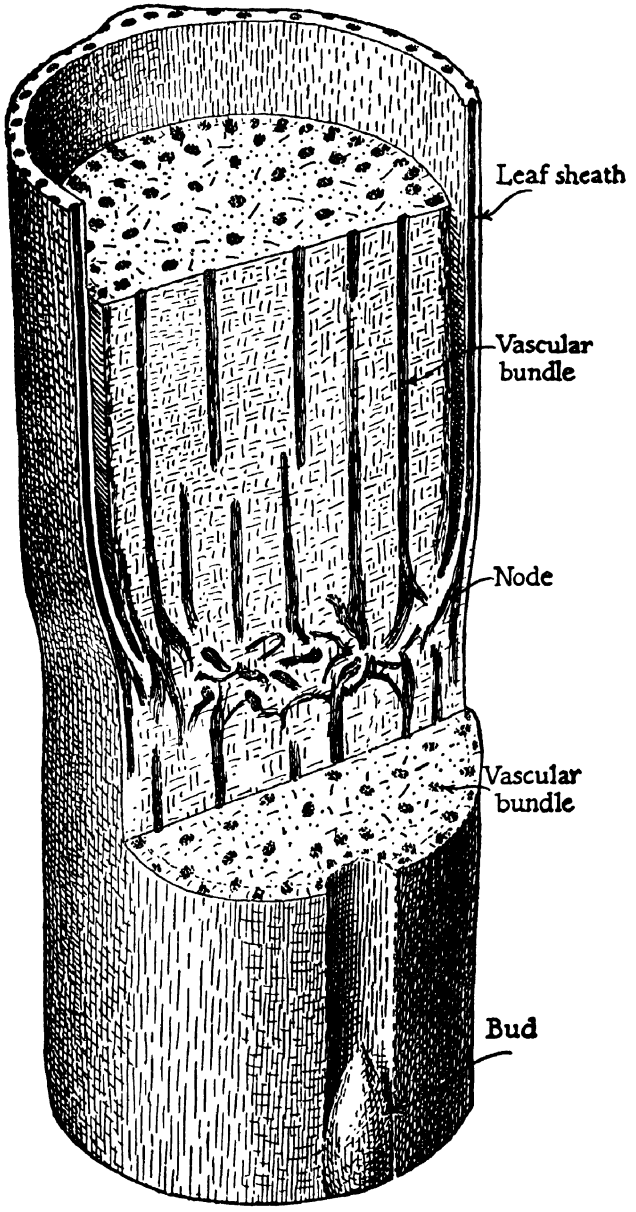

FIG. 98. Arrangement of tissues in a solid monocot stem (*Panicum*). Courtesy of World Book Co.

bamboo stem, and no big bamboo stem was ever a slender bamboo stem (Fig. 99). The diameter of monocot stems usually does not increase from year to year. There are, however, some exceptions. In the stems of some monocots such as palms and yuccas a temporary cambium de-

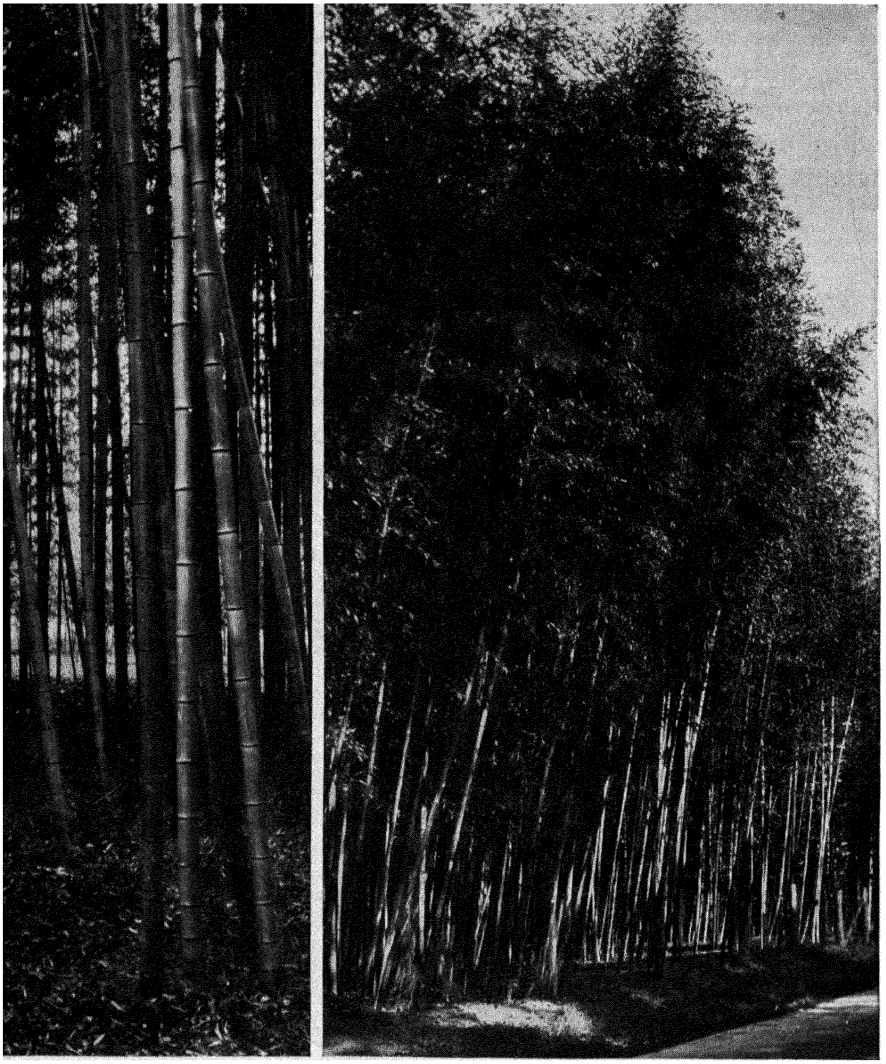

FIG. 99. Interior and exterior view of bamboo forest at Savannah, Georgia. Photo from United States Department of Agriculture.

velops periodically from cells in the cortex of the stem. The stem thus increases in diameter from time to time (Fig. 100).

Place of growth in length. The place of growth in length of the stem may be recognized by both its external and internal appearance. At the top of the stem the leaves are relatively small and young, and several of the internodes are not fully elongated. Internally, parenchyma is the

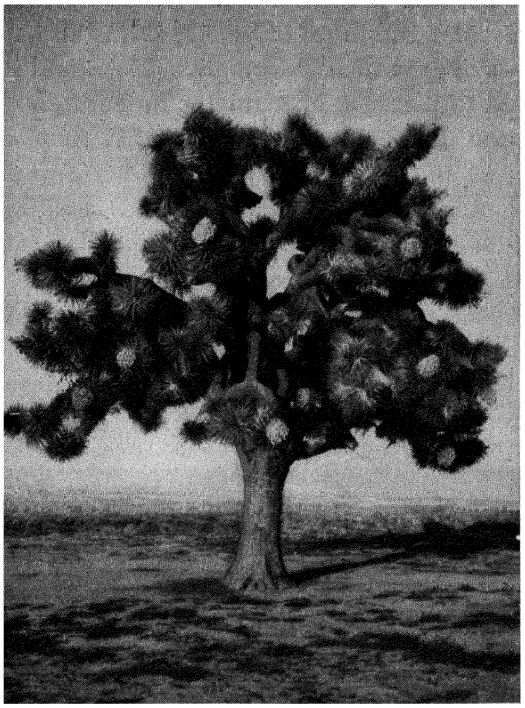

FIG. 100. The Joshua tree, an arborescent yucca, in bloom. Mojave Desert near Kramer, Calif. Photo by U. S. Forest Service.

most prominent tissue. At the extreme tip only parenchyma is present (Fig. 32, page 69). We have already seen (Chapter XXIII) how such external factors as light and gravity may influence the direction of growth of an elongating stem tip. To see the growing tip of a grass stem one must first carefully remove the ensheathing leaves. Unless the plant is very young the stem tip will be bearing rudimentary flowers entirely hidden within the leaf sheaths. As the grass stem grows, the bases of the internodes are the last parts of the stem to stop elongating and become mature.

Size of stems. The forerunner of the whole stem system of a plant is the apical meristem in the bud (plumule) of the embryo (Fig. 8, page 11). Through the formation and enlargement of cells in this apical meristem the stem elongates and axillary buds develop from cortical and epidermal cells along its sides. From some of these axillary buds lateral branches develop, each of which also has an apical meristem.

Although there are seasonal periods of growth and dormancy, it might

appear that the stem of a perennial plant would have unlimited growth in length. The vascular cambium of woody stems also is perennial, with alternating periods of growth and dormancy. Trees and shrubs, therefore, might be expected to increase in diameter indefinitely.

From observation, however, it is evident that there are limits to the age of trees and also to both height and diameter growth of stems. Furthermore, among the different species there is a wide range in these limits. The smallest species of trees never exceed a few feet in height and a few inches in diameter. Among herbaceous plants there are many species that are even more restricted in age, height, and diameter. The tallest trees may exceed 300 feet, and the diameter of some trees may become more than 30 feet. Vines in the tropics may become a thousand feet or more in length.

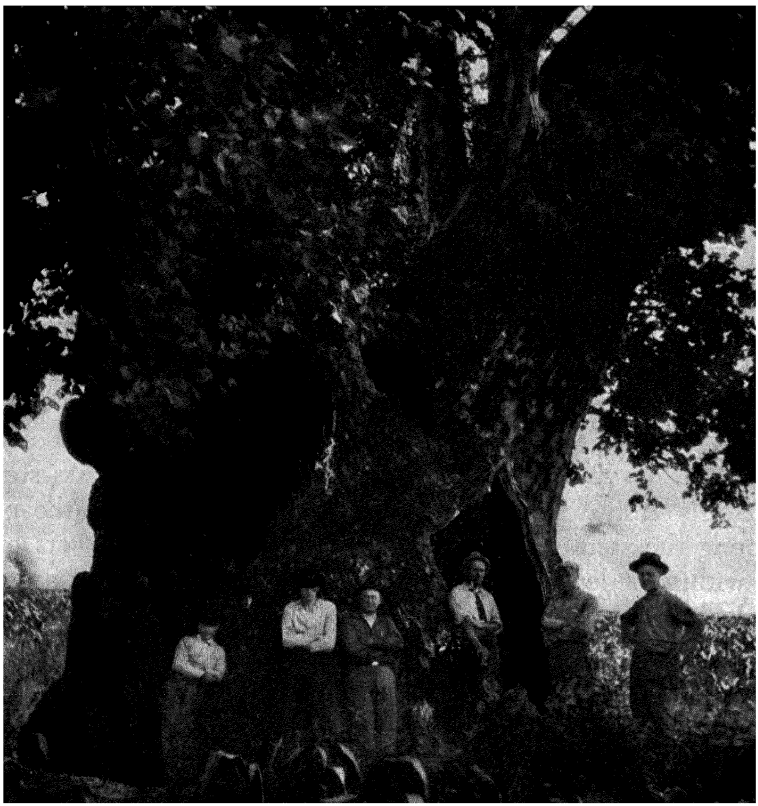

FIG. 101. A giant sycamore 45 feet in circumference at breast height. White River Valley, Indiana. Photo by G. W. Blaydes.

Many of us are impressed with the superlative. Large trees, tall trees, and old trees elicit considerable interest as shown by their frequent mention in the press (Fig. 101). Some of the present-day trees are the largest and have attained the greatest age of any plants that ever existed (Fig.



FIG. 102. Big Tree or Sequoia in the Sierra National Forest, where trees as large as those pictured above are common. They are limited to unglaciated areas in the canyons of the Sierra Nevada Mountains. Photo from the U. S. Forest Service.

102). What determines the limits of age, size, and height? It would be interesting to consider some of the factors correlated with size limits, but space can be given here only to a few suggestions and to a summary of reports of the largest trees (Table 11). What world events were in progress when these trees were seedlings?

That the stem may have potentialities of unlimited growth may be demonstrated with plants, such as English ivy, that propagate readily from cuttings. To do this it is necessary only to use repeatedly the upper part of the same stem as a cutting and to keep it in an environment that is favorable to continuous vegetative growth. That is, it must not be

TABLE 11. Maximum Sizes and Ages Attained by Certain Trees

Name of Tree	Location	Diameter	Height	Age
Western yellow pine	Western N. A.	8 ft.	230 ft.	500 yrs.
Sugar pine	California	12 ft.	300 ft.	600 yrs.
Douglas fir	British Columbia	25 ft.	417 ft.	700 yrs.
Redwood	California	28 ft.	360 ft.	1000 yrs.
Big tree (sequoia)	California	35 ft.	330 ft.	4000 yrs.
Big cypress of Tule	Oaxaca, Mexico	50 ft.	140 ft.	3000 yrs.
Western juniper	California	14 ft.	80 ft.	3000 yrs.
White pine	Tennessee	11 ft.	170 ft.	350 yrs.
Sugar maple	Wabash Valley	4 ft.	120 ft.	..
Bur oak	Wabash Valley	8 ft.	170 ft.	..
Tulip	Wabash Valley	10 ft.	200 ft.	..
Sycamore	Southern Indiana	16 ft.	150 ft.	..
Black walnut	Wabash Valley	6 ft.	150 ft.	..

placed in an environment in which the terminal vegetative bud will become a flower bud. Similarly, artificial cultures of root tips, described in Chapter XXI, are evidence that the apical meristem of a root tip has potentialities of unlimited growth if it is repeatedly removed from the remainder of the root system and kept in a suitable environment. What then are the factors that limit the growth in length of stems and roots when they are attached to the whole plant?

Processes in stems. All the processes characteristic of a vegetative cell occur in the cells of stems. In addition, there are certain processes that occur in some vegetative cells but not in others. Photosynthesis does not occur in all vegetative cells, but such processes as respiration, digestion, and assimilation do. On the other hand, photosynthesis occurs in any cell of a leaf, or a stem, or a root that contains chlorophyll and is exposed to a suitable environment. But many leaves and stems do not contain chlorophyll. All we can say is that in most ferns and seed plants photosynthesis occurs more abundantly in leaves than in stems and roots.

When all kinds of leaves, stems, and roots are compared, there are very few processes that can be said to be distinctly characteristic of any one of these three types of vegetative organs. Perhaps there is no process that occurs in all stems that does not occur in some roots or some leaves. There are very few species of plants which have leaves that bear other leaves; roots may never bear leaves, but there are also certain kinds of stems that do not bear leaves. Flowers do not develop directly from leaves or from roots; neither do they develop on all types of stems. When water and salts move from the soil to the leaves of a dandelion plant, the

distance they move through the roots is many times the distance they move through a stem. There are certain species of plants in which photosynthesis occurs primarily in the stems. There are others in which the absorption of water and inorganic salts occurs primarily in the leaves and stems. The reader may find it both interesting and instructive to add to these examples of similarities among plant organs.

On the basis of what has been learned so far, it should not be difficult for the reader to formulate intelligent answers to questions that may be asked about stem processes. Why may the girdling of a tree result in its death? Why do people girdle trees? Why may they sometimes fail to obtain the desired results? Why may the leaves soon wilt when the girdle is made deep enough to include a few cylinders of sapwood? If a tree is wounded, will it "bleed to death"? How does healing occur? What is the gravest danger to which a tree is exposed when it is wounded, and how may it be prevented? How do trunks of trees become hollow? Why may hollow trees live for many years? If a nail is driven in a tree will it continue to remain the same distance from the base of the tree as the tree increases in height from year to year? Why are there anastomosing longitudinal ridges and crevices in the bark of a tree? What tissue of a tree is used as a source of lumber? Why do plants bearing leaves absorb more water from the soil than they do when leaves are removed? Why may a young tree have a longer growing period during the summer than an older tree of the same species? Why may the new branches of a pollarded tree grow several feet in length and bear numerous leaves in a single season, while those of an unpollarded tree may grow but a few inches in length and bear relatively few leaves? Can you add other questions, and answer them?

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CHAPTER XXVIII

TISSUES AND PROCESSES OF STEMS

Some of the general regions of stems discussed in the preceding chapter are composed of several kinds of tissues. This is particularly true of the cortex, the bark, and the stele. On the other hand, the pith, vascular cambium, endodermis, cork cambium, cork, and the epidermis each consist of a single tissue. Moreover, some of the tissues of stems are *complex tissues*, being composed of a system of several kinds of cells. This is particularly true of xylem and phloem, if we regard each of these as but one tissue.

Stem tissues that develop from cells in the apical meristem are called *primary tissues*. Those that develop from cells in the vascular cambium, or cork cambium, are called *secondary tissues*. In stems of most monocots, therefore, all the tissues are primary tissues. In stems of woody plants nearly all the xylem and phloem and the cork are secondary tissues; and the others, together with the first strands of xylem and phloem adjacent to the pith, are primary tissues. The only primary tissues that may still be present in the trunk of a large tree are the pith and a small amount of primary xylem. On the other hand, stems of herbaceous plants such as coleus consist mostly of primary tissues. Certain microscopic structures in these tissues will be given further attention.

Apical growth and the origin of primary tissues. At the extreme apex of the stem there is a group of small, closely packed, isodiametric, meristematic cells, the apical meristem. Immediately below it is a zone of cells in various stages of enlargement, some of which are also dividing. In the apical meristem food is being changed into new protoplasm, pectic compounds, and cellulose, as the cells divide and the daughter cells become as large as the mother cells. In the zone characterized by cell enlargement, growth of the cell wall, vacuolation, and the osmotic absorption of water are prominent processes. Apparently there is a continued synthesis of protoplasm, and the protoplasm that is present is being pushed out against the cell wall by the enlargement of the vacuole formed by the coalescence of many smaller vacuoles accompanying the

entrance of water. In the zone of cell enlargement, and especially toward its lower end, some of the cells are visibly different from others; that is, the results of cell differentiation are becoming evident (Fig. 32).

Various types of cell differentiation in stem tips may be noted; (1) some of the cells soon become the primordia of leaves and axillary buds; (2) these axillary buds, and sometimes the terminal bud, while still meristematic, may become either vegetative buds or flower buds (Fig. 83 in Chap. XXVI); (3) some of the cells may retain their meristematic condition and become the vascular cambium; (4) many other cells merely enlarge with or without evident change in form and composition, and, because of their position, origin, shape, and differences in cell walls, may be recognized as belonging to the epidermis, cortex, pericycle, phloem, xylem, or pith; and finally (5) the cross walls of some of the xylem cells partly disintegrate, leaving long tubes, or vessels, the lateral walls of which become thickened and lignified, with spiral thickenings that are particularly conspicuous. Numbers (1) and (2) above may be considered organ differentiations in meristematic tissue, while numbers (4) and (5) are tissue differentiations in enlarging and maturing cells. All the tissues formed by the differentiation of cells that originated in the apical meristem are primary tissues.

The above description applies to both woody and herbaceous stems of dicots. It applies also to growing stem tips of pines and other conifers, except that xylem vessels do not develop in conifers. Secondary xylem and phloem soon begin to develop from cambial cells. In stems of monocots, such as grasses, in addition to the apical meristem there is a temporary zone of meristematic cells at the base of each internode. This is the softest and weakest part of a growing grass stem. In young woody stems a cork cambium develops from cells in the cortex, and a layer of cork may develop on the new stem segment before the close of the first growing season. In some species of plants latent root primordia develop from parenchyma cells in the pericycle.

Just below the apical meristem short internodes, as well as nodes bearing primordia of leaves and axillary buds, are recognizable. Ultimately, flower primordia develop either from the apical meristem or from the meristems of axillary buds. The cells in the center of the apical meristem are forerunners of pith, which is surrounded by longitudinal strands of primary xylem.

The pith. Since the pith develops directly from the central cells of the apical meristem, it increases in length as the stem elongates; thus, it is

continuous from year to year in perennial stems. In time the cells of the pith usually die, and the protoplasm disintegrates. All soluble substances may diffuse out, and only the cell walls remain. In stems of some plants (walnut, hackberry, etc.), some of the cell walls also disintegrate or collapse, and the pith becomes chambered. In many species of herbs all the cells of the pith soon disintegrate and the stem becomes hollow. The stems of all these herbs are solid at the tip where the pith is young and intact.

In perennial plants the pith, or certain cells in it, may live from one to many years: one year or less in the European larch, 10 years in Scotch pine, 17 years in horse chestnut, 27 years in gray birch, and more than a century in a columnar cactus of the American desert. The pith cells in this cactus not only remained alive from 100 to 150 years, but when the pith was wounded some of the cells near the wound divided and formed new tissues.

The epidermis. The epidermis of the stem is continuous with that of the leaves and is comparable to it in most respects. The outer wall is usually thick and heavily cutinized. Glaucous stems, like glaucous leaves, are covered with wax. Epidermal hairs are the rule rather than the exception. Stomates are present, though usually not as abundant as in leaves. In many stems they ultimately become ruptured by lenticels that develop from cortical cells beneath them. The first cork cambium that develops in stems occasionally originates in epidermal cells.

The epidermis of a leaf lives as long as the leaf. This is also true of some stems; but in perennial stems that increase in diameter by cambial growth, the epidermis is soon ruptured, except in those plants where it continues to grow for a few years.

The cortex. When all types of stems are compared, the cortex is found to be a very diversified region. It consists primarily of parenchyma cells. The outer layer of cells just beneath the epidermis is often referred to as a *hypodermis*; the inner layer of cells adjacent to the pericycle is the *endodermis*. Each of these layers of cells may be parenchyma and differ little if at all from neighboring cells, or they may be easily distinguished by the shape of the cells and thickness of cell walls. The hypodermis may be composed of ordinary parenchyma cells, sclerenchyma cells, collenchyma cells, or palisade cells similar to those in leaves.

The first cork cambium in a stem frequently develops from the hypodermis. The development of cork from cork cambium is similar, whether it occurs in herbaceous stems, woody stems, roots, or any other plant

organ (Fig. 103). Cork cells are short-lived; but the cell walls, which are composed primarily of layers of suberin and lignified cellulose lamellae, last indefinitely because very few kinds of non-green plants can digest them. On stems that increase in diameter by cambial growth, however, the cortex is ruptured and sloughed off.

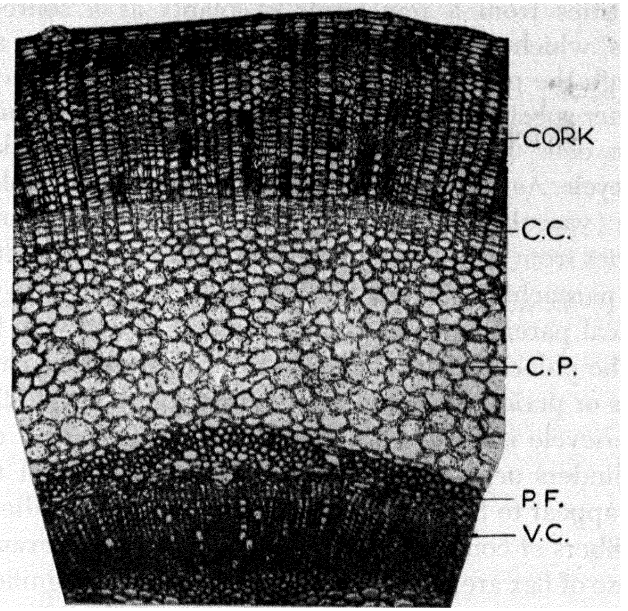

FIG. 103. Photomicrograph of a portion of a cross section of geranium stem in which the cork and cork cambium (C.C.) are evident. C.P., cortical parenchyma; P.F., pericycle fibers; V.C., vascular cambium.

In herbaceous plants the cortex may live as long as the stem does, but in many woody stems it may die and be sloughed off while the stem is comparatively young. New cork cambiums periodically develop in deeper-lying tissues. When cork develops in the pericycle, it prevents the diffusion of water from the xylem to the cortex, which soon dies. In beech the cortex lives and grows as long as the tree is alive. It is also long-lived in birch and certain other trees. Chlorenchyma is present in the cortex of most young aerial stems.

Sclerenchyma and collenchyma are frequently present in the cortex. In some species of plants there may be many other kinds of cells in the cortex, such as isolated sclerenchyma cells (stone cells or grit cells), groups of stone cells surrounded by a cambium, and isolated cells or groups of cells containing anthocyanins, essential oils, tannins, or cal-

cium oxalate crystals. Various canals or ducts, such as resin ducts, essential oil ducts, and latex tubes, may also be found in the cortex of some stems. No one of these features, however, is limited to the cortex or even to the stem of a plant.

Latex, the milky juice found in many species of plants, is collected in large quantities from a few kinds of plants as a source of rubber. Latex tubes, which originate from cells in the embryo in some species, grow through the parenchyma tissues of the plant as if they were parasites. In other species they are formed by the disintegration of scattered parenchyma cells. Resin ducts are surrounded by special kinds of cells.

The pericycle. As noted earlier, the pericycle is the peripheral cylinder of the stele (vascular cylinder) and in cross section appears as a ring of cells. It varies from one to several cells in thickness. When it is composed entirely of parenchyma it may be difficult to recognize. In fact, in some stems cortical parenchyma appears to extend all the way from the epidermis to the phloem; that is, there is no visible differentiation of either endodermis or pericycle. When sclerenchyma (pericycle fibers) is present, the pericycle is easily recognized. These fibers may occur as continuous cylinders or as separate strands, and because of their location they often appear to be the outer part of a vascular bundle. Some of the important fibers of commerce are pericycle fibers—for example, flax and hemp. Those of flax are mainly cellulose, and are less lignified than hemp fibers.

The pericycle is important in one other way. It is the region in which the primordia of lateral roots, and frequently those of adventitious stems, develop. It is from the pericycle that roots usually develop on stem cuttings. In some species, such as willow and cottonwood, root primordia develop in twigs on the tree and remain dormant unless the twig is exposed to conditions favorable to their further development.

The phloem. The phloem is a complex tissue in which several kinds of cells may usually be recognized with the aid of the microscope. The chief food-conducting cells are the *sieve tubes*, which are generally elongate, short-lived, and interconnected through perforated diaphragms called *sieve plates* (Fig. 104). Associated with the sieve tubes, perhaps in all the vascular plants except ferns and gymnosperms, are long-lived, slender parenchyma cells called *companion cells*. Various other parenchyma cells, not associated directly with the sieve tubes, may also be present. All these cells together constitute the part of the phloem in

which conduction of food may take place and in which starch frequently accumulates.

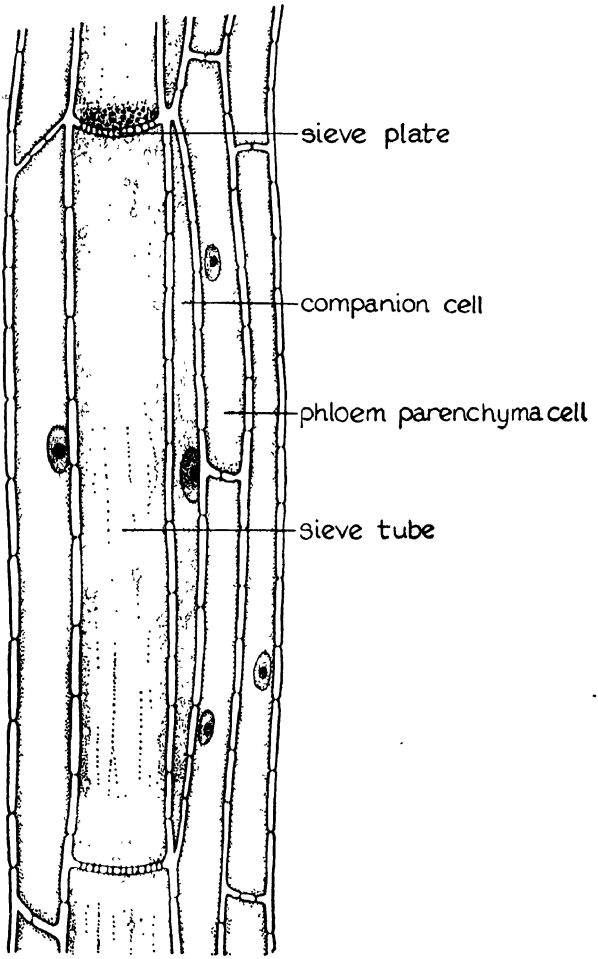

FIG. 104. Types of cells in the phloem of a gourd stem.

In the phloem of many vascular plants, except ferns, some gymnosperms, and most herbs, there are sclerenchyma cells, known as *phloem fibers*, comparable to the fibers of the pericycle. These fibers may occur in bands, as hollow cylinders surrounding softer tissue, singly, or irregularly. The commercially important fiber, jute, is obtained from the phloem of the jute plant. The individual phloem fiber is a long, tapering cell, usually with lignified walls. Short thick-walled cells, called *stone cells*, may occur in the phloem either associated with the fibers or alone. In a

few plants, such as sycamore and beech, the stone cells are the only sclerenchyma cells in the phloem.

Vascular rays are present in most plants having a vascular cambium. That part of the ray extending from the cambium into the phloem is the *phloem ray*, and it varies considerably in size, shape, and appearance in different species of plants.

In stems of most trees and shrubs the epidermis, cortex, and pericycle are present for only a few years. The tissues outside the cork cambium gradually die, and ultimately a new cork cambium develops from parenchyma cells in the phloem. The cylinder of cork formed from this cambium prevents diffusion of water to tissues external to it. The whole outer bark soon dies, cracks, and sloughs off.

In the birch and cork oak there are conspicuous cylinders of cork that resemble annual rings of the xylem, but in most species such rings are not evident. These cylinders are due to alternating layers of thin-walled and thick-walled cells. The thin-walled cells separate easily, and this results in the separation of the papery sheets of birch bark and the scaly bark of the sycamore. External masses of cork in such trees as cork oak accumulate in layers several centimeters in thickness and are of great commercial importance.

Stems of pumpkin, squash, tomato, potato, and several other kinds of plants differ from the usual by having phloem both external and internal to the xylem.

The xylem. The xylem of a woody dicot is a complex tissue composed chiefly of *vessels*, or *water-conducting tubes*; *tracheids; wood fibers; xylem parenchyma cells,* and *xylem ray cells.* A vessel may be several millimeters, several feet, or even yards in length. The length of a vessel depends upon the number of end walls that disintegrate in the row of cells from which it is formed. Old vessels may be closed by tyloses, outgrowths from adjacent xylem parenchyma (Fig. 105A).

In the xylem of conifers the vessels and sometimes the fibers are absent; the chief cells are tracheids and xylem ray cells. The tracheids are both water-conducting and wood cells. They are thick-walled and spindle-shaped, and have thin areas or *pits* in the walls (Fig. 105B).

Certain features of the xylem are more easily understood in relation to the growth of the cambium.

The vascular cambium. In order to see the cambium of stems clearly, one must have thin sections cut from *growing* stems of dicots or conifers. Between the easily recognized xylem and phloem in cross sections of

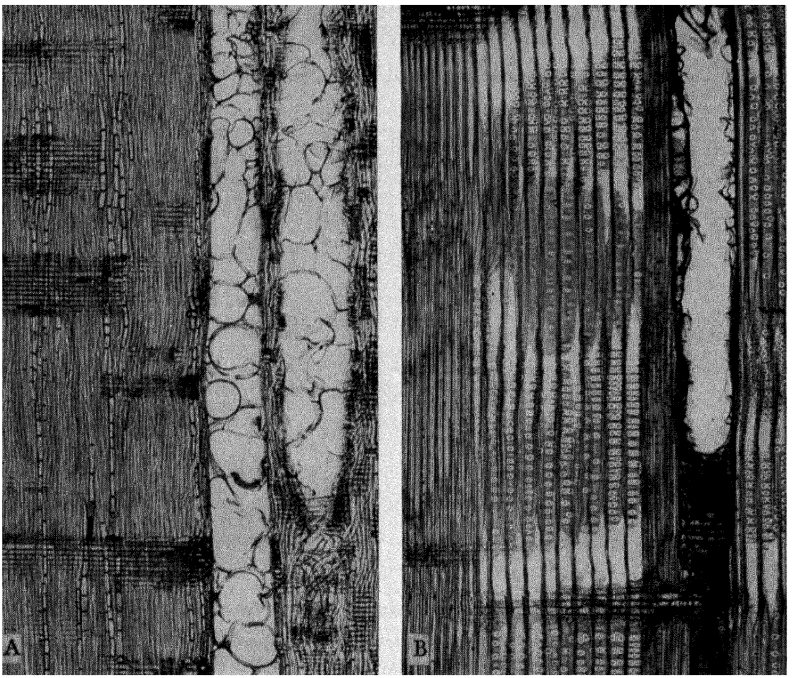

FIG. 105. Radial longitudinal sections of wood of (A) white oak and (B) long leaf pine. In the former wood fibers, xylem rays, and vessels filled with tyloses may be seen. In the latter section tracheids with bordered pits, xylem rays, and a resin duct are visible. Photos from Forest Products Laboratory.

these stems there is a region composed of several layers of thin-walled cells. The cells near the middle of this region are very small and thin-walled. These are the cambial cells from which additional xylem and phloem develop by cell division, enlargement, and differentiation and bring about an increase in the diameter of stems. Adjacent to and on both the phloem and the xylem sides of this cambium there are a few layers of cells which are thin-walled but inceasingly larger at greater distances from the cambium. One may therefore see from one to several layers of cells in the processes of enlargement and differentiation between the cambium and the mature phloem on the one side and the cambium and the mature xylem on the other (Fig. 106).

In the larger stems the cambium is a closed cylindrical sheath between the xylem and the phloem, that is, between the xylem and the bark; but in the younger part of the stem it is present only in the individual vascular bundles, which are separated from one another by broad rays of

pith-like parenchyma. As the young stem increases in age cambium usually develops from the parenchyma cells between the bundles and becomes a complete cylinder in the stem (Fig. 107).

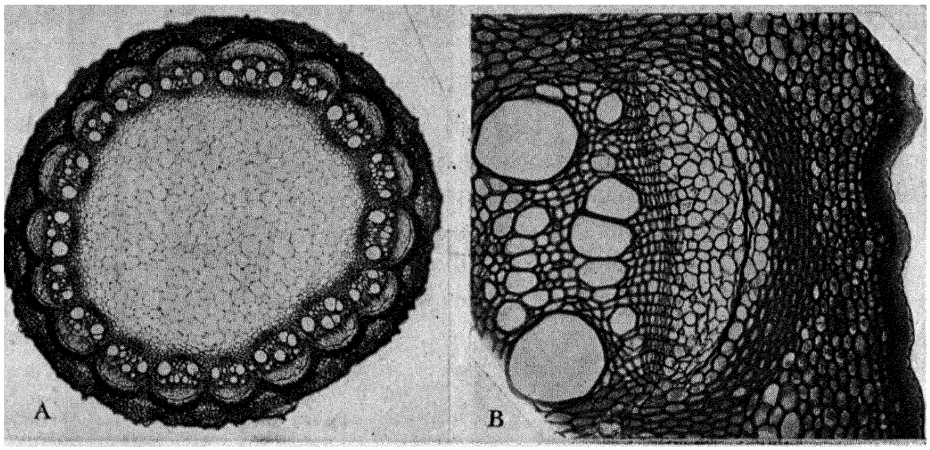

FIG. 106. A, photomicrograph of a cross section of a stem of moonseed vine; B, one of the vascular bundles, adjacent pericycle fibers, and cortex greatly enlarged to show the small cambium cells in contrast to the enlarged and differentiated cells of the xylem and phloem. The outermost phloem cells have been crushed by the enlargement of the inner younger cells formed by the division of cambial cells.

Since the xylem of woody perennials increases in diameter from year to year, it presses against the encircling bark. Some of the cells of the bark become crushed, and the outer dead parts of the bark are ruptured. As a result, the outer bark of woody perennials is usually furrowed and irregularly broken.

In most parts of the world cambial growth is limited to a few months of each year. In woody perennials of temperate climates it begins in the young twigs about the time the buds begin to open in spring, and somewhat later in the older branches and trunk of the tree. Two or three months later the cambium becomes dormant in the trunk of the tree and remains in that condition until the following spring. Each season cambial growth may begin first in the twigs or in the larger branches. Growth of the cambium appears to be dependent upon hormones from the leaves, but the evidence upon which this inference is based is too limited for final conclusions at present.

The xylem cells and vessels that develop in spring are usually larger than those that develop toward the close of the growth period in summer.

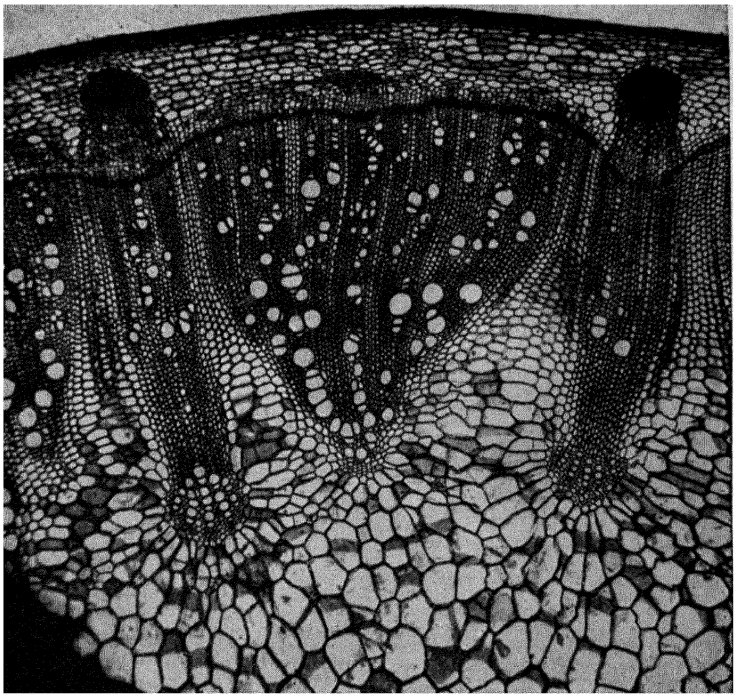

FIG. 107. Photomicrograph of a small portion of a cross section of a sunflower stem in which a continuous cambium has developed between the original bundles of the younger stem as pictured in Fig. 97.

Consequently the appearance of the inner portion of each annual ring of xylem as seen in cross section is quite different from that of the outer portion of the ring. Without these differences in *spring wood* and *summer wood* the annual rings of growth would not be evident to the eye.

The width of the annual rings in particular species varies with the age of the individual plant and with the fluctuations in environmental factors from year to year. In certain localities the effects of fluctuations in water supply and humidity are more prominent than those of all other factors combined. Tree rings may therefore be used, along with other data, as an index of periods of drought and of abundant moisture. Such studies have shown that there are rather definite and predictable cycles of periods of drought. Comparison of annual rings of living trees with those of wooden beams used in dwellings in the southwestern part of the United States has made it possible to date quite accurately certain events

in the lives of the cliff dwellers and other ancient peoples as far back as a thousand years or more.[1]

Ring-porous, diffuse-porous, and non-porous wood. When the vessels

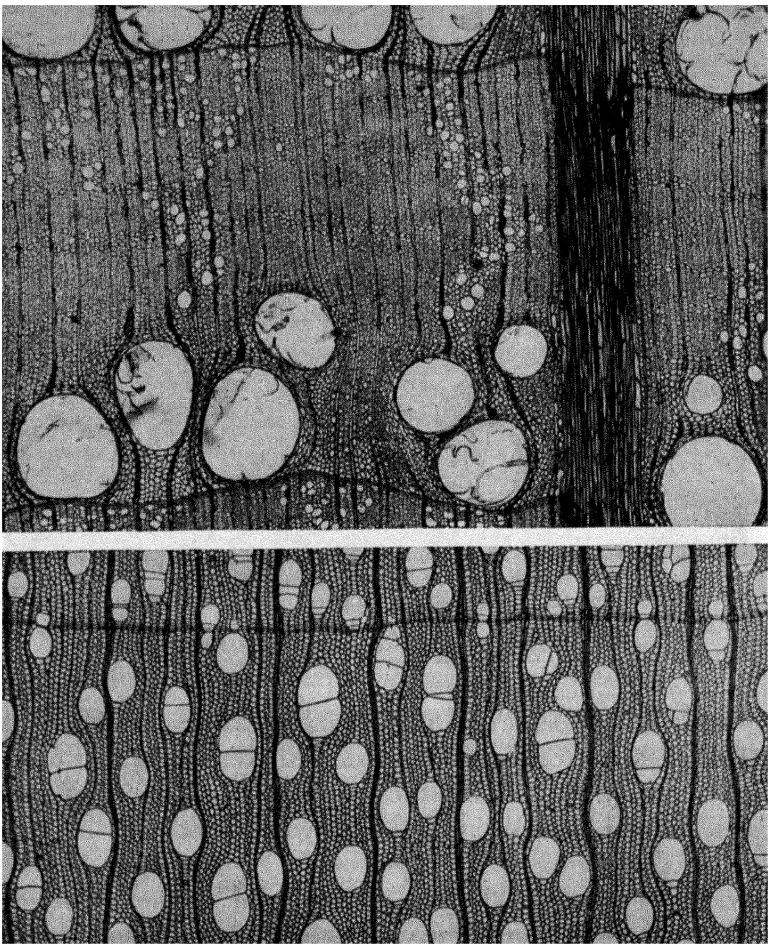

FIG. 108. Ring porous wood of white oak (A, above), diffuse porous wood of river birch (B, below). Photos from Forest Products Laboratory.

and xylem cells that develop in spring are large and numerous (Fig. 108A), the annual rings are particularly conspicuous. Such wood is *ring-*

[1] Papers by A. E. Douglass and Waldo S. Glock. Carnegie Institution of Washington, D. C. Leonardo da Vinci, over 400 years ago, recorded the relation of tree-ring growth to weather conditions. The matter did not receive serious attention, however, until 1901 when Douglass began to report his observations.

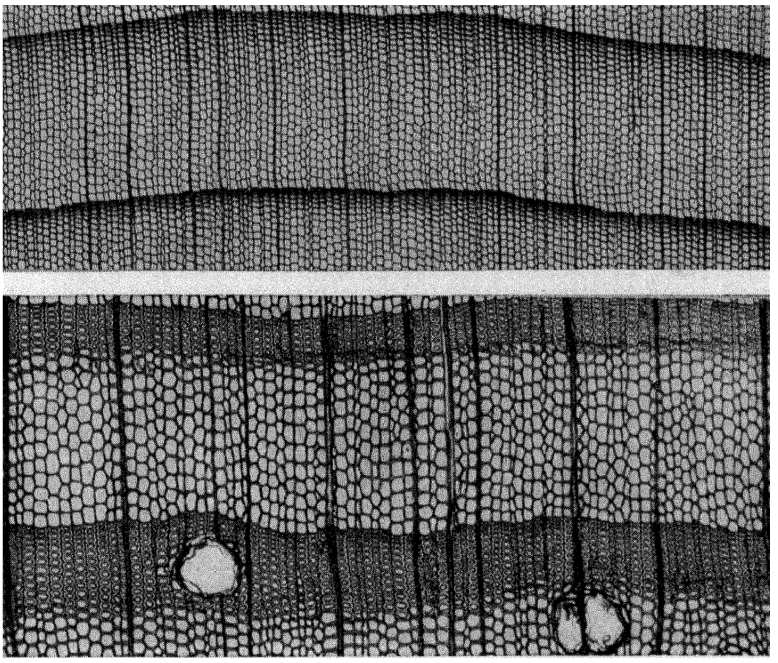

FIG. 109. Non-porous woods of arbor vitae (above) and of long leaf yellow pine (below). The large openings in the latter are cross sections of resin ducts. Photos from Forest Products Laboratory.

porous. If the vessels are of about the same size and are scattered uniformly in the annual ring (Fig. 108B), the wood is said to be *diffuse-porous*. In conifer stems, where no vessels occur, the wood is *non-porous* (Fig. 109). These facts are useful in the identification of woods of different species.

Grain of wood. When boards are cut from stems and polished, various patterns of wood are often conspicuous. Such patterns are dependent on the relative size of the cells and vessels of spring and summer wood, on the width of the annual rings, and on the plane in which the saw passes through the log with reference to the xylem rays (Figs. 110 and 111). "Quarter-sawed" boards are cut parallel to these rays. Tangential or "slab" cuts at various angles to the rays result in a variety of patterns. The summer wood is harder than the spring wood and takes a finer polish; and this difference is the cause of the often attractive grain patterns of furniture, panels, and cabinet work. In perfect radial sections the grain appears as straight lines crossed by patches of xylem rays.

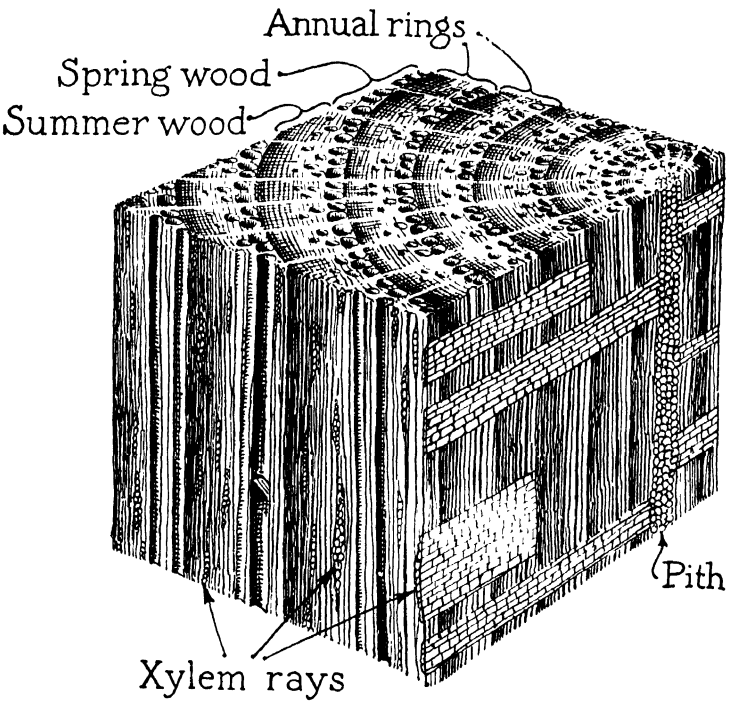

FIG. 110. Diagram of a block of oak wood, magnified to show the arrangement of tissues which underlies the patterns on polished wood surfaces. Courtesy of World Book Co.

When the cut passes through several annual rings, as in slab-cut boards, the pattern is most striking. Xylem rays in oaks and some other trees are prominent, and in quarter-sawed boards from such trees the rays appear as the light-colored areas.

If the annual rings are narrow, the wood is "fine-grained"; if they are wide, "coarse-grained." Some patterns of wood have special names. The "silver grain" of quarter-sawed oak refers to the large wood rays. If the patterns are wavy in appearance, as they sometimes are in birch, cherry, and chestnut, the wood is regarded as "curly grain." The best known is the "bird's-eye grain" of certain maples. This is caused by the presence of numerous partly dormant buds from which minute, embedded lateral stems develop. These small "stems within a stem" are the "eyes" of the wood seen in tangential section.

The monocot stem. Since the stems of monocots were discussed with those of dicots and conifers, some of the major facts about them may be summarized. The vascular bundles are scattered throughout the stem (Fig. 98). No cambium, except temporary vestiges, occurs in the bundles,

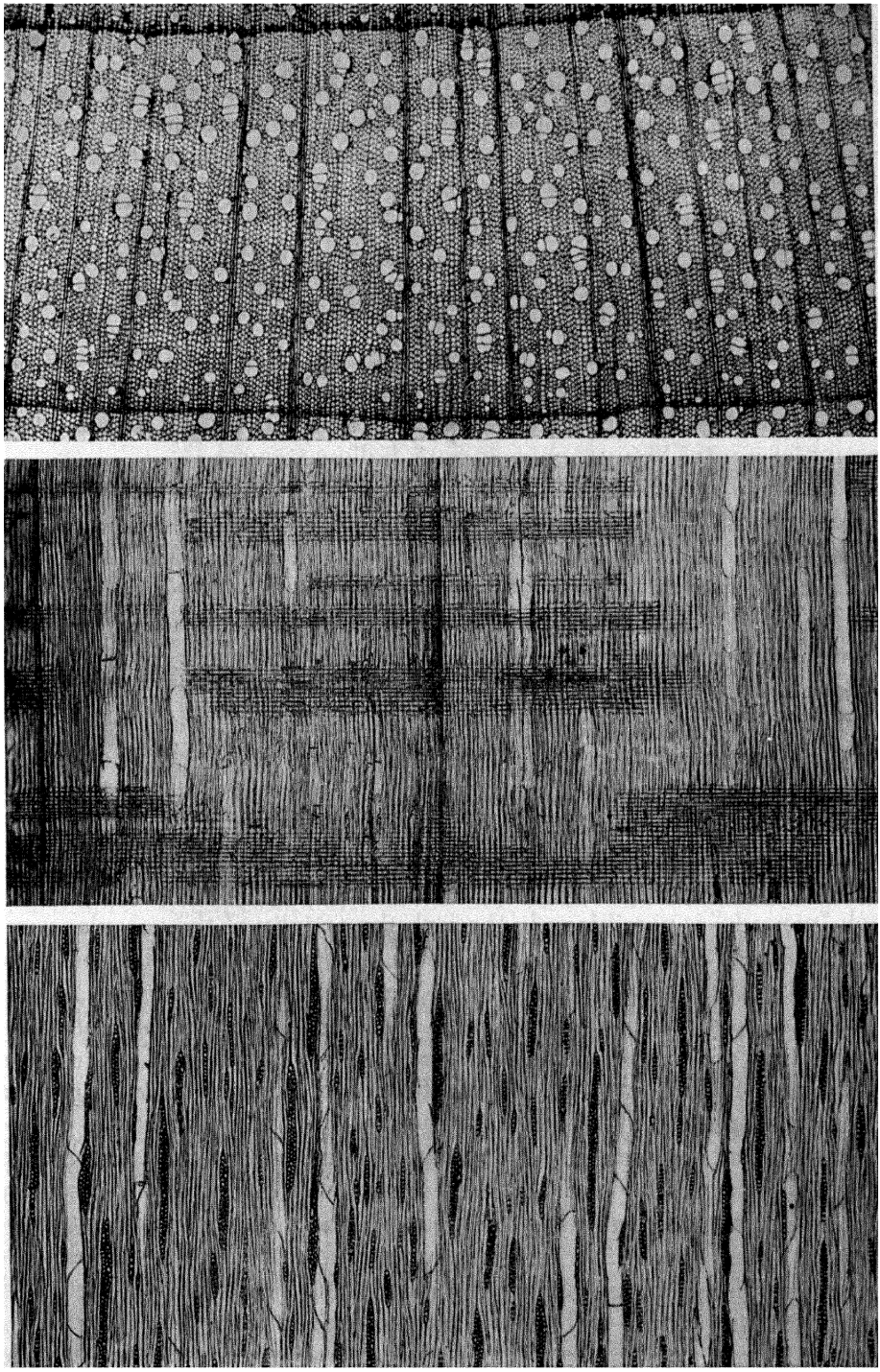

FIG. 111. Transverse, radial, and tangential sections of wood of sugar maple. Photos from Forest Products Laboratory.

and hence secondary growth, so evident in dicots and conifers, does not occur. The bundles are composed of xylem and phloem surrounded by a bundle sheath of more or less sclerenchyma-like cells. Growth in length occurs at the apex and also at the bases of several of the uppermost internodes. The epidermis is composed of hard, thick walls and may be subtended by several rows of thick-walled cells, the *hypodermis*. The epidermis, together with the hypodermis, is sometimes called the *rind*; this is evident in the corn stem.

The remainder of the stem consists of parenchyma. It is usually impossible to distinguish pericycle or cortex or pith. In some few monocots the central region is devoid of bundles, and the central parenchyma resembles a pith. Many monocots have hollow stems.

Because of the absence of a cambium, stems of most monocots do not increase in diameter after the cells are mature. The bamboo and corn, for example, grow to considerable heights but remain slender. Many perennial monocots have underground stems that elongate each year and enlarge the area occupied by the plant. Such aerial stems as those of palms, dragon tree, and yucca have secondary thickening. Cells in the pericycle or parts of the undifferentiated parenchyma become meristematic, and from them additional parenchyma and new vascular bundles develop.

Healing of wounds. As a result of the injurious effects of winds, ice, insects, and fungi, areas of living tissue on trees and branches may be killed or completely removed. Girdling a tree is another way of destroying its living tissue. It is perhaps evident by now that "recovery" from such "wounds" is possible only through the activity of the vascular cambium. Expert "tree surgeons" are able to save valuable trees, apparently ruined by mechanical injury, disease, and decay, by removing the injured areas and covering the exposed tissue with wax, tar, or other substances that reduce water loss and prevent the entrance of destructive organisms. If the injured area is not too large, the scar may in time be covered completely by tissue that develops from a cambium.

Grafting and budding. The importance of the cambium has long been recognized in grafting and budding. Many cultivated plants, especially fruit trees, do not "come true to seed" and must be propagated vegetatively. Sometimes it is commercially advisable to use vegetative multiplication, instead of seeds, for other reasons. One common practice used in perpetuating plants without the use of seeds is grafting.

In grafting, a twig or stem (the scion) of one plant is attached to the

stem or root of another plant (the stock). If the cambiums of the stock and the scion are in perfect contact and if proper precautions are taken, union of the meristematic tissues takes place rapidly. There are many types of grafting (Fig. 112), and reference to any manual on horticul-

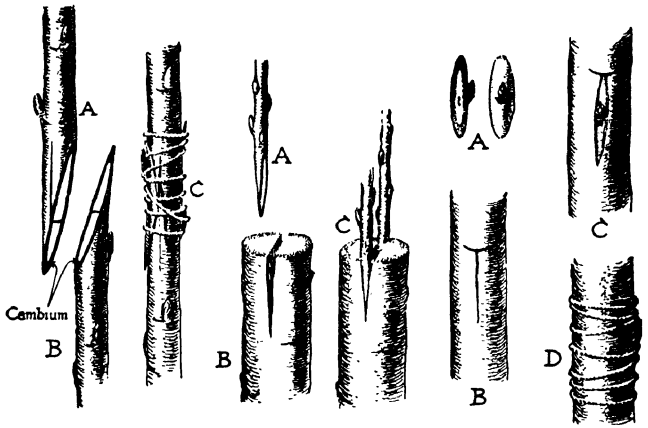

FIG. 112. Methods of grafting and budding. At the left, whip grafting; in the middle, cleft grafting; at the right, budding. A, represents the scion, and B, the stock. C, the scion and stock are joined. In both grafting and budding, success depends on bringing the cambium of the scion into contact with the cambium of the stock. Courtesy of World Book Co.

tural practices will indicate the preferred methods for different kinds of plants. Budding or bud grafting differs from twig grafting only in the fact that a bud and some additional tissues are inserted in a T-shaped slit in a branch. If the cambiums of the bud tissue and the branch are in contact, the two pieces soon unite.

It is evident that neither twig grafting nor budding is possible in stems without cambiums, as for example in corn, wheat, rye, and many other grasses. A further discussion of grafting is given in Chapter XXXV.

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CHAPTER XXIX

ROOTS: DEVELOPMENT AND STRUCTURES

To complete the story of the water and salt relations of plants we shall have to examine the underground parts of plants that have roots. The soil is a part of the immediate environment of these plants. The water in the upper layers of the soil, where most roots grow, is transitory. It enters from rain and melting snow and moves out by seepage, by evaporation, and through the plant. Only a portion of it is held in the interstices among the innumerable particles of the soil. From these interstices the water moves into the roots and upward into the stems and leaves and then into the air by transpiration. We have seen that in many plants the amount of water that passes through them during a growing season is large in comparison with either the volume of the plant or the water necessary for photosynthesis and other plant processes. How such large amounts of water can enter the plant from the soil will be better comprehended when we see how roots develop and become distributed among the soil particles.

Types of roots. When the seeds of most plants germinate, the first part of the embryo to enlarge and push through the seed coats is the *hypocotyl*, having at its lower end a *root primordium*. The hypocotyl is the part of the embryo between the *cotyledons* and the primary root, and is really the base, or the first-formed part of the stem of many plants (Fig. 8). This initial expansion of the embryo is due to cell enlargement. The hypocotyl may ultimately elongate from a small fraction of an inch to several inches shortly after germination. Following the emergence of the hypocotyl from the seed coats, the cells at the lower end of the root primordium begin to divide, and from this primordium the *primary root* develops. The hypocotyl appears to be lacking in the embryos of some plants, such as the grasses (Fig. 113). The plumule appears to be separated from the primary root principally by a node. If a hypocotyl is present in this type of embryo it is quite small and does not elongate when the embryo germinates.[1]

[1] The term *radicle* is variously used by different writers to refer either to the rudimentary root of the embryo or to both the root and the hypocotyl.

The primary root continues growth vertically downward for several days at least, and sometimes for weeks or even months after germination. Usually *lateral roots* grow from it and elongate either horizontally or obliquely downward. These are the *secondary roots*; and when still smaller branches develop from the secondary roots, they are called *tertiary roots.*

During the germination of seeds like those of corn and wheat, two or more small roots may develop from the base of the first internode of the embryo, and still later others from the second and third nodes of the stem. By the time the corn plant is two months old there is usually a whorl of roots at each of the eight lower nodes. Each successive whorl appears about one week later than the one below it. These and all other roots that originate from stems or from leaves are *adventitious roots.* All the roots of a plant—primary, secondary, tertiary, and adventitious—may be called collectively its *root system.* The primary root with all its branches may be called the *primary root system*, and all the adventitious roots of a plant its *adventitious root system.*

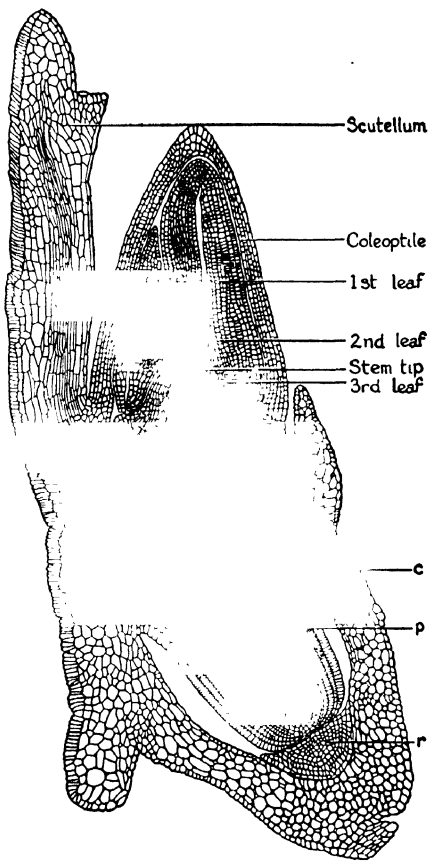

FIG. 113. Median section through a wheat embryo; c, coleorhiza; p, primary root; r, root cap. After M. A. McCall, *Journal of Agricultural Research.*

A mature corn root system comprises both of these root systems, but the primary root system is limited in growth. Hickory trees, English plantain, and dandelion plants from seed have primary root systems consisting of a large taproot and minor secondary roots. All plants artificially propagated by cuttings have adventitious root systems. The root systems of plants that grow from bulbs, tubers, and other underground stems likewise are only adventitious root systems after the first season from seed. The above terms are useful in classifying roots according to their origin.

Another way of classifying roots is based on their form and appear-

ance. When they are slender, elongate cylinders, such as those of grasses, they are called *fibrous roots*. If the primary root continues its downward course and becomes the principal large root of a plant, it is often called a *taproot*. Sugar beet, mullein, sunflower, pigweed, walnut, hickory, alfalfa, and red clover have taproots. Taproots are of two types, woody and herbaceous, with many gradations between. Those of hickory and walnut are woody. Those of beets, long conical radishes, dahlias, and sweet potatoes are usually herbaceous and greatly thickened. They are composed mainly of parenchyma cells with relatively few woody cells. Such *thickened herbaceous roots* are often referred to as fleshy roots.

The beets and radishes of commerce are not entirely roots. The upper part of each one consists of a thickened hypocotyl and the short stem to which the rosette of leaves was attached (Fig. 114). The edible part of some varieties of globe radishes is almost entirely thickened hypocotyl.

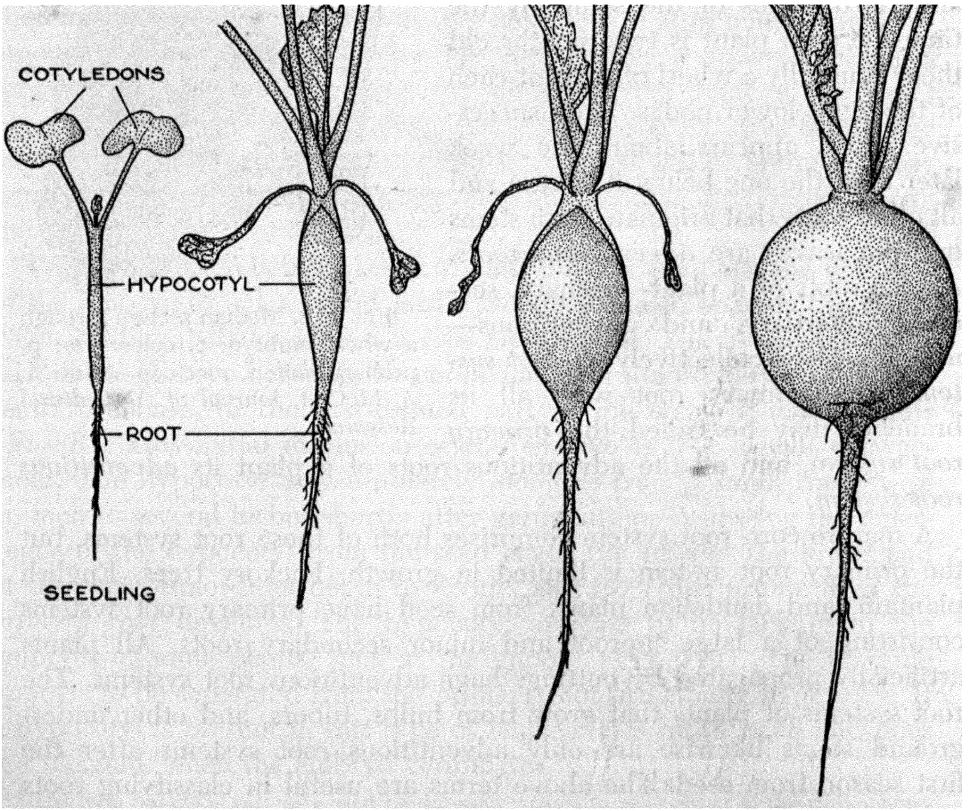

FIG. 114. Globe radishes develop primarily from the hypocotyl of the seedling.

Mature corn plants in the field usually have "prop roots" that have developed from the lower nodes above the ground. Pandanus, mangrove, and other tropical trees like the banyan and fig, have adventitious roots from the main trunk and also from the lateral branches of the crown (Figs. 115-118). When these so-called "prop roots" and "drop roots"

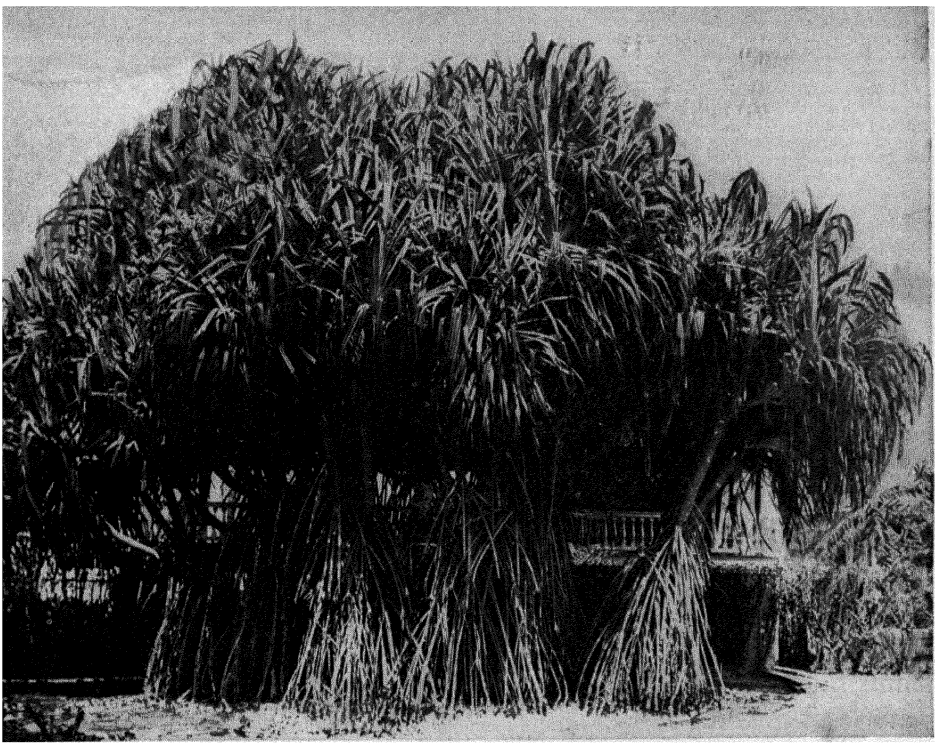

FIG. 115. Prop roots of pandanus, a tropical shore plant, planted in Florida. Photo by W. Fifield.

have grown into the soil, they become additional supports and have the same relation to the soil as primary root systems.

Many vines, such as the Virginia creeper, English ivy, poison ivy, and trumpet creeper, have *aerial roots* which become attached to the trunks of trees, walls of buildings, or rock cliffs, and anchor the slender shoots far above the height to which the stem can support itself. Orchids, bromelias, and many ferns in the tropics live as *epiphytes*, that is, perched on the branches of trees and shrubs (Fig. 119). These plants also have aerial roots which form masses below the leaves and not only attach the



FIG. 116. Prop roots of red mangrove (*Rhizophora*) in Bermuda. Photo by B. E. Dahlgren, Chicago Natural History Museum.

plants but also in some species become the only region of entrance of water and mineral salts.

Finally, there are the root-like organs of parasites, such as dodder and mistletoe, which grow into the tissues of the host plant and connect the tissues of the parasite with those of the host. Such roots are also called *haustoria*. Through them pass not only water and inorganic salts but also foods made by the host plant.

When the seedling of the common dodder, which is a mere thread-like stem two or three inches in length, comes in contact with a living green plant, it coils about it and a row of haustoria develops wherever the stem is in contact with the host. The haustoria penetrate between the cells of the host plant to the water-conducting and food-conducting tissues (Fig. 120). The dodder then grows rapidly, branches, and makes new contacts; and its haustoria penetrate the tissues of other parts of



FIG. 117. Banyan tree with prop roots that resemble trunks. Hawaii. Photo by U. S. Forest Service.



FIG. 118. The strangling fig. The tree on the left started as an epiphyte and its roots may be seen encircling the trunk on which it started; the specimen on the right began as a seedling in the soil. Photo by G. W. Blaydes.



FIG. 119. Epiphytic bromelias on live oaks in southern Florida. Photo from New York Botanical Garden.

the same green plant or those of other nearby plants. The haustoria embedded in woody stems may survive from one season to another, and from them the dodder plants propagate vegetatively each year.

Internal structure of roots. A limited observation of root systems is sufficient for one to see that roots are usually largest at or near their junction with the base of the stem and gradually taper in size to slender and tender tips. From these facts one may infer that the root tip is the zone of growth in length. Since the older portion of a root toward its base is the largest, there must be some means by which roots increase in diameter.

If a cross section of a young root of a tulip tree is compared with a

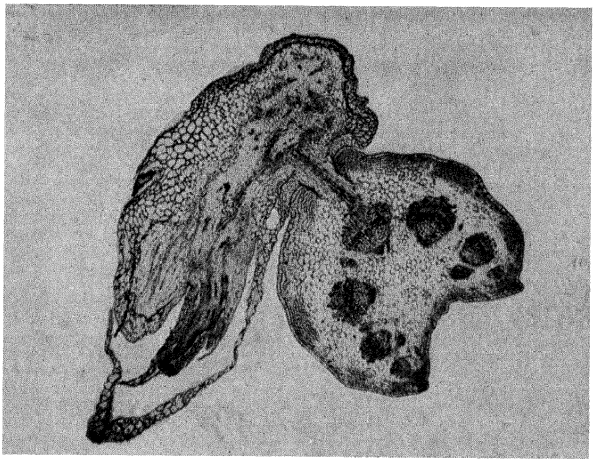

FIG. 120. Section of stem of dodder above and a cross section of petiole of host plant below. A haustorium from the dodder has grown through the cortex to a vascular bundle in the petiole.

cross section of a woody twig, the same kind of tissues in the same order of arrangement may be seen, except that no pith will be found in the root. From the center of this woody root outward therefore, there are, in order of occurrence: xylem, vascular cambium, phloem, pericycle, endodermis, cortical parenchyma, cork cambium, cork, and epidermis if it has not already become broken and sloughed off (Fig. 121). In most of the roots that have been studied the first cork cambium originated in the pericycle and the cortex was soon sloughed off.

The larger roots of a tree, like the larger stems above ground, consist only of the vascular cylinder (stele) and the cork that develops periodically from temporary cork cambiums derived from pericycle or from phloem parenchyma. Obviously, water and mineral salts do not enter roots where they are enclosed by a cylinder of cork. They enter only the youngest zone of tree roots that have not become enclosed in cork.

The growing root tips of many plants are sufficiently transparent so that when they are examined with a hand lens or low-power microscope, one may easily recognize the terminal root cap, the central vascular cylinder surrounded by a cortical cylinder, and the numerous root hairs which protrude from the epidermis a short distance back of the apex (Fig. 122). Root hairs are not present on the roots of all species of plants, and their abundance on others varies in different environments.

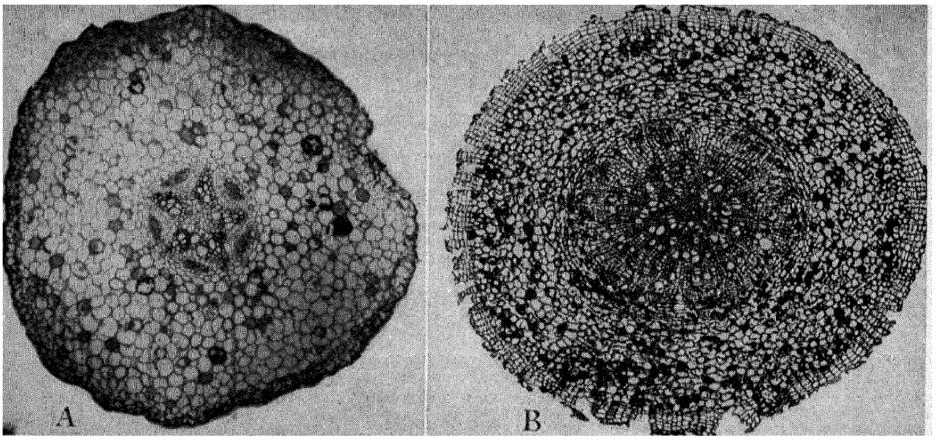

FIG. 121. Photomicrographs of cross sections of roots of a tulip tree (*Liriodendron*) in which the arrangement of tissues is evident: A, a young root; B, a 2-year-old root.

The terminal portion of the root, then, is the zone of origin of certain root tissues, the zone of growth in length and of growth curvature, and the principal zone through which water and salts enter many kinds of plants.

Tissues of roots. When longitudinal sections of the growing tips of stems and roots are compared, certain similarities and differences are easily recognized. The three zones characterized in general by cell division, enlargement, and differentiation (maturation); and the three longitudinal cylinders represented by the epidermis, cortex, and vascular cylinder are common to both. In some roots these three cylinders are distinguishable all the way to the so-called growing point in the center of the zone of cell division, which lies just above the root cap (Fig. 123). In other roots the differentiation of cells in these three regions is not obvious so near the growing point.

The four regions (root cap, epidermis, cortex, and primary vascular axis) of the growing tip of the root all originate from cells formed in this growing point. The root cap is a cup-shaped mass of cells renewed by cell division and enlargement at the lower side of the growing point and sloughed off on the outer surface by disintegration of the middle lamellae of the cell walls, accompanied by abrasion when the roots are growing in the soil.

In the zone characterized by cell enlargement there are also some cell

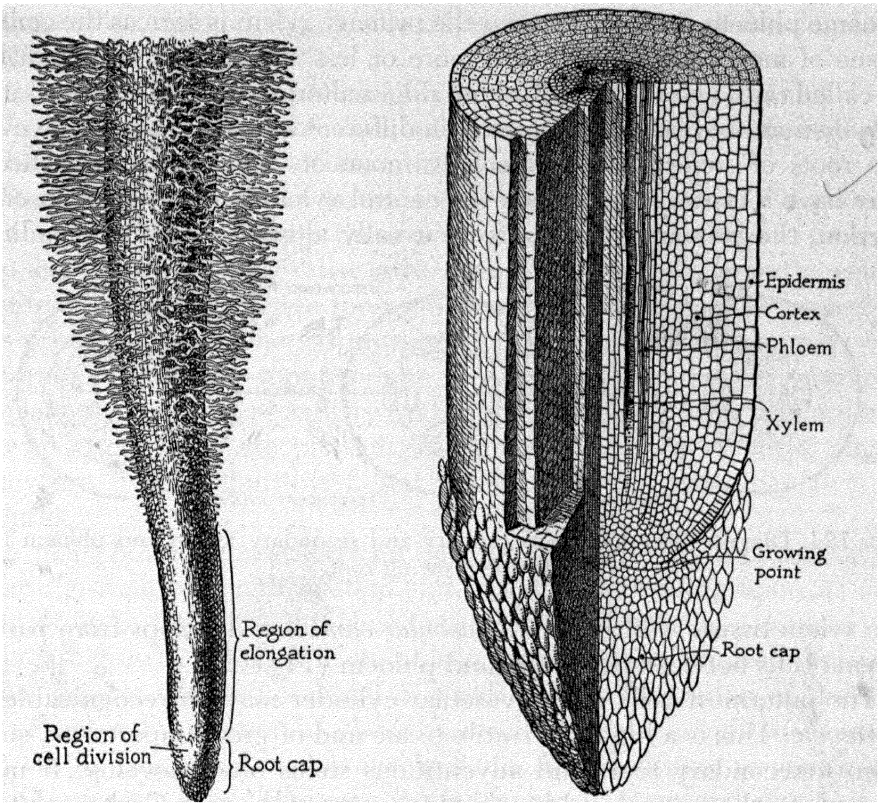

FIG. 122. Relative position of root-hair zone and region of growth in length in a root tip. Courtesy of World Book Co.

FIG. 123. Diagram of the general arrangement of tissues in a root tip. Courtesy of World Book Co.

division and cell differentiation. Farther up the young root, differentiated cells become more and more conspicuous. The epidermal cells elongate parallel to the axis of the root. As elongation slows down, *root hairs* begin to appear as tubular extensions of some of the epidermal cells, and within a few hours they attain their complete elongation at right angles to the surface of the root.

Near the center of the vascular cylinder rows of cells extending lengthwise in the root become conspicuously large. These cells are the forerunners of the primary xylem vessels. The cross walls disintegrate, and spiral thickenings are formed along the longitudinal walls before the protoplasm disintegrates. Other strands of cells in the vascular cylinder

become phloem. In cross sections the primary xylem is seen as the central tissue of most roots and is often more or less star-shaped, although the so-called radii (ends of longitudinal ridges alternating with troughs) may vary in number from 2 to 5 or more in different kinds of plants. However, the roots of some plants, especially monocots and herbaceous dicots, may have a central pith. When the central xylem is star-shaped in cross section, the primary phloem tissue usually alternates with the radii of

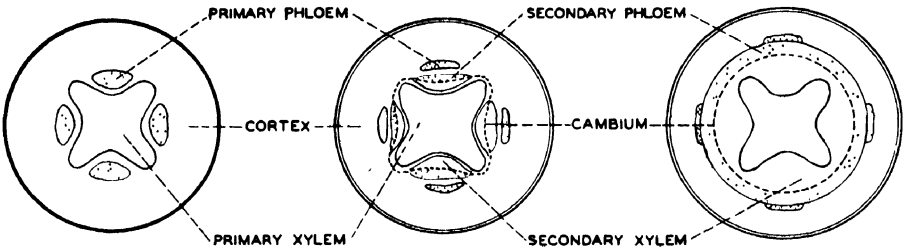

FIG. 124. Diagram of relations of primary and secondary xylem and phloem in a young growing root.

the xylem tissue. A little later a *vascular cambium* develops from parenchyma cells between the xylem and phloem (Fig. 124).

The outermost cells of the vascular cylinder may be recognizable as *pericycle*. This is a highly versatile tissue and of great importance, since from it secondary roots and adventitious stems often develop. It may, through further growth, add to the thickening of the root. Cork cambiums usually develop from the pericycle in young roots.

The inner layer of the cortex adjoining the pericycle usually becomes more or less recognizable as an *endodermis*. The thickness of the cortex varies greatly in roots of different kinds of plants. In very young roots it is usually the most conspicuous part. The first cork cambium in the young roots of some plants may develop from cortical parenchyma.

Among the last tissues to appear in a young root are the primordia of lateral roots. Unlike the primordia of axillary branches of stems, these root primordia develop not from the young epidermal and cortical cells near the apex but from deeper lying tissues (usually the pericycle or, in older roots, the phloem) at some distance from the apex. Renewal of cell division in scattered groups of cells in the pericycle results in root primordia that grow outward through the cortex and emerge through the epidermis as secondary roots. Lateral roots are said, therefore, to have an *endogenous origin*, in contrast to the *exogenous origin* of the stems that grow as axillary branches. Stem branches may also have an

endogenous origin, especially the adventitious stems that develop from roots.

Lateral roots often appear mainly in two or more rows up and down the root, because most of the root primordia originated opposite the radially arranged ridges of the primary xylem.

Some of the differences in the apical regions of stems and roots may now be noted. In stem tips there is no structure comparable to the root cap, even in the rhizomes that grow in the soil. The cells from the center of the apical meristem are forerunners of pith which is surrounded by the primary xylem, whereas in most roots they are the forerunners of a central xylem. At the root tip there are no lateral organs comparable to the lateral primordia of axillary buds, foliage leaves, or the primordia of flowers. Root hairs are present near the tips of roots of most plants. They are usually short-lived, but in some species they may live for months.

A plant hormone necessary for cell enlargement may increase or decrease growth in length in stem and root tips depending upon its concentration in the cells. But the concentration of hormone necessary to decrease growth in length in stems is in the order of a hundred thousand times greater than is necessary in roots. The concentration of the hormone naturally present in plants is usually great enough to decrease growth in length in roots but not in stems. Such facts are needed if one is to understand the difference in geotropism in stem and root tips, as shown in Chapter XXIII. The direction of growth of young lateral roots, like that of lateral stems is influenced by apical dominance.

Secondary growth of roots. Most of the root tissues mentioned above are primary tissues that developed from the cells of the apical meristem. Secondary growth in thickness results primarily from the development of a vascular cambium as a cylindrical sheath between the xylem and phloem. From the cells formed by this cambium, increase in xylem and phloem occurs as in stems.

The secondary growth may result in breaking and loss of epidermis. The cortical tissue may continue enlarging for a time, or it too may be broken and sloughed off. The pericycle survives in roots of some kinds of plants much longer than in others. The thickened herbaceous roots of some plants, such as those in long conical radishes and sweet potatoes, are the result of growth of the vascular cambium plus further division of the parenchyma cells of xylem, phloem, or pericycle. The concentric rings seen in cross sections of beets are the cut edges of a series of cone-

shaped layers of tissue (Fig. 125). The innermost cone is formed by the growth of the primary vascular cambium. The others are formed by the growth of a series of anomalous secondary cambiums, which may originate from parenchyma cells in the phloem or in the pericycle. The thickened portions of turnips and conical radishes are largely xylem; but in parsnips the tissues external to the xylem are most prominent. Increase in thickness of bark, especially of roots of trees and shrubs, is partly the result of the development of cork from cork cambiums.

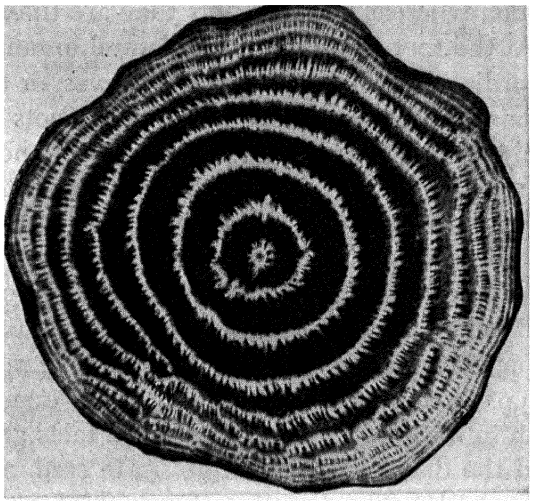

FIG. 125. Concentric rings of tissues visible in cross sections of beet roots formed by the development of a succession of secondary cambiums in pericycle and phloem parenchyma. Photo by E. F. Artschwager, *Journal of Agricultural Research*.

The size and extent of root systems. The primary root of a seedling continues its downward extension into the soil. Root hairs develop within a few hours, and lateral secondary roots within a few days. If the plant has a taproot system, the primary root continues growth for weeks or months, and under favorable conditions may penetrate the soil to a depth of 5, 10, 20, and even 30 feet. The roots of most plants, however, develop in the upper 3 to 5 feet of soil. In regions of abundant rainfall and high water table, root systems in general are nearer the surface than in regions subjected to periodic drought (Fig. 126). In deserts there are many species of cacti with widespreading root systems less than a foot below the surface, and species of yuccas and desert shrubs nearby with roots which penetrate deeply.

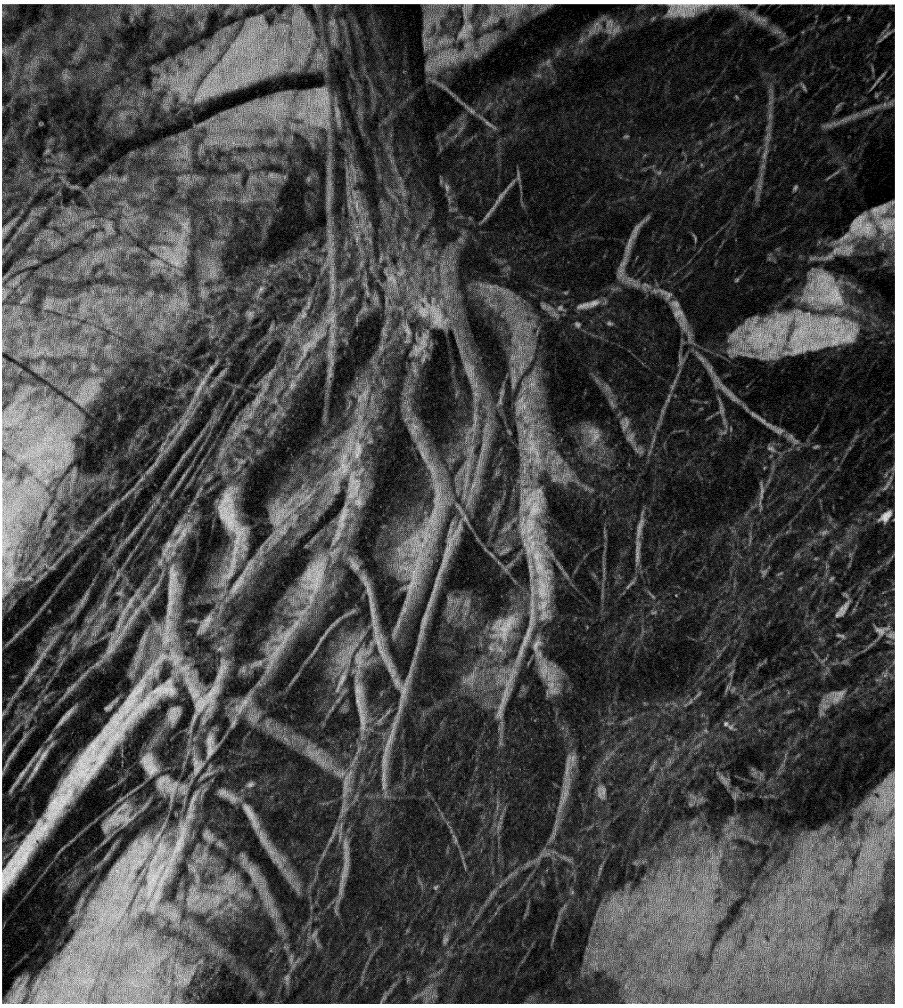

FIG. 126. Roots of hemlock and spruce on a rocky slope in the Smoky Mountains. The layer of mosses and ferns under which they first grew have been washed away. The terminal roots are located deep in the crevices of the rock. Photo by E. N. Doan.

Contrary to common belief, roots do not grow through dry soil in search of water (Fig. 127). When a portion of the root system of a plant is exposed to moist soil and the remainder of its system to dry soil, the portion in moist soil grows extensively, while the portion in dry soil grows but little or not at all, depending upon whether water coming from the roots wets the soil enough in advance of the root tip.

The horizontal distribution of the root system of a plant is not dependent upon either the diameter or the height of the part above ground. The frequent statement in popular literature that the horizontal spread

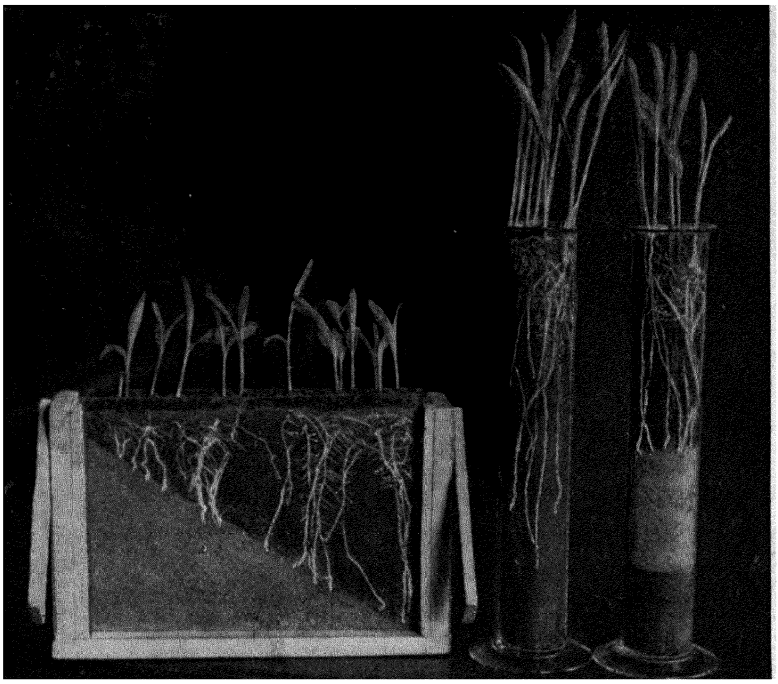

FIG. 127. Effects of dry soil (lighter color) on the growth of roots. Photo by F. H. Norris.

of the root system of a tree is the same as the diameter of the crown is erroneous. Isolated trees on a lawn or campus may have a horizontal spread of roots as much as 4 to 5 times the diameter of the crown. A young pear tree was found to have a horizontal spread of roots 9 times the diameter of its crown.

Plants closely crowded together do not have as extensive root systems as isolated ones. The more extensive root system may or may not occur with the larger crown. The root system of a corn plant at Lincoln, Nebraska, commonly has a horizontal spread of about 7 feet and a vertical penetration of about 6 feet. At Wooster, Ohio, the horizontal spread of the root system of a corn plant is generally about 3 feet, and the depth about 2 feet. These figures represent differences in the growth of root systems due to the combined effects of heredity, climate, and soil.

Many factors affect the development of root systems. The striking differences in form of the root systems of different species of plants are expressions of different heredities in similar environments. But expres-

sion of heredity may vary greatly in different environments. The wild ancestors of our cultivated varieties of beets and radishes had comparatively slender and woody roots. The thickened herbaceous characteristics of these cultivated varieties are hereditary, but under certain conditions of temperature and length of day the roots fail to thicken; that is, this particular hereditary potentiality is not expressed under certain environmental conditions. It will be helpful to visualize root systems as we do the crowns of trees. Certain specific characteristics are often evident, but in different environments their development may be greatly altered.

In considering the factors that affect the growth of root systems, one should not forget that sugar and hormones from the leaves are essential factors in root growth, and that any factor that influences the supply of these substances to the roots indirectly affects their growth (Chapter XXI). Gravity affects the direction of growth of roots but cannot be classified as either an atmospheric or a soil factor. Among the factors of the soil environment that affect physiological processes and growth in root systems are compactness or texture of the soil, water, oxygen, carbon dioxide, soil temperature, inorganic salts (essential, nonessential, and toxic), acidity and alkalinity, and soil fungi and bacteria. Only a few of these factors will be mentioned further in this chapter.

The compactness of the soil indirectly affects the growth of roots through its effects upon aeration and the rapidity of the movement of water and mineral salts. Directly it affects the penetration of roots. Many clay soils may become so hard during dry seasons that germinating seeds at the surface die through failure of the roots to enter the soil. Root systems in general are less extensive in compact soils, and root growth occurs mainly in the crevices of such soils. Soils of coarse texture are not good soils because, in spite of good aeration, the supply of water and available salts is often deficient under natural conditions. Between these two extremes of fineness and coarseness are the soils known as loams, in which roots grow best.

When roots grow through alternating layers of coarse and fine soils, far more branching and development of lateral roots occur in the layer of loam. Trampling, as it occurs in paths in gardens and greenhouses or on trails and roadways, makes the soil compact. Pioneer roads abandoned for a century or more are still evident in forests because few plants can grow in such compact soils. Excellent virgin soils that were thousands of years in forming become more compact through careless farm prac-

tices, partly because of the oxidation of organic matter in them and partly by the removal of the surface layers down to the more compact subsoil. The failure of plants to grow well on many abandoned farms is due not so much to lack of essential salts as to the compactness of the soil. The social significance of these facts has but recently been recognized by the general public.

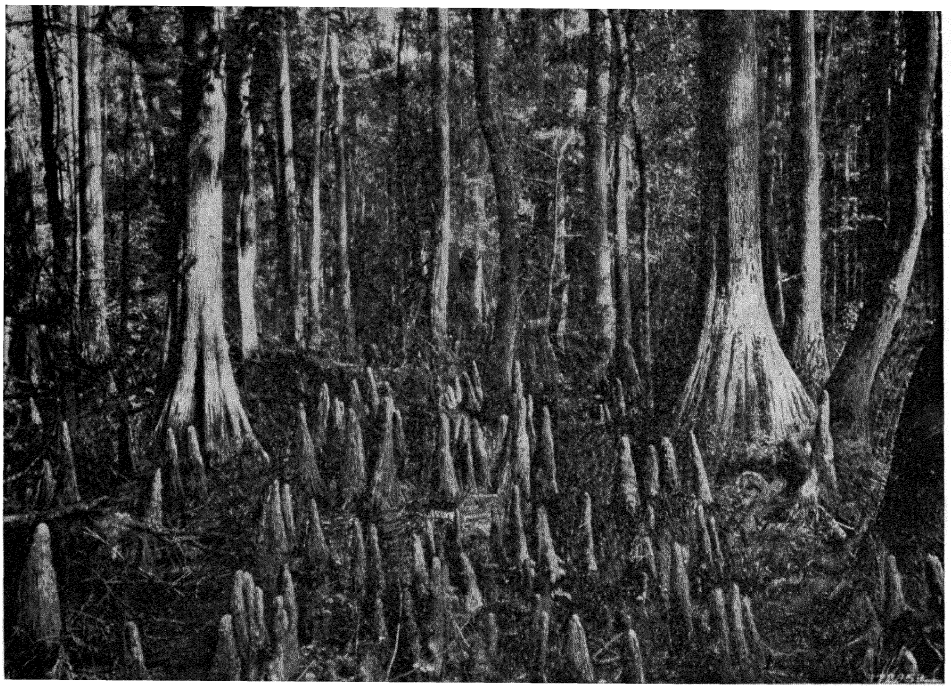

FIG. 128. Development of "knees" from the roots of bald cypress when growing in lowlands annually submerged by floods. Photo by U. S. Forest Service.

Available oxygen has an immediate effect on respiration, and consequently on growth. The roots of some kinds of plants, such as willow, cottonwood, and cypress, can survive and grow in much lower concentrations of free oxygen than roots of many other kinds of plants (Fig. 128). Oxygen is not necessarily obtained from the soil air by some plants, such as those growing in swamps or in partly submerged areas. Many of these marsh plants have continuous air cavities extending throughout the plant. The green shoots above may well have an excess of oxygen in the daytime, and there is always some

movement of oxygen from the atmosphere into the air cavities through open stomates.

Windfalls frequently display the root systems of trees that have grown on bogs and swamps (Fig. 129). Often none of the larger roots has



FIG. 129. Major root system of an arbor vitae tree overthrown by a wind storm. The tree had been growing in a bog and the uppermost layers of peat were lifted with the roots. Photo by G. W. Blaydes.

penetrated the substratum more than one foot. The roots that lived and attained age were those just beneath the surface. Toward the close of the last century, thousands of miles of fences were made of these flat root bases of white pine set up side by side, enclosing pastures after lumbering had denuded the land. Yet when white pine stumps were pulled from sandy upland, they had several roots an inch or more in thickness down to ten feet below the surface.

The effects of submergence in rapidly flowing water differ from those

of stagnant water largely because of the different amounts of oxygen available. When plants are being considered, the expression "good drainage" should be interpreted as good oxygen supply rather than water movement.

The well-known fact that the roots of willows, cottonwoods, and elms will develop excessively in drain pipes and stop the flow of water is due to the combined result of constantly available moisture and oxygen.

The more direct effects of *temperature* on root development are largely expressions of the fact that higher soil temperatures accelerate and lower ones retard development. In polar regions the soil may be constantly frozen a few feet below the surface; only the upper layers thaw in midsummer. Root systems there are usually very shallow.

The available *inorganic salts* in a soil may increase or decrease root development. Low concentrations of nitrogen in the form of ammonium compounds and nitrate may restrict it. If nitrogen is present in greater concentration and the manufacture of proteins is not curtailed, average root systems are formed. Excessive amounts of nitrogen may result in larger root systems in some plants and in smaller ones in others, accompanied in both cases by excessive development of the tops. Consequently, one frequently finds greater development of roots *in proportion to the shoots* in poor soils than in soils rich in nitrogen.

Large amounts of salts, such as occur in salt and alkali flats in dry regions, become limiting factors to most plants, and only a few species survive these conditions. When salts accumulate to 2 per cent of the dry weight of the soil, practically all flowering plants are killed.

With the effects of all these factors in mind, one should be able to explain some of the examples of root distribution that he encounters in the field, in road cuts, and in excavations, and the many diagrams of root systems available in botanical literature.

Root surfaces compared with leaf surfaces. Many studies of the relation between the depth and extent of root penetration and the height and size of the shoots of plants have been made. The relative weights of roots and shoots of many economic plants have been studied at the agricultural experiment stations, particularly following different methods of cultivation, crop rotations, frequency of cutting, and the addition of fertilizers. Few studies have been made of the areas of entire root systems, including the finest roots and root hairs, in relation to the areas of leaves and stems.

The total areas of tops and roots of winter rye grass have been meas-

ured in detail. Some of the results as reported are given here. The plant grew for 4 months in a fertile soil contained in a wooden box a foot square at the top and 22 inches deep; that is, somewhat less than 2 cubic feet of soil. The plant had 80 shoots with an average of 6 leaves per shoot, and was about 20 inches tall at the end of the experiment. The total exposed surface of the top of the plant was 51.4 square feet. The number, length (if placed end to end), and area of the roots are best seen from the accompanying table.

Roots	Number	Total Length	Total Surface
Main roots	143	214 ft.	1.5 sq. ft.
Secondary	35,600	17,800 ft.	45.0 sq. ft.
Tertiary	2.3 million	574,000 ft.	758.6 sq. ft.
Quaternary	11.5 million	1.4 million ft.	1,748.9 sq. ft.
Total	14 million	2 million ft.	2,554 sq. ft.
Root hairs	14 billion	6,000 miles	4,321 sq. ft.

From these figures one may see that the total surface of the roots is about 130 times that of the shoots. The presence of nearly 14 million roots and 14 billion root hairs with a total surface of 6800 sq. ft. in less than 2 cu. ft. of soil shows how completely every part of the soil may be penetrated. The roots are thus in contact with much of the water surrounding the soil particles and with the salts and other compounds dissolved in the soil water.

If we assume an average daily rate of growth during the four-month experimental period, 3 miles of new roots and 50 miles of new root hairs (100,000,000) were added each day. In nature the daily invasion of new soil masses might be of great importance if the water content of a soil were decreasing, or if the soil solution of inorganic salts were very dilute.

In the chapter on transpiration it was shown that the principal evaporation surface is the mesophyll when the stomates are open. The mesophyll surface of winter rye grass is perhaps 6 times that of the epidermis of the shoots. Even when the stomates were open, the plant described in this experiment had an absorbing surface 22 times that of the evaporation surface.

When the root systems of winter rye grass were compared with those of oats, and of bluegrass under *field* conditions, the following relative results were obtained:

	Number of Roots	Total Length	Total Surface
Oats	4,700	150 ft.	50 sq. in.
Winter rye grass	6,400	210 ft.	78 sq. in.
Bluegrass	84,500	1,250 ft.	332 sq. in.

From these figures it is evident why bluegrass is so effective in forming turf and in preventing soil erosion. Further evidence of its copious root system is obtained when a comparison is made of the roots of three grasses growing in the field under similar conditions. An examination of sample volumes of soil, 3 inches in diameter and 6 inches deep (42 cu. in.) showed that for each cubic inch of soil:

Oats had 15 sq. in. of root surface and 150,000 root hairs.

Winter rye grass had 30 sq. in. of root surface and 300,000 root hairs.

Bluegrass had 65 sq. in. of root surface and 1,000,000 root hairs.

The roots of oats occupied 0.55 of 1 per cent of the soil volume; those of winter rye grass 0.85 of 1 per cent; and those of bluegrass 2.8 per cent.

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CHAPTER XXX

ROOTS: PROCESSES AND SOIL RELATIONS

If we include both subterranean and aerial roots in our purview there are few processes in leaves and stems that do not also occur in roots. Cell division, enlargement, and differentiation; respiration; transpiration; sugar, fat, and protein syntheses; digestion; assimilation; absorption and movement of water and mineral salts; and the translocation and accumulation of substances are just as characteristic of roots as they are of leaves and stems. Some of these processes, however, are not equally prominent in every type of leaf, stem, or root.

Photosynthesis in roots is limited to those roots which become green when exposed to light, and is characteristic especially of the epiphytes, such as tropical orchids, bromelias, and ferns. However, the roots of many land plants exposed by current and wave action along lake shores and stream banks may become green and add to the sugar supply of the root. Transpiration occurs from the roots of epiphytes, and from any other root surfaces exposed to air, either above or below the soil surface.

The soil environment. Before discussing the other processes occurring in roots we should consider a few of the conditions in the soil as an environment in which roots grow. First of all the soil is a mass of larger and smaller particles of minerals derived from underlying rocks, or carried in from adjoining regions by water, ice, and wind. Through the centuries this "parent material" of the soil is modified by weathering which includes rainfall and drought, freezing and thawing, solution and precipitation, leaching and chemical reorganization.

Meanwhile plant stems and roots have thickly penetrated all the surface layers every year, and the lower layers at least every few years. All or parts of these organs have died each year, and their organic compounds have been incorporated in the soil. These compounds become the food supply of an enormous population of bacteria, fungi, and minute animals that alter the organic residues and, according to conditions, in-

crease or decrease the available organic compounds and the water-holding capacity of the soil, as well as its texture and penetrability.

The interstices among the irregular soil particles make up from a third to a half of the soil volume. After a rain they are partly or entirely filled with water (Fig. 130). The air in these interstices constitutes a "soil

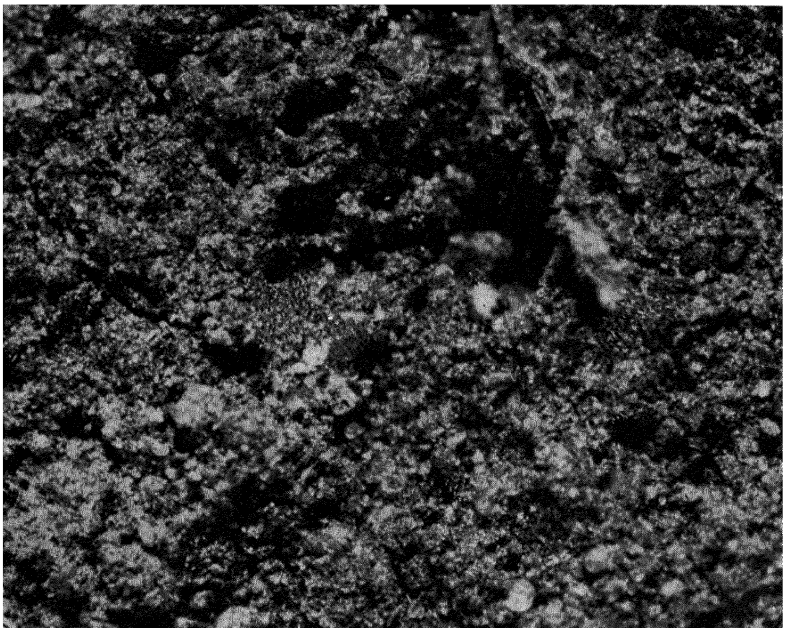

FIG. 130. Arrangement of soil particles and interstices in a cultivated field. Photo by L. D. Baver.

atmosphere." Water movement in these spaces is for the most part by capillarity, and to a slight extent by gravity. The lateral movement is almost as rapid as the downward movement.

Following a rain the water gradually approaches an equilibrium in which similar parts of the soil mass have about the same water content. Water vapor is also diffusing through the soil mass and some of it diffuses out of the pores at the soil surface. Soluble salts are likewise diffusing in the soil solution from the regions in which they are more highly concentrated. They are also carried about during mass movement of the water in the soil. Owing to electrical forces, some of the mineral ions become adsorbed (electrically held) on the surfaces of soil particles until replaced by others.

Oxygen diffuses into soil from the atmosphere and is also carried into it in solution in rain water. Within the soil atmosphere is the oxygen necessary for respiration in roots and countless numbers of small plants and animals that inhabit the soil. Sometimes its concentration in the soil is very low.

Carbon dioxide, because of its high solubility in water, enters the soils in rain water especially if that water percolates through a layer of leaf litter, duff, and humus at the soil surface. It also diffuses into the soil air and soil solution from respiration in roots and soil organisms. Soil air may contain as much as 5 to 15 per cent of carbon dioxide.

In temperate regions soils may undergo rather rapid temperature changes at the soil surface, where in the summer time fully exposed areas may be heated as high as 120° to 140° F., or even higher. Temperature fluctuations gradually decrease from the surface downward until the temperature is more or less stabilized at about the average annual temperature of the locality.

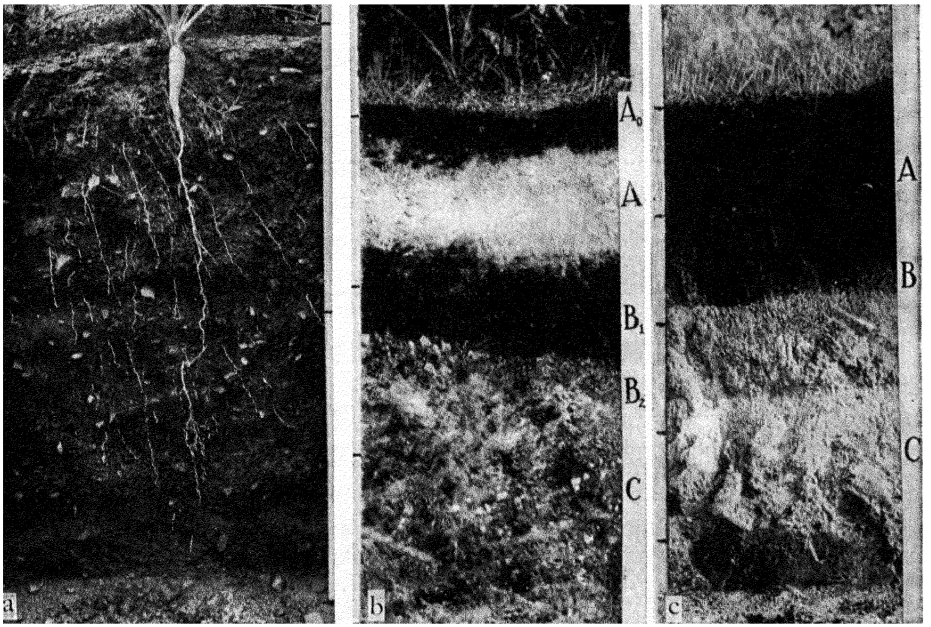

FIG. 131. Profile of a cultivated soil (a) with the roots of a carrot in place; the profile of a mature soil (b) that developed beneath a northern coniferous forest; and (c) the profile under a northern mixed prairie. One-foot intervals are indicated at the side of each picture. Photos, (a) from H. C. Thompson, Cornell Univ.; (b) and (c) from C. E. Kellogg, United States Department of Agriculture.

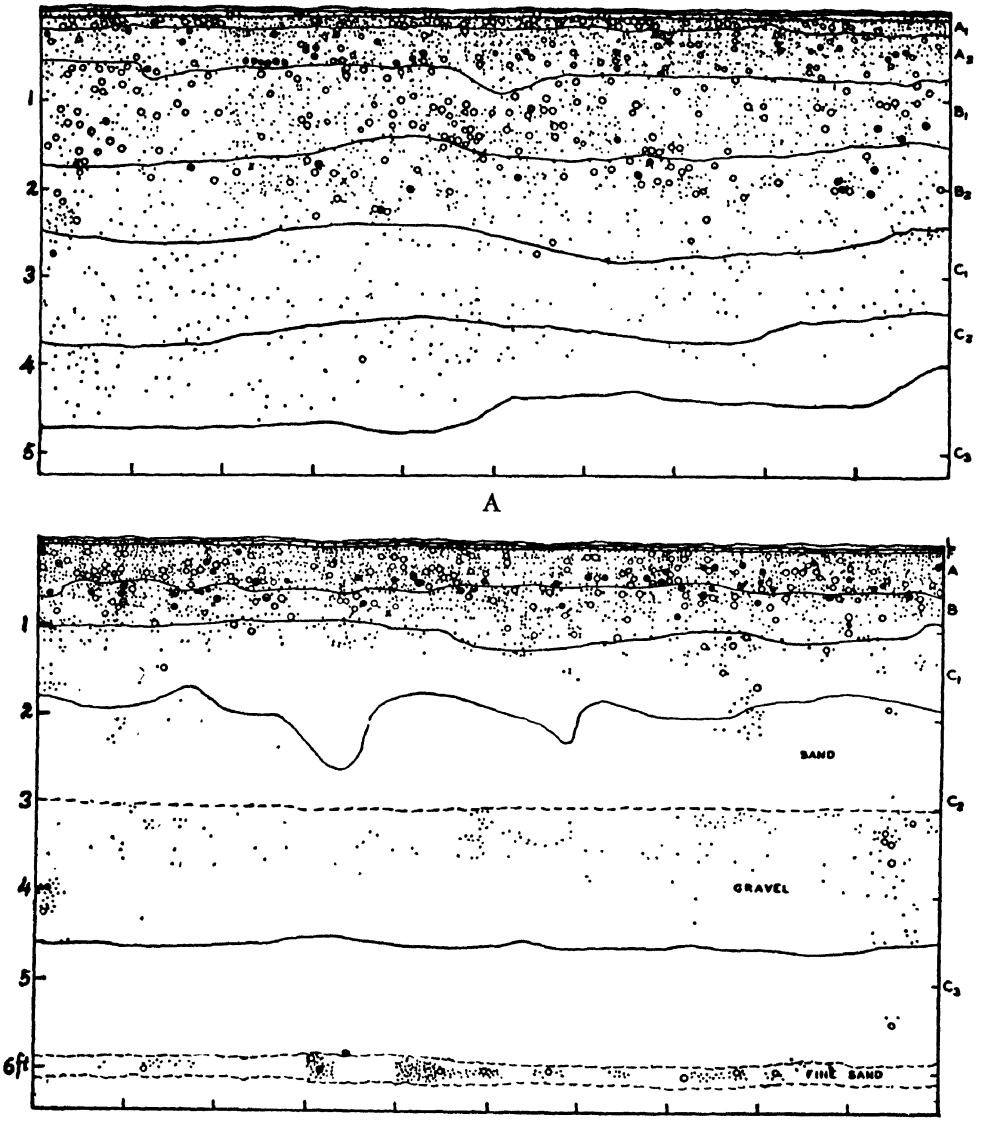

FIG. 132. Two diagrams illustrating the distribution of the roots of white pine in soil profiles having layers of different texture, color, water content, and aeration. After H. J. Lutz, *Yale Forestry Bulletin 44*, 1937.

Diagram of soil profile (A). Uppermost layers of white pine debris and fungous mycelia. Horizon A, fine sandy loam, dark brown above, light brown below. Horizon B, fine sandy loam, brown slightly mottled. Horizon C, loam above, coarse sand below.

Diagram of soil profile (B). Loamy coarse sand in horizon A; color brownish gray, mottled. Horizon B, dark brown coarse sand. Horizon C, gray in color. gravelly, coarse sand except layer of fine sand at 6 ft. below surface.

After all these soil processes and activities have continued for hundreds or thousands of years, a soil usually has attained maturity and certain characteristic chemical and physical properties and water-holding capacities. Its constituents become arranged in layers or horizons of varying thickness beginning at the soil surface and ending below in the parent material. These layers may differ greatly in composition, reaction, and structure, but some parts of most root systems extend into each of them (Figs. 131 and 132).

Roots growing in a soil, then, are developing in a highly dynamic medium, in which chemical, physical, and biological processes are continuous, and in which the available soil water, soil solutes, and soil air may be as variable as those of the atmospheric environment in which the foliage and stems develop.

Field capacity and wilting percentage of soils. With reference to the actively growing plant there are two critical points in the water relations of a soil. The first is the amount of water that is held in equilibrium against further movement by gravity and capillarity in a given soil under field conditions. One may visualize this condition by assuming that a large mass of a uniform soil after a prolonged drought has become *air dry* to a depth of 5 feet. This soil still contains some water—about 1 per cent if composed of sand, and as much as 5 per cent if clay. Seeds do not germinate and seedlings do not survive under these conditions.

Suppose now that an inch of rain falls on this soil and it all penetrates the interstices between the soil particles. If the soil were sandy it might moisten the upper layer to a depth of a foot. If the soil were a fine clay only a few inches would become moist. After a day or two the water in the moist layer of soil has become uniformly dispersed. Neither capillarity nor gravity causes it to move farther downward. The soil water is now at equilibrium, and films of water surround the soil particles but do not fill the larger spaces among them. The water held at equilibrium is commonly called the "field capacity" of a soil. Sandy soils have a field capacity of about 5 per cent, and clay loams about 35 per cent (Fig. 133).

If a second rain of one inch followed, capillary forces would cause the water to move through the moist layer into the dry layer just beneath, and at equilibrium the fine soil would be moist to a depth of several additional inches, and the sandy soil another foot.

Under these conditions, seeds can germinate and seedlings grow rapidly. The roots of seedlings have a continuous water supply as their

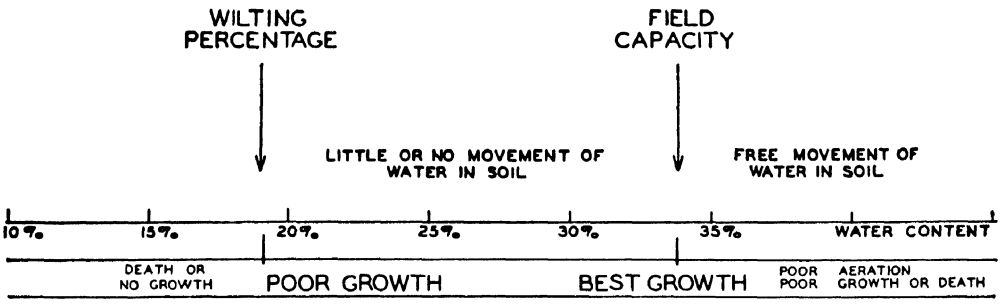

FIG. 133. Plant development in relation to water content of a clay loam.

innumerable branches and root hairs penetrate to all parts of the moist layer. Oxygen is abundant in the soil air and respiration is not restricted.

Let us now assume that no more water is added. After a few weeks, depending on the temperature, the young plants begin to wilt in the middle of the day, but recover their turgidity at night. The rate of absorption of water is not equal to the rate of transpiration during midday, but at night it is greater than the water loss. After several more days, however, the plants wilt and do not recover at night. In spite of the large root surface, water no longer moves from the soil to the plants, and they become *permanently wilted*. The *wilting percentage* is the amount of water present in a soil under these conditions. It varies from 1 to 10 per cent in sandy loams, from 15 to 20 per cent in fine clay loams.

Absorption of water by osmosis. Thus far we have visualized osmosis as occurring in each individual cell, in which the water inside the vacuole is separated from the more concentrated water outside the cell by the differentially permeable cytoplasmic membrane. It is possible also to visualize a whole root as one osmotic unit; that is, the water in the xylem vessels in the central cylinder of the root is separated from the water in the soil by the cambium and bark (phloem, pericycle, cortex, epidermis), which may be considered as one complex differentially permeable membrane.

These relations may be demonstrated by means of a thickened root, such as that of carrot. To simplify the problem, one may remove most of the xylem of the root with a cork borer and regard the cavity thus formed as one large xylem vessel, in lieu of the many original vessels removed by the cork borer. A glass tube may be securely attached to the top of the root to represent the continuation of a xylem vessel into the stem of the plant. If the cavity in the root made by the removal of

natural xylem is filled with a sugar solution and the root is then immersed in water, the sugar solution slowly rises in the attached glass tube.

The observed phenomena may be duplicated by substituting for the carrot root a long porous clay cup in the walls of which there is a differentially permeable membrane of copper ferrocyanide.[1] In the carrot root the differentially permeable membrane is considered to be all the layers of living cells between the xylem vessels and the water surrounding the root.

This demonstration is probably analogous to the movement of water from the soil through the cortex to the xylem vessels in a living root under certain conditions. When the stems of some plants, growing with an ample water supply, are cut off an inch or two above the soil, water may exude from the cut surfaces. Under these circumstances large quantities of sap exude from the stumps of a few kinds of plants, such as birch and grape. The water may exude from these stumps against a pressure of one or two atmospheres, which would be sufficient to push water to the tops of small trees. Such pressures, however, are lacking at the time of year when the water loss from leaves is greatest. During that time the water is being pulled upward in the roots and stems at a rate that far exceeds the rate of exudation.

Guttation. The extremely wet grass one often sees on lawns at night and early morning is not always a result of the formation of dew. When the humidity in the air is high and the soil is moist, each blade of grass has a glistening drop of water at its tip. This loss of water in liquid form at the ends of veins of leaves is called *guttation*. Early-morning golfers are often annoyed by the fact that this water contains sugar, because when the water evaporates from their hands and from the handles of golf clubs a sticky sirup remains.

Guttation may be demonstrated in the leaves of many kinds of plants by placing bell jars over well-watered plants in pots or by attaching leaves or branches to a water faucet by a hose connection. Guttation may also occur in plants in greenhouses when excessive amounts of water have been added (Fig. 134). The veins of the leaves are continuous with those of the stems and roots, and where they end in the leaves there may be an open meshwork of parenchyma cells covered by an epidermis containing stomates or pores. Guttation is probably the result of conditions

[1] The copper ferrocyanide membrane is formed in the walls of a porous clay cup previously soaked in water, if the cup is filled with a solution of potassium ferrocyanide and immersed in a solution of copper sulfate.

exemplified by the carrot-root demonstration without any artificial manipulation of the structures of the plant. In other words, guttation may be the result of the processes by which pressure is built up in the xylem vessels of the root system by the osmotic absorption of water across the complex membrane of tissues external to the xylem. This pressure may become great enough to push water up the vessels and out of the ends of the veins of some of the leaves of a plant.



FIG. 134. Guttation in leaves of tomato in a moist atmosphere. Photo from J. H. Gourley.

During early autumn, when the soil is warm and moist and the air is nearly saturated with water vapor, drops of water exude from the points on the leaf margin of oaks, maples, cottonwoods, and other trees. This is another example of guttation, often mistaken for dew.

Absorption of water by pull of transpiration and osmosis. The phenomena of guttation and "bleeding" from cut stems have sometimes led to the conclusion that the pressure developed in roots is the cause of the upward movement of water in tall stems under all conditions.

However, if a hole is bored through the bark of a tree and an inch or

two into the wood and a glass tube filled with water is quickly attached by a tight-fitting rubber stopper, one may readily discover whether the water in the trunk of the tree is under pressure or under tension. If the lower end of the tube is immersed in a vessel of water and there is internal pressure, water will flow into the vessel; if there is tension, water will flow into the tree. The best time to set up such an experiment is during a light rain, or in the early morning before sunrise. Gauges that register both positive and negative pressures have been used in similar experiments.

In most experiments it was found that in late spring and early summer, when transpiration is highest, there is tension, not pressure, and that water may be drawn from the vessel into the tree. This would be difficult to explain on the basis of root pressure.

An experiment described on page 321 may be used to detect water tension and pressure in roots. If a plant is cut off when transpiration is

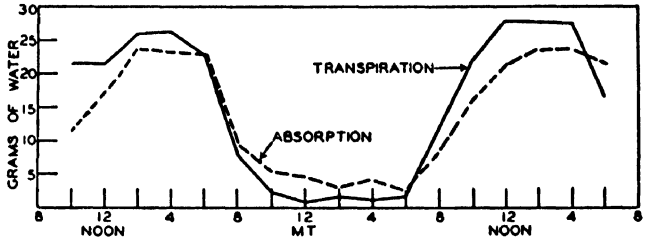

FIG. 135. Curves of hourly rates of absorption of water, and the simultaneous rates of transpiration. Internal water tension, or pressure, results. Data from P. J. Kramer.

rapid, and a water-filled tube is immediately attached to the stump, the water level in the tube falls. Even when the soil is wet, positive pressures and consequent rise of water in the tube do not occur until after a lapse of one-half to two hours' time. In this experiment it appears that, despite osmotic relations in roots, the root cells were not fully extended. Some of the water evidently had been drawn out of the roots by transpiration in the leaves above (Fig. 135).

Additional evidence that the water content of tree trunks decreases during periods of rapid transpiration is the fact that the diameter of tree trunks varies with the time of day. It is least in the afternoons of clear, hot days, and greatest in the early morning hours (Fig. 136).

The flow of maple sap. The flow of maple sap from trees in early spring

is conditioned not only by the effects of root pressure but also by the presence of gases in the xylem tissues. The flow is greatest during the period when freezing temperatures occur at night and daytime tempera-

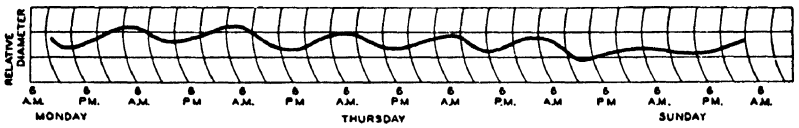

FIG. 136. Daily variations in the diameter of the trunk of a Monterey pine. The contraction of the wood cells is a result of tension on the water columns due to transpiration. Stems of plants shrink in diameter in the afternoons when the rate of transpiration is relatively high. Data of D. T. MacDougal (1936).

tures are well above the freezing point. At this season the sugar content of the tree is high. Transpiration is low because the buds have not yet



FIG. 137. Method of collecting "sap" from sugar maple.

opened and absorption of water by the roots is active. When the twigs and smaller branches are warmed by the sunlight, the gases in the xylem expand. The resulting pressure added to the pressure developed in the roots causes the sap to flow from the tap-holes in the trunk (Fig. 137).

When the leaves have begun to develop, the "sap pressure" becomes negative, sap ceases to flow from the tap-holes, and (with experimental equipment) water is drawn into the tree instead of being forced out.

During the maple sap season, most of the sap and sugar flows out before noon of any one day. The total yield of sugar from different trees is roughly proportional to their summer leaf areas. When three taps were made in a tree, one at the top of the root, another at a height of four feet, and a third just below the branches, one-half of the yield came from the tap four feet from the ground, one-fifth from the root tap, and the remainder from the upper tap. These are some of the more interesting facts about the flow of maple sap. From the experimental data now available it is evident that a satisfactory explanation of the flow of maple sap will include not only root pressure and gas pressure, but also other internal relations now unknown.

Dead root systems. If water is pulled upward in stems through xylem cells that are dead, what will be the effect of killing the roots without injuring the stem? An answer to this question may be obtained by killing the roots of plants with hot water. Of course the living membranes of the roots of these plants will be destroyed and osmotic movement of water ended. When such experiments were performed, it was discovered that not only may the plants continue to live for a week or two but the transpiration rate increases, and in some plants becomes several times as great if the soil is wet. Under what conditions and in how many ways are living root systems superior to dead root systems?

Absorption of inorganic salts. Not only does water enter plants from the soil, but inorganic salts also enter from the soil solution. When plants grow freely suspended in water, as the algae in the microcosm described in Chapter XX, soluble salts in the water may diffuse into any cell of the plant. In rooted plants the salts enter mainly through the root system. A smaller amount may enter through rhizomes, or even through leaves and young stems that have been covered by a film of salt-containing water. This is particularly true of leaves of Spanish moss, pineapple, and other plants of the bromelia family. The peculiar leaves of the pitcher plant exemplify another condition in which salts may diffuse directly into the leaves. Perhaps many other leaves with cup-like bases in which water collects during rains similarly absorb a small amount of salts directly.

Salts in solution may diffuse directly into the root tip and root hairs, or the outer layer of pectic compounds on the root hairs may be in such close

contact with soil particles that the salt ions adsorbed on their surfaces may move from one to the other without actually being in solution. Thus the entrance of a salt into roots is influenced not only by the concentration of the salt and the permeability of the protoplasm, but also by the electrical charges on its ions and those on the surfaces of soil particles and of root cells. The physical and chemical processes involved in the absorption of salts other than simple diffusion are so complex that we shall omit further consideration of them.

It may be noted, however, that any salt in the soil surrounding the roots may enter the plant. Neither the kinds nor the proportions of salts found in plants bear any necessary relation to "what the plant needs." After the ions of a salt have entered a plant they may remain in solution, become a part of organic molecules, form salts with organic acids and bases, accumulate in crystalline form, or be adsorbed on the surfaces of the colloidal particles in the protoplasm and cell walls. The ease with which some of the ions of a salt may be removed from the protoplasm without killing the cells may be demonstrated by placing leaves of elodea in water at 90° F. for an hour or two. Some of the calcium in the protoplasm is set free and forms beautiful crystals of calcium oxalate with the oxalic acid that was already free in the vacuoles of the cells.

Relation of inorganic salts to plant development. Most people know that the growth of a plant is often improved after certain salts have been added to the soil, and that the practice of applying fertilizers containing salts of nitrogen, phosphorus, and potassium to fields and gardens would be discontinued if it were not profitable. On some kinds of soils it is profitable to apply salts containing certain other elements.

Fig. 138 illustrates the relative development of a tomato plant when nitrogen or some one of several mineral elements is not present in the salts added to the sand in which the roots grow. It is customary to refer to these plants as having grown in a sand culture; that is, the pots were filled with pure quartz sand, and then a culture solution, made by placing a known amount of certain chemically pure salts in distilled water, was added from time to time. Perhaps no chemical element is absolutely lacking in these experiments. Many kinds of chemical elements were in the compounds in the seed from which each plant grew, and it is impossible to obtain absolutely pure sand, water, or salts. It is quite evident, however, that any one of several elements may be so deficient that the plant grows but little and fails to complete its entire life cycle.

The characteristic differences in growth and appearance of a plant,

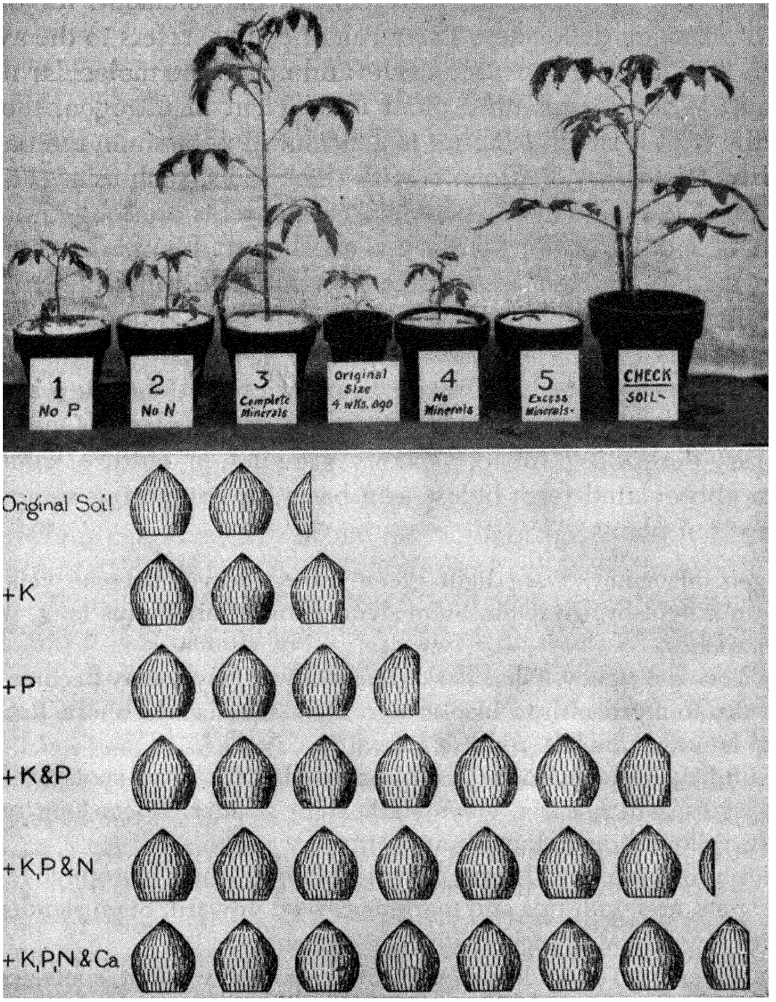

FIG. 138. Relative growth of plants in relation to the concentration of various ions of inorganic salts: Upper—tomato plants; lower—a diagrammatic representation of the effects of ions on the yield of hay in an unplowed meadow in southern Greenland. The ions added to different parts of the meadow are indicated on the left. Each haystack represents a yield of 1,000 pounds. The yields indicated are averages per acre of 8 successive harvests. Data from Danish Experiment Station of south Greenland.

when the supply of some element is inadequate, are referred to as deficiency effects, or symptoms, in respect to that element; for example, effects of nitrogen deficiency. The term, of course, refers to the available nitrogen in ammonium or nitrate salts and not to the molecular nitrogen in the air. When a cucumber plant is deficient in nitrogen, the apical end of the fruit is small. When it is deficient in potassium, the basal end of the fruit is small. When plants with thick roots, such as sweet potato, are deficient in potassium or phosphorus, the roots are long and slender because of a failure of cell division in the cambium. Continued cell division in the meristem appears to be related to the fact that mobile ions of potassium and phosphorus accumulate most abundantly in apical meristems.

Several investigators have made summaries of deficiency symptoms of each of several elements in different species of plants. One of these summaries describing tobacco plants growing in culture solutions is given in abbreviated form below as a basis for comparing symptoms in other kinds of plants.

Nitrogen deficiency. Plant light green. Lower leaves become yellow, die, and dry to a light-brown color. Stem slender and short. Roots long, with few lateral branches.

Phosphorus deficiency. Plant dark green. Lower leaves may become yellow, die, and dry to a greenish to black color. Stem slender and short. Roots long, with few lateral branches, reddish brown in color.

Potassium deficiency. Lower leaves mottled, with dead spots at tips and along margins, which curve downward. Stem slender. Roots long with few branches; yellowish and slimy in appearance.

Magnesium deficiency. Lower leaves chlorotic (no chlorophyll), usually without spots, and with tips and margins curved upward. Stem slender. Roots long, with few lateral branches; slimy in appearance.

Iron deficiency. Young leaves chlorotic, usually without spots, principal veins green. Stem slender and short. Root short, with abundant short laterals, brown in color. Terminal bud of stem remains alive.

Manganese deficiency. Young leaves chlorotic with scattered dead spots. Leaf appears checkered because of the green color of the small veins. Stem slender. Roots not abundant; brownish in color. Terminal bud of stem remains alive.

Sulfur deficiency. Young leaves light green, no dead spots. Veins lighter green than intervein tissue. Stem short and slender. Roots white, abundant and much branched. Terminal bud of stem remains alive.

Calcium deficiency. Young leaves in bud curved and hook-like; die at tips

and margins. Terminal bud dies. Roots short, much branched, dark brown in color.

Boron deficiency. Young leaves in terminal bud at first light green at base; later disintegration is evident, followed by twisted growth. Terminal bud dies. Roots have many short laterals; brown in color.

If one were to attempt a complete explanation of each deficiency effect, it would be necessary to know the first effect of the chemical element on one or more processes in the cell and then to show that without these first effects certain other processes would not occur. This is not easy to do, and with our present knowledge it is usually impossible. Perhaps the reader would be content to say that chlorosis in the absence of magnesium is the result of the fact that magnesium occurs in the chlorophyll molecule and no chlorophyll could be made without it. But how shall we explain chlorosis in the absence of iron or of manganese? We cannot, of course, pursue this problem in detail in a general textbook, but we may emphasize certain useful perspectives.

In previous chapters each of the major plant processes (photosynthesis, respiration, digestion, assimilation, etc.) was presented in a simple manner. That is, the products used and the products formed were named, and it was usually noted whether oxidation, reduction, condensation, or hydrolysis was involved. We omitted the series of intermediate steps in each of these major processes, partly because many of them have not yet been discovered, and also because they involve many complex chemical compounds. For example, in muscles of animals, glycogen is changed to lactic acid, and vice versa. It is now fairly well established that at least 10 different enzymes and as many kinds of intermediate products are formed during these major changes. Furthermore, nearly every one of these enzymes and intermediate products is adequately active only when phosphorus is present and temporarily combines with them; that is, phosphorus is a catalyst in these processes. It appears to be a catalyst in most of the major processes in living cells, and for that reason has been referred to as "the dynamite of living cells." Many other elements, such as iron, manganese, magnesium, and potassium, are also catalysts in some of the major processes that occur in cells.

From the above discussion it is obvious that one cannot understand all the relations of the mineral elements to cell processes until all the steps in each of these processes are fully known. We may, however, at this time summarize the relations of the elements already discussed in previous chapters. We have seen, for instance, that nitrogen, sulfur, and

phosphorus are constituents of protein molecules; that nitrogen and magnesium are constituents of chlorophyll; and that calcium forms salts with pectic acid in cell walls. Carbon, hydrogen, and oxygen are omitted from this discussion, since, with the exception of oxygen in a few compounds like carotene, they are constituents of the molecules of all the substances of which cells are composed.

We have also seen that the ions of some of these elements are catalysts in cell processes. Others affect osmosis through their influence upon the permeability of protoplasm and to a minor extent upon the concentration of water in the vacuole. It was noted that sodium, which is not essential to most plants, increases the permeability of protoplasm and that calcium annuls this effect. This is but one example of numerous balancing effects of the different ions in cells. Almost any ion may influence the permeability, viscosity, and water content of protoplasm. Some of them even cause death of the cells in one or the other of these ways. The whole complex of organic acids, bases, and inorganic salts, especially of phosphorus, is capable of so many interrelated reactions that fluctuations in the acidity of the cell seldom become fatal.

Chemical elements essential to plants. If a botanist had been asked in 1920 to list the external conditions necessary to the complete development of a green plant, his reply would have been about as follows: the absence of destructive and toxic agencies; the presence of a suitable temperature, length of day, and acidity; adequate light, water, free oxygen, carbon dioxide, and certain soluble salts containing the elements of nitrogen, phosphorus, potassium, sulfur, magnesium, calcium, and iron. Today he would add that there must also be a trace of salts of manganese, boron, copper, molybdenum, and zinc. He would also say that other elements may be found essential to plants, at least to some plants. Perhaps the last five elements named above are not essential to all plants. Even calcium is not essential to certain algae and fungi.

During the 19th century, botanists and agriculturists got along fairly well on the conclusion that only 10 elements are essential to plants. Later it was observed that copper-containing sprays sometimes improved the growth of plants, and that molds would not grow and reproduce repeatedly in the same glass vessels unless a trace of zinc was added. The first cultures of molds had obtained sufficient zinc from the new glass.

These observations did not constitute a final proof that these elements are essential. Final proof was obtained only when all the containers used were of pyrex glass. The water used in the water cultures prepared for

green plants and in the nutrient media prepared for non-green plants was redistilled several times, until its total metal content was less than 0.0002 part per million (0.0002 ppm.). The salts used were recrystallized until the metal impurities in them were less than 0.0001 ppm.

To cite but one example, it was discovered at the University of California that the symptoms of manganese, zinc, and copper deficiencies in tomato plants disappeared when the culture solution contained 0.5 ppm. of manganese, 0.05 ppm. of zinc, and 0.02 ppm. of copper. The copper deficiency symptoms also disappeared when the leaves were merely sprayed with a very dilute solution of copper sulfate. Increased amounts of these elements soon result in toxic effects; 2 ppm. of copper in the culture solution was injurious to tomato plants.

Several botanists have proposed culture solutions in which many kinds of green plants will grow well. The following is an example:

Water	1,000.00 cc.
KH_2PO_4	0.31 gm.
$Ca(NO_3)_2.4H_2O$	1.04 gm.
$MgSO_4.7H_2O$	0.54 gm.
$(NH_4)_2SO_4$	0.09 gm.
Very small quantities of $FeSO_4$, H_3BO_3, $MnSO_4$, $ZnSO_4$, and $CuSO_4$.	

Water cultures in tanks. Botanists have studied the growth of plants in water cultures in small laboratory vessels for nearly a century. When the size of the vessel was increased to that of a small tank, the process attracted public attention. It is necessary to stretch "hardware cloth" across the top of the tank and cover it with a thin layer of such substances as peat or excelsior that will keep the seedlings upright. If all the factors are properly adjusted, many kinds of plants will grow and reproduce in these "tank cultures" as well as they do in highly fertile soils. Tank culture has been commercialized under the name "hydroponics."

Anyone can play with the idea of tank culture; but the means of maintaining a proper supply of salts and of testing its commercial value are problems that can be solved only by research students. The most modern tank-culture apparatus found in greenhouses consists of a tank filled with cinders or coarse gravel, into which the culture solution is pumped from another reservoir at stated intervals during the day and allowed to drain out immediately. Various modifications of the apparatus may also be used (Fig. 139). The apparatus can be constructed to run automatically.



FIG. 139. A convenient method of repeatedly adding a culture solution to plants potted in gravel. Each bucket contains a prepared solution and is connected to a pot by means of a rubber hose. At intervals the bucket is hung on the suspended hook above the pot until the solution flows into the gravel. It is then returned to the shelf below the pot and the solution drains from the gravel into the bucket. Photo by J. D. Sayre, Ohio Agricultural Experiment Station.

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CHAPTER XXXI

INITIATION OF FLOWERS

Many plants bloom regularly only at certain seasons of the year. We all know that some of them bloom much earlier during the growing season than others. Without giving much thought to these familiar facts, we might casually assume that a plant blooms when the temperature is just right, or when it has reached the right age to bloom. But anyone who is aware of the behavior of plants in greenhouses or in window boxes may have noted that some of these plants likewise bloom only at certain seasons of the year, or that they do not bloom at any season.

Some of the plants that bloom regularly only during the summer may bloom in winter if the room is lighted during the first half of each night. Likewise, some that regularly bloom only in autumn, or in greenhouses during the winter, will bloom in midsummer if they are placed in a dark room from the middle of the afternoon until the next morning for several successive days.

Cocklebur plants that grow from seeds in late summer may be in bloom two or three weeks later. Those that begin growth from seeds in late spring may grow vegetatively for several months before the first flowers appear.

If the germinating seeds or seedlings of certain plants are exposed to continuous low temperature for a few weeks, they may bloom sooner than those kept warm at all times. In the eastern United States certain varieties of apple and pear bloom abundantly in alternate years. When facts such as those listed above are considered, one may feel that casual explanations of why plants bloom when they do may be inadequate or even erroneous.

All seed plants have a period of youth during which the growth of roots, stems, and leaves precedes the formation of flowers and fruits. The length of this purely vegetative period may vary from a few weeks to many years, depending upon the species of plant and the habitat in which it is growing.

The occurrence of flower primordia in buds is the first visible evidence

of flower formation. Their first appearance can be detected only by examining thin sections of buds with a microscope. During the winter many of the buds of trees and shrubs contain rudimentary flowers that may be recognized without a microscope (Chapter XXVI). Evidently the initiation of these dormant rudimentary flowers occurred sometime during the previous growing season.

In the latitude of Ohio the initiation of flower buds on trees of apple, peach, plum, and cherry usually occurs sometime during the last two months of summer. The initiation of flower primordia in many shrubs, such as currants, gooseberries, and cranberries, also occurs during these months. In the early spring-flowering plants that grow from the terminal bud in bulbs, the differentiation of flower primordia occurred sometime during the preceding growing season.

The opening of flower buds, the relatively rapid enlargement of the different parts of flowers, and the subsequent development of fruits the following spring are familiar to all. In annuals, biennials, and many herbaceous perennials, the initiation of flower primordia and the subsequent development of flowers and fruits occur during the same season.

Since the fruit and the parts of a flower are composed of cells, one may reasonably infer that the processes of growth in them are similar to those in leaves, stems, and roots. Here again the formation, enlargement, and differentiation of cells are influenced by food, water, hormones, and all the other factors that affect the growth of cells. As in leaves, an abscise layer may develop at the base of each of these floral structures, and they may abscise and fall off at maturity or in some earlier stage of development. During certain years this abscission may be so excessive that the ground beneath a tree is covered with a layer of abscised flowers and young fruits. Biloxi soybeans which grow where they are exposed to light 14 to 15 hours each day may bloom, but no fruits develop. The initiation of flower primordia, therefore, may occur when conditions are unfavorable to the further development of both flowers and fruits. It is because of this fact that attention has been called to each of these three processes: initiation of flower primordia, flowering, and fruiting. In the cultivation of plants one strives to maintain a combination of conditions that is favorable to all three of these processes.

The formation of seeds in fruits is dependent upon the formation of pollen and gametes and is the result of a long series of processes that will be considered in Chapter XXXIII. These, too, are influenced by external conditions.

In this chapter the initiation of flower primordia will be given most attention. The further development of these primordia to full-grown flower structures and fruits will be mentioned occasionally.

We shall have to turn our attention once more to the growing stem tip, for it is from this meristem that all flower primordia develop. They may develop from the stem tip in the terminal buds of main stems or of lateral branches, as in roses, zinnias, dahlias, petunias, and asters. In these plants there is a change from a vegetative bud to a flower bud.

Flower primordia may also develop from the unelongated stem tips of axillary buds, as in rose of Sharon, hibiscus, hollyhock, bindweed, mullein, and coleus. In these latter plants the fully developed flowers are later seen along the sides of the stem in the axils of leaves. The leaves subtending the axillary flowers may be large, as in hibiscus, or they may be small green bracts, as in coleus. The stem tips from which these flowers developed never bore leaves (Fig. 83, page 249).

Observable differentiation of flower primordia. In the longitudinal section of a vegetative bud (Fig. 32) the apical meristem and the primordia of the lateral foliage leaves and of axillary buds are evident. When such a bud changes to a flower bud, no more primordia of foliage leaves and axillary buds are formed; but a number of small mounds or ridges of cells develop from the apical meristem in regular arrangement. In the simplest cases the lowest and outermost mounds of these cells are the primordia of the sepals of the flower, and they are usually the first to appear (Fig. 140). Just above them are the primordia of the petals of the flower, then the primordia of stamens; and finally the center of the meristem becomes the primordium of the pistil. The order in which these different primordia become visible is not the same in all species of plants. This short stem tip, with the several mounds of meristematic cells, is the beginning of a flower.

Physiological differentiation precedes the occurrence of flower primordia. Back of all visible changes in development there are, of course, changes in physiological processes and conditions. What we see are merely the consequences of the accumulated physiological conditions. What are these conditions?

Among the conditions postulated to be important in flower formation, two—namely, specific hormones called "florigens," and the relative amounts of carbohydrates and proteins in the plants—have been given the most attention in recent years. While an unqualified specific answer

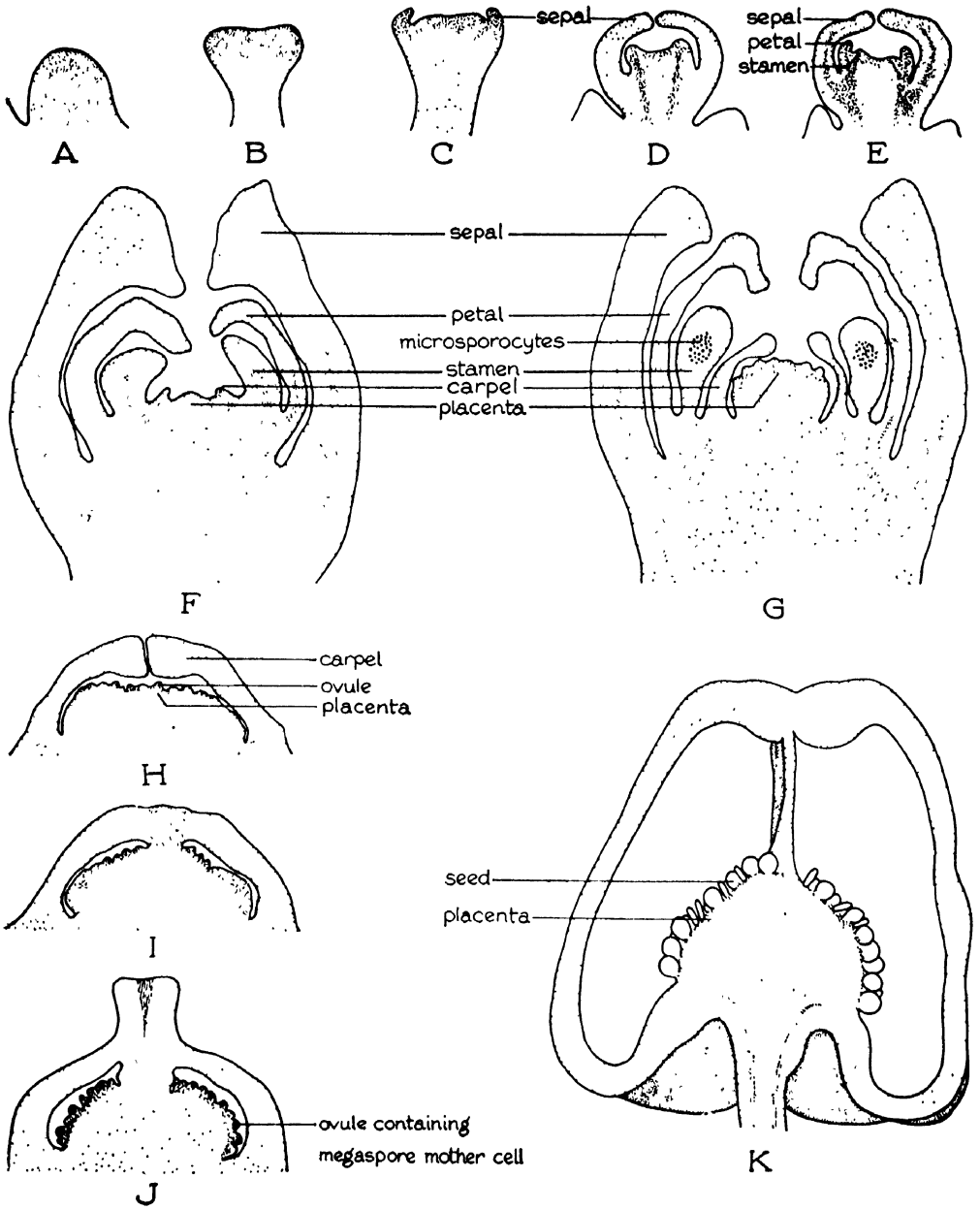

FIG. 140. Primordia of the parts of a flower and the forerunners of fruit and seeds of pepper. A, the vegetative stem tip previous to the development of flower primordia; B-G, early stages in the development of flower primordia; H-K, stages in the development of fruit and seeds. A-J, after H. L. Cochran, *Journal of Agricultural Research*. K, drawn from a photograph by H. P. Stuckey and J. A. McClintock.

to the above question is impossible today, some of the facts relating to it may be of more interest than the answer.

The leaves of begonia may be used as a means of vegetative multiplication; that is, if the base of a leaf which has been broken from a plant is placed in moist soil, a complete individual plant will develop from it. If the plant from which the leaf was taken is about to bloom, the new individual that grows from the isolated leaf will grow but little and bloom within a short time. On the other hand, if the original plant is vigorously vegetative, the new individual from the isolated leaf will grow much larger and for a long period of time before flowers develop on it. From such experiments as these a German botanist (Julius von Sachs) suggested in 1893 that flower formation may be dependent upon specific chemical substances made in the leaves. At that time, and for several years later, the idea that a small amount of some chemical substance formed in the plant could have such a profound influence on its development attracted little serious consideration.

A few years later, another German botanist (Georg Klebs) began a series of experiments in which he was able either to keep plants in a vegetative state for many years or to bring about flower formation and sexual reproduction in a relatively short time. He thought that all his experimental data could be explained on the basis of the influence of light, inorganic salts, and other external factors upon the nutrition of the plants, especially upon the synthesis and accumulation of carbohydrates in relation to other products. He concluded that the initiation of flower primordia is dependent upon a previous accumulation of physiological conditions.

In 1918, two American botanists (E. J. Kraus and H. R. Kraybill) described their experiments with tomato plants in which the number of flowers formed, flower development, and subsequent fruit development varied with external conditions that influence photosynthesis and protein synthesis in plants. From the discussions in previous chapters (XIII-XVI) we are aware of the ways in which certain external factors could be changed and thereby alter the relative rates of photosynthesis and protein synthesis in plants. Following this report many investigators, working with several kinds of plants, performed hundreds of experiments in attempts to discover the relation of the relative amount of carbohydrates and proteins to the development of all parts of plants.

These investigators showed that no organ of a plant grows well unless it is well supplied with both carbohydrates and proteins, or with the con-

ditions by which it can make these two kinds of foods. Flowers and fruits will grow no better than leaves, stems, or roots without these foods. Nor will they grow well when conditions are favorable to the synthesis of only one of them. Many facts of both practical and scientific interest were discovered. Some of them have been included in previous chapters.

Most of these investigators think that these foods are not a direct cause of the initiation of flower primordia. When cultivated plants in gardens, orchards, and fields are exposed to conditions favorable to both photosynthesis and protein synthesis, they usually grow well and bear an abundance of flowers and fruits. It is possible, however, that other processes essential to the initiation of flower primordia also occur best under these same conditions, and that the foods are important because they are a necessary source of material and energy in the growing cells of the primordia and of the expanding flowers and fruits.

Following the definite proof of hormones in plants about 1928, several botanists became interested in testing Sachs' idea that the initiation of flowers is dependent upon specific hormones made in the leaves. From the results of numerous experiments performed since that time it appears reasonably certain that hormone-like substances are made in the leaves which promote the initiation of flower primordia, and that probably others inhibit it. The evidence back of this conclusion and the differences discovered in the plants investigated cannot be presented in this short chapter, but a few facts selected from two of the reports are too interesting to be omitted.

No initiation of flower primordia occurs in plants of cocklebur (*Xanthium pennsylvanicum*) growing in an ordinary greenhouse if the plants are exposed to continuous light for 16 hours each day. Under these conditions they remain vegetative indefinitely. If the daily light period is shortened to 9 hours, microscopic flower primordia are evident within 5 days, and the plants are in bloom in about 2 weeks. If only one branch bearing mature leaves is exposed to a daily light period of 9 hours, and another branch of the same plant is exposed to the 16-hour daily light period, flowers develop on both branches. Finally, if only one mature leaf on the plant in the 16-hour day is exposed to a short day of 9 hours, flowers develop on all branches of the plant.

Whatever it is that passes from the leaves exposed to the short days and promotes the initiation of flower primordia on the part of the plant exposed to the 16-hour day, it passes both up and down the stems. It

also diffuses across a graft between two branches of the same or different plants, even if direct contact in the graft is prevented by the insertion of lens paper.

Approach grafting was employed in these experiments; that is, portions of the sides of two stems were shaved to the cambium, and the two shaved surfaces were bound together without removing either stem from the plant. The leaves above the graft on one stem were then exposed to a 9-hour daily light period. Those on the other stem were exposed to the 16-hour day. Flowers developed on both branches.

As in the cocklebur the initiation of flowers in soybean plants also occurs only during relatively short days, but there is one striking difference. If the leaves on one part of a plant are exposed to short days and those on the remainder of the plant to long days, flowers develop only on the branches exposed to short days.

This localized effect has also been reported as occurring in other plants, such as cosmos, chrysanthemum, tobacco, and poinsettia. But it has been shown that in soybeans if the leaves are removed from the branches exposed to long days when the experiment is started, flowers develop on these branches also. If the leaves are removed from the branches exposed to short days, no flowers develop. From these facts one might infer that there are at least two substances that influence the initiation of flowers in soybeans: one made in leaves exposed to short days which induces the initiation of flowers, and the other one made in leaves exposed to long days that inhibits it.

Environmental factors. By this time it is probably evident that environmental factors, through their effects upon processes and conditions within the plant, may affect the initiation of flower primordia. Of these factors light and temperature are often the most important and will be discussed further.

Light. When light is mentioned as a factor, one should know whether intensity, quality, or daily duration is being considered. From investigations made to date it appears that in the initiation of flower primordia, the so-called red rays of light are more effective than the blue, and green is least effective of all.

Many plants have been known to grow and die in light of low intensity without bearing flowers and fruits. Some of them may live in this purely vegetative state for many years. Whether the failure of flower formation in deep shade is the result of deficient photosynthesis, hormone synthesis, or of some other internal condition is unknown. The in-

tensity of light, through its influence upon photosynthesis, is a very important factor in the growth of flowers and fruits after they are initiated.

The daily duration of light to which plants may be exposed is often the most potent of all external conditions in the initiation of flower primordia.

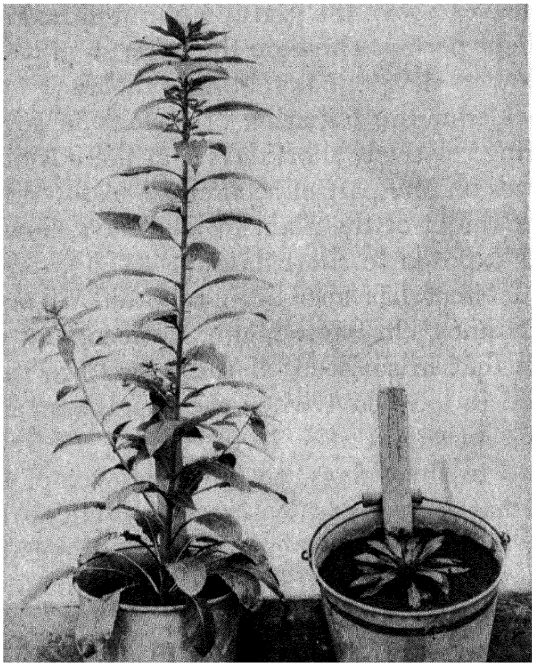

FIG. 141. The effect of long and short days on the evening primrose. Both plants were brought into the greenhouse in November. The one at the left was exposed to natural winter daylight and also to illumination from an electric light from sunset to midnight for about two months. The one at the right was kept under the same conditions, except that it was exposed only to the natural winter daylight. This is a typical long-day plant, in nature flowering when the days are long. W. W. Garner and H. A. Allard, U.S.D.A.

This fact was first clearly recognized in 1920 by two American botanists (W. W. Carner and H. A. Allard), of the U. S. Department of Agriculture (Figs. 141 and 142). They suggested the term *photoperiod* for the daily light period, or for any other period of continuous light to which the plants were exposed; and the term *photoperiodism* to refer to the recognized effects of the light period on the development of the plant.

The photoperiod. The daily light period to which plants may be ex-

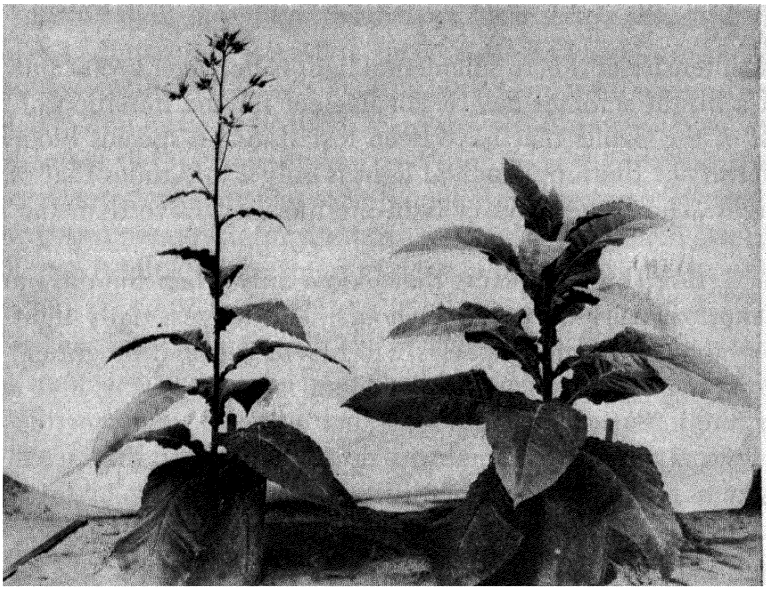

FIG. 142. Effects of length of day on tobacco plant. Both plants grew in a greenhouse during the winter. The plant at the right was exposed to daylight and also to electric light from sunset to midnight, while the plant at the left was exposed to natural daylight only. This is a typical short-day plant. When exposed to long days, this variety will grow 15 feet or more in height and produce upward of 100 leaves. W. W. Garner and H. A. Allard, U.S.D.A.

posed influences not only the initiation of flowers, but also physiological processes in plants that affect the growth of all plant organs. Here only a few of its relations to the initiation of flower primordia will be discussed.

Since the species and varieties of plants are inherently different, they are not all affected in the same way when exposed to the same photoperiod. Garner and Allard recognized three different groups of plants with reference to length of day and flower formation.

First, there are the long-day plants, which bloom only when the days are relatively long, usually more than 12-14 hours. The shortest daily photoperiod under which one of these species will bloom is called its critical photoperiod. When exposed to continuous light many of these species grow and reproduce; others fail to survive. These are the plants that regularly bloom in the long days of summer. During the short days of the growing season they remain vegetative, often as rosettes. They will also bloom in greenhouses in winter if the daily photoperiod is lengthened by means of electric lights. This supplemental electric light

need not be very intense. The main thing is that the daily photoperiod be lengthened.

If the intensity of this supplemental light is between 1/500 and 1/2000 that of a bright summer day, it is sufficient for the initiation of flowers in most of the plants that have been tested. Some species bloom when the intensity of the supplemental light is only 2 to 5 times that of bright moonlight. The longer rays of light are more effective than the shorter ones.

Second, there are the plants that bloom only when the days are relatively short, usually under 12-14 hours. The longest daily light period under which one of these species will bloom is called its critical photoperiod. These are the plants that bloom in early spring and autumn. That is, the initiation of flowers in them occurs during short days. The young flowers may grow to maturity during the season they are initiated, or they may remain dormant until the following spring, as they usually do in trees and shrubs.

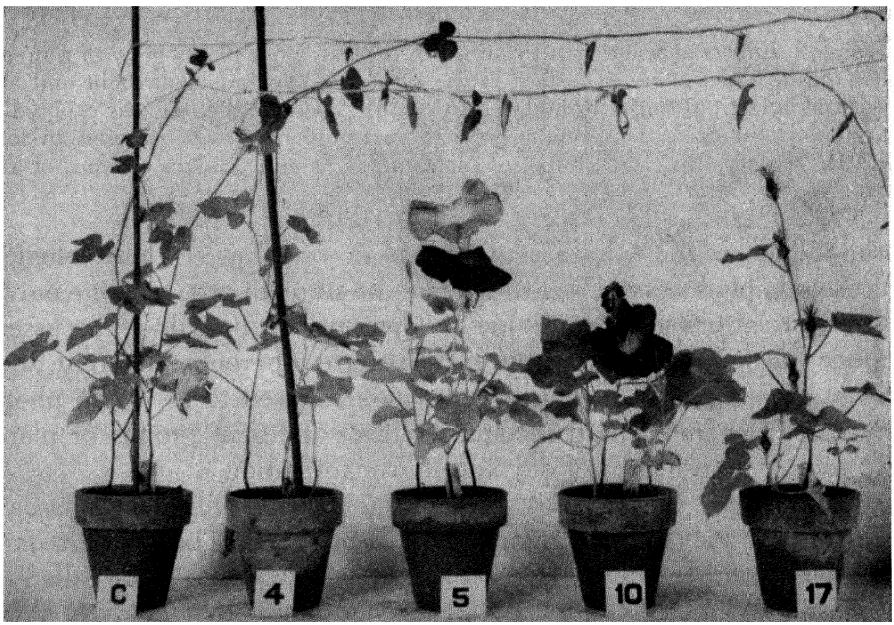

FIG. 143. Effects of length of day on vegetative growth and flower formation in morning glory. C, control plant exposed to long days from time of germination. Figures indicate the number of short-day periods to which the other plants were exposed during the seedling stage. All plants completed their development in long days. Photo by Victor A. Greulach.

Herbaceous short-day plants that have been tested bloom during the long days of summer if for a few successive days they are placed in a dark room from about the middle of the afternoon until the next morning (Fig. 143). The number of these short-day exposures that are effective depends upon the species of plant and also upon the temperature. One or two exposures are sufficient to initiate flower primordia in some plants. Short days are necessary for the further growth of the flower primordia after they are initiated in some species, whereas in other species the flowers may continue to develop in either long or short photoperiods.

These short-day plants will bloom even when exposed to the long days of summer if the intervening dark period is made longer, for example, from the evening of one day to the morning of the second day thereafter. The dark period must be continuous. If it is interrupted, even by very short light periods, flower primordia do not form. Such facts as these have led some investigators to suggest that the short-day plants should be called long-night plants. An idea of the importance of the long dark period may be obtained by comparing the behavior of the plants under different photoperiods as summarized in Table 12.

TABLE 12. Initiation of Flowers in Cocklebur in Relation to the Length of Alternating Periods of Light and Darkness

Length of Light Period in Hours	Length of Dark Period in Hours	Condition of Plant After 15 Days
8	16	In bloom
4	8	Vegetative only
16	8	Vegetative only
16	32	In bloom

If short-day plants are exposed only to long daily light periods, they remain vegetative for an indefinite time and grow much larger than when they are exposed to short days. Advantage is sometimes taken of this fact. After the plants have grown to some desired size in long days, they may be transferred to short days. In this way larger plants with a greater number of flowers and fruits may be obtained. If the seeds germinate in spring the plants are exposed to long days in early

summer and to short days in late summer and autumn without being transferred. What is the explanation of the differences in the blooming of the cocklebur plants mentioned in the third paragraph of this chapter?

Finally, there is a third group of plants, in which the initiation of flowers occurs during either long or short photoperiods, although it may occur more readily in one type of photoperiod than in the other. These plants are called *day-neutral* plants. They may bloom any time during

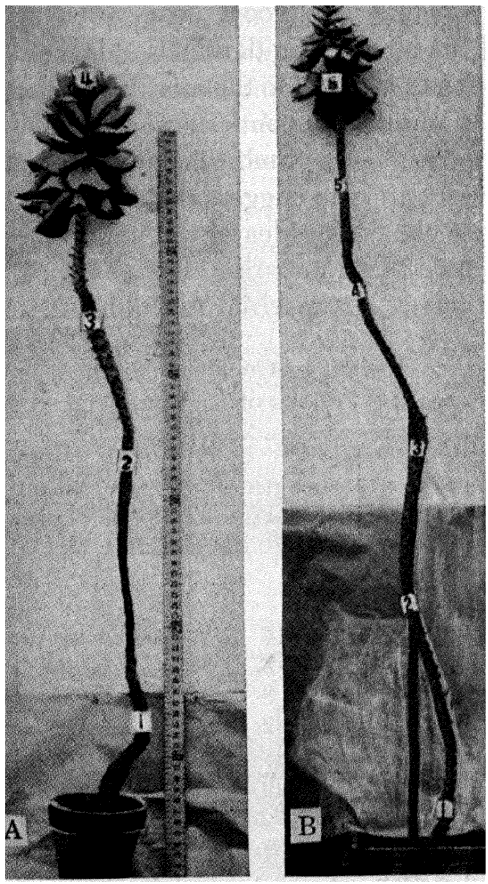

FIG. 144. Photographs of a cabbage plant kept in a greenhouse at about 67° F. At the end of two years plant (A) was more than 6 feet tall and had borne 4 compact heads of leaves at the points indicated by the figures 1, 2, 3, 4. At the end of 2.5 years it had borne 6 heads (B). When it was transferred to a cool (55° F.) greenhouse, flower primordia developed and the plant bloomed within a few months (B). Photo from H. C. Thompson.

the growing season. Hybrid roses, chickweed, dandelion in gardens and lawns, and tomatoes and buckwheat in greenhouses are familiar examples of day-neutral plants.

Temperature. Both the degree and the duration of any particular degree of temperature are important factors in the development of plants. Under certain conditions the initiation of flowers may be influenced more by temperature than by the length of day. Some species, such as beets,



FIG. 145. Effects of temperature on vegetative growth and the formation of flowers in celery. The four plants pictured on the left grew in a cool (60° F.) greenhouse; at the same time those on the right grew in a warm (70° F.) greenhouse. Photo from H. C. Thompson, Cornell University.

stocks, and celery, do not bloom when kept continuously at a relatively high temperature in greenhouses. Cabbage, a biennial, may grow vegetatively as a perennial if kept continuously at 70° F. (Figs. 144 and 145). Some plants of temperate climates when transported to the tropics similarly remain vegetative. Low temperature delays the time of flower formation in some species and shortens it in others. In many species the initiation of flowers occurs sooner at a moderate temperature than at either a low or a high temperature.

Much more striking, however, is the fact that the initiation of flowers may occur much sooner in some plants if the germinating seeds or the young seedlings are exposed to a low temperature for a short time. For example, wheat plants bloom sooner if the germinating seeds are exposed to a low temperature. Celery and beets, which are regularly biennials in the latitude of New York, grow as annuals if the seedlings

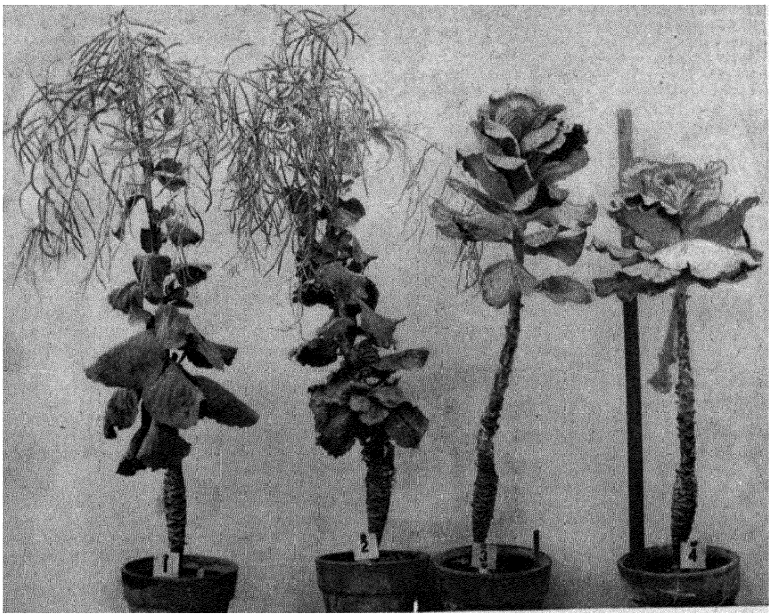

FIG. 146. Preconditioning effects of temperature on the development of flower primordia in cabbage plants. The four plants pictured above grew in the field during Summer. The two on the right were transferred directly from the field to a warm greenhouse, while the two on the left were brought from the field and kept at 40° F. for 2 months before they were placed in the warm greenhouse. Photo from H. C. Thompson.

are exposed to a temperature of 40° F. for about one month. Some of the effects of temperature at these early stages of development persist in the plant as it continues to grow and finally result in an earlier initiation of flowers (Figs. 146 and 147). This phenomenon may be referred to as *preconditioning*. That is, the plants bloomed sooner because they were preconditioned by a low temperature during some earlier stage of their development. Likewise, a similar preconditioning occurs when short-day plants are exposed to a long dark period. Our present knowledge of



FIG. 147. Preconditioning effects of temperature on the development of flower primordia in celery plants. The plants pictured in the center row grew in a cold frame (40-50° F.) for 35 days during their seedling stage before they were transferred to the field. The plants in the next rows in the foreground were kept in a warm greenhouse during their seedling stage. They have continued to grow vegetatively, while those in the center row have borne flowers and seeds. Photo from H. C. Thompson.

plant physiology is not sufficient to enable us to explain these preconditioning effects either of temperature or of light.

Since the initiation of flowers may be either promoted or inhibited by temperature or by the photoperiod, one of these external conditions may either annul or accentuate the effects of the other. What happens when the effects of the one are opposed to the effects of the other in a particular plant? At the present time one may obtain an answer to this question by only one of two ways. Someone may have already discovered the answer and reported it. If the answer cannot be found in botanical literature, the only way to obtain it is by a series of experiments.

When a plant is exposed to a length of day near its critical photoperiod, it is more readily influenced one way or the other by changes in temperature or some of the factors that affect photosynthesis and protein synthesis. For example, barley is a long-day plant; when exposed to a photoperiod near its critical day-length it will bloom or remain vegetative, depending upon the temperature and upon the factors that affect the relative rates of photosynthesis and protein synthesis. What has just been said may be made clearer by the following summary:

Photoperiod	Long Day	Intermediate Day (Length Near Critical Photoperiod)	Short Day
Long-day plants that have been tested by experiments	Usually bloom	Variable, dependent upon several other factors	Usually remain vegetative
Short-day plants that have been tested by experiments	Usually remain vegetative	Variable, dependent upon several other factors	Usually Bloom

The greater variability in behavior of plants exposed to intermediate day-lengths near their critical photoperiod includes not only the variability in the initiation of flowers, but also the variability in the further development of flowers and fruits and the processes involved in seed formation. Changes in vegetative structures, such as growth in height



FIG. 148.

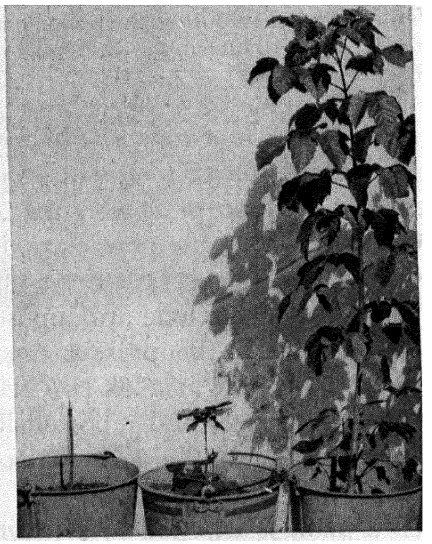

FIG. 149.

Fig. 148, the plant on the right, an apple seedling that grew more rapidly with 10 hours' daily illumination than the control plant on the left with a full day's illumination. In contrast, the maple seedlings (*Acer negundo*) on the left in Fig. 149 were dwarfed and forced into dormancy by shortening the illumination period to 10 hours, while the plant exposed for the full length of day grew rapidly. The photograph of the apples was made July 13 and that of the maples September 22 by W. W. Garner and H. A. Allard. Photo from U. S. Dept. Agric.

and the formation of tubers, are also more variable under these photoperiods, because the influence of other environmental factors on them is relatively more pronounced.

Plants may also be classified as long-day and short-day types with respect to tuber and bulb formation, root growth, stem growth (Figs. 148 and 149), deciduous and evergreen habit, kinds of flowers, and yield of crop plants.

Tubers ordinarily develop at the ends of rhizomes of Jerusalem artichoke during the short days of autumn. They will also develop during



FIG. 150. Photographs of the roots, underground stems, and bases of the aerial stems of Jerusalem artichokes (*Helianthus tuberosus*). The plants on the left were exposed to the long days of summer, those in the center and on the right were covered with a dark cloth from 4 P.M. to 9 A.M. each day, but only the tips of those on the right were covered. The elongated rootstocks of the plants on the left, and the thickened tubers of the others are evident. Photo by P. W. Zimmerman and A. E. Hitchcock, Boyce Thompson Institute.

midsummer if the photoperiod is artificially shortened each day by placing the plants in a dark room or by covering the leaves and stems aboveground with a black cloth. Darkening of the stem tips alone is sufficient to initiate tuber formation in artichokes (Fig. 150).

Girdling. In certain habitats young apple trees and other orchard trees may remain vegetative for several years before they bear flowers and

fruits. What can one do that will result in the initiation of flowers in such plants? It has been known for a long time that if a branch of one of these trees is girdled (ringed), it will bear flowers and fruits sooner than other branches on the tree. If the trunk of the tree is girdled, numerous branches on the tree will bear flowers and fruits sooner. If one wishes to avoid killing the tree in this way, the girdle should be very narrow, about one-eighth of an inch. It should be so protected that no parasites can enter the wound and that complete healing by the growth of a new cambium over the wound can occur within a few months. Merely cutting through the bark by drawing a knife blade around the trunk of the tree may be as effective in initiating flowers as making a wider girdle. How may one explain the initiation of flowers that results from girdling?

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CHAPTER XXXII

FLOWERS, FRUITS, AND SEEDS

Flowers are the precursors of fruits and seeds, and within the seeds are the embryos of a new generation of plants. The growth of the parts of a flower from the primordia in a flower bud is but the first of a series of processes and structures that ultimately result in sexual reproduction in seed plants. As we proceed with further chapters some of the interrelations of sexual reproduction and other plant phenomena will become evident.

The rapid expansion of an opening flower is mainly the result of cell enlargement by growth of cell walls accompanied by the osmotic absorption of water. Most of the cell division and a considerable amount of cell differentiation, including the differentiation of some of the reproductive cells, occurred in the flower bud before it opened.

Interest in flowers, however, is not limited to sexual reproduction. The widest general interest lies in the pleasure of seeing them on cultivated plants and also on plants growing under natural conditions. The flowers sold for decorative purposes are valued annually in millions of dollars.

Flowers are also sources of nectar and perfumes. But the direct economic importance of flowers is small when compared with the value of the fruits and seeds that develop from them. The accumulated food in these organs is one of the most important commercial products of cultivated plants.

The colors, shapes, and sizes of flowers; the forms and arrangement of the parts of a flower; and the arrangement of flowers and fruits of a plant are as definite as are the forms and arrangements of leaves. Because of this inherent constancy of form and structure, the specific differences in flowers and fruits, as well as in leaves and stems, are used in classifying plants. Some appreciation of this use of flowers may be gained first-hand by comparing the flowers of a few common plants such as lily, bean, tomato, mint, morning glory, rose, carrot, and sunflower.

The flower. Numerous flowers are commonly recognized by their form, color, texture, fragrance, or other distinguishing feature. In fact,

flowers are often regarded as something distinct from the rest of the plant, as is shown by the very common advertisement, "Plants and Flowers for Sale." Few people realize that about one-half of the species of plants bear flowers.

The variety in floral organs is probably greater than that in other organs of plants. Many flowers are conspicuous, but others are quite inconspicuous and appear as aggregates of scales and bracts, as in grasses, alders, poplars, and birches. Technically, even a young pine cone may be regarded as a type of flower. Such cones, however, lack both sepals and petals. Flowers vary in size from the nearly microscopic flower of *Wolffia* to the "fleshy" flower of *Rafflesia*, nearly three feet in diameter. Although nearly all colors and almost all conceivable blends and mixtures of colors may be found in flowers, the most common are green, white, and yellow. In the flora of Ohio, for example, the percentages of different flower colors are approximately 36 green, 21 white, 20 yellow, 15 blue to purple, and 7.5 red to pink. Locally and seasonally one or another of these flower colors may predominate in the landscape.

The flower is a short stem bearing floral organs and its development is similar in many respects to that of a branch from a vegetative bud.

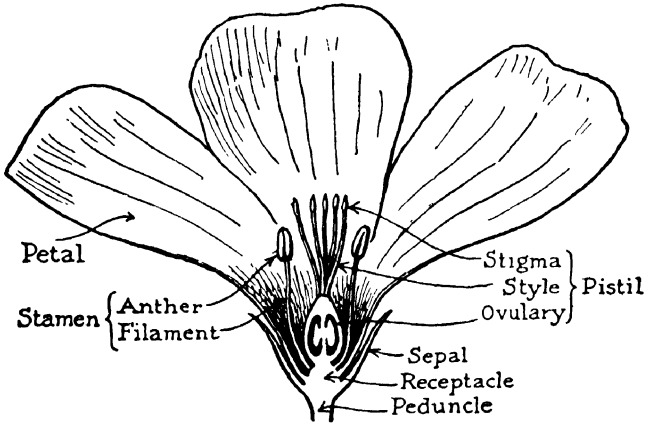

FIG. 151. Vertical section through a complete flower (Flax). Courtesy of World Book Co.

Mounds of meristematic tissue are formed by cell division at the growing tip of a stem or floral axis. From them the parts of the flower develop as lateral structures, in much the same way as ordinary leaves develop from similar mounds of tissue (Fig. 140). There is, however, little or no elongation of the internodes between the floral organs; consequently flowers

are usually compact structures, with the parts in close spirals or whorls (cycles). In the more primitive types of flowers, floral organs are spirally arranged; in the more complex types they are usually cyclic and also fewer in number (Fig. 151). The best way to study flowers is first to examine a few common ones critically and then to amplify these initial studies by further observation of some of the hundreds of different kinds available each season.

A simple flower. The flowers of tulip and sweet pea exemplify two common forms of simple flowers. The floral organs of the tulip (Fig. 152) are arranged in cycles of three at the top of the flower stalk or peduncle. This end of the peduncle is slightly enlarged and is known as the *receptacle*. The outermost cycle of leaf-like structures growing from the receptacle is the *calyx*, composed of three *sepals*. In the enlarging flower bud these sepals are green. They may remain green or become variously colored as the flower matures, depending upon the variety. Except for position, the next cycle is very similar to the first; its three *petals*

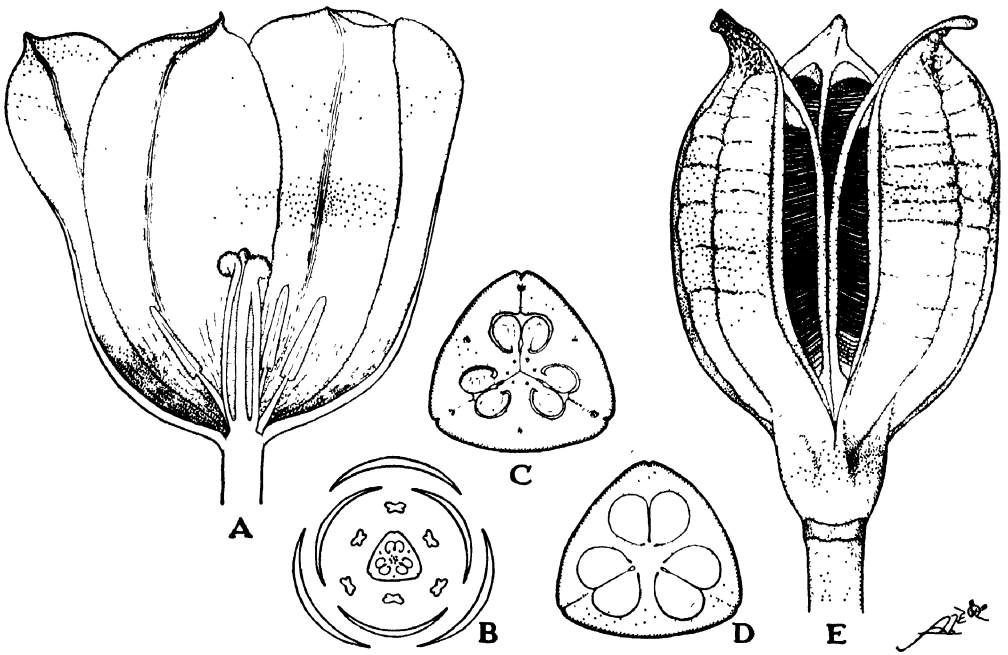

FIG. 152. Flower, fruit, and seeds of tulip. A, vertical section through center of flower; B, diagram of cyclic arrangement of the floral organs; C, enlarged cross section of the pistil in which the three carpels and six of the ovules are evident; D, cross section of a mature pistil in which the ovules have become seeds; E, a mature fruit which has split open along the midrib of each carpel.

constitute the *corolla*. The calyx and corolla together are often called the *floral envelope* or *perianth*. The next two whorls of organs are less leaf-like in appearance and each consists of three *stamens*. The stamens in one cycle alternate with the sepals; those in the other cycle alternate with the petals. Each stamen has a stalk or *filament* terminating in a pollen-bearing *anther*. The *pistil* is centrally located in the flower and is composed of three leaf-like parts, the *carpels*. The slightly thicker lower portion of the pistil is the *ovulary*,[1] which tapers apically into a neck-like structure, the *style*, at the summit of which is the three-lobed *stigma*. Each lobe of the stigma is in line with the midrib of a carpel.

If the ovulary is cut or broken crosswise the ovules from which seeds develop may be seen. If the carpels are pulled apart lengthwise, the six vertical rows of ovules are easily seen. As the pistil enlarges and becomes a fruit, the ovules become seeds.

The foregoing is a description of the usual tulip flower. Variations may be found, some of which are inherent in the variety of tulip, while others are the result of the conditions in which the bulbs are stored during their dormant period.

The calyx of the pea flower (Fig. 153) like that of bean is green, and the four or five sepals are united except at their tips which may appear as large teeth or calyx lobes. The corolla is variously colored and is composed of five petals, so unlike in form that special terms have been applied to them. One, the "standard," is broad and encloses the others in the bud; the two lateral petals are "wings"; and the remaining two are more or less united ventrally, forming the "keel" and enclosing the stamens and pistil. Of the ten stamens, one is free; but the filaments of the other nine are united in a tube surrounding the pistil.

The pistil of the pea or bean consists of a single carpel but usually contains several ovules attached to a longitudinal ridge at one side of the ovulary. The region to which an ovule is attached is called a *placenta*. The leaf-like nature of the carpel is clearer when a green pea pod is opened along one side and spread out flat. If a cross section of the pod is made, the ovules appear to be borne on the fused margins of a folded leaf.

The stamens, petals, and sepals of such flowers as the tulip develop

[1] The ovulary of the pistil is often referred to as an ovary. The term ovary is used to designate a very different sort of structure in animals. Later on we shall see that the origin of egg-bearing structures in plants is quite unlike that of the ovule-bearing structures. It seems preferable, therefore, to use the term ovulary to refer to the ovule-bearing structure in plants.

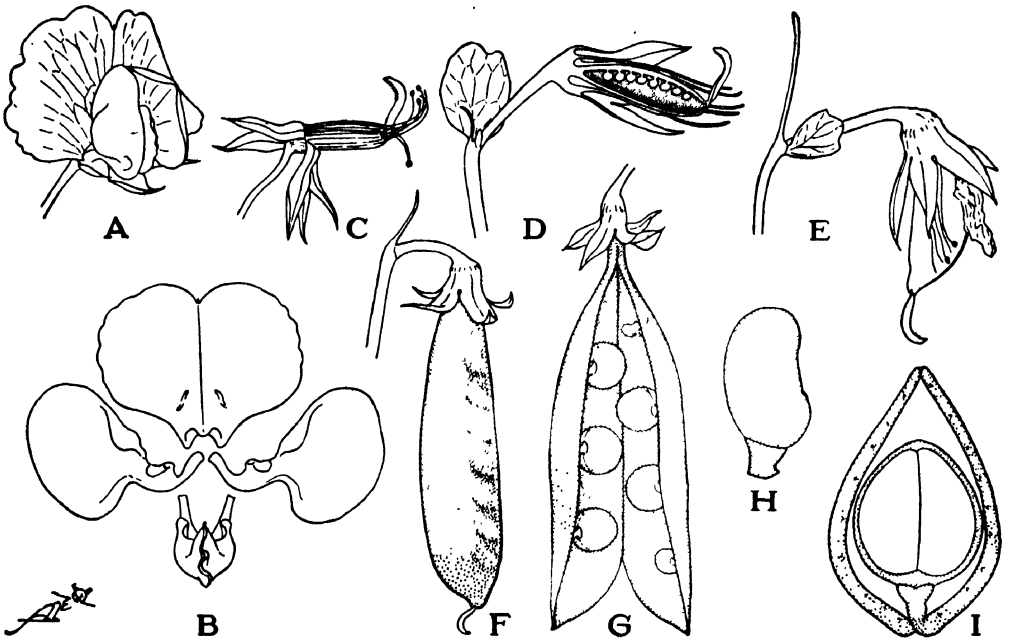

FIG. 153. Flower, fruit, and seeds of the garden pea. A, the flower; B, the five petals; C, flower with petals removed so that the stamen tube which surrounds the pistil may be seen; D, arrangement of ovules as seen in a longitudinal section of the pistil; E, F, and G, stages in the development of the fruit from the pistil and of the seeds from ovules; H, a young ovule enlarged; I, enlarged cross section of a young fruit to show that it is composed of one carpel and that the ovules are borne on the infolded margins of the carpel.

from separate primordia. The growing carpels, however, are united and a compound pistil develops from them.

A pistil that develops from one carpel, as in beans and peas, is a simple pistil. In the flowers of some plants, such as the buttercup, the carpels do not unite, and many simple pistils develop separately in the same flower.

Still other plants have flowers in which the calyx and corolla are tubular because the sepals and petals are united in a tube as they develop.

Such unions of the parts of a flower take place between flower primordia, and the tubular structure develops thereafter as a unit. The calyx of the flower of peas, for example, begins as five separate sepal primordia near the apex of the receptacle. Shortly, however, later growth at the bases of these primordia results in a complete collar of tissue. Continued growth of this collar and of the lobe of each sepal results in a cup-shaped calyx tube with five lobes at its margin. The ten stamen

primordia likewise begin as separate mounds of tissue, but nine of them soon become united at their bases, leaving the tenth stamen primordium free. Fusions of floral parts are common and of great variety, as may be seen if numerous flowers are examined.

In many flowers, such as those of apple, there is a *floral cup* composed of the united bases of sepals, petals, and stamens. This floral cup may

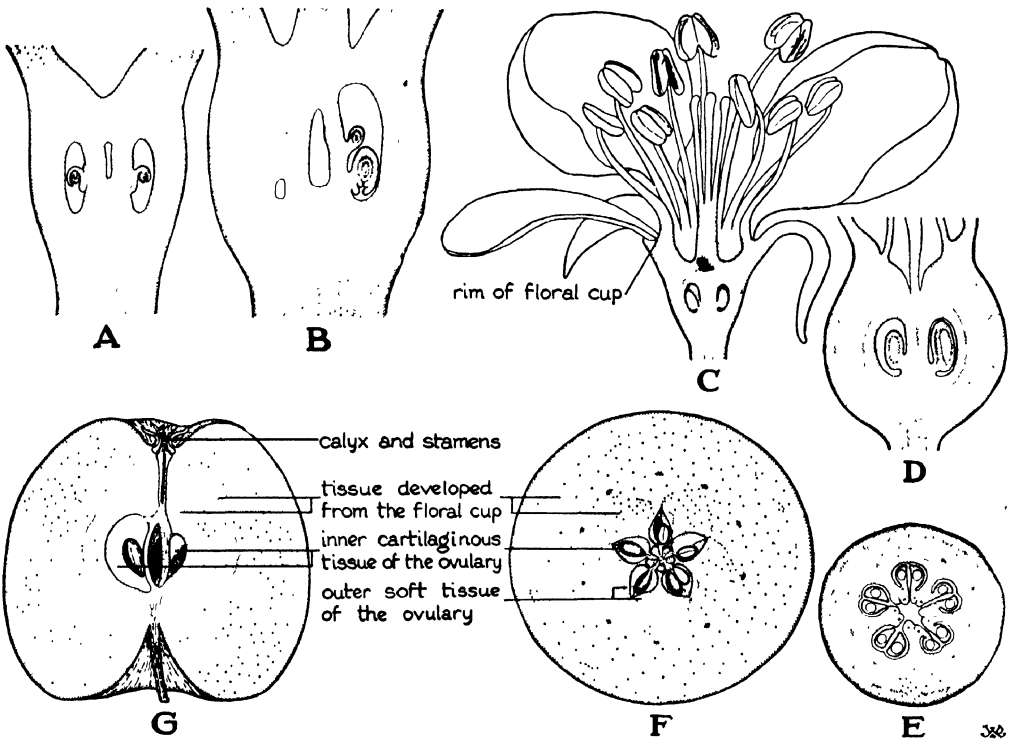

FIG. 154. Flower, fruit, and seeds of apple. A-D, vertical sections through flowers of different ages. In C, which is about 2.5 natural size, all the parts of the flower have been drawn. The tissues of the ovulary and the floral cup are united. A and B are about 9 times natural size and were made before the flower buds opened. C and D are about 2.5 natural size and were made soon after the petals abscised. E, cross section of a young fruit in which the five carpels and ten of the ovules are evident; F and G, cross and longitudinal sections of a mature fruit, about one-half natural size.

partially or completely enclose the ovulary and become united with it. The upper parts of the stamens and the lobes of the calyx and corolla appear to be attached to the rim of the cup (Fig. 154). Furthermore, while the ovulary develops as the core of the apple, the floral cup grows and becomes the edible part of the fruit.

The floral cup of the English walnut is still more complex. The primordia of bracts below the pistillate flower become united with those of the floral organs, and by further development become the husk of the mature fruit. The hard shell of the nut develops from the two-carpellate ovulary; the "meat" within is an embryo surrounded by thin seed coats.

The floral cups of some flowers, such as those of the cultivated shrub, pearl bush, abscise when the flower is mature and do not form a part of the fruits.

Flowers of grasses and sedges have nothing closely resembling a calyx or a corolla; in them the stamens and pistils are enclosed by small

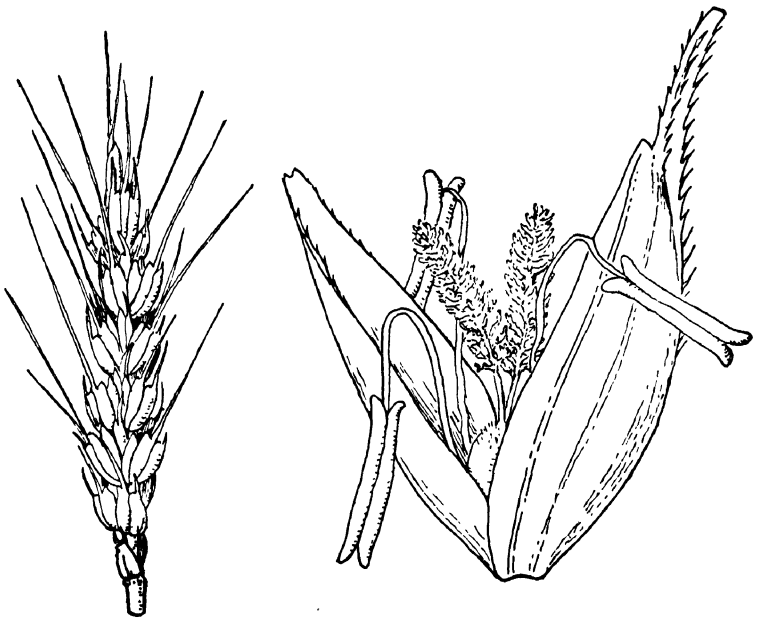

FIG. 155. Spike and flower of wheat (*Triticum vulgare*). The two floral bracts, or glumes (lemma on the right and palet on the left), enclose three stamens and a pistil with two plumose stigmas. At the base of the flower inside the glumes are two minute scales, the lodicules, which are not evident in the above figure. Courtesy of World Book Co.

scales or bracts, which are usually green and are often referred to as glumes (Fig. 155).

Flowers composed of calyx, corolla, stamens, and pistils are referred to as *complete*. They are said to be *perfect* if they have both stamens and pistils, regardless of the presence or absence of calyx or corolla, because stamens and pistils are the essential parts of flowers. Not infrequently

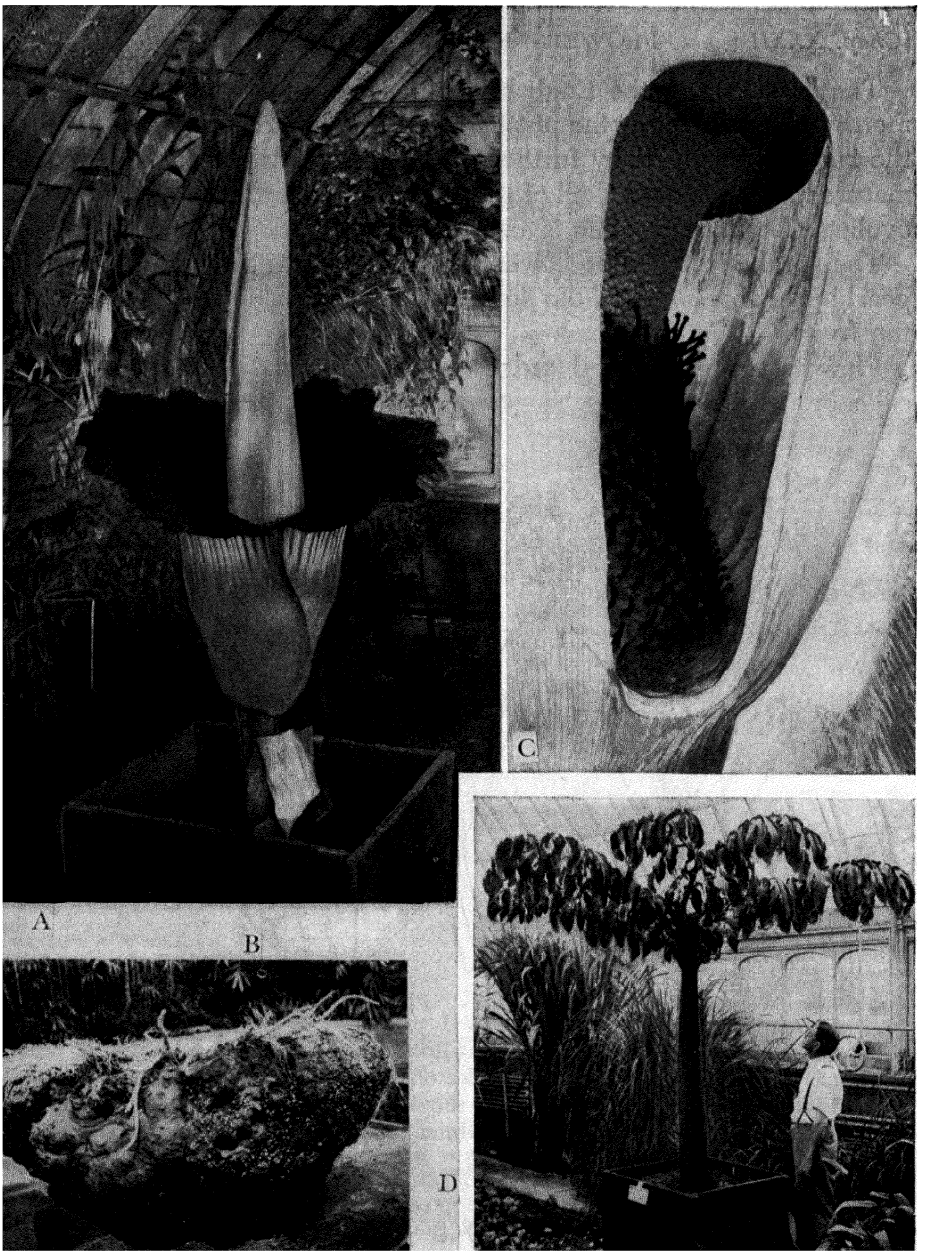

FIG. 156. Sumatra's giant krubi (*Amorphophallus titanum*) in bloom. This plant has the largest flower cluster of the Arum family. The spadix shown above was 8.5 feet tall and the circumference of the spathe was 12 feet 10 inches. The corm B from which it grew weighed 113 pounds. In C the staminate flowers (above) and the carpellate flowers (below) may be seen through the opening cut in the spathe. D shows a leaf of a similar but smaller plant. Further details have been published by W. H. Camp, *Jour. N. Y. Bot. Gard.* 38:177. 1937. Photos from New York Botanical Garden.

flowers have stamens but no pistils, and other flowers on the same plant or in the same inflorescence have pistils but no stamens. These flowers are termed *staminate* and *pistillate*, respectively. In the inflorescence of jack-in-the-pulpit, *Amorphophallus* (Fig. 156), and other aroids stami-

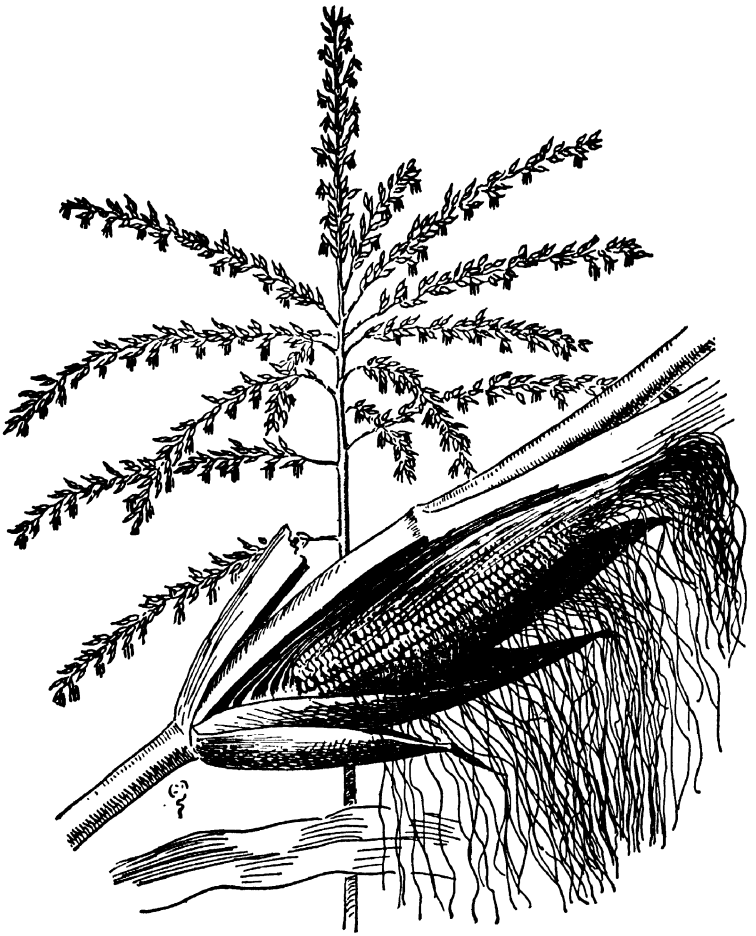

FIG. 157. Flowers of the corn plant. The staminate flowers are borne in a large open panicle (tassel). The pistillate flowers are arranged in a spike (ear), enclosed by sheathing leaves. The only part of a pistillate flower exposed to the outer air is the end of the long style (silk). Courtesy of World Book Co.

nate flowers occur on the upper part and pistillate flowers on the lower part of the same floral axis. Maize, or Indian corn, has staminate flowers on "tassels" and pistillate flowers on "ears" (Fig. 157), but the environment may greatly affect this arrangement.

Many trees of Christmas holly, willow, and poplar have only staminate

flowers; others have only pistillate flowers. Hemp plants likewise usually bear only staminate or only pistillate flowers. Such plants are said to be dioecious (Greek "two households"), in contrast to monoecious (Greek "one household") plants on which both staminate and pistillate flowers, or perfect flowers, occur. Some plants are monoecious in certain environments and dioecious in others.

Flower clusters. The flowers of some plants, such as those of tulip and trillium, grow singly at the ends of solitary unbranched peduncles. But

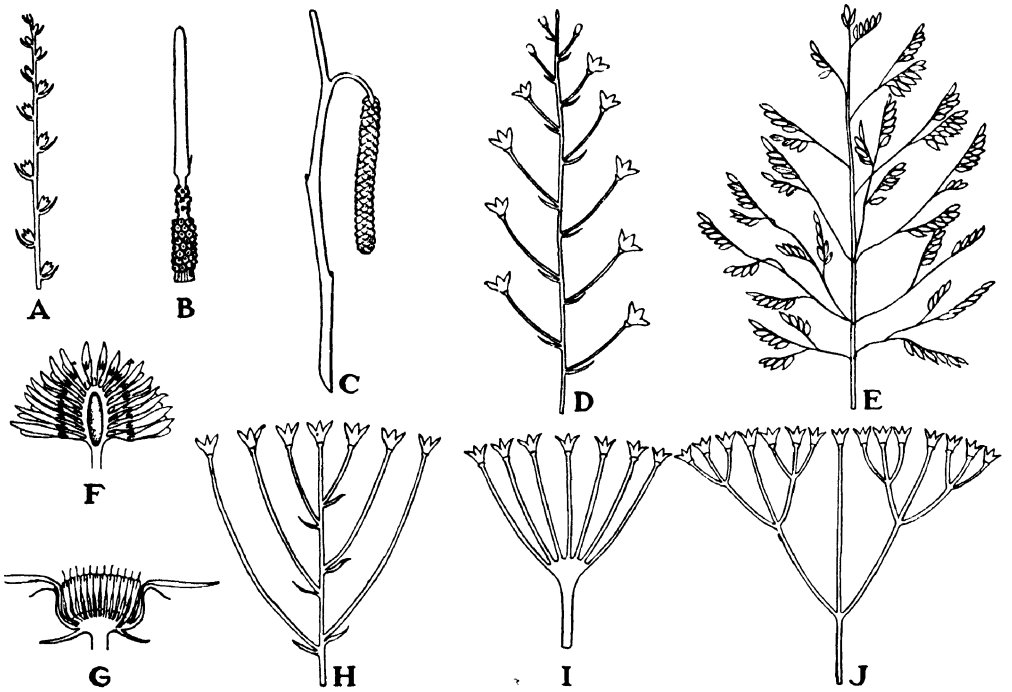

FIG. 158. Diagrams of ten types of flower clusters (inflorescences): A, spike; B, spadix; C, catkin; D, raceme; E, panicle; F, head; G, head with disk flowers and ray flowers; H, corymb; I, umbel; J, compound umbel. See also illustrations in Chapter LI.

in many species of plants the peduncle branches; and each of its ultimate branches, the pedicels, terminates in a single flower. The flowers are thus grouped in various types of clusters called *inflorescences*. (Fig. 158). Flowers may also be clustered along the sides of the main floral axis, or on numerous small lateral branches at the upper part of a plant.

The variety of flower clusters is so great that a special terminology is necessary to describe them. The *spike* exemplified by the common plan-

tain, wheat, and cat-tail has numerous flowers which are sessile, or nearly so, on an erect and elongate axis. If the axis is fleshy, as in calla lily and jack-in-the-pulpit, it is called a *spadix*. A *catkin* is a spike-like cluster of flowers, but drooping and scaly, as in willow, cottonwood, oak, hickory, and birch. When the pedicels of the individual flowers are longer, as in the inflorescence of yellow toad-flax, pepper-grass, and snapdragon, the arrangement is designated a *raceme*. Rounded or flat-topped clusters of milkweed and carrot are *umbels*, while those of the hawthorn are *corymbs*. The pedicels of umbels all originate in the apex of a stem, whereas those of corymbs are axillary outgrowths along the sides of the floral axis. If the peduncle, or floral axis, is repeatedly branched, as in the inflorescence of yucca and many grasses, the cluster is called a *panicle*. The flowers of red clover, dandelion, and sunflower are sessile and grouped in a compact *head*. The head of flowers of dahlia, daisy, cosmos, and sunflower is often mistaken for a simple flower because the ray flowers have the appearance of petals and beneath them is an involucre of green bracts that resembles a calyx. There are other types of inflorescences, but the foregoing are the common ones, and usually they are not difficult to recognize.

There are, however, many intergradations among the classified types of flower clusters. Sometimes it is a matter of choice whether a particular spike is short enough to be called a *head*, fleshy enough to be called a *spadix*, or scaly and pendant enough to be called a *catkin*. In spikes, racemes, and panicles the inflorescence continues to elongate at the tip during the period of flowering, and it may even revert to a vegetative condition as it ordinarily does in pineapple. Elongation usually does not occur in heads, umbels, or in certain other types of inflorescences in which the central terminal flower develops first.

Flowers as forerunners of fruits. One has but to compare the pistil with the mature fruit of such plants as tulip or sweet pea to see many points of similarity. If successively younger fruits are examined, it soon becomes evident that the fruits of these plants develop solely from the pistil or from the ovulary. Such simple fruits, therefore, are merely the result of further growth of the carpels after pollination has occurred. If the stigma and style wither and die, only the basal part of the carpels, the ovulary, becomes the fruit. The enlarged and mature ovulary may be thin and membranous, hard and thick, or soft and juicy. It encloses the seeds and is often referred to as a *pericarp*.

The simpler fruits of all flowering plants consist only of enlarged

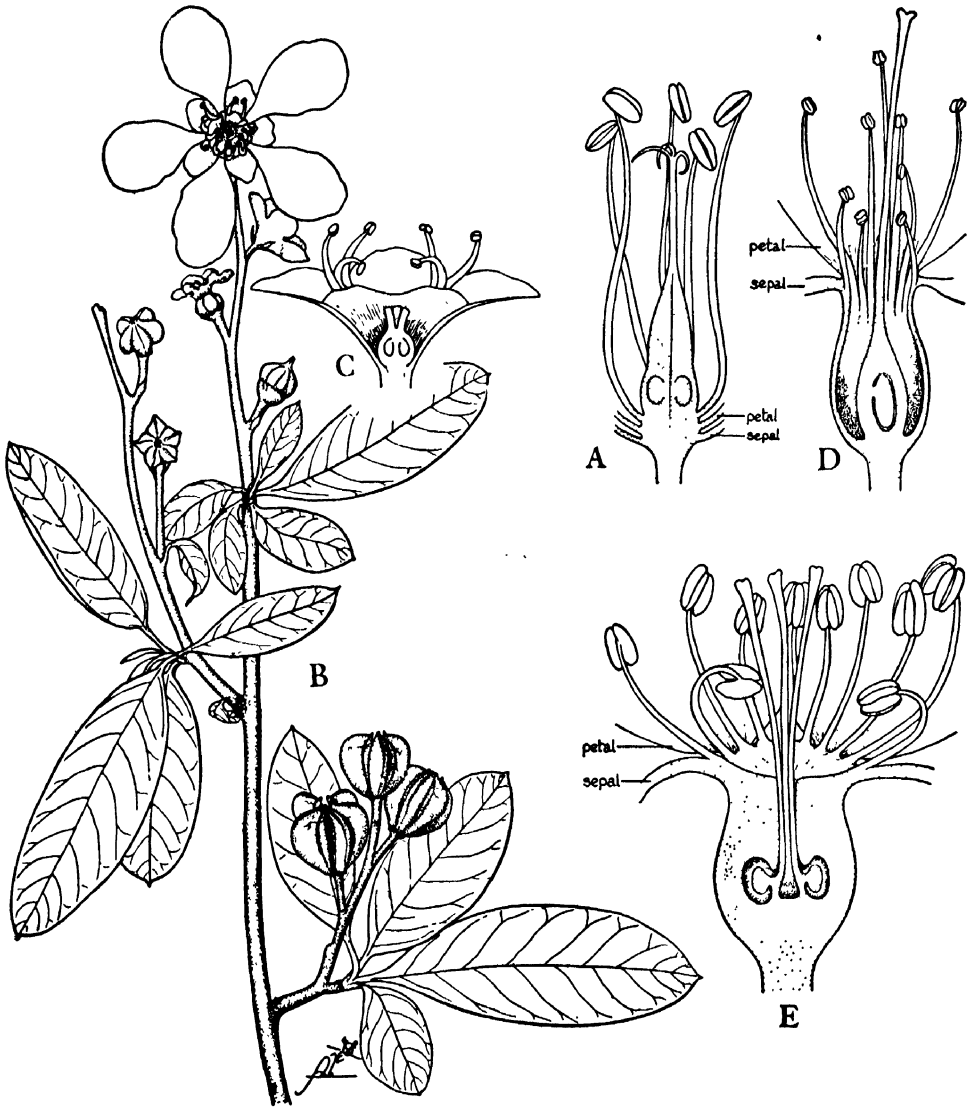

FIG. 159. Types of flowers in relation to fruits. A, flower of cranesbill (*Geranium*) in which the floral organs develop separately on the receptacle and the base of the pistil is above the bases of the stamens, petals, and sepals (hypogynous). The pistil alone becomes the fruit. B, flowers and fruits of pearl bush (*Exochorda*) in which the bases of the stamens, petals, and sepals develop as a floral cup around the base of the pistil (perigynous). The floral cup abscises and the pistil alone becomes the fruit. C, vertical section of a flower of pearl bush; D, vertical section of a perigynous flower of peach; E, vertical section of a flower of pear in which the floral cup surrounds and is united with the ovulary (epigynous), and becomes a part of the fruit.

carpels, or pericarp. The more complex fruits of flowering plants are composed in part of enlarged carpels and in part of other structures which develop from the receptacle, floral cup, or other parts adjacent to the flower. The edible portion of an apple and the rind of a banana, for example, develop from the floral cup and surround the ovulary. In the flowers of many plants, such as apple, rose, banana, gooseberry, blue-

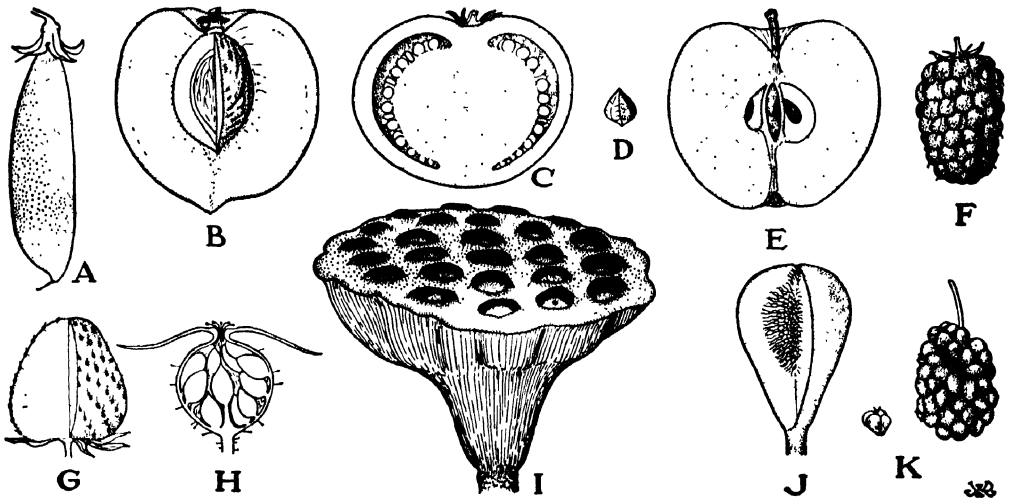

FIG. 160. Types of fruits: A, legume (pea); B, drupe or stone fruit (peach); C, berry (tomato); D, akene (buckwheat); E, pome (apple); F-G, several ripened pistils on the receptacle of one flower, aggregate fruits (blackberry and strawberry); H, several pistils enclosed in an enlarged urn-shaped floral cup (rose); I, several pistils embedded in the enlarged apex of the floral axis (water lotus); J, an enlarged stem tip with a central cavity containing many small flowers (fig); K, a single flower of mulberry with thickened sepals and also the whole flower cluster ripened as one compact fruit. J and K are types of multiple fruits.

berry, cucumber, and sunflower, the floral cup partly or wholly encloses the ovularies of the pistil and becomes a part of the fruit (Fig. 159). The cups of acorns and the husks enclosing hickory nuts apparently develop from involucral bracts that grow below the flower. We may therefore consider a *fruit* as a plant organ that develops from one or more carpels, together with any other closely associated flower part that may enlarge and ripen with the carpels (Fig. 160).

To many persons the term "fruit" refers only to certain edible structures, such as apples, pears, plums, and apricots, that grow on trees. In certain practices the *fruits* of many herbaceous plants, such as tomato, string bean, okra, pepper, cucumber, and squash, are popularly called

"vegetables." Vegetable salads may even contain the seeds of beans and peas. The term "vegetable" is not a technical term. Sometimes it is used synonymously with the term "plant," as in the expressions "vegetable kingdom" and "vegetarian." We shall soon see that in everyday language the fruits of many plants are not ordinarily distinguished from seeds.

Types of fruits. The variety of fruits appears to be as great as that of the flower from which they develop. In the course of a year everyone eats or otherwise encounters many types of fruits, and it may be of interest to be able to recognize the principal structures of the more familiar ones. Botanists and horticulturists often try to distinguish two general types of fruits: the *simple fruits*, which develop solely from an ovulary or pistil, and *complex fruits*, which develop from ovularies and a variety of adjacent structures. Fine distinctions are not always made. A tomato, for example, is usually regarded as a simple fruit, although, as in the fruit of pepper (Fig. 140), the placenta probably originates mainly from the apex of the receptacle.

Several types of simple fruits are easily recognized. If young bean pods and young peach fruits are cut crosswise, the cut surfaces of

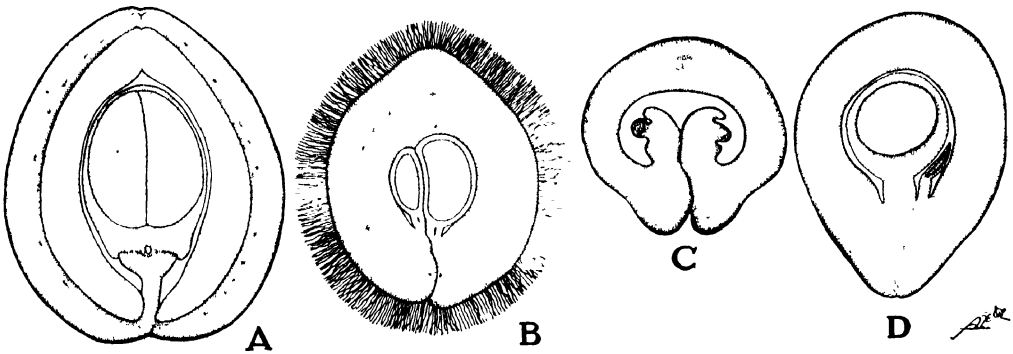

FIG. 161. Cross section of three young simple fruits each composed of a single carpel. The ovules develop from the infolded margins of the carpel, best seen in C, which is a cross section of a very young pistil of a plum flower. A, cross section of a young bean pod in which one ovule is evident; B, cross section of a young peach with two ovules; D, cross section of a plum in which one of the two ovules has failed to become a seed. The cells in the innermost tissue of the carpels of peach and plum ultimately become thick-walled and form the hard "pit" or "stone" of the fruit.

these two types of fruits are seen to have certain features in common (Fig. 161). Each consists of a single carpel with united margins. The ovule or young seed visible in each section is attached by a short stalk to one of the infolded margins of the carpel. The bean pod may con-

tain from one to many ovules or seeds, but usually only one of the two ovules in a fruit of peach becomes a seed. Another significant similarity in these two fruits is the two obvious layers of tissue in the carpel. The inner of these two layers in the peach ripens dry and stony, whereas the outer layer ripens soft and juicy. In the bean pod both of these layers ripen dry and hard. The fruit of grape is a third type of simple fruit in which the whole ovulary ripens soft and juicy.

The peach is an example of *stone fruits*, or *drupes*. Other examples of stone fruits are plum, cherry, olive, apricot, mango, almond, and the fruits of hackberry, poison ivy, basswood, and American holly. The suture formed by the fusion of the margins of the single carpel of these drupes is usually evident as a slight groove on one side of the fruit. The almond differs from the other fruits in the list in that the entire fruit becomes dry at maturity. The coconut likewise resembles a stone fruit, but it consists of three carpels, both layers of which ripen dry and hard.

The grape exemplifies the *berry type* of fruit. Other examples are persimmon, date, avocado, nightshade, lemon, orange, grapefruit, and tomato.

Simple dry fruits may be one-seeded and indehiscent, as the *akene* of buckwheat, and the *grain*, or *caryopsis*, of wheat, corn, and other grasses. They are said to be indehiscent because they do not split open when mature. In all grains the ovulary wall is united with the coats of the single

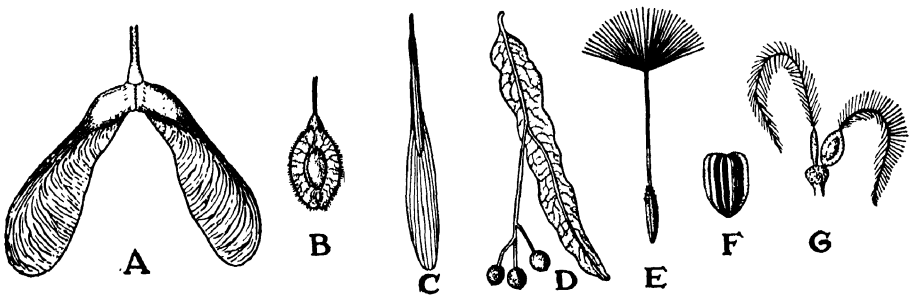

FIG. 162. Several types of simple fruits: A, maple; B, elm; C, ash; D, basswood; E, dandelion; F, sunflower; G, clematis.

seed. The shelled nuts of hickory, pecan, walnut, oak (acorn), and chestnut as they appear on the market are similar to akenes. The individual fruits of sunflower, dandelion, and other plants of the composite family are also called akenes, but they are not simple fruits, for they consist of an ovulary united with a floral cup (Fig. 162). The winged fruits of maple, ash, and elm are similar to akenes.

A large number of simple dry fruits are many-seeded and dehiscent. The *legumes* of the pea and the bean split along two sutures: the *follicles* of milkweed and larkspur split along one suture; the *capsules* of tulip, cotton, and okra consist of more than one carpel and split along several sutures. The *pyxis* of plantain, purslane, and pigweed splits crosswise.

Representative examples of some of the more familiar complex fruits are the apple and the cucumber, the raspberry and the strawberry, and the mulberry and the pineapple.

The fruits of apple, pear, quince, hawthorn are called *pomes*. The core resembles a drupe in that the cartilaginous part is the inner layer of the ovulary and is surrounded by a soft juicy layer that develops from the outer tissue of the ovulary. Most of the edible part, however, develops from the floral cup.

The fruit of the cucumber likewise develops from the ovulary and adherent floral cup, but does not have the inner cartilaginous tissue. Other examples are gooseberry, currant, cranberry, blueberry, banana, pomegranate, guava, coffee, gourd, pumpkin, squash, muskmelon, and watermelon.

In each pistillate flower of a strawberry are many separate pistils on an enlarged receptacle. As the receptacle enlarges and becomes the major part of the fruit, the pistils ripen as separate akenes and are partly embedded in the receptacle. Because of this assemblage of pistils on one receptacle the strawberry is called an *aggregate fruit*. Other examples are blackberry and raspberry, in each of which the separate pistils ripen as small drupes, or drupelets. When a raspberry is ripe the closely adhering aggregate of drupelets separates from the receptacle. In the fruit of wild roses the group of ripened pistils is enclosed by a floral cup.

When fruits from several flowers are united in a compact mass, the entire assemblage is a *multiple fruit*. The formation of multiple fruits varies with the kind of plant. In the fruit of the fig the enlarged fleshy receptacle is hollow, and on its inner surface there is a compact layer of simple fruits that developed from the enclosed flowers. The flowers of the pistillate catkin of the mulberry surround the floral axis in a compact mass as the sepals become thickened and succulent. The multiple fruit of pineapple also develops from a spike-like cluster of flowers in which the floral axis, flowers, and subtending bracts all become enlarged and united in a single mass (Fig. 163).



FIG. 163. Pineapples in Hawaii. The entire flower cluster of each plant becomes a compact multiple fruit. Photo from U. S. Forest Service.

The seed. We have already seen that the ovulary contains ovules, which ultimately become seeds. Seeds are unlike in size, form, composition, and in several other ways. The seeds of some orchids are almost microscopic in size, while those of a few tropical legumes and of certain nut-bearing trees may be several inches in diameter. From a study of a few kinds of seeds one may learn to recognize their essential parts.

The *seed coats* of the castor bean, for example, consist of a hard outer layer and a thin papery inner membrane. The seed coats enclose the *endosperm* and the *embryo*. The embryo is the young plant of another generation of castor bean. It consists of a very short stalk (*hypocotyl*) and two thin, colorless leaves, or *cotyledons*. Between the bases of the two cotyledons is a bud—the *plumule*—from which the stems and leaves of the seedling develop. No root is visible in the embryo; but when the seed germinates, the basal tip of the hypocotyl elongates, and from its root primordium a *primary root* develops. The seedling that develops from the embryo of a germinating seed is at first dependent upon the food which accumulated in the cells of the embryo and endosperm while they were developing in the seed.

The seed of the kidney bean differs from that of the castor bean in the absence of an endosperm. It consists only of an embryo enclosed by

seed coats. The embryo consists of a hypocotyl, a plumule, and two large, greatly thickened cotyledons. All the accumulated food in a bean seed is in the embryo. The seeds of many other plants, such as species of legumes, mustards, hickory nuts, and pumpkins, also lack endosperms.

The grain of corn, like that of wheat, consists of a grain coat, a large endosperm, and an embryo, which is near the inner end of the seed. There is a single large cotyledon (*scutellum*) more or less enclosing the hypocotyl and the plumule (Fig. 113). Because of the fact that the corn grain develops from both the ovule and the ovulary wall, it is really a fruit. The grain coat is composed of seed coats plus the adhering ovulary wall, or pericarp.

Monocots and dicots. From our early study of the vegetative organs of a plant we learned that monocots and dicots may be recognized partly by the venation of the leaves and the arrangement of the vascular bundles in the stem. The flower parts of monocots are often in 3's or 6's, while those of dicots are often in 4's or 5's or in some multiple of these numbers. The terms refer, however, to the number of cotyledons[2] in the embryo of the seed. The seeds of bean, squash, apple, and ash, along with many others, have two cotyledons, and these plants are called *dicots*; the seeds of wheat, corn, rye, and other grasses contain but one cotyledon, and such plants are *monocots*.

Gymnosperms and angiosperms. Conifers, such as pines and spruces, bear seeds on the upper sides of overlapping scales arranged in a cone. The seeds are not enclosed by the scales but are exposed on their flat open surfaces. Plants bearing seeds in this manner are termed *gymnosperms* ("gymnosperm" means "naked seed"). Most seed plants have carpels united in the form of a distinct pistil. The seeds enclosed in the ovulary of the pistil are covered, or "hidden"; hence the name, *angiosperms*.

Dissemination of seeds. When seeds are mature they may become separated from the fruit or the parent plant in several ways. The seeds may be expelled from fruits such as legumes and capsules when the ovulary walls dry out, twist, or curl and shrink. The one-seeded fruits, such as the akene and the grain, become free by abscission from the receptacle. The seeds in many fruits, such as those in pomes, nuts, drupes, and berries, are set free only by the decay of the fruit.

[2] "Monocots" and "dicots" are abbreviations now in rather general use for the longer terms "monocotyledons" and "dicotyledons."

Seeds may be scattered by wind, by water, by birds and other animals, and by means of temporary lodgment on moving vehicles, such as automobiles, airplanes, trains, and ships. Perhaps the most important natural agent in the dissemination of seeds is the wind. Many seeds are light in weight, have relatively large surface areas, and may be carried many miles by air currents. Larger and heavier seeds may be washed great distances downstream, particularly during time of flood. Animals scatter seeds in several ways: (1) the seeds may be eaten and survive the

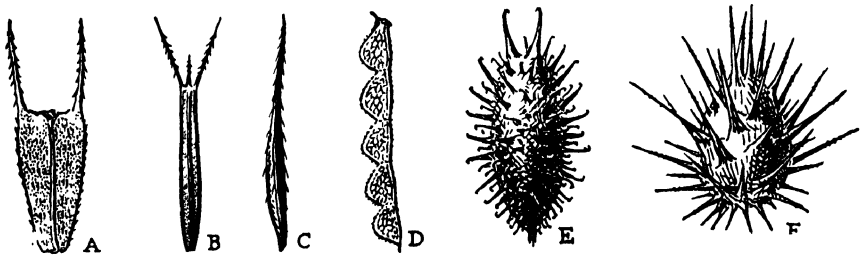

FIG. 164. Fruits frequently transported by animals: A, beggar-ticks (*Bidens*); B, Spanish needles (*Bidens*); C, sweet cicely (*Washingtonia*); D, tick trefoil (*Desmodium*); E, cocklebur (*Xanthium*); and F, sand bur (*Solanum*). Courtesy of World Book Co.

digestive juices of the animal; (2) the walls of the fruit enclosing the seeds may be spinous, prickly, or otherwise roughened and become entangled in the fur and hair of animals; (3) the fruit coats may be sticky and adhere to the feet of birds or other animals (Fig. 164). Man is one of the main agents in the dispersing of seeds, especially when it comes to carrying them across the continent or from one continent to another. Dissemination of seed does not necessarily result in the wider distribution of the plant. Germination of the seed does not occur except when the environment is favorable; and even then the seedling may fail to develop or may be destroyed.

Economic value of flowers, fruits, and seeds. These three plant organs are the primary economic products of floriculture, horticulture, and agronomy. Corn in the United States alone is a billion-dollar crop. This is its value to those who cultivate and harvest it. It may then be converted to pork in the body of a pig, or to eggs in the body of a chicken; or man, by means of industrial processes, may place it on the market as meal, corn flakes, hominy grits, starch, glucose, syrup, alcohol, acetic acid, dextrin, mucilage, sizing paste, corn oil, artgum, rubber, or any one of a hundred other products. The economic value of a plant organ

is thus intimately related to the uses made of it and to the number of people who make a living wholly or in part by cultivating the plants that bear it or by preparing it for ultimate consumption. Some commercially important seeds are those of wheat, oats, barley, rice, cotton, beans, peas, coffee, peanuts, coconuts, almonds, pecans, walnuts, filberts, and pistachios. Economically the seeds of the grasses are the most important; then come those of cotton and the legumes.

The cultivation of plants for their seeds is the most important economic phase of agriculture. The secondary industries related to it include shipping, marketing, feeding of domesticated animals, industrial processing, scientific investigation of processes and of the uses of products, and the dissemination of information about agricultural methods and procedures.

The number of kinds of commercially important fruits and flowers is large, but their total economic value is much less than that of seeds. Among the commercially important fruits of the world are bananas, breadfruit, dates, figs, olives, plantains, apples, grapes, plums, apricots, peaches, tomatoes, pineapples, melons, and several varieties of citrous fruits. The secondary industries related to the cultivation of plants for their fruits include, in addition to those listed for seeds, greenhouse culture, extraction of juices, canning, drying, freezing, and cold storage which make them available at all seasons of the year. Other industries related to the cultivation of plants for their flowers include the numerous flower shops, the keeping of bees for honey, and the manufacture of perfumes.

The economic value of flowers, fruits, and seeds and of the products derived from them thus amounts annually to many billions of dollars, and a large percentage of the population finds a means of livelihood either by cultivating the plants or by preparing and distributing the harvested products for final consumption.

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CHAPTER XXXIII

SEXUAL REPRODUCTION IN FLOWERING PLANTS

Sexual reproduction occurs in nearly all kinds of plants. In angiosperms, commonly called flowering plants, and in gymnosperms (pines, firs, spruces, and other cone-bearing plants) it is associated with the formation of seeds. With a few exceptions the processes of sexual reproduction and seed formation in these two groups of plants are similar, but in this chapter all statements about seeds and seed plants refer particularly to angiosperms.

A complete account of the principal events in the sexual reproduction of seed plants must include a description of how the embryo and endosperm come to be in the seed, how pollen develops in the anther, and how pollen is related to the formation of seeds and fruits.

Since seeds develop from ovules, and since the seed coats, embryo, and endosperm are each composed of cells, one may infer at once that each part of the seed grows from certain cells in the ovule. The origin of the embryo of a seed plant, like the origin of the embryo of other organisms, usually is a fertilized egg—a cell formed by the union of an egg and a sperm.

From what cells, then, do the eggs and sperms develop in a seed plant? What is the precursor, or forerunner, of the endosperm of a seed? Of the pollen grain in the anther? Each of these several structures develops from others in a definite order or sequence; and to know the story of sexual reproduction one must learn which processes and structures are the precursors of others.

Deviations from the usual sequence may occur. The results of some of these deviations are familiar objects. Seedless fruits, seeds without endosperms, seeds with more than one embryo, identical twins, and abscission of pistils are consequences of certain departures at some particular stage in the usual story of reproduction. One must be able to visualize this usual story in order to appreciate such deviations as those just mentioned, to compare sexual reproduction in seed plants with that of other organisms, and to understand its relation to heredity. To do this

we need to know only what happens in the stamen and pistil of the flower. Sepals and petals are merely accessory structures. We may begin with the stamen.

What takes place in the stamen? At certain seasons of the year the stamens become mature, their anthers open or dehisce, and from them millions of powdery grains known as *pollen* or *pollen grains* are released. What is their origin and how have they developed? To answer this question it will be necessary to begin with a young anther.

In a cross section of a very young anther the cells look alike; but in sections of slightly older anthers there may be seen four groups of meristematic cells quite distinct from the remaining cells, and known as the *sporogenous* (spore-forming) *tissue* (Fig. 165). Further differentiation in this tissue results in special spore precursor cells called *microspore mother cells*, or *microsporocytes*. Each mother cell becomes separated from the others and divides. The anther now contains numerous cells attached in groups of two (dyads). When these cells divide, the resulting daughter cells appear in groups of four (tetrads) and are known as *microspores*. Each microspore mother cell, therefore, is really the grandmother cell of four microspores. At maturity the microspores fall apart and are seen as separate cells. Many microspores are ordinarily formed in an anther at about the same time, and the parts of the anther enclosing them are *microsporangia* (microspore cases).

Each microspore at first contains a single nucleus. When this nucleus divides, the microspore technically becomes a 2-nucleate *pollen grain* and the microsporangium may now be termed a *pollen sac*. One of the two nuclei in the pollen is the forerunner of the sperms and is known as the *generative nucleus*; the other one is referred to as the *tube nucleus* because of its relation to the growth of the pollen tube from the pollen grain. A subsequent division of the generative nucleus,[1] either in the pollen grain or in the pollen tube, results in two *male gametes*, or *sperms*. Dehiscence of the anther and shedding of the pollen occur in most plants before the sperms are formed. In the anthers of many plants the wall between certain pollen sacs may open so that by the time of dehiscence of the anther the original four microsporangia have become two pollen sacs.

We shall interrupt the story of what is happening in the stamen

[1] These nuclei are surrounded by cytoplasm, but the individual cells are not always enclosed by distinct cell walls. It is more convenient, therefore, to observe and refer to the nuclei than to the cells of which they are a part.

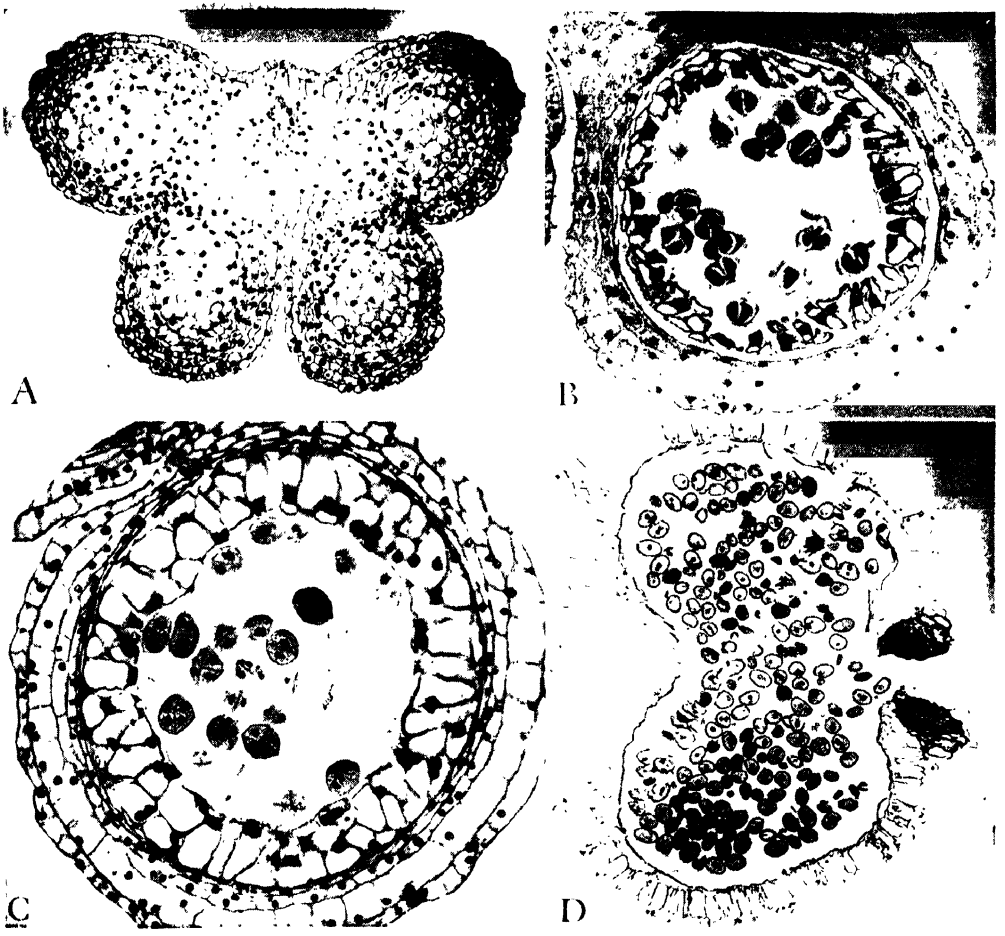

FIG. 165. Formation of microspores and pollen in the anther. A, cross section of a young anther with four microsporangia containing microspore mother cells; B, an enlarged cross section of one microsporangium containing cells in groups of two formed by division of the microspore mother cells; C, a slightly older stage in which further cell division has resulted in microspores adhering in groups of four; D, the microspores have separated and some of them have become pollen grains. Two of the microsporangia have become one pollen sac, which has split open along one side.

at this point, and return to it after we have found out what is occurring in the pistil.

What takes place in the pistil? The externally visible parts of a pistil are the stigma. style, and ovulary. If a young ovulary is broken in two or dissected, it will be seen to contain one or more small roundish bodies known as ovules.

In a very young ovulary the ovules are seen as small mounds of cells that have developed from a particular part of the ovulary termed the placenta. In microscopic sections of these young ovules all the cells look alike; but in sections of a slightly older ovule one cell near the tip is seen to be larger than any of the others. This cell is a *megaspore mother cell*, or *megasporocyte*. From this cell through successive cell divisions there results a group of four (tetrad) *megaspores*. Three of the megaspores ordinarily disintegrate, and only one develops further.

By this time the ovule has enlarged and its three parts—the stalk, nucellus, and integuments, or coats—can be recognized (Fig. 166). Since the megaspores develop within it, the ovule may be called a *megasporangium*. The integuments do not quite enclose the ovule at one end, thus leaving a small pore known as the *micropyle*. After the first nuclear division the megaspore technically becomes a 2-nucleate *embryo sac*. Through subsequent nuclear divisions the embryo sac finally contains eight[2] nuclei, one of which becomes the *female gamete*, or *egg*. Two other nuclei unite and form the *fusion nucleus*. The embryo sac thus becomes 7-nucleate. Of these the egg and fusion nucleus are the important ones. The other five nuclei are usually transient and disintegrate, though in certain species of plants some of them divide and a small group of cells develops from them; occasionally an embryo may develop from one or more of them.

The pollen in the stamen now becomes important in our account of sexual reproduction.

Pollination and growth of the pollen tube. Upon the dehiscence of the anther and shedding of the pollen from the pollen sacs, some pollen grains either fall upon or are carried by some means to the stigma of the same or of another flower. The transfer of pollen from the anther to the stigma is called *pollination*. This process may be brought about by wind, water, insects, man, and gravity. On the stigma the pollen grain germinates almost immediately, and a *pollen tube* develops from it. The stigma is covered with a sticky fluid of sugars, acids, and other substances, and the pollen grain will usually germinate best on stigmas of the same or closely related plants. Pollen grains of many kinds of plants germinate when placed in solutions of sugar and water.

The pollen tube grows rapidly, penetrates the stigma, and extends

[2] In the embryo sacs of some plants, such as trillium, the number of nuclei is four. One becomes the egg, two form the fusion nucleus, and the fourth disintegrates. Several other deviations in embryo sac development in other plants are known, but only the usual type of embryo sac will be described here.

through the style into the ovulary and finally to the ovule (Fig. 167). This distance in most plants is short; but in the style of corn, which is the silk, the pollen tube must often elongate more than a foot before

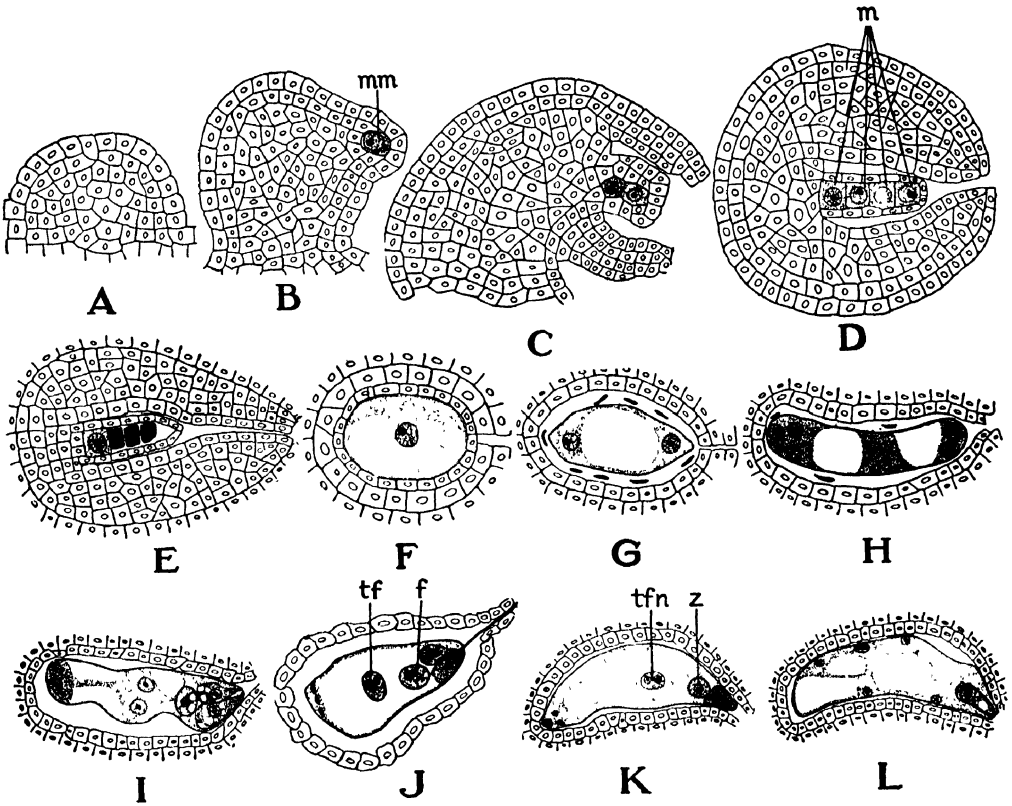

FIG. 166. Stages in the development of an ovule and a young seed of pepper. A-D, formation of four megaspores (m) from a megaspore mother cell (mm) in a young ovule; E, disintegration of three of the megaspores; F-I, development of an 8-nucleate embryo sac from one of the megaspores, a fusion nucleus is formed by the fusion of the two nuclei near the center of the sac, only a little of the surrounding ovule tissue is represented; J, fertilization (f) and triple fusion (tf); K, zygote (z) and triple-fusion nucleus (tfn); L, early stages in the development of the embryo and endosperm of the seed. After H. L. Cochran, *Journal of Agricultural Research*, with some modification.

it penetrates the ovule. The direction of its growth is influenced by chemical conditions within the pistil. A part of the distance it is growing in channels and intercellular spaces. Resistance to its growth between closely packed cells is decreased by enzymes which bring about softening of the tissues through which the tube grows. During the growth of the tube, the nuclei are near the growing end. The pollen

tube enters the embryo sac, often through the micropyle; the end of the pollen tube swells and bursts, and the two sperms are released. The tube nucleus then disintegrates. The embryo sac now contains, in addition to the five transient nuclei, an egg, a fusion nucleus, and two sperms.

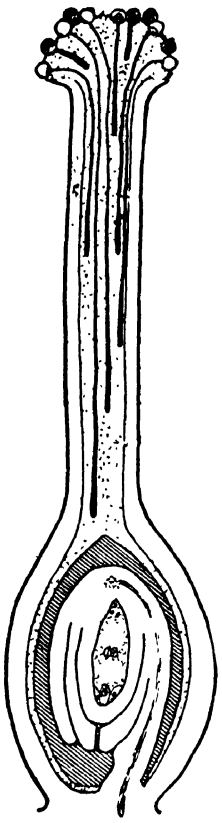

FIG. 167. Diagram of a pistil with germinating pollen grains and pollen tubes of various lengths. The embryo sac is in the 7-celled stage, with a central fusion nucleus and an egg (below). Fertilization occurs when a sperm from a pollen tube unites with the egg. After J. T. Buchholz. Courtesy of World Book Co.

Fertilization. The next event is the fusion of one sperm with the egg, resulting in the *fertilized egg*, or *zygote*. The union is called *fertilization*. The other sperm unites with the *fusion nucleus*, and the resulting 3-nucleate structure is the *triple-fusion nucleus*, also inappropriately called the *endosperm nucleus*. The union of the three nuclei is termed *triple fusion*.

The embryo and the endosperm. The fertilized egg soon begins to grow, and many cell divisions result in a tissue known as the *embryo* (Fig. 168). The sugar used in the growth of the embryo must have come from the green parts of the plant on which the flowers were borne. The embryo, when mature, is differentiated into cotyledons, hypocotyl, and plumule, as noted in the preceding chapter. It is a new plant.

While the embryo is developing in the ovule, another *tissue*, known as the *endosperm*, may develop from the triple-fusion nucleus (Fig. 169). The cells of the embryo and endosperm often contain considerable food, chiefly oils, starch, and protein. The conditions in these cells are particularly suitable to the conversion of sugar to these more complex foods. In seeds of many plants the endosperm is very small or absent, because it failed to grow. In such seeds the cotyledons of the embryo are usually large and contain most of the food.

The embryo and endosperm of an angiosperm differ little in their origin, but in their final outcome they are quite unlike. The endosperm, when present, makes its complete growth within the seed, and ordinarily no other structures develop from it; the embryo, on the other hand, is the young stage of a new generation of plants.

The seed and the fruit. The growth and hardening

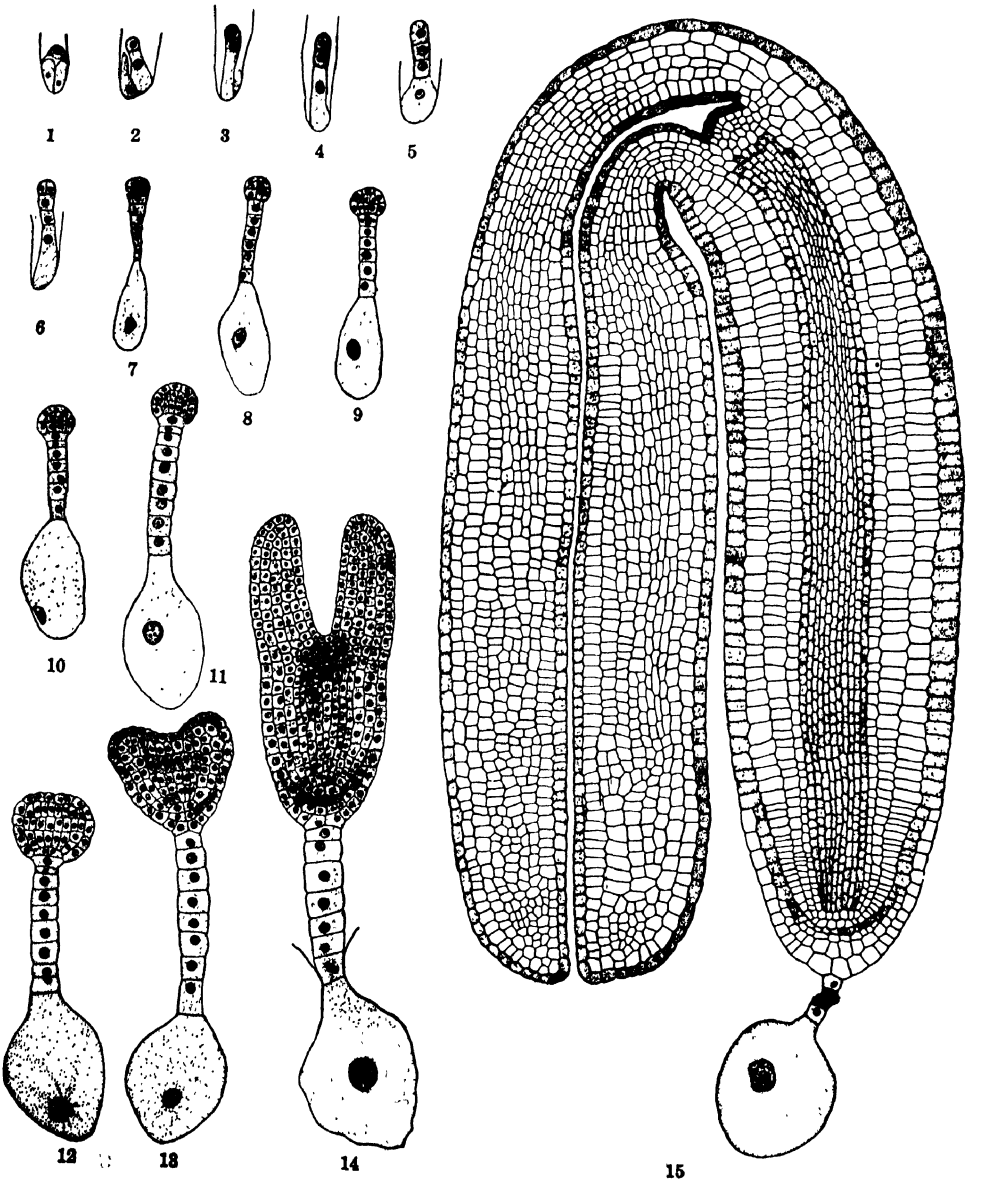

FIG. 168. Stages in the development of the embryo of shepherd's purse (*Bursa*) from the fertilized egg to the mature seed. Drawings by Mabel Schaffner.

of the ovule coats result in the seed coats which enclose the endosperm and embryo. These three structures—embryo, endosperm, and seed coat —are the principal parts of the *seed*. The seeds of numerous plants, however, consist of an embryo surrounded by seed coats only. Growth and various other changes in the ovulary result in the formation of a *fruit*,

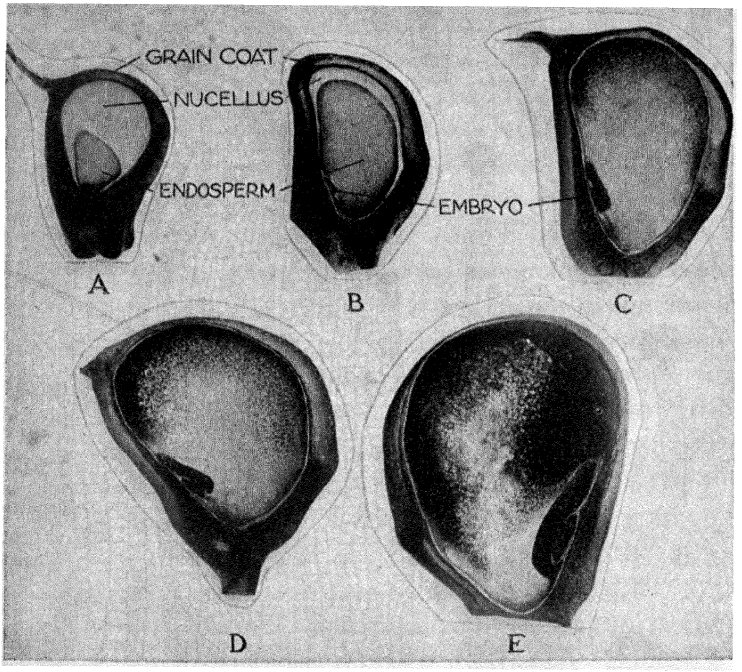

FIG. 169. Stages in the growth of embryo and endosperm in a developing grain of corn: A, 5 days after pollination; B, 10 days; C, 13 days; D, 15 days, and E, 20 days after pollination. Photos by Lois Lampe.

although none of its structures is the direct result of fertilization. Sometimes structures adjacent to the ovulary also grow and form a part of the fruit.

The life cycle of a flowering plant. We have now observed the series of changes in the flower known as sexual reproduction, leading directly or indirectly to the formation of fruits and the different parts of the seeds. If a seed is planted, a seedling may develop from the embryo. At first, food used in germination and in early seedling growth comes from the cotyledons of the embryo or from the endosperm. As soon as chlorophyll is formed in the seedling, however, photosynthesis may occur, and we have the usual green plant with which we are quite familiar.

Upon further growth of the seedling and completion of the vegetative stage, buds containing flower primordia develop. Through the series of events we have just described, spores and gametes develop in certain floral structures, and upon the formation of zygotes by union of gametes a new generation of plants is initiated. This life cycle from zygotes to

gametes and the formation of zygotes of a new generation may be repeated indefinitely.

The life cycle of a flowering plant may be analyzed from another point of view which may be stated briefly now, and then reconsidered after the life cycle of a fern has been discussed. A plant in which microspores and megaspores[3] develop may be termed a *sporophyte* (spore-bearing plant). The parts of the flower in which spores develop are often referred to as *sporophylls* (spore-bearing leaves); hence, the stamens may be thought of as *microsporophylls* and the carpels of the pistil as *megasporophylls.*

Eggs and sperms, collectively called gametes,[4] are also formed during the life cycle of a seed plant. In ferns and mosses, gametes develop in small multicellular plants that grow free upon the soil. Since these plants bear gametes they are called *gametophytes.* If this terminology is applied to seed plants, then the pollen grain plus the pollen tube in which the sperms are formed is a *male gametophyte* (sperm-bearing plant), and the embryo sac containing the egg is *female gametophyte* (egg-bearing plant).

The gametophytes of flowering plants are almost microscopic in size, non-green, and parasitic upon the tissues of the sporophyte. The gametophyte phase may be thought of as alternating with the sporophyte phase in the life cycle. The life cycle then is composed of two phases, each bearing the particular reproductive cells from which the other develops. The endosperm, however, is neither gametophyte nor sporophyte; it is termed the *xeniophyte.*

Summary of the usual sequences of events in sexual reproduction. The formation of fruits and seeds from flowers usually follows the sequence of events described in the preceding pages. Summary statements of these events are: (1) the formation of microsporocytes, microspores, and pollen in regular sequence within the anther of the stamen; (2) the development of two sperm nuclei from the generative nucleus within the pollen grain or the pollen tube; (3) the formation of one or more ovules in the ovulary of the pistil; (4) the formation in regular sequence within each ovule of a megasporocyte, an active megaspore, and an

[3] It is customary to use the term "microspore" to refer to the precursor of a pollen grain, and the term "megaspore" to refer to the precursor of the embryo sac, even though the terms are sometimes literally inappropriate, since in many flowering plants there is little difference in size and sometimes the microspore is the larger of the two.

[4] Eggs and sperms are called "megagametes" and "microgametes" respectively by some authors.

embryo sac with an egg nucleus and a fusion nucleus; (5) pollination; (6) the germination of the pollen grain and growth of the pollen tube from the stigma to the ovule; (7) the fusion of one sperm with the egg—fertilization—and the fusion of the other sperm with the fusion nucleus —triple fusion; (8) the development of the embryo from the fertilized egg; (9) the development of the endosperm from the triple-fusion nucleus in seeds of some plants; (10) the formation of seed coats from the ovule coats; and (11) the development of the fruit from the ovulary and other parts of the flower. The fertilized egg and embryo are the early stages of a new generation.

Deviations from the usual story of sexual reproduction. An examination of a seed of lima bean or garden pea reveals the *absence of an endosperm.* Seeds of such plants as onion, grapefruit, and pine often have more than one embryo, a condition known as *polyembryony.* Fruits of certain varieties of sunflower, orange, grapefruit, and grape are seedless, a condition referred to as *parthenocarpy.* What deviations from the usual story of sexual reproduction would result in these phenomena?

Plants such as the common dandelion have seeds containing viable embryos which developed from unfertilized eggs: a process termed *parthenogenesis.*

In the seeds of some plants, such as corn cockle, coffee, water lily, spinach, and pepper, the nucellus grows and becomes much enlarged, and foods accumulate in it just as they do in the embryo and endosperm. When mature, this tissue resembles the endosperm in appearance and is known as the *perisperm.* Sometimes it is merely a thin compressed membrane within the seed coats.

The failure of pollination and fertilization often results in the abscission of the pistil and no fruit develops. The early fall of immature fruits such as those of apple, peach, pear, and plum may of course be caused also by the invasion of parasites and by other unfavorable conditions. In spite of numerous exceptions, pollination and fertilization are generally necessary for the development of fruits and seeds in the great majority of flowering plants.

Growth of an absciss layer and subsequent separation of cells in the base of a pistil, or base of a young pedicel, are similar to the abscission processes that occur in the base of the petiole of a leaf (page 73 and Fig. 35). These processes in a petiole are affected by auxins coming from the leaf blade, but in pistils and pedicels they are affected by auxins

coming from pollen, ovules, and placentas. Hormones from placentas may also affect the germination of pollen on stigmas.

Ectogony. Pollination and fertilization directly affect the development of the embryo and of the endosperm because of the union of the sperms with the egg and with the fusion nucleus. They may also affect the abscission of the pistil as well as the chemical composition, the color, and the time of ripening of the fruit. Their influence on the development of structures outside of the embryo and endosperm may be referred to as *ectogony.*

Considerable study has been made of the effect of pollination and fertilization on the fruit of the date palm. The pollen from staminate flowers of several different varieties of palm was artificially transferred to the pistillate flowers of a single species of palm. The development of the fruits varied with the source of the pollen. The fruits varied in size, in shape, and in the time of ripening. Some fruits ripened as much as 10 days earlier than others.

Ectogony is undoubtedly the effect of hormones from the pollen tube and the developing embryo. From tests we now know that certain ectogonous effects may be obtained in plants such as tomato, squash, tobacco, and petunia merely by the application of extracts of pollen to the stigma, or to the cut end of a style from which the stigma has been removed. By this means abscission of the pistils may be prevented, and fully formed seedless fruits may develop from them.

Xenia. The effect of the sperm upon the development of the endosperm may be visibly evident. If, for example, pollen from a certain corn plant that had grown from a seed with blue endosperm is transferred to the stigma of another corn plant that had grown from a seed with white endosperm, and if triple fusion follows pollination, the resulting endosperm may be blue. Similar effects may be seen in form, shape, and chemical composition of the endosperm. The immediate effect of the pollen parent on the endosperm of the ovule parent is known as *xenia,* and will be described further in a later chapter.

Self- and cross-pollination. The transfer of pollen from anther to stigma of the same flower or of another flower on the same plant may be termed *self-pollination.* The transfer of pollen from the anthers on one plant to the stigmas on another plant is ordinarily referred to as *cross-pollination.* In Chapter XXXVII, however, it will be shown that two plants may be genetically identical, and what appears to be cross-pollination is equivalent to self-pollination. For example, plants that

develop from cuttings, or by other vegetative means, from the same individual are usually genetically identical. They are merely isolated branches of that individual. This is an important distinction to make in practice because many varieties of horticultural plants, such as certain varieties of apple and cherry, bear little or no fruit unless they are cross-pollinated. Cross-pollination is often referred to as *crossing*, and self-pollination as *selfing*.[5]

Pollination in itself is important in sexual reproduction only when it is followed by fertilization. Promiscuous cross-pollination may occur among numerous kinds of plants that are in bloom at the same time, but unless they are closely related no cross-fertilization occurs; that is, they are *cross-sterile*.

Cross-pollination is often necessary to sexual reproduction, and in some cultivated plants it is important in increasing yield and size of fruit. Self-pollination may not be followed by fertilization in rye and certain orchids because the pollen tube fails to grow on the stigma except when the plants are crossed; and in avocado, plantain, red clover, and lettuce because anthers and pistils do not mature simultaneously. Self-pollination does not occur in willows, palms, hemp, and many other plants because the stamens and pistils do not develop on the same plant. If fertilization occurs in a plant only when it is crossed with another one, the plant is said to be *self-sterile*. Self-sterility in *Petunia violacea* appears to be due to a hormone formed in the placenta which inhibits pollen germination and pollen-tube growth unless the pollen comes from a different variety.

Self-pollination is, however, usual in oats, wheat, barley, tobacco, and many other plants because the pollen is shed before the opening of the flowers. A small amount of crossing may occur when insects eat parts of the young flowers and move from one plant to another.

The avocado, or alligator pear, has complete flowers, but often no fruit develops. This was puzzling to the owners of avocado orchards

[5] The terms self- and cross-pollination are variously used by different writers, depending upon whether the flower, the "individual plant," the variety, or the species of plant is chosen as the basis of comparison. Since the chief value of these terms lies in the use we may make of them in discussing various horticultural procedures and heredity in seed plants, the more appropriate uses of them will become clearer in the following six chapters.

The term self-pollination has also been used in an entirely different sense to refer to pollination by direct contact of anther and stigma in contrast to the transfer of pollen by wind, insects, or other external agents. For example, as the pistils of sunflower approach maturity the styles curve downward and bring the stigmas in direct contact with the anthers below them. In spite of this "marvelous adaptation" sunflowers are self-sterile! The term "contact pollination" might well be used when self-pollination occurs in this way.

until careful observations showed certain peculiarities in the time of flower opening. Each flower opens twice. In some varieties this may be the morning of one day and the afternoon of the next day; in other varieties, the afternoon of one day and the morning of the third day. At the first opening the pistils are mature but the pollen has not been shed. At the second opening the anthers dehisce, but the stigmas are too mature for the pollen to germinate. Evidently self-pollination in avocado does not result in fertilization and the production of fruit. If these two varieties of avocado grow sufficiently close together, cross-pollination and fertilization may take place, and good yields of fruit result. The whole process is, however, complicated by the erratic opening of the flowers, and by the insects that transfer the pollen.

Dissemination of pollen. In the flowers that remain closed during ripening, as in oats and wheat, gravity plays an important part in pollination. A few plants, such as eel grass, certain pond weeds, and the water buttercup, are pollinated by water-borne pollen. Often the pistillate flowers develop just at the surface of the water, while the staminate flowers may be formed below the surface. The staminate flowers rise to the surface in large numbers, and the pollen eventually comes in contact with the stigmas.

In the great majority of land plants, particularly where cross-pollination occurs, wind and insects are the most important agents of pollination. Pollen grains vary widely in form (Fig. 170). Pollen may be carried many miles by air currents, but the pollen of most plants under

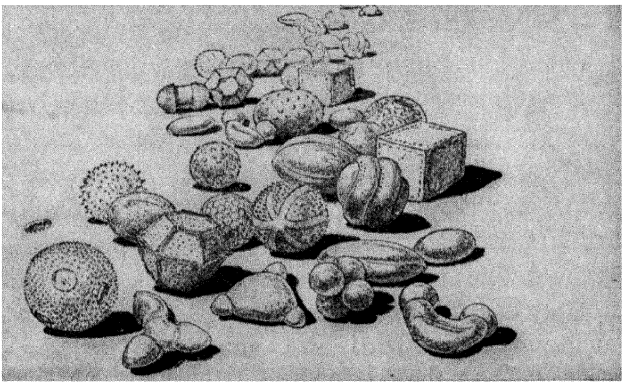

FIG. 170. Various forms of pollen grains. From W. Hamilton Gibson.

natural conditions remains viable but a short time, usually not more than a day or two. Under artificial conditions and proper drying it may be kept alive for a few weeks or even months. It has been reported that the pollen of date palms has been kept viable from two to eighteen years. The number of pollen grains that develop in the anthers on a single plant is often prodigious. A single corn plant, for example, may have as many as 50 million pollen grains. The number of seeds that develop in an ear on this same corn plant will rarely exceed 1000.

The importance of incidental pollination brought about by bees, wasps, flies, and other insects that use pollen and nectar as a source of food has been known for years (Fig. 171). The current statements that

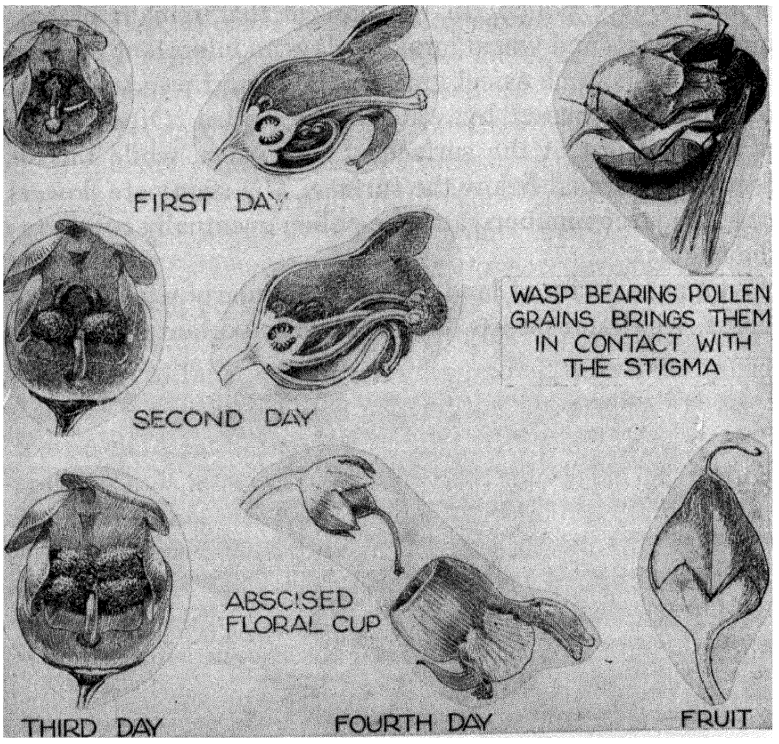

FIG. 171. Successive stages in the development of the flower, pollination, and growth of fruit in the common figwort. From W. Hamilton Gibson.

insects are more likely to visit flowers having a striking color, a special appearance, or a large size have little if any foundation in fact. Such matters cannot be discussed with certainty until more experimental data

are available. Some of the facts and speculations about the relation of flowers to pollination by insects may be found in the books cited at the end of this chapter.

The most remarkable cases of pollination by insects are those in which the plants have become dependent upon certain insects for the transfer of pollen. Cross-pollination of red clover is brought about primarily by bumblebees, and pollination of several of our horticultural plants is accomplished mainly by honeybees. The pollination of the widely cultivated yucca by the Pronuba moth is even more remarkable. The female moth deposits her eggs in the ovulary of the yucca flower, collects pollen from the anthers, carries it to the tip of the pistil, and then pushes it down inside the tubular stigma. The young larval insects which develop from the moth eggs inside the ovulary eat some of the developing seeds, but not all of them. The mature moths do not live long enough to see their offspring, but the instinct to deposit eggs in the pistil of the yucca flower and then pollinate it reappears through heredity in each generation of moths. The relation of the fig to a parasitic fig wasp is equally dependent, but much more complicated.

All such cases of specialization are, of course, the result of a long series of heritable variations during the millions of years that flowering plants and insects have been in existence. An enormous variety of heritable differences in floral structures has evolved and survived, but attention is usually directed only to those that appear to influence pollination, and to those we find desirable for decoration or for the classification of plants. Those of no survival value to the plant, or of no direct value to man, are usually ignored except by a few special students who find in them numerous contradictions to the claims of those who have an eye only for useful or allegedly useful structures.

Pollen and hay fever. Many people suffer every year from hay fever and "seasonal asthma," caused by unusual effects of pollen of certain species of plants upon the mucous membranes of the eyes, nose, throat, and bronchial tubes. The worst onslaught of hay fever is usually in late summer and is caused by the pollen of plants such as ragweeds, cocklebur, sagebrush, pigweeds, and thistles. Early-season hay fever may be caused by the pollen of such plants as maples, willows, birches, tulips, and grasses. The number of plants to which one person or another is allergic is large.

The sufferer is frequently affected seriously only by the pollen of one or a few species of plants, and these can be ascertained by proper skin

tests under the directions of specialists. When the pollen to which the individual is allergic has been ascertained, the physician may inject dosages of extracts specially prepared from the offending pollen. In this way complete or partial immunity to the pollen may usually be acquired. As an alternative the sufferer, once having found out what plants caused his discomfort, may—during their period of pollination—go to regions where these particular plants do not grow.

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CHAPTER XXXIV

GROWTH, DORMANCY, AND GERMINATION OF SEEDS

From the child who is thrilled by the story of Jack's miraculous beans that grew to sublime heights in a single night, to the world tourists who are perennially duped by the peddlers of Egypt with their living grains of wheat allegedly taken from the tombs of the Pharaohs, most persons are curious about how long seeds remain alive, why some seeds germinate readily and why the seeds of other equally common plants fail to germinate within a few weeks although the embryo appears to be in perfect condition. These phenomena have been studied experimentally in recent years and some of the results will be discussed in this chapter.

From zygote to mature embryo. The germination of the zygote is the beginning of the development of the embryo of a new plant similar in most respects to that in which the zygote was formed. Through cell division and some enlargement the embryo soon consists of a small body of meristem cells. In seeds of some plants, such as those of orchids, development of the embryo ceases at this early stage. In seeds of most plants, however, cell division, enlargement, and differentiation continue, and an embryo with well-defined cotyledons, hypocotyl, and plumule results. This development of the embryo of a seed plant occurs inside the ovule. Meanwhile the ovule coats grow and become seed coats. The nucellus also grows in the seeds of a few kinds of plants, but in most seeds it either becomes a negligible structure, or is entirely destroyed by the growth of the other seed structures.

The growth of the embryo is thus definitely limited by the tissues that enclose it. As its supply of water and oxygen decreases, and the dead seed coats prevent further expansion, the embryo ceases to grow and becomes dormant.

If the young embryos are removed from the ovules and placed in a sterile culture medium containing inorganic salts, water, and sugar, with oxygen available, they do not become dormant but continue to grow as seedlings. When the immature embryos of certain varieties of peach are planted under these conditions the plants are better than those that

develop from the embryos of seeds that matured within the fruit. Sometimes during excessively wet weather the embryos of corn, wheat, and other grains germinate almost immediately after maturity. In these wet seasons one frequently finds embryos continuing growth inside the ears of standing corn in September, and wheat and oats sprouting in the shocks on the field during midsummer.

Extreme cases of embryo development are found in seeds of such plants as Christmas holly, orchids, and mangrove. The embryo of the holly is merely a minute spherical body of cells when the fruit turns red in December. This clump of cells grows very slowly during a period of 8 to 12 months. The germination of the seed is further complicated because the developing embryo cannot break out of the hard fruit coat until the coat is partially decayed.

Orchid seeds also consist of comparatively few cells and do not germinate unless they are artificially supplied with sugar or unless fungi digest the insoluble food in the surrounding substrate. The balloon-shaped green seedlings become readily visible only after a lapse of 6 months, and at the end of two years seedlings in many species are less than an inch in height.

The seeds of mangrove, on the other hand, germinate while the fruit containing them is still attached to the tree. The hypocotyl emerges from the seed and fruit and becomes more than a foot in length and a half inch in diameter. Then this great hypocotyl, with a tiny plumule at its apex and a root primordium at its heavier basal end, drops from the tree into the mud below, and rapid development of plumule and roots follows (Fig. 172).

The embryos of most plants, however, are fully developed within the ovule, but the seed will not germinate immediately. Seeds of these plants germinate only after a longer or shorter period of time has elapsed, even though placed in environments with water, oxygen, and temperature conditions ordinarily suitable for growth.

From embryo to seedling. Some of the processes in embryos during germination have been described in Chapter II and Chapter XXIX. If several seedlings are watched as they emerge from the soil, certain striking differences in their growth are evident.

When the castor bean germinates, the lengthening of the hypocotyl raises the cotyledons, endosperm, and broken seed coats above the soil surface. The cotyledons rapidly expand in area and slough off the remaining endosperm tissues and seed coats. The cotyledons are thin blade-like

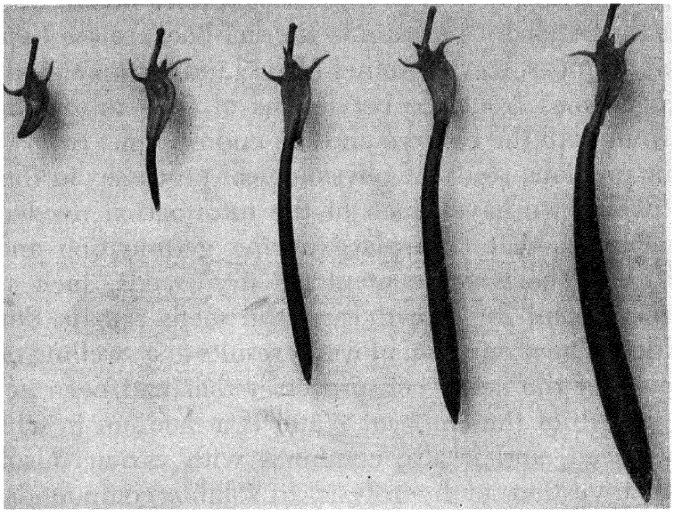

FIG. 172. Development of mangrove seedlings. The tree (*Rhizophora mangle*) grows on tidal mud flats in the tropics and semi-tropics. The seed in the fruit pictured on the left germinates while the fruit is still attached to the tree. The embryo grows a foot or more in length before it drops to the ground and becomes rooted. This plant does not live in fresh water. See Fig. 116, page 298. Photo from Chicago Natural History Museum.

structures, and most of the food used during germination comes from the enclosing endosperm. By the time the endosperm has dropped, the cotyledons have doubled or trebled in area. Meanwhile they have become green, and photosynthesis has begun. Further growth is dependent on sugar and other foods made within the green seedling.

The cotyledons of the common bean and lima bean are likewise raised above the soil surface. There is no endosperm, and the initial growth is dependent solely upon the food contained within the embryo. As the growth of the plumule proceeds, the cotyledons shrivel and abscise within two or three weeks. By this time a shoot containing two or three leaves has developed from the plumule.

The growth of roots during the germination of seeds of grasses was described in Chapter XXIX. The hypocotyl of grasses does not elongate, and the cotyledon remains in the soil. The plumule, which is enclosed in a sheath (the coleoptile), grows upward through the soil, and by its enlargement breaks through the sheath. The plumule of a grass seed is thus the forerunner of all the plant that appears above the surface of the soil.

During the germination of peas, scarlet runner beans, corn, sorghum, and acorns the cotyledons remain in the soil because the hypocotyl does not elongate. In peas, scarlet runner beans, and acorns the initial food of the seedling comes from the cotyledons of the embryo; in corn and sorghum, from both the embryo and the endosperm.

From our previous study of physiological processes in the vegetative organs of plants, we have much of the information needed to understand the changes that take place during germination and the early seedling stages. The water content of "dry" seeds, such as corn and wheat, is insufficient for growth, and the seeds remain dormant until water is added. The absorption of water results in a swelling of the tissues and a renewal of the many cell processes that had been active during the initial growth of the embryo. Water is a medium in which enzyme activities proceed, and it also combines with various insoluble foods during their digestion, or hydrolysis, to soluble compounds. It is likewise the medium in which soluble foods and soluble inorganic salts move or are moved about in the developing seedling. The greater part of the enlargement of the seedling is the result of the osmotic absorption of water and the increase in size of the vacuoles of the enlarging cells.

Oxygen is essential during germination because of the many oxidation-reduction processes that occur in the complex protoplasmic system, especially in the transformation of foods into more permanent cell structures.

"Favorable" temperatures obviously refer to those temperatures in which the complex colloidal system of the protoplasm and physiological activity are best maintained, since upon this condition permeability and the coordination of many essential physical and chemical processes depend. But temperatures ordinarily best for the rapid growth of plants are not best for the germination of all kinds of seeds.

The upward growth of the shoot and the downward growth of roots of seedlings are primarily the result of the distribution and influence of hormones described in Chapter XXIII.

Changes in foods during germination. The chemical changes that occur in germinating seeds have been studied by means of gross chemical analyses at frequent intervals during the germination process. The changes have also been followed by observation of small seeds, or thin sections of seeds, through the microscope with appropriate chemical tests. It is not difficult to follow the transformation of starch, for example, as it is hydrolyzed to dextrin and sugar. The recognition of the different sugars is somewhat more difficult, as described in Chapter XII.

The disappearance of fats and proteins through digestion is not difficult to observe, but methods of detecting the intermediate and end products are somewhat complicated (Fig. 173).

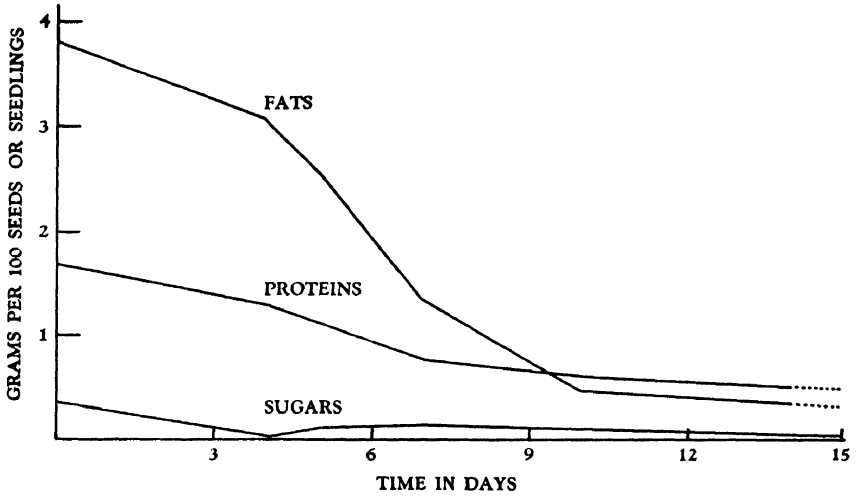

FIG. 173. Changes in amounts of foods in the cotyledons of germinating sunflower seeds. The sugar moves out of the cotyledons into the hypocotyl about as rapidly as it is formed from the disappearing fats and proteins; some of it is temporarily condensed to starch. Data from E. C. Miller.

A part of the sugar is oxidized in respiration, and during germination the temperature of seeds is raised slightly by the heat energy liberated. Another part of the energy is used in the chemical transformations involved in the synthesis of pectic compounds, the constituents of protoplasm and certain other parts of the cell. As a result of respiration, seeds and seedlings progressively decrease in weight if germination takes place in the dark.

Delayed germination. The seeds of most wild plants do not germinate immediately after they fall from the plant, even when placed in conditions ordinarily most suitable for rapid growth. Even under experimental conditions the seeds of many plants germinate only after the lapse of several weeks or months, or even years. The length of the delay in germination of seeds of different plants is often a specific characteristic. The seeds of hundreds of species, both wild and cultivated, have been tested and the conditions most favorable for their germination have been discovered. Germination of these seeds does not occur previous to certain changes in the composition and structure of the embryos or of seed

coats, even after the seeds are apparently mature. These changes are referred to as *after-ripening*. Delayed germination may result from a number of factors, which may be considered in three groups:

1. Delayed germination, the result of environmental conditions outside the seed.
2. Delayed germination, the result of conditions within the seed, but outside the embryo.
3. Delayed germination, the result of conditions within the embryo itself.

The delayed germination in the last two groups is the result of true dormancy in seeds, since the cause of dormancy is within the seed.

Germination delayed by the environment. Environmental conditions profoundly affect the growth of the embryo, both before and after the seed appears to be mature. In temperate regions winter temperatures are too low for the germination of most seeds, and in our southwestern deserts summer temperatures are too high for the germination of many seeds, even though moisture conditions are favorable. Temperatures that facilitate germination vary with the plant species, but comparatively few seeds germinate below 50° F. Continued exposure to temperatures either unfavorably high or low results in no germination or in stunted seedlings. At temperatures above 70° F. the root systems of some plants develop very slowly, and vigorous plants rarely form. The embryos of two water plants, wild rice and eel grass, die soon after maturity unless stored at temperatures just above the freezing point in moist situations.

The effects of environmental conditions on the growth of embryos and seedlings are not always limited to this period of growth. They may continue to influence the subsequent development of the plant, even if the environment is changed. Rapid germination of seeds and growth of seedlings are not necessarily beneficial to the subsequent growth of the plants. The relative growth of shoots and roots and the length of the vegetative period may be influenced by the temperature at germination and early growth of seedlings (Chapter XXXI).

Prolonged droughts obviously restrict germination, and are often a source of great agricultural losses when they follow the planting of seeds of crop plants. Germination may be stopped at any stage from the swelling of the seed to the emergence of the seedling above the soil surface.

The seeds of such plants as willow, cottonwood, and elm will germi-

nate immediately after being shed, but are soon killed by desiccation.[1] The chances of growth of such seedlings and their survival are therefore greater on wet banks, stream and pond margins, and in unoccupied wet lands. The seeds of silver maple rarely germinate if their water content falls below 30 per cent.

Oxygen deficiency most frequently results from the burial of seeds too far below the soil surface, especially of tight clay loams. Flooding of soils by continuous rains may so compact the soil and fill the spaces between particles that aeration becomes almost zero. Oxygen deficiency is a constant condition in the ooze at the bottom of lakes, ponds, and permanent marshes and swamps. Here the diffusion of oxygen from above not only is very slow, but the mud and ooze have an enormous population of bacteria and other organisms that use O_2 as fast as it diffuses from the water. These bottom organisms also release CO_2 in large quantities; and when the CO_2 accumulates about seeds it may of itself become a cause of delayed germination.

Most seeds will germinate in either light or darkness, but a long list of species has been published in which better germination was obtained in light. Among these plants are bluegrass, certain varieties of tobacco, mullein, carrot, mistletoe, evening primrose, loosestrife, and willow herb. On the other hand, light interferes with the germination of some seeds, among which are species of *Phacelia*, *Nigella*, waterleaf, and onion. After a period of suitable storage some of these seeds germinate in either light or darkness. There is evidence that light may alter seed coats in some seeds, and in certain others may affect the embryos or the endosperms. Some of these seeds will germinate when alternating periods of higher and lower temperatures are substituted for light. Of the light rays in the visible spectrum, in general the red to yellow rays seem to facilitate germination, while the blue to violet rays retard it.

Germination delayed by seed and fruit coats. There are many seeds with embryos enclosed by very hard and tough coats: either seed coats or fruit coats. The common pigweed, the water plantain, Christmas holly, and the bloodroot have coats so resistant to mechanical pressure that expansion of the embryo cannot occur until the coats are partially destroyed by soil organisms or by some other means. These coats may

[1] The seeds of some of these plants can be dried and kept alive for a time under special experimental conditions. Willow seeds, for example, may survive for several months in a refrigerator if they are placed over 50 per cent H_2SO_4 in a small vessel. The relative humidity in the vessel would be almost 13 per cent. Similarly sugar cane seeds live longer in an atmosphere of carbon dioxide kept dry with calcium chloride.

delay germination in nature for months or years. The embryos of Christmas holly do not become dormant, and most of them perish before the surrounding coats are sufficiently weakened by decay. Under natural conditions only about one holly embryo in ten million germinates. In horticultural practice the best germination of holly seeds has been obtained by keeping the seed bed above 70° F.

Seed and fruit coats may often exclude water from the endosperm and embryo. These coats may be impervious to water because of the presence of wax, suberin, resin, and certain structural features. Embryos thus entombed germinate in nature only when the coats have been partly digested by bacteria and other organisms. Seeds of red clover and numerous other legumes have seed coats impervious to water. In lotus and certain stone fruits, it is the fruit coat that is impermeable.

In horticultural practice such seeds may be treated for a few minutes, or for longer periods, with strong sulfuric acid until the impervious layer of the coat is altered or removed. These seeds may also be scarified by means of sandpaper, sharp sand, and special scarifying machines until the coats are partially removed. Often only the two outermost layers of cells need to be broken. Legumes are noted for the great variation in the "hardness" of the coats of the seeds from a single harvest.

Oxygen likewise may be excluded from embryos by impermeable seed and fruit coats. An example of delayed germination due to oxygen deficiency has been discovered in cocklebur. There are two seeds in each bur, the lower of which is near the surface and germinates freely after the fruit is shed. The upper embryo, however, is surrounded by tissue that is rather impervious to oxygen, and it does not germinate when the concentration of oxygen is low, even if the coats are destroyed. Both these conditions delay germination for additional months or years, as compared with the lower embryo. Certain grasses and some of the plants of the sunflower family also have seed and fruit coats that are not very permeable to oxygen.

Intermittent germination of seeds of a species over a period of years is probably an advantage to a plant in nature. In horticulture, forestry, and agriculture it is uneconomical because it results in uneven-aged stands of crop plants, and delays the starting of nursery stock.

Germination delayed by conditions within the embryo. When the seed of the ginkgo tree falls to the ground its embryo may consist of only a few cells, and sometimes fertilization has not yet occurred. During ensu-

ing months the embryo grows and its three parts become differentiated. Germination of the seed occurs after the embryo has fully developed in the seed. To this class of seeds with only rudimentary embryos belong those of buttercup, anemone, adder's tongue, holly, columbine, and hepatica. Some of these seeds germinate more rapidly in dilute sugar solutions than in water. The dormant period of these seeds is a time of active chemical and morphological development of the embryo. The embryo itself is not dormant.

A second group of plants with fully formed embryos have seeds that are also truly dormant when shed. These seeds undergo a process of *after-ripening* in which certain chemical changes in the embryo slowly occur. They do not germinate at once when planted under external conditions ordinarily suitable for growth; but if the seed coats are removed and the embryos are treated with a dilute acid, some of them germinate comparatively soon. The dormancy of these embryos is conditioned by chemical processes.

Little is known about the processes that occur during dormancy, but it is wrong to assume that all dormant seeds contain a "resting embryo." Experiments have shown that during after-ripening of this last class of seeds the embryos become more acid, enzymes are more abundant, complex carbohydrates and proteins are hydrolyzed, and respiration is increased. These are merely the superficial, easily tested indicators of more important, but unknown, steps in the reorganization of the protoplasmic system.

To this group of seeds with embryos in which an increase in acidity appears to be a primary part of the process of after-ripening belong those of apple, rose, cherry, sugar maple, giant ragweed, basswood, cotoneaster, peach, and plum.

After-ripening may be hastened in many of these seeds by storing them at a temperature of 40° F. Other seeds after-ripen soonest at a temperature nearer 50° F., and still others after-ripen best with daily fluctuations in temperature as low as 40° F. and as high as 70° F. Moist acid peat probably is the best medium in which they may be placed during the dormant period. Table 13 is a summary of some of the results of after-ripening tests made at the Boyce Thompson Institute for Plant Research. Most of these seeds were stored dry until February, and were then stratified, or mixed with moist granular peat, and placed at a variety of temperatures.

TABLE 13. Temperature and Length of Stratification Periods for Seeds to Obtain the Best Yield of Seedlings.

Plant	Most Effective Temperature	Effective Temperature Range	Time Required for Best Results
Jack pine	32° F.	32–41° F.	60 days
Sugar pine	50° F.	32–50° F.	90 "
Pitch pine	41° F.	32–50° F.	30 "
Eastern white pine	50° F.	32–50° F.	60 "
White spruce	32° F.	32–41° F.	60 "
Sitka spruce	32° F.	32–50° F.	30–60 "
Arizona fir	32° F.	32–41° F.	30 "
Bald cypress	41° F.	32–50° F.	30 "
Eastern red cedar	50° F.	32–50° F.	65 "
Lily of the valley	41° F.	32–50° F.	150 "
Blackberry lily	41° F.	41–50° F.	120 "
Cotoneaster—best results in covered cold frames out of doors			280 "
Apple	41° F.	41–46° F.	60–70 "
French pear (stored dry 6 months)	41° F.	41–50° F.	90 "
Carolina rose	41° F.	32–50° F.	90 "
Apricot, carpel intact	50° F.	32–50° F.	45 "
Apricot, carpel removed	41° F.	32–50° F.	25 "
Red Japanese maple	41° F.	32–50° F.	100–120 "
Tropical pawpaw	50° F.	32–50° F.	100 "
Flowering dogwood	41° F.	32–50° F.	120 "

These results were secured under carefully controlled conditions. One can hardly avoid wondering how long the dormant period of these seeds may be in nature, and, if prolonged, what fraction of the embryos escapes destruction by bacteria, fungi, and the innumerable animals near the soil surface. Is it one in a million or one in a billion?

Longevity of seeds. Present knowledge of how to shorten the period of delayed germination of seeds gives some insight into the factors involved in the preservation of seeds through a long period of time, alive but ungerminated. Some seeds have greater longevity when rapidly dried in a desiccator and stored in sealed vessels or in an atmosphere of carbon dioxide. This is true even for seeds that survive but a short time in nature where oxygen is abundant and the seeds are alternately wet and dry.

It has been clear for many years that lowering the temperature to near the freezing point lengthens the period of vitality of most seeds. Sealed storage of dry seeds at refrigerator temperatures apparently prolongs the life of embryos still further and is now used by commercial seedsmen. A comparison of the results obtained with delphinium seeds emphasizes

the effectiveness of low oxygen and low temperature storage conditions on the retention of viability.

TABLE 14. Percentage Germination of Air-dried Seeds of Delphinium Stored in Sealed and Open Containers at About 70° F. and 46° F. (Data from L. V. Barton.)

Storage Condition	11 mos.	22 mos.	3 yrs. 10 mos.	5 yrs. 9 mos.	9 yrs. 3 mos.
Open, 70° F.	57%	44%	00%	00%	00%
Sealed, 70° F.	75	80	50	15	00
Open, 46° F.	50	41	31	5	00
Sealed, 46° F.	70	45	66	80	76

The longest known period of survival of any seed is that of the lotus, *Nelumbo nucifera*. At the British Museum seeds kept in dry storage germinated after 150 years. Recently viable seeds of this same species were recovered from a lake bed in Manchuria that had been buried by a landslide centuries ago. Measurements made of the radioactive carbon in these seeds have been interpreted as evidence that the burial of the seeds occurred about 1000 years ago. The hard seeds of the legumes are well known for their longevity; there is a record of 158 years for a species of *Cassia*. Most agricultural seeds live for 10 or 20 years, but the hard seeds of many crop legumes are viable after 40 to 60 years. It should be noted, however, that the percentage of germination at the end of the longer periods is usually very low. A number of seeds of wild plants with hard coats have records of longevity up to 90 years.

We still lack authentic records of the longevity of seeds stored in hermetically sealed containers. The longest records are those derived from "hard seeds" which represent seeds with embryos sealed individually. Putting seeds in sealed containers is merely duplicating the conditions within hard seed coats, for it likewise results in excluding oxygen and water from embryos.

A diagrammatic record of the famous experiments by Beal at the Michigan Agricultural College is given in Fig. 174. Beal buried the seeds in the soil in inverted open bottles in 1879. Bottles containing the seed mixture have been dug up at five-year intervals and the number of living seeds tested, with the results shown in the diagram.

Why do dormant seeds die? This question has been asked for many years and many answers have been proposed, but none of them has been

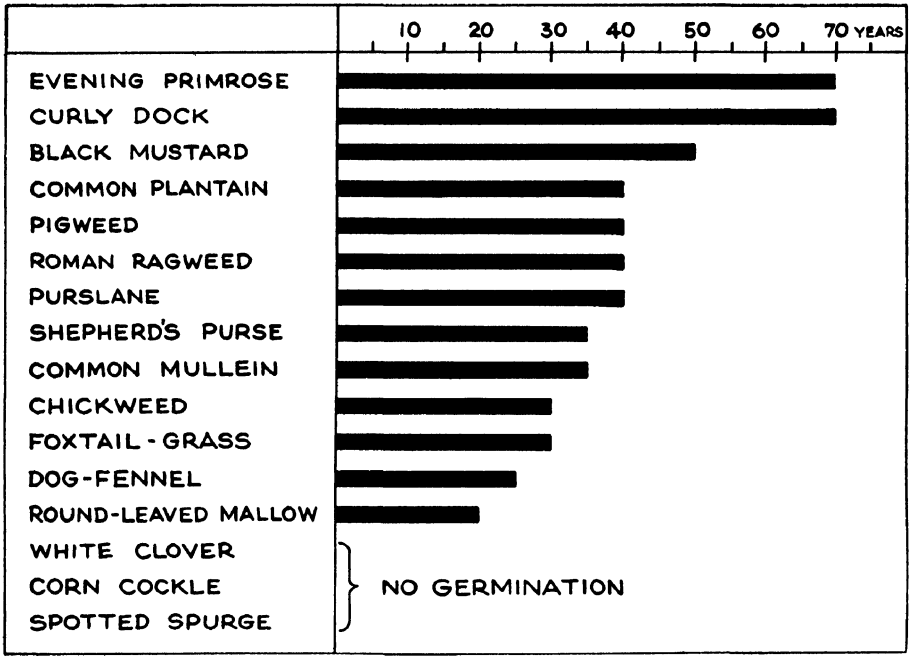

FIG. 174. Longevity of embryos of seeds in Beal's experiment.

completely satisfactory. The earlier suggestions that the change from viable to non-viable seeds is the result of the oxidation of the food supply and the destruction of the enzymes seem to have been adequately disproved. Foods in seeds have been carefully analyzed and the chemical changes are slight. The enzymes, on the other hand, seem to be just as active as before death. Evidence against the idea that the food has been completely oxidized is the dry storage of minute one-celled algal spores in sealed soil samples for 30 to 40 years and their germination when the soils were moistened.

Later it was suggested that death is due to the coagulation of the proteins in the cells. This had in its favor the fact that there is a similarity in the curve of longevity of seeds at high, medium, and low temperatures and the curve of coagulation of proteins at corresponding temperatures. Coagulation of proteins in cells might disrupt the organization of the protoplasm. Changes in the protoplasmic lipoids might likewise destroy the organization.

A more recent answer is suggested by the discovery that the seedlings derived from old seeds, from X-rayed seeds, and from heated seeds are similar in survival, in growth, and in variability. Moreover, similar irregularities in nuclear structures have been observed in microscopic

studies of the nuclei of the cells after these three different treatments. From these facts it appears that prolonged storage of seeds results in the breakdown of nuclear organization and the mechanism of heredity. This answer has more experimental results to commend it than the preceding ones, and it seems to be the best one at the moment.

Caution. Anyone interested in the preparation, storage, or germination of particular kinds of seeds should not depend wholly on the generalized statements concerning the best methods. There is now a considerable body of data available regarding these techniques, and it should be searched before attempting to prepare, store, or plant the seeds of valuable plants.

Another precaution may also save time and disappointment. One should first of all be sure that the seeds have embryos inside them, since there are seeds that look perfectly normal on the outside but lack the most essential part of a seed. One should also make sure that the parts inside the seed coat are in a healthy condition, that they have not become infected by bacteria and fungi, or infested by insect larvae.

The references below will be helpful in seeking further details about seeds, their preservation, and their germination.

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CHAPTER XXXV

VEGETATIVE MULTIPLICATION OF FLOWERING PLANTS

Most flowering plants may increase in number by either of two methods: (1) the formation of special reproductive cells and seeds—*sexual reproduction,* or (2) the development of a separate individual from one or more vegetative cells of a plant—*vegetative multiplication* or *vegetative propagation.* The vegetative organ, or any fragment of it, from which the separate individual develops may be referred to as a *vegetative propagule,* in contrast to a seed.

If two or more separate individuals develop from single vegetative cells or from branches of the same plant, they are merely isolated parts of it. They are "chips off the same block," not a new generation of plants. These facts are most readily appreciated when vegetative multiplication by cuttings is considered.

We may, for example, cut a thousand twigs from a willow tree in early spring and place the basal end of each twig in moist aerated soil. These severed twigs are *cuttings.* Within a few weeks roots develop from the lower nodes of each cutting, and branches grow from the buds above the soil. Thus within a short period of time we can secure a thousand young willow trees, which may in turn become large trees.

These thousand separate trees, however, are as much alike inherently as are the unsevered branches of a single tree; and in all matters pertaining to pollination, sex, and heredity they should be considered as branches of the tree from which the cuttings were taken. Branches of each of these thousand trees may in turn be used as cuttings, and so on *ad infinitum.* In this manner a single generation of a willow tree may be perpetuated and multiplied indefinitely. It is often convenient to have a name to refer to all the individuals which through repeated vegetative multiplication have a common origin. Such individuals are collectively called a *clone.* Their common origin is the embryo of the first individual of the clone (Fig. 175).

In practice this concept of a clone is often considered too broad. Clones of sweet potato plants develop from sprouts which originate

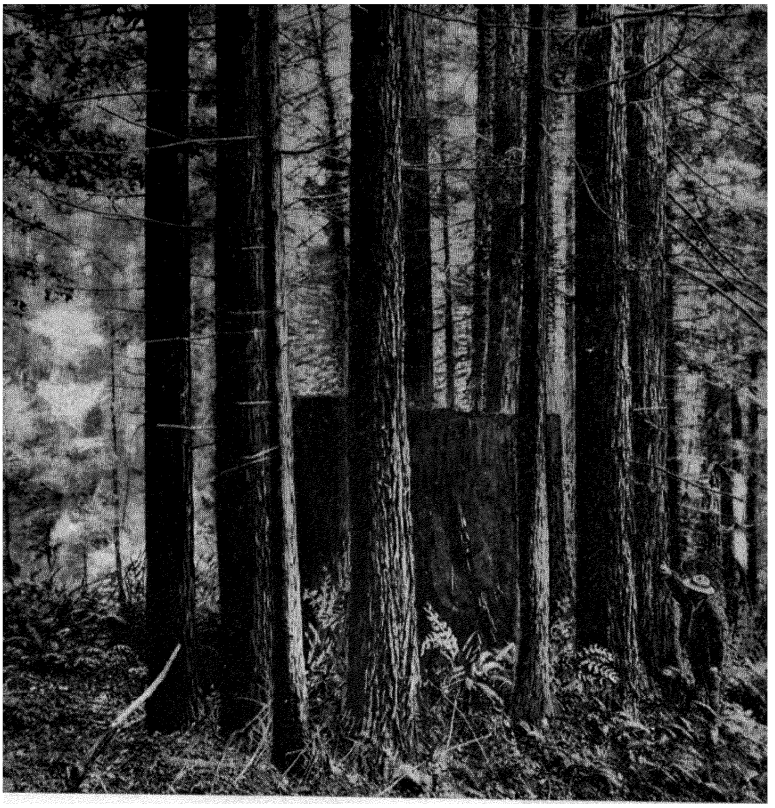

FIG. 175. A miniature clone of redwood trees which originated vegetatively as a group of sprouts from the roots of an older tree which has been cut down. Photo from U. S. Forest Service.

from cells in the roots. How shall we regard the vegetative descendants from the red and yellow roots of the plant pictured in Plate IV (opposite page 436)? Those from red roots continued to have red roots; those from yellow roots had yellow roots. Shall we call those from the yellow roots a clonal variety of the original clone, or shall we regard them as the beginning of a separate clone? If we choose the latter we have the convenience of considering clones as groups of individuals that are alike in heredity, but the task of always being sure they are.

Vegetative multiplication may occur by either of two ways: by the natural separation and further development of vegetative parts of a plant, or by the further development of segments cut from a plant by man and placed under various suitable conditions. Man promotes vegetative

propagation among cultivated plants by collecting, storing, and transplanting naturally occurring vegetative propagules; and by cuttings.

Among the vegetative parts of a plant that may become separated naturally and develop as separate individuals are the branches that grow from runners, rhizomes, and roots; offsets or sprouts that grow from the bases of stems; plantlets that develop from leaves; and the familiar bulbs, corms, and tubers with terminal and lateral buds from which new shoots and roots develop (Chapter XXVI). Methods by which plants multiply vegetatively from these naturally occurring vegetative propagules will be described first.

Abscised leaves and stem segments. Under natural conditions the abscised stem segments of some plants and abscised leaves of others are vegetative propagules. Embryos develop from vegetative cells in the notches of the leaves of bryophyllum and kalanchoe (Fig. 176). From these embryos roots develop first in leaves of *Bryophyllum calycinum*, and shoots develop first in leaves of *Bryophyllum crenatum* (Fig. 194). The plantlets on the leaves of some varieties of kalanchoe abscise before the leaves do. On falling to the ground they continue growth, forming a clone beneath the larger plant.

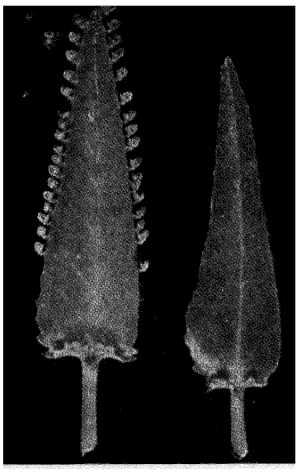

FIG. 176. Kalanchoe leaves. Young plants have originated from cells near the margin of the older leaf on the left. Photo from P. W. Zimmerman.

Abscised lateral buds of some species of sedum and lily fall to the ground and new individual plants develop from them. Similarly abscised stem segments and fruits of certain cacti become vegetative propagules. In pastures where these cacti are weeds the stem segments may be scattered rather rapidly by grazing animals. The abscised stem segments of such plants as willow and cottonwood appear to be of no importance in propagation. Vegetative multiplication of some water plants, such as elodea, occurs frequently from broken fragments of leafy stems. The elodea in the canals and rivers of central Europe is said to have been dispersed vegetatively from clones introduced from America about 1840.

Runners and other "creeping" stems. Runners are common means of vegetative multiplication of strawberry, of some ferns and grasses, of water hyacinth, and of numerous other plants (Fig. 177). As many as a

dozen runners from 3 to 10 feet in length may grow from a single strawberry plant during one season. Roots and shoots of new strawberry plants develop at every other node of each runner. Secondary runners develop from the alternate nodes and also from the new strawberry

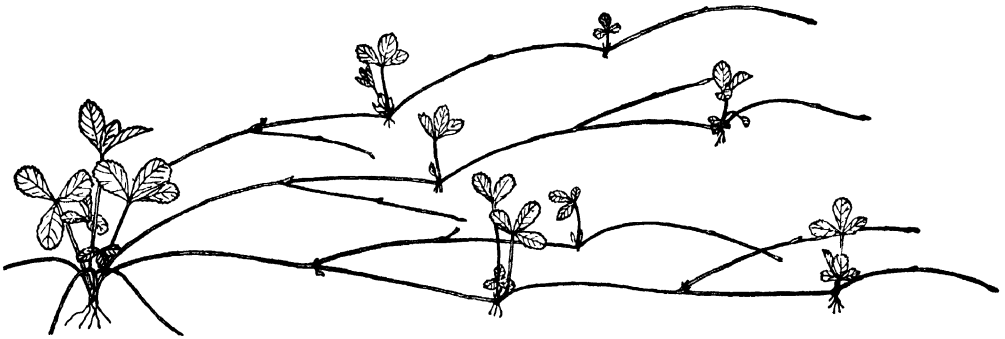

FIG. 177. Clones of strawberry plants develop from runners. Note the regular occurrence of new shoots and secondary runners at alternate nodes.

plants. By this means a clone of a score or more strawberry plants may develop from a single plant during one summer. Under cultivation, the new plants may be lifted from the soil and reset in rows. In nature they become separated by the death of the connecting runners.

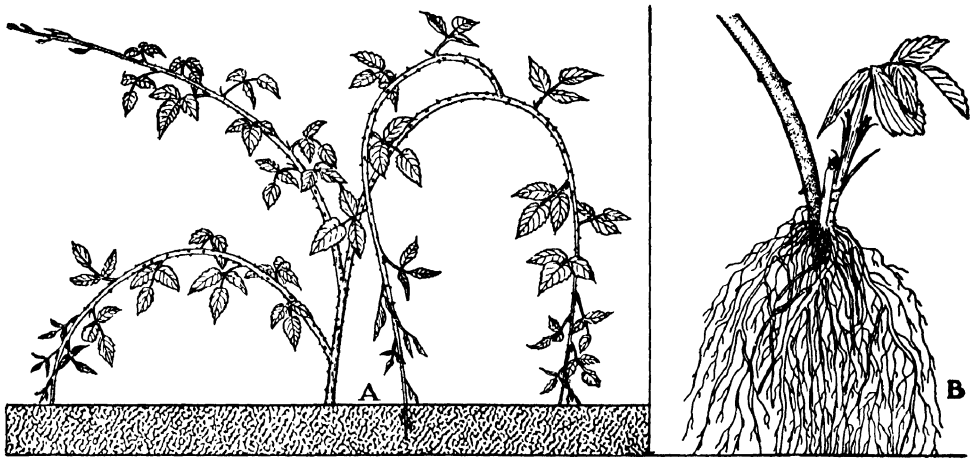

FIG. 178. Tip-layering of black raspberry. In late summer when the ends of the branches bear very small leaves and have a rat-tail appearance, they are buried vertically in holes dug in the soil (A). After adventitious roots have developed from the buried nodes the stem tip begins to grow upward (B). The rooted tips with a portion of the old canes attached are dug up and reset early the following spring before the tip has emerged from the soil.

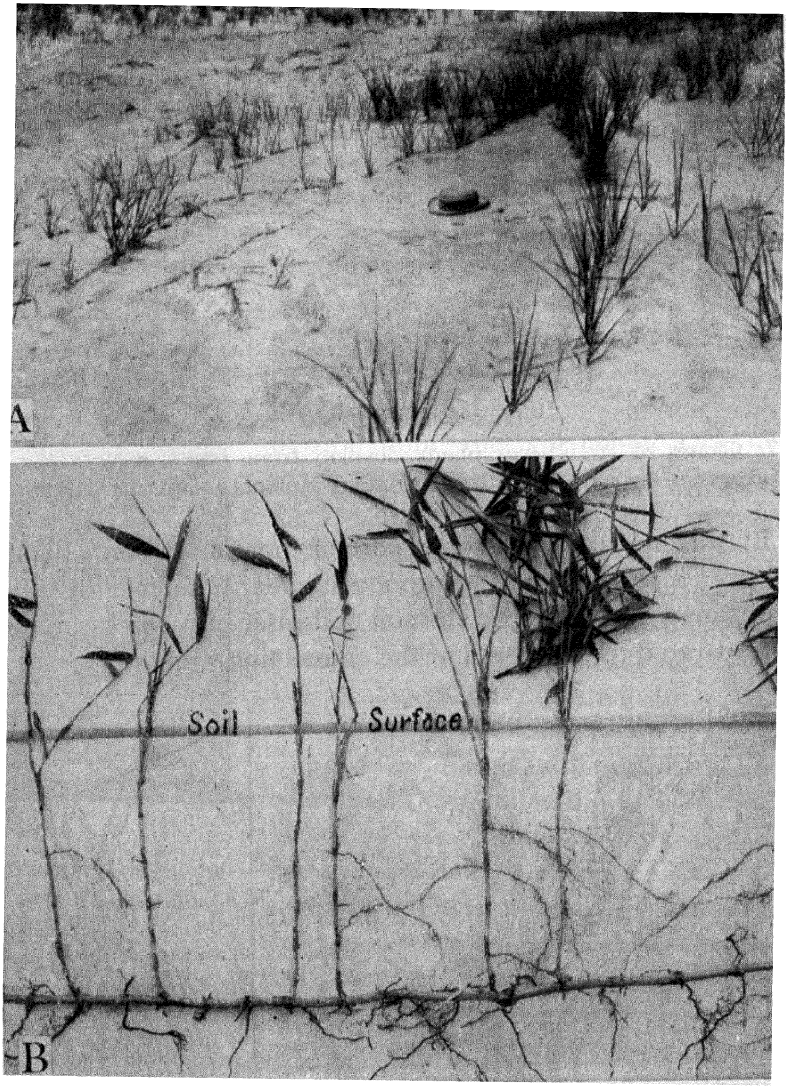

FIG. 179. A, aerial shoots of beach grass from the rhizomes of a single plant; B, aerial shoots from a rhizome of bamboo (*Arundinaria*) 10 inches below the soil surface.

Vegetative multiplication may also occur at the nodes of leafy prostrate stems, and at the nodes of elongated stems of such plants as raspberry, grape, and honeysuckle, which bend over and come in contact with moist soil. In horticultural practice the stems of such plants are bent over and some of the nodes or whole stem tips are covered with soil: a procedure called *layering* (Fig. 178). The terminal buds of the buried stem grow upward and adventitious roots grow from the oldest buried nodes. The rooted branches may then be severed from the parent plant and transplanted.

In bog forests propagation of trees by layering occurs naturally when the lower branches of spruce and arbor vitae lie on the ground or are pressed down by snow. This method of propagation may be more frequent among bog plants than propagation by seeds. Layering by leaf tips occurs in a few species of plants, such as the walking fern.

Rhizomes. Many perennial grasses, ferns, mints, and a host of other plants have rhizomes from the nodes of which roots and aerial shoots develop (Fig. 179). The rhizomes may elongate each year by the growth of terminal buds. When the older parts of these rhizomes die, groups of individuals of the clone become separated and are new centers of dispersal by growth of rhizomes.

As a result of this method of propagation, certain perennial grasses and other perennial herbs become the dominant plants of the vegetation of lawns and meadows, and of the natural prairies and plains in various

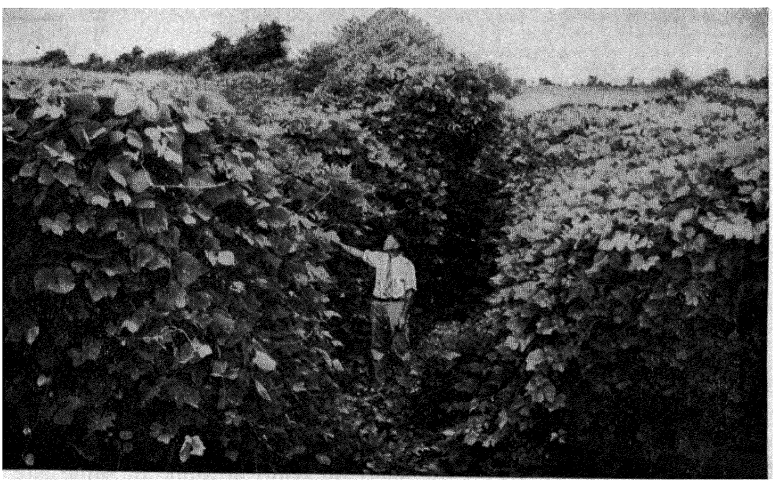

FIG. 180. Erosion stopped by the kudzu vine. The ditch is now being filled by the accumulation of silt. Photo from the U. S. Soil Conservation Service.

parts of the world. Since their roots and rhizomes are perennial, shoots from buds on rhizomes begin to grow rapidly in spring and soon overtop the annual plants, which start from seeds each year. Similarly cattails, rushes, sedges, and water lilies frequently exclude many other plants from certain habitats. Their rhizomes may grow several feet in length each year, and the plants occupy new areas rapidly.

Abandoned farms and denuded areas about cities are first occupied by a mixed population of annual, biennial, and perennial weeds; but the perennials increase their area year by year through vegetative multiplication and finally exclude nearly all the annuals and biennials.

For the prevention of soil erosion in gullies and on freshly made em-

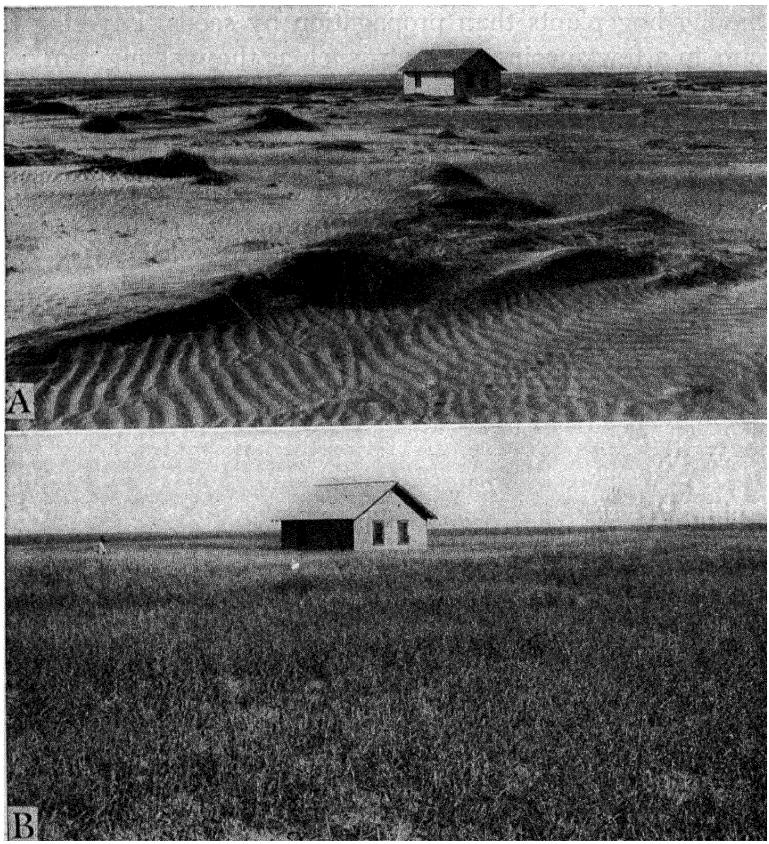

FIG. 181. A, an area in northwest Texas where death of crops and native plants during a prolonged drought was followed by wind erosion. B, same site after the soil had been stabilized by grasses planted according to methods devised to control this type of erosion. Photo from U.S. Conservation Service.

bankments quick-growing perennials that multiply by means of rhizomes, creeping stems, and sprouts from roots should be planted first. For a permanent vegetation on such areas one may prefer a bluegrass turf or trees; but these plants usually become established too slowly to be used as pioneers unless some means of temporarily preventing soil erosion is employed. A few trees and shrubs, such as black locust and the creeping honeysuckle, which multiply vegetatively by branches from roots, or from creeping stems, soon become established on such areas. Kudzu vine has been used to prevent gullying in the Southern States (Fig. 180). In

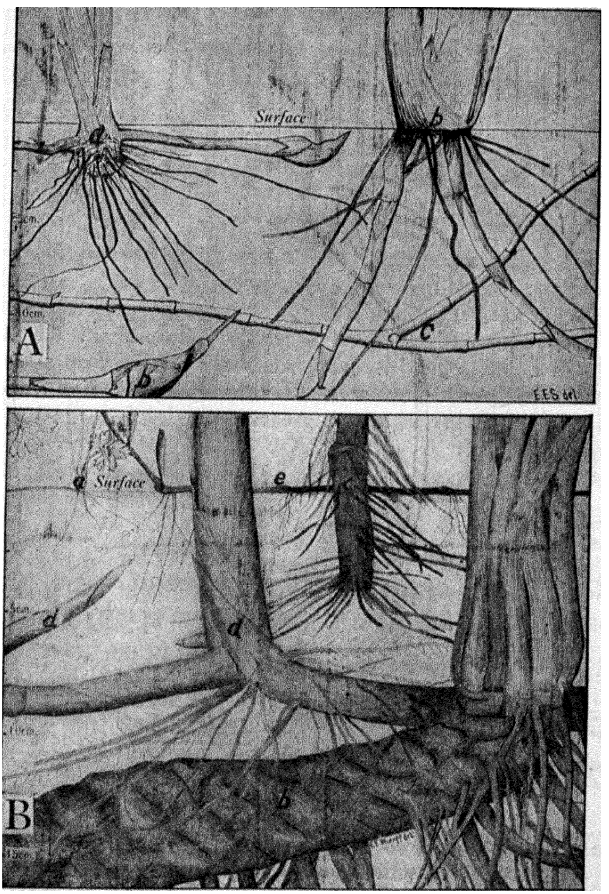

FIG. 182. Depth of rhizomes below soil surface: A, a, bur-reed (*Sparganium*); b, broad-leaved arrowhead (*Sagittaria*); c, swamp persicaria (*Polygonum*).

B, a, yellow water crowfoot (*Ranunculus*); b, large yellow pond lily (*Nymphaea*); c, water parsnip (*Sium*); d, cat-tail (*Typha*); e, mild water smartweed (*Polygonum*). Sketches by E. E. Sherff.

the West Central States grasses have been employed in stabilizing wind-blown farm lands (Fig. 181).

Pieces of rhizomes are often planted in preference to seeds. Rhizomes of each species grow at a fairly definite depth below the surface of a particular soil (Fig. 182). If they are planted below or above this depth they grow up or down to the specific soil level.

When weeds, such as couch grass, bindweed, flowering spurge, and nettle, grow among crop plants, their rhizomes may be broken and scattered when the crops are being cultivated, and the weeds become still more abundant.

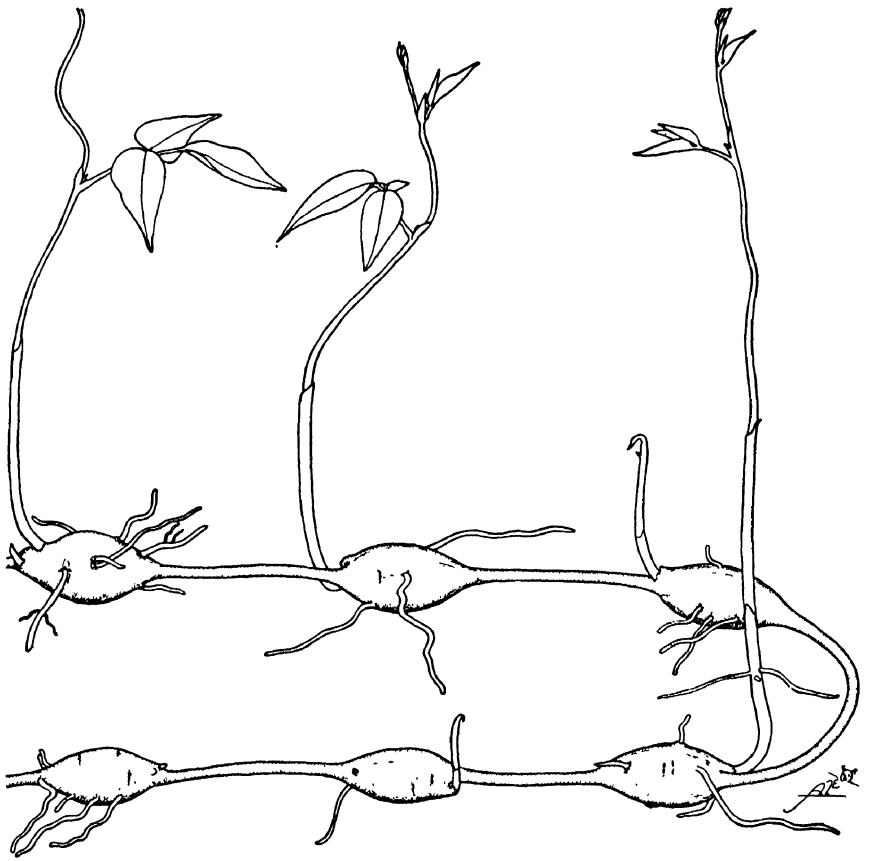

FIG. 183. The groundnut (*Apios tuberosa*) has many edible underground tubers from which aerial shoots develop.

Tubers. The tubers or thick terminal portions of rhizomes of Irish potato are a means of vegetative multiplication common to many herbaceous plants (Figs. 183 and 185). The wild species of potato are native

to the highlands of tropical America, where they grow naturally as perennials. In the latitude of central Ohio the tubers left in the field are killed by low temperature in winter. But farther north, where the temperature of the soil beneath deep snow may remain above freezing, the cultivated potato may in some local areas live indefinitely as a perennial.

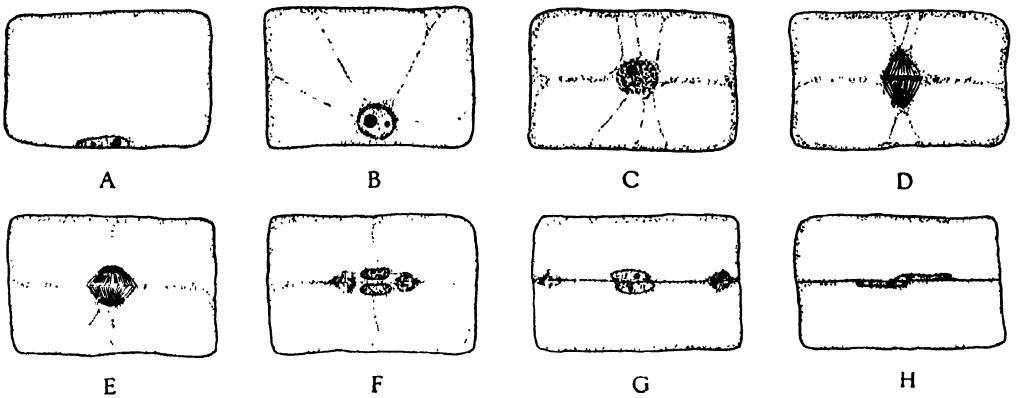

FIG. 184. Semi-diagrammatic drawings of a sequence of stages in the division of a vacuolate cell in the pith of a growing stem tip. A similar sequence of events occurs in older vacuolate cells that divide during the healing of wounds in cuttings. A, a vacuolate cell. B, early evidences of division in a vacuolate cell: the nucleus becomes spherical, and cytoplasmic strands extend through the vacuole. C, the nucleus becomes centrally located, and numerous anastomosing cytoplasmic strands radiating from the nucleus form a diaphragm across the center of the cell. D-E, duplication of the nucleus (described in Chapter XXXVII). F-H, the cytoplasmic diaphragm divides into two layers between which a cell wall is formed. From studies reported by E. W. Sinnott and R. Block.

The tubers of many kinds of plants survive the temperature of winter even if snow is not deep or present throughout the cold season. Such plants are classified as perennials; but the vegetative propagules, the tubers, develop annually and live only through parts of two growing seasons. Each year leafy shoots with roots at their bases develop from buds in the so-called eyes of the tuber. As these shoots grow to mature plants, another crop of tuber-bearing rhizomes develops.

The buds of tubers, like those of many other stems, have a definite dormant period; and when they grow, apical dominance is also evident (Chapter XXVI). If the temperature of the storage bin is unsuitable during this period, or if artificial treatments of the buds with thiourea to break their dormancy are excessive, apical dominance may be annulled, and inferior plants result. If the tubers are planted before the

dormant period is completed, the tops of the young sprouts may enlarge and become tubers instead of growing into upright green shoots. The development of sprout tubers may also occur on tubers from which ordinary sprouts have been removed several times (Fig. 185D).

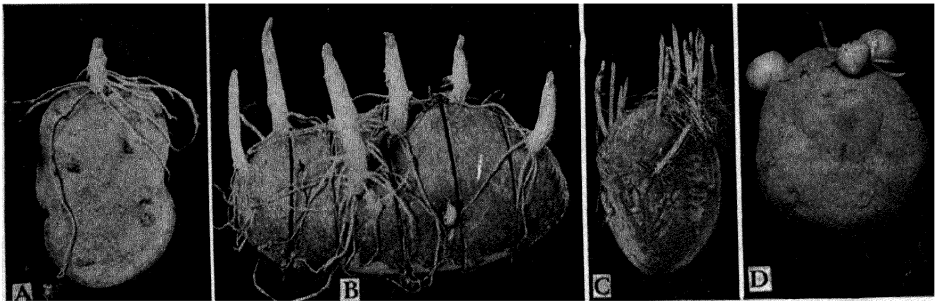

FIG. 185. Growth of potato sprouts. A, apical dominance; B, apical dominance is annulled when the tuber is cut into several pieces which are planted separately; C, apical dominance partially annulled and vigor of sprouts decreased by storage at high temperatures (33-34° C.) for a year; D, repeated removal of sprouts on tubers in storage results in the growth of sprout tubers. A-C from C. O. Appleman; D from J. Bushnell.

Corms and bulbs. The corms of gladiolus and crocus, and the bulbs of onion and tulip are examples of other types of vegetative propagules common to many herbaceous plants. These organs develop annually from lateral buds, and when mature they become separated from the parent plant (Fig. 186A). Like tubers, they usually live through parts of two

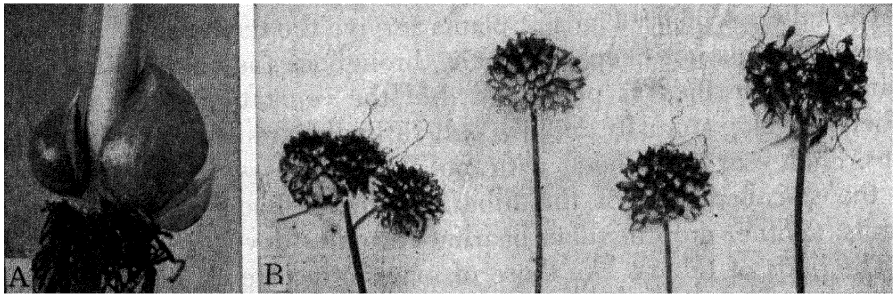

FIG. 186. Vegetative multiplication of wild garlic by bulbs: A, roots and base of flowering shoot from old bulb and three new bulbs which have developed from lateral buds; B, clusters of small bulbs, or "sets," in the flowering heads of aerial shoots. Vegetative multiplication by these small bulbs is so effective that garlic often becomes abundant in pastures. Courtesy of World Book Co.

growing seasons. Bulbs or bulblets may develop from buds on aerial stems also, as in certain varieties of lily and onion (Fig. 186B). Some water plants have bulblike compact winter buds which become separated by the death of the older parts of the stem. These buds float about in the water or settle to the bottom of the lake or pond. In the following spring roots and shoots develop from them.

Gardeners do not usually transplant bulbs and corms until after the tops of the plants have died. These propagules may also be stored and shipped, but the temperatures to which they are exposed may greatly affect the subsequent growth of plants from them. Improper storage temperatures are sometimes the cause of worthless plants. Diseases caused by viruses which spread throughout the plants may also become a menace to the bulb industry. Intelligent inspection of the growing plants and of the bulbs placed on the market, accompanied by reasonable laws and their enforcement, is the only means of protecting the purchaser of bulbs.

The buds of bulbs and of corms have definite periods of dormancy, and the best plants are not obtained unless the dormant period is passed



FIG. 187. Rhizome of *Eryngium* with distinct annual segments and branches, seen from the side, and from below. From H. S. Jurica.

under suitable conditions. Tubers, corms, and bulbs, like rhizomes, have fairly specific levels of growth in the soil. If they are planted below or above this level, the new ones are formed a little nearer to it each succeeding year. This phenomenon appears to be related primarily to light.

Offsets and basal sprouts. Many plants, both herbaceous and woody, multiply vegetatively by offsets, sprouts, and tillers, all of which have a similar origin from lateral buds near the base of the stem (Figs. 187 and 188). This process occurs annually in some species of plants, such as rose, sedum, aster, and goldenrod; but in shrubs and trees the lateral

buds may have been dormant for many years (Fig. 84). Under natural conditions the plants become separated by breaking away naturally or through the death of the parent plant. In practice these vegetative propagules may be severed from the parent plant and transplanted.



FIG. 188. Owing to its rapid vegetative multiplication by runners, the water hyacinth, which is a floating plant, may completely cover the surface of slow-flowing streams in the southern states and the American tropics. Photo by G. W. Blaydes.

Apical dominance at the tops of many plants prevents the growth of shoots from the base of the stem. When the stems of such plants are cut off, sprouts often grow profusely from the stumps. If regeneration by sprouts from the stumps is allowed to occur naturally after the trees of a forest have been cut down, the next forest is largely a sprout forest, or coppice. Since the sprouts on the stumps have a root system already established in the soil, they may grow more rapidly than seedlings with a comparatively small root system. Unfortunately, as the sprouts from the larger stumps increase in age, their dead heartwood may be destroyed by the same fungi that cause decay of the stumps.

If the forest is repeatedly cut, such trees as chestnut and linden, which

sprout profusely, become increasingly abundant in subsequent forests. Forests composed almost entirely of chestnut have resulted from this practice. When the sprouts originate from parts of the plant below ground, and especially from roots, they are frequently called "suckers."

There are many plants, such as lilac, plum, cherry, sumac, black locust, silver poplar, and bindweed, that multiply vegetatively by the growth of shoots, or sprouts, from adventitious buds in the roots (Fig. 189).

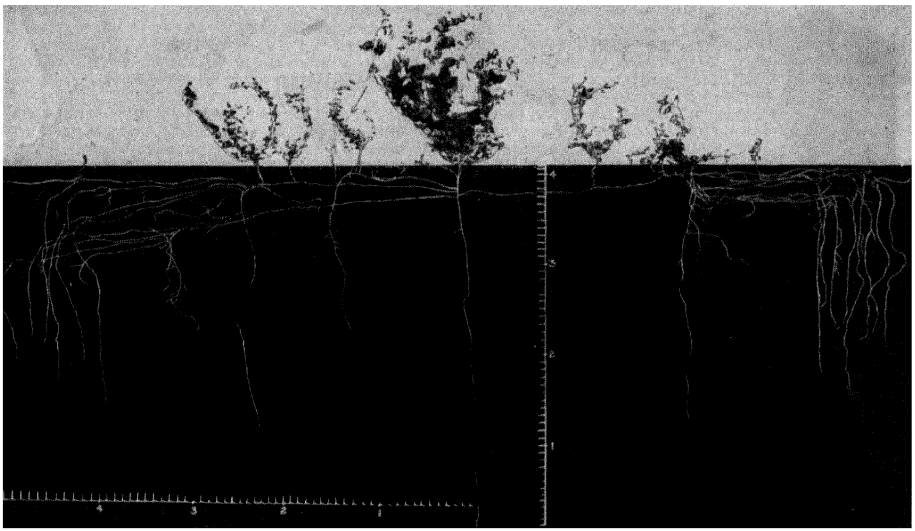

FIG. 189. The field bindweed (*Convolvulus arvensis*) multiplies rapidly by the growth of aerial shoots from buds on vertical rhizomes which develop at intervals from the many lateral roots. The plant pictured above had been growing for 14 weeks. The scale is in feet and inches. The larger shoot near the center grew from the embryo in the seed. The lateral roots grow horizontally for a foot or more and then curve downward. Near the bend a second crop of laterals develop; when they curve downward a third crop develops from them, and so on throughout the season. Photo by J. C. Frazier, Kansas Agricultural College.

Thickets of such plants are often formed in this manner. Ordinarily shoots grow from the roots of many other plants only after the tops have been removed—for example, dandelion or cottonwood. New sweet potato plants are obtained from old roots each season by moving them from storage bins to warm moist propagating beds for a short time. Dozens of new plants may be obtained from each root. Leaves of the sweet potato plant may also be used as vegetative propagules.

Vegetative multiplication not limited to leaves, stems, and roots. Vegetative multiplication occurs more frequently in stems and roots than in other organs of seed plants. It is known to occur in many kinds of leaves and also in bulb scales, fruits, cotyledons, hypocotyls of embryos, zygotes, endosperms, and in the coat and nucellus of an ovule. Later on it will become evident that the development of embryos from unfertilized

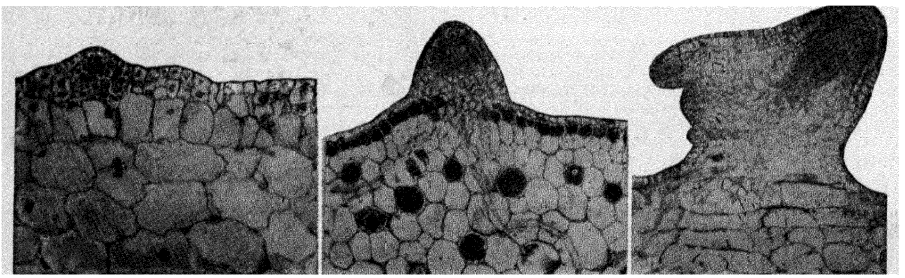

FIG. 190. Stages in the development of an embryo-like bud from the epidermis of *Crassula*. From Ilda McVeigh.

eggs in dandelion is genetically equivalent to vegetative multiplication. Whether the new individual develops from a single cell or a group of cells, both root and stem primordia resembling those of an embryo soon become differentiated (Fig. 190). Among the bacteria, fungi, and algae, vegetative multiplication by single cells is a regular phenomenon.

Cuttings. Man, however, is not limited to naturally occurring vegetative propagules, because he has learned how to utilize cuttings from various parts of the plant. Among ornamental plants propagation by cuttings alone greatly exceeds that by all other methods. Trees and shrubs cultivated for their fruits are usually started from cuttings used as grafts. A few of them, such as black raspberry and hazel, are started by layering. Red raspberry, banana, and pineapple are started by offsets and sprouts from the base of the stem or from roots. Sugar cane is started from short stem segments bearing several lateral buds. Cuttings may be made from stems, leaves, or roots and are valuable means of insuring the propagation of varieties that do not reproduce true from seeds.

Stem cuttings. Shoot primordia are already present in the terminal and axillary buds of a stem cutting. Preformed root primordia may also be present, as in branches of willow, cottonwood, and flowering currant. Adventitious root primordia may develop from parenchyma cells in the

pericycle or from cells in the phloem or cambium of the stem (Fig. 191). They do not develop readily in stem cuttings of some plants, and not at all in others.



FIG. 191. Cross section of a root of *Cissus* in which lateral root primordia have developed from cells in the pericycle at points directly external to the vascular bundles of the main root. Photomicrograph from N. E. Pfeiffer, Boyce Thompson Institute.

Stem cuttings may be placed directly in soil, moist sand, peat, and other media. They may also be grafted on the stem or roots of another plant.

When a stem cutting is placed in a suitable "rooting medium," roots grow from the morphologically basal end, and new shoots develop from the apical buds. The development of these apical shoots prevents the growth of shoots from buds further down the stem. Likewise the growth of basal roots prevents the growth of roots farther up the stem, even though preformed root primordia are present. This apical dominance is so pronounced in both roots and stems that it is seldom reversed, except by drastic changes in the physiological condition of the cuttings.

The origin and growth of the roots depend upon sugar and hormones, particularly thiamin, from the leaves (Chapter XX). Consequently when cuttings are made of herbaceous plants ("slips"), or of the young stem segments of woody plants (soft-wood cuttings), the origin of roots and their rate of growth are influenced by the leaves left on the cuttings

(Fig. 68). They are also influenced by such external factors as water, oxygen, temperature, and light.

Perhaps with further research, stems of nearly any plant may be used successfully as cuttings. In addition to the factors mentioned above, the origin of roots in stem cuttings varies with the age of the plant, with conditions under which it grew, with the part of the stem taken as a cutting, with the season of the year, and with the presence of special chemical substances.

Besides the natural hormones some thirty different chemical compounds, when applied artificially, accelerate and increase the initiation of root primordia in parenchyma cells in almost any part of the plant. Some of these compounds are of value in shortening the time of root

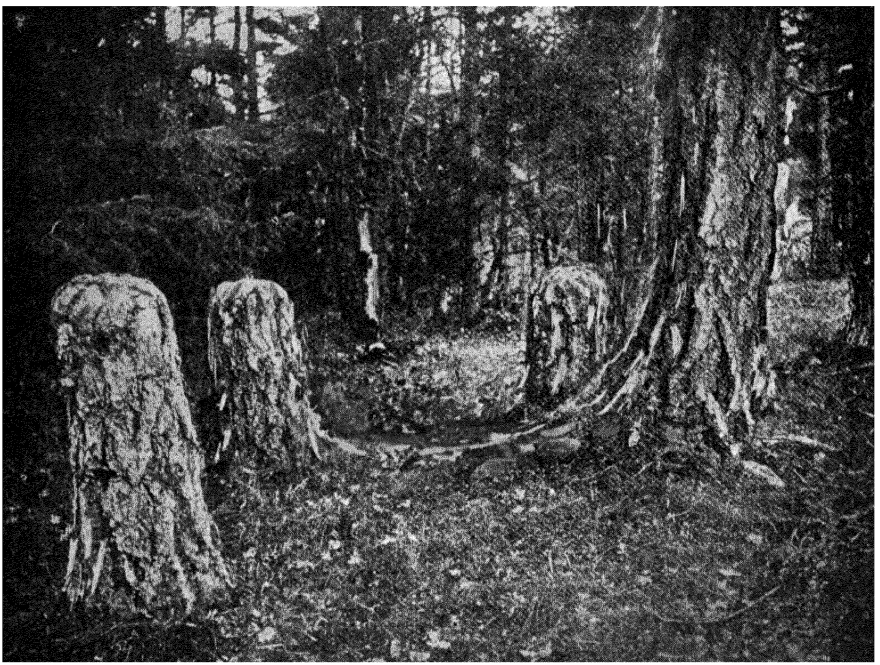

FIG. 192. Photograph of three living and growing stumps of Douglas fir (*Pseudotsuga taxifolia*) in a moist, cool valley of southern British Columbia. These trees do not sprout when cut. These stumps derive their food supply from the large living tree at the right by way of lateral root grafts, some of which appear above the soil level. Note that the cut surface has healed over. There is good evidence that the oak-wilt fungus gets from one black oak tree to others nearby through naturally formed root grafts. Photo by C. A. Pemberton. From A. H. R. Buller's *Researches on Fungi*, Vol. 4, page 141. Courtesy of Longmans, Green & Co., London.

formation in cuttings of certain varieties in which the initiation of roots is very slow.[1]

The relative amount of shoot and root growth from a cutting is affected by the presence of carbohydrates and proteins within it. Both grow well if there is a good initial supply of each of these foods. But if carbohydrates are abundant and proteins are scarce, root growth is much better than shoot growth.

The physiological condition of cuttings greatly influences their behavior. If the plant is dormant, the cuttings do not live unless they are kept in cool moist conditions until adventitious roots have begun to develop. If the plant is just beginning to bear flowers, the cutting may grow but little and then bear flowers.

Grafting. Artificial grafting is a method of promoting vegetative propagation when cuttings do not root readily, and when the plants do not reproduce true from seeds. Most varieties of trees cultivated for their fruits are perpetuated by some method of grafting.

Grafting consists in attaching a cutting, the *scion*, to the root, stem base, or branches of another plant, the *stock*. The scion may be a twig bearing several buds, or it may be a single bud attached to a small piece of bark. If two plants are growing close together the bark may be removed from convenient points on branches or main stems, which may then be bound together at these points. This is called approach grafting. When the union between the stems is complete, the parts of either that are not desired may be cut away.

Valuable trees that have been girdled by animals or by extremes of temperature may be saved by bridge grafting, in which opposite ends of each of several twigs are inserted as grafts beneath the bark on the upper and lower edges of the girdle.

The parts of plants used in grafting are illustrated by diagrams in Fig. 193. The cambiums of the stock and scion must be brought into close contact. The grafted sections are then bound together with a string, and the junction is covered with waxed tape to prevent drying and the entrance of destructive organisms.

The cambium and other meristematic cells at the cut surfaces grow

[1] Three of these compounds most valuable in promoting plant propagation on a commercial scale are indole butyric acid, naphthalene acetic acid, and indole acetic acid. Others important scientifically are indole propionic acid, ethylene, propylene, acetylene, and carbon monoxide. Directions for applying these compounds to cuttings of different varieties of plants may be found in publications from the Boyce Thompson Institute of Plant Research, and also in circulars from chemical supply companies that market them under such trade names as "hormidin," "auxillin," and "rootone."

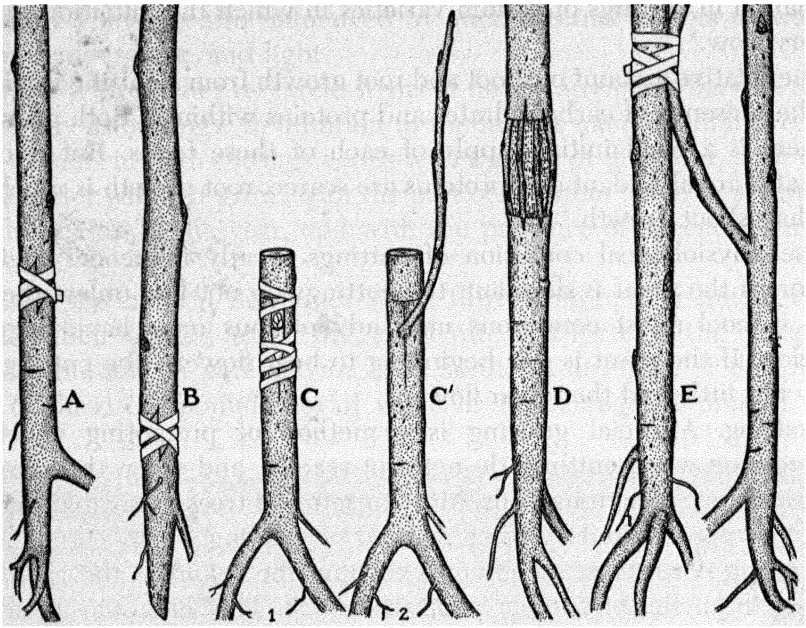

FIG. 193. Parts of plants used in grafting: A, stump or crown grafting; B, piece-root grafting; C, C′ budding; D, bridge grafting; E, approach grafting.

and form *wound tissue*, or *callus*. In successful grafts, new cambium cells develop from some of the cells in the callus and unite the cambiums of stock and scion. The new xylem and phloem tissues formed become continuous; and water, salts, sugar, hormones, and other soluble substances move across the junction.

If this union of tissues fails to occur, the scion dies. If the union is not well formed, the movement of water and salts to the scion and of sugar to the stock is restricted and growth of the whole plant is slow.

The fundamental features of bud grafting are similar to those of twig grafting. If the bud of a peach tree is grafted in place in late summer, healing occurs within a few weeks, but the bud remains dormant until the following spring when a branch develops from it in the usual way. To insure the growth of the grafted bud, the stem is cut off just above it to remove the source of apical dominance. Branches will develop from the buds the same year the graft is made, if the buds formed the previous year are collected in winter and kept on ice until the graft is made in June.

Established grafts are commonly obtained only among related plants, as among varieties of peach, apricot, and plum, or among varieties of

apple, pear, and quince. Intergrafting among genera is possible in plants of the potato family, and in plants of the sunflower family, but intergrafting between families of plants is rare. The idea that horticulturists can make a kind of "table d'hôte" plant through multiple grafting of tomatoes, cucumbers, potatoes, apples, beans, and other plants is not based upon reliable data.

Effects of scion and stock upon each other. Removing a cutting from a plant and placing it in soil, or grafting it on to the stem or root of another plant, does not change its heredity. Both the stock and the scion retain their inherent qualities, but do not acquire new ones from each other. Each of them, however, is a part of the environment of the other. They become physically united as parts of the same individual, and as such they are subject to the interrelation of the parts of an individual as described in Chapter XXI.

The scion is dependent upon certain processes in the roots of the stock, and the stock is dependent upon certain processes in the leaves of the scion. Sugar, hormones, and other soluble substances pass from one to the other. Nicotine, for example, may pass from a tobacco stock into the stems and leaves of a potato scion. It is reported that when potato and tomato are intergrafted with jimson weed, an alkaloid, atropin, from the jimson weed accumulates in the tuber of the one and the fruit of the other. As a result of these interrelations, the growth of roots and tops, the size and flavor of fruits, and the time of flowering may be altered.

Graft chimeras. A stem primordium may develop by the division and enlargement of cells at the area of contact of scion and stock. If some of the cells of this primordium develop from one or more cells in the base of the scion and some of them develop from adjoining cells in the stock, the young stem tip will be composed of the two kinds of cells, which may be referred to briefly as "scion cells" and "stock cells." Since this stem tip is the forerunner of a leafy branch, these cells are the remote forerunners of all the tissues that develop in it (Fig. 32). Consequently whole tissues in the leaves and stems of this branch may be composed entirely of the one or the other kind of cell. The epidermis, for example, may be composed entirely of scion cells, and the other tissues entirely of stock cells. Such compound structures are called *chimeras*; and since they develop from the junction of a graft, they may be called *graft chimeras* to distinguish them from *mutant chimeras*, which originate *within* cells by processes described in Chapter XXXIX.

In time flower primordia may develop on stem tips of this branch. These flower primordia may develop entirely from scion cells, entirely

from stock cells, or from both kinds of cells. If the primordium of the pistil develops from both kinds of cells, some of the tissues in the resultant fruit will resemble those in the fruit of the scion, and others will resemble tissues in the fruit of the stock.

When the tissues characteristic of one kind of plant surround those of the other, the chimera is said to be *periclinal*; when neither tissue surrounds that of the other, but each appears in distinct sectors, the chimera is *sectorial*. Incomplete periclinal chimeras appear superficially to be sectorial.

Experimental attempts to increase the number of chimeras include wounding or cutting across the stem at the junction of stock and scion after they have become united.

Advantages of grafting. Grafting is a valuable means of perpetuating desired varieties of plants that do not multiply readily by other methods of vegetative propagation or reproduce true from seeds. There are also certain other advantages, three of which will be mentioned briefly.

The range of distribution of a variety may be extended if it can be grafted on root systems that grow better than its own roots in certain habitats. For example, peach trees may grow better on the roots of plum in poorly drained soils, and plum trees may grow better on roots of peach in light or sandy soils. The root systems of some varieties of pear grow well in light, well-drained soils, others in heavy, poorly drained soils.

The destructive effects of insects, fungi, and bacteria on roots may be avoided by grafting the desired variety on root systems that are immune to these parasites. A classical example is the avoidance of the destructive effects of the root louse, *Phylloxera*, on roots of the wine grape, *Vitis vinifera*, of France by grafting the European grape on an immune species of American grape, *Vitis labrusca*. Similarly, certain susceptible varieties of apple are grafted on the roots of other varieties immune to the woolly aphis. English walnut is protected from the fungus *Armillaria* by being grafted on black walnut, which is immune to it.

Plants, such as apple, have a long vegetative period before they bear flowers and fruits. The shoots of apple seedlings will bear fruit in two or three years if they are grafted on the branches of a tree that has begun to bear flowers and fruits. Advantage is sometimes taken of this fact in testing the quality of apple seedlings that would otherwise not bear fruit for ten years.

Root cuttings. Root cuttings are made from several kinds of plants, such as blackberry, red raspberry, plum, cherry, horse-radish, apple, Japanese quince, sumac, phlox, and anemone. The cuttings, which are

usually 2 to 3 inches long, are covered with about one-half inch of soil. They differ from stem cuttings in the absence of preformed shoot buds. Owing to the polarity of the roots, adventitious shoot buds usually develop from the upper, or basal, end of the cutting and roots develop from

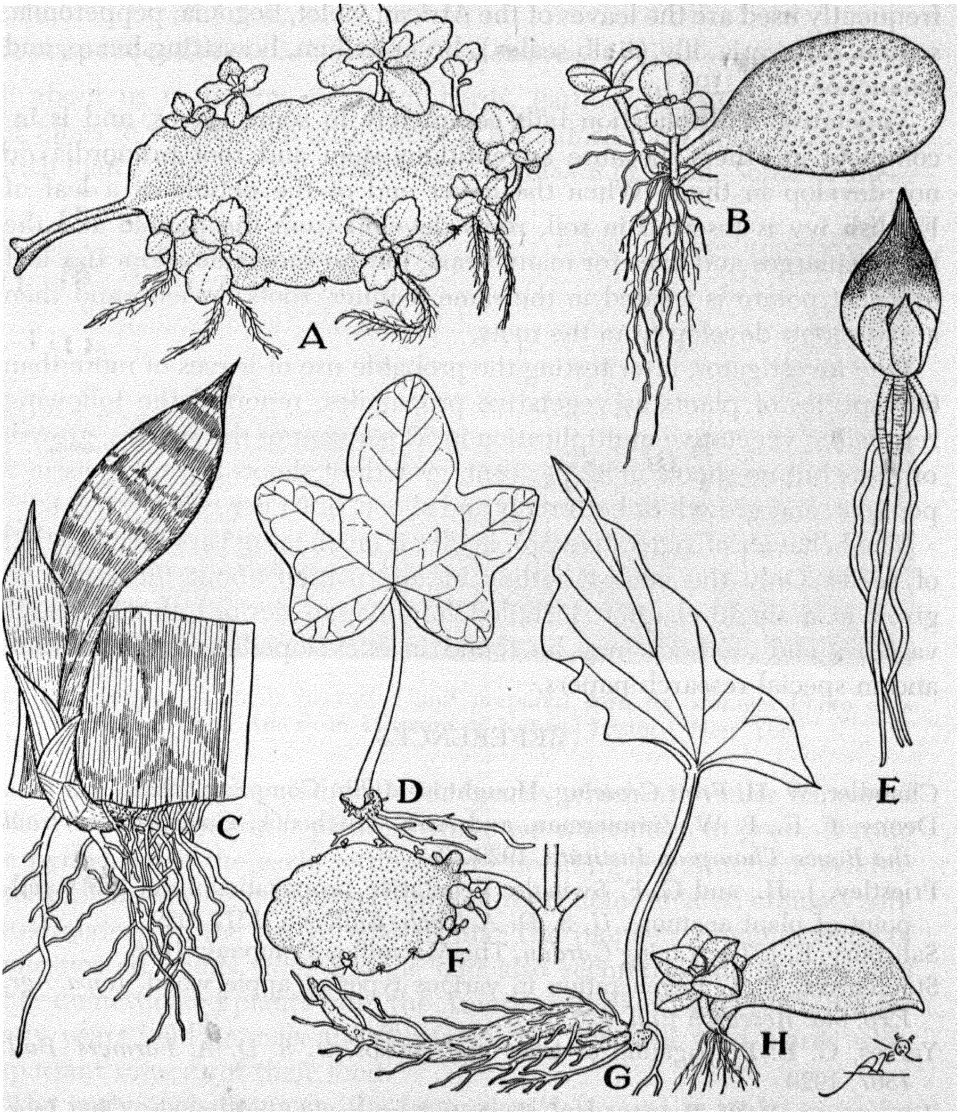

FIG. 194. Vegetative multiplication of plants from leaf cuttings: A, *Bryophyllum calycinum;* B, *Crassula;* C, *Sansevieria;* D, English ivy; E, bud scale of lily; F, *Bryophyllum crenatum;* G, yam; *H, Echeveria.*

the tip. Some plants, such as apple, which fail to propagate from stem cuttings taken from the crown of the tree, propagate readily from root cuttings. Moreover, sprouts from the roots of apple may be used as stem cuttings, in contrast to branches from the crown.

Leaf cuttings. For many years floriculturists have used the leaves of certain species of plants as vegetative propagules. Among those most frequently used are the leaves of the African violet, begonia, pepperomia, sedum, echeveria, lily (bulb scales), bryophyllum, bowstring hemp, and kalanchoe (Fig. 194).

Vegetative multiplication fails completely in some leaves, and is incomplete in others, because adventitious stem and root primordia do not develop in them. When the lower end of the petiole of a leaf of English ivy is inserted in soil, roots develop from the petiole and the blade enlarges and lives for many years, but no shoots develop. If a leaf of sweet potato is treated in the same manner, roots develop and then aerial shoots develop from the roots.

One investigator, after testing the probable use of leaves of more than 600 species of plants as vegetative propagules, reported the following results: no vegetative multiplication in 32 per cent of the species, growth of roots but no shoots in 42 per cent, growth of shoots but no roots in 2 per cent, and growth of both roots and shoots in 24 per cent.

The behavior of vegetative propagules is much more variable than that of seeds. Only the merest outline of information about them can be given in a single chapter. Detailed information desired about specific varieties and methods may be found in encyclopedias of horticulture and in special research papers.

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CHAPTER XXXVI

ORIGIN OF PLANTS USED BY MAN

All about us in forests, fields, orchards, gardens, lawns, and even in test tubes in commercial and research laboratories are numerous plants which man values for the various uses he makes of them. Some of these



FIG. 195. Iroquois Indians harvested and prepared corn for storage. Photo of a diorama from American Museum of Natural History, New York.

plants are the uncultivated, or wild, species which are either harvested where they are found, or planted where we want them to grow. During the period when the early settlers were invading the American wilderness and converting it to farms, some of their domesticated animals subsisted mainly on the native wild plants. The pioneers brought seeds of domesticated plants from Europe and also secured seeds of corn and other domesticated plants from the American Indian (Fig. 195), but for many years wild animals and the fruits and seeds of wild plants were important sources of their food.

The native vegetation on the farms was destroyed to make room for domesticated plants; but in certain practices, especially those in which

the plants of the forest are needed, we still use many of the native wild species. The origin of these wild species will be considered in a later chapter. Many of the plants we use, and especially our crop plants, have been obtained from wild species by repeated selection of more desirable variations, and in recent times by selection accompanied by controlled pollination. Even forest trees are now being selected and artificially pollinated to obtain varieties with certain desired qualities.

When man transfers plants from the wild state and provides artificial environments favorable to their growth and propagation, he observes many of the variations that naturally occur in them and eventually selects and maintains certain of the new varieties. These cultivated varieties are often referred to as agronomic, horticultural, and garden varieties, or briefly as domesticated plants.

Many domesticated plants are unable to survive in the natural conditions that prevail over most of the area in which they are cultivated. Domesticated annuals, for instance, may perish because their seeds do not survive from one growing season to the next unless they are preserved in artificial conditions. Some domesticated varieties, such as special hybrids of corn, are reobtained each season only by carefully controlled pollination. On the other hand some domesticated plants, through seed dispersal, may become distributed and continue to persist as weeds in fields and along roadsides, but they usually do not survive in areas occupied by native plant communities.

A heritage from prehistoric man. Nearly all of our more important species of cultivated plants were domesticated by prehistoric man. Numerous new varieties have been obtained from these domesticated plants within historic times, but the domestication of additional wild species has been limited largely to plants chosen for decorative purposes or for their fruits and their forage value.

On the basis of our present knowledge of plants, we may, with reasonable certainty, enumerate the major steps by which prehistoric man secured domesticated plants. First, there was a recognition of certain valuable parts or properties in the wild ancestors. For a time these parts were collected from the plants wherever they were found in a wild state. Later particular species were intentionally cultivated. Variations in the heredity of the cultivated individuals continued to occur by the same process that brings them about in plants in the wild state. Under the conditions of cultivation, seeds or vegetative propagules of some of the variants were either consciously or unconsciously selected and planted

more abundantly than others. Continued variation accompanied by selection through many thousands of years resulted in cultivated varieties that differ in many ways from their wild ancestors.

There is good evidence that long before historic times man began to notice and select desirable variants of the plants on which his existence depended. The primitive tribes in the interior of New Guinea, whose civilization today is considered by ethnologists to correspond to the late Stone Age, distinguish and name the numerous varieties of sugar cane they are cultivating.

Man may also unconsciously select and promote the propagation of certain varieties of cultivated plants. Owing to the occurrence of natural variations, a field of crop plants usually consists of a mixture of several varieties just as the population of a city is composed of many different kinds of people all of whom are members of the same species. Experiments have shown that in a mixed population of crop plants some varieties may produce more seeds than others, have a greater number of ripe seeds at harvest time, or have seeds that germinate more readily when planted. Consequently in a mixed population of plants that propagate by seeds, certain varieties may gradually increase and others decrease in abundance without any conscious selection on the part of man (Table 15).

TABLE 15. Changes in a Mixed Crop of Wheat During a Five-year Period Without Any Conscious Selection by the Farmer. Percentages of the varieties and species in the crop during the first season of the test are given in column A; at the end of five years in column B.

Wheat Varieties	A	B
Triticum vulgare lutescens	72.0%	7.6%
" " ferrugineum	10.9	82.4
" " erythrospermum	9.3	5.7
" " milturum	6.1	4.3
" durum, " compactum	1.7	0.0
	100.0%	100.0%

The evolution of cultivated plants has occurred over such a long period of time and resulted in such marked changes in the plants that botanists have had great difficulty in discovering the wild ancestors of some of

them. Compare, for instance, our present varieties of cabbage, kohlrabi, cauliflower, kale, and Brussels sprouts with the mustard-like wild ancestor from which these cultivated varieties were derived (Fig. 196).

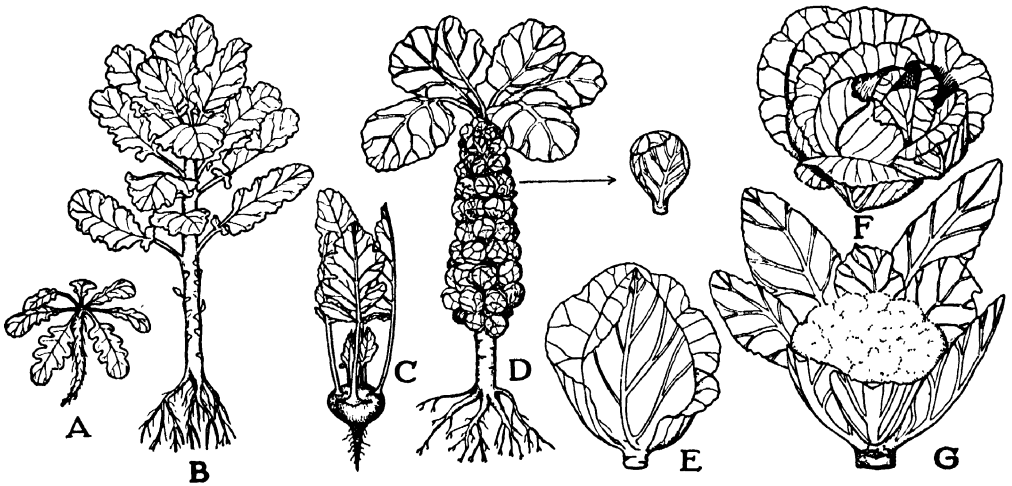

FIG. 196. Domesticated varieties derived from the wild cabbage, *Brassica oleracea* (A), a native of Europe. B is kale, *Brassica oleracea acephala*; C, kohlrabi, *B. oleracea caulo-rapa*; D, Brussels sprouts, *B. oleracea gemmifera*; E, pointed-head cabbage, *B. oleracea capitata*; F, round-head cabbage, *B. oleracea capitata*; G, cauliflower, *B. oleracea botrytis*.

The wild ancestors of the domesticated plants of Eurasia are better known than those of America. Corn is the only important cereal that originated in America. Its wild ancestor was a grass; but in spite of a prolonged search for this grass, it is still unknown today.

When Columbus arrived in America, the Indians of the New World were cultivating several distinct varieties of corn, potatoes, sweet potatoes, kidney and lima beans, peanuts, pumpkins, squash, tomatoes, pineapple, pepper, arrowroot, sunflower, Jerusalem artichoke, beach strawberry, tobacco, cotton, and many other plants (Fig. 197). These plants were domesticated by prehistoric man in the highlands of Mexico, Central America, and the northwestern part of South America: the regions in which the Incas, Mayas, and Aztecs later developed their remarkable civilizations. Previous to the voyage of Columbus none of these domesticated plants of America was known in Europe, and none of the domesticated plants of Europe was known in America. Within each hemisphere, however, several important crop species had become widely distributed. The Indians were cultivating corn in many local



FIG. 197. Woodland Indians cultivated corn, sunflower, squash, and tobacco. Photo of a diorama from American Museum of Natural History, New York.

areas between what is now Canada and Argentina, while in Eurasia wheat and rice were just as extensively cultivated. Some of the importance which the early American Indians attached to their domesticated plants is reflected in their art (Fig. 198).

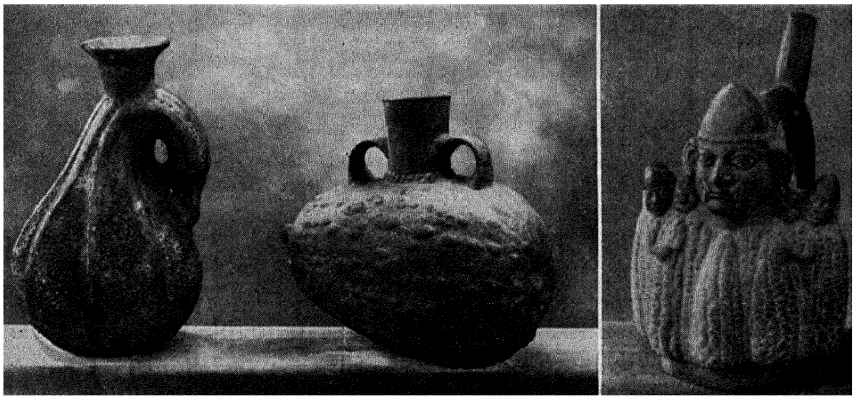

FIG. 198. Ancient Peruvian pottery. Photo from American Museum of Natural History.

In the eastern hemisphere the principal centers in which the basic crop plants originated are certain parts of central Asia, Asia Minor, central and southern China, northern India and perhaps Ethiopia: the regions in which the earliest civilizations of Eurasia later became most highly developed. Among the cultivated plants on which these early civilizations of Eurasia depended were the cereals (wheat, barley, rye, rice, millet, oats, sorghum), soybeans, and several common vegetables and edible fruits. Most of the cultivated forage crops (clovers and grasses) also originated in the eastern hemisphere (Fig. 199).



FIG. 199. Forage crop—red clover and timothy.

Civilization in the past depended upon an unfailing supply of plants as the primary source of food just as it does today. During his long existence upon the earth as a primitive nomad, early man depended upon plants in the wild state. Furthermore, his migrations were conditioned by the abundance, or the scarcity, of wild plants. The kinds of wild plants used by prehistoric tribes in all parts of the globe are numbered in the thousands. The Indians who lived in what is now the United States and Canada used as a source of food more than 1000 species of plants, only a few of which were ever cultivated (Fig. 200).

Many others were used as sources of material for weaving, medicine, and personal equipment (Figs. 201 and 202).



FIG. 200. Woodland Indians collected and boiled maple "sap" as a source of sugar. Photo of a diorama from American Museum of Natural History, New York.

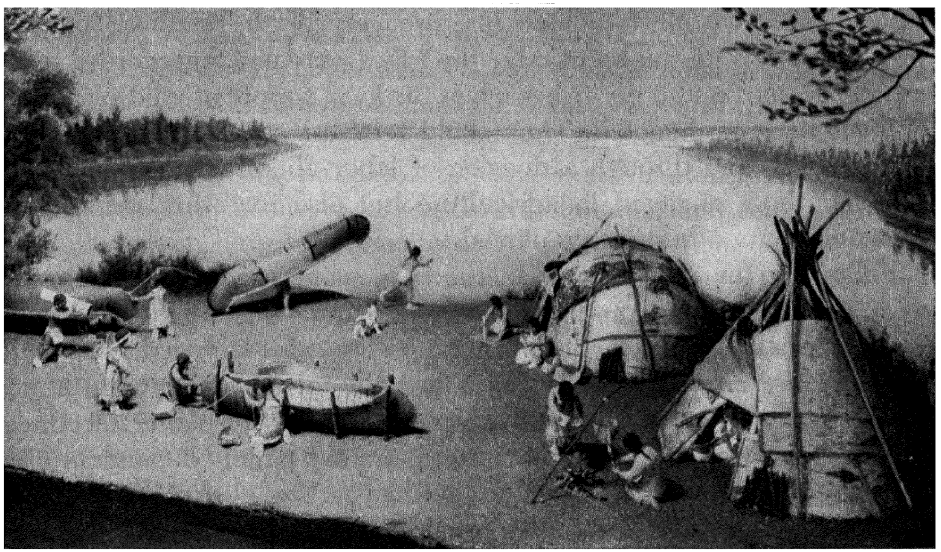

FIG. 201. Birch bark industries of North American Indians. Photo of a diorama from American Museum of Natural History.



FIG. 202. Basswood bark fiber industries of eastern woodland Indians. Photo of a diorama from American Museum of Natural History.

No civilization of any note was possible prior to the development of a primitive agriculture. Among the more valuable accomplishments of prehistoric man we must include his discovery of the methods of plant propagation. With this knowledge the tribes were no longer forced to live as nomads and raid other tribes when the local supply of wild plants and animals became depleted. They could establish stable abodes in moist fertile areas, and through a division of labor obtain food sufficient not only for those engaged in agriculture but also for other members of the community otherwise employed.

Following the discovery of methods of plant propagation, primitive man, by transporting and planting seeds and vegetative propagules, could permanently occupy new areas. Without this knowledge the early civilization that developed in the Nile Valley would have been impossible, for Egyptian agriculture was accomplished with plants introduced from Eurasia. In the United States today we are largely dependent upon plants that were first domesticated in other parts of the world. The most outstanding exceptions are our forest trees.

The evolution of cultivated plants has gradually progressed since prehistoric times to the present. Today this progress is accelerated by a more

rapid introduction of foreign species from all parts of the world, accompanied by intelligent control of plant breeding and a clear understanding of the different types of variations that occur in plants.

The introduction of foreign species is merely an attempt to secure plants with other heredities. The ancient caravan trade routes were important means of distributing plants in the early days. Botanic gardens, and more recently experiment stations, became centers of receiving, testing, and distributing these foreign plants. Plant scientists at the U. S. Department of Agriculture annually obtain numerous varieties of probably desirable plants and distribute them to appropriate testing stations throughout the country. They have secured and tested a total of more than 8000 varieties of wheat collected from more than 50 different countries.

Plants are now critically selected with reference to a number of qualitative and quantitative characteristics, such as yield and quality of certain organs and tissues, chemical composition, relative development in different soils and climates, and immunity to causal agents of disease.

New varieties obtained by control of plant breeding. Man no longer depends entirely upon the selection of chance or fortuitous variations as a means of securing new varieties of plants. He has learned how to control plant breeding and obtain more desirable varieties (1) by combining the desirable heredities of two or more kinds of plants, (2) by eliminating or preventing the expression of undesirable heredity in otherwise desirable plants, and (3) by first eliminating undesirable hereditary qualities in two or more kinds of plants and then combining the desirable heredities.

Plant breeding is controlled by means of pollination. Plants, such as wheat, peas, and beans, in which close pollination and self-fertilization naturally occur, have to be manipulated differently than plants, such as corn, in which open pollination and both cross-fertilization and self-fertilization naturally occur. In open pollinated plants the pollen of the stamens of a flower may come in contact with the stigma of the pistil of the same flower, of flowers of the same plant, or of flowers of other plants.

The term close pollination is used here to refer to the fact that in some species of plants pollination usually occurs before the flower buds open. A very small amount of cross-pollination and cross-fertilization occurs in these close pollinated plants. In some varieties of wheat it may be as much as 4 per cent. Insects that break through the floral envelope may become agents of cross-pollination in closed flowers.

When the pollination of plants which are naturally open pollinated is controlled so that only selfing can occur, several different kinds of progeny are obtained from the same parent. That is, the plant does not "breed true." It is a hybrid, and its mixed parentage becomes evident in its progeny (Fig. 203). But if each individual in its progeny is selfed, and if this process of selfing is repeated in all individuals for several successive generations, several different kinds of plants are eventually ob-

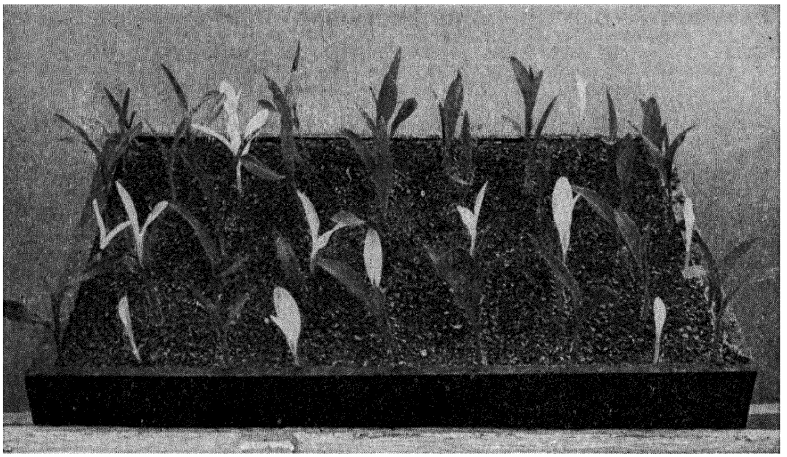

FIG. 203. Hybrid segregation in corn. Photo by G. W. Blaydes.

tained, each of whose progeny appears uniform when growing in a similar environment. In this way several inbred lines of plants are obtained from the original hybrid parent.[1] Further inbreeding results only in a continuation of uniformity in the progeny of each inbred line. Inbred plants are pure-line plants with respect to many of their characters. In contrast to hybrids, pure-line plants continue to breed true. Plants that naturally have only close pollination are natural inbred and pure-line plants.

Pure-line plants of some species, such as those of corn, may be less desirable than the hybrid varieties obtained by cross-pollination because they are smaller, less vigorous, or more susceptible to parasites, or have fewer seeds and fruits than the hybrids. More desirable and uniform hybrids may be obtained by restricting cross-pollination to certain se-

[1] Probably more than 2000 inbred lines of corn have been obtained by this method, and several hundred of them have been used as a basis of securing better varieties of hybrid corn. Some of the inbred lines of corn are albinos and perish in the seedling stage. Certain others also fail to grow to maturity and reproduce.

lected pure-line plants (Fig. 204). Environment affects the development of a pure-line plant just as it does that of any plant; but changing the environment does not change its characteristic of breeding true to type.

Compared with plant selection, the controlling of plant breeding is a very modern occupation. Prehistoric man, by the introduction and cultivation of closely related species and varieties of plants in the same



FIG. 204. Uniformity of height and maturity in hybrid corn of similar genetic composition. Photo by G. H. Stringfield, Ohio Agricultural Experiment Station.

locality, was unconsciously responsible for cross-pollination and the consequent hybrid varieties that developed as a result of cross-fertilization. On the other hand, the ancient practice of collecting pollen-bearing branches from staminate trees of dates and tying them among the flowers of pistillate trees to insure the development of fruit resulted in some wholly unintended limitation of cross-pollination. In the wild state, the staminate trees of dates are as abundant as the pistillate trees, and the pollen is distributed by wind. More than 5000 varieties of dates are now under cultivation.

Intelligent efforts to control plant breeding through pollination depended upon the discovery of sex in plants and of the dependence of sexual reproduction in seed plants upon pollination. The experiments of Camerarius from 1691 to 1694, by which he showed that embryos do not develop in seeds in the absence of pollination, were the first definite

proof of sex in plants.[2] The experiments of several other investigators during the 18th century were necessary to show that sex occurs in all seed plants and that pollen is essential to the sexual process in them.

The actual process of fertilization as the union of a sperm cell with an egg cell was unknown prior to the middle of the 19th century, and was first discovered in the algae. The union of the egg in the embryo sac with a sperm from the pollen tube was first noted in 1884. The fact that the endosperm of seeds develops from the triple-fusion nucleus formed by the union of one sperm from the pollen tube with the fusion nucleus of the embryo sac was discovered in 1898. The first careful experimental study of the hybridization of plants is accredited to Koelreuter, 1761-66.

Nevertheless, a considerable amount of controlled plant breeding was accomplished by the method of trial and error previous to the 20th century. Many new varieties of cultivated plants were obtained by crossing individuals of domesticated varieties with each other and with wild species. Some new varieties were also obtained by crossing wild plants with each other. The Concord grape, for instance, was obtained by Ephraim Bull in Massachusetts by crossing two wild species. This variety, which is now cultivated in most temperate regions of the earth, was selected in 1853 from among 22,000 progeny of the two wild parents.

Toward the close of the 19th century new varieties of domesticated plants were being obtained by foreign introductions, by cross-pollination and inbreeding, by mass selection, and by single-line selection.

As already indicated, a crop of cultivated plants is likely to be a mixed population of several different varieties. In mass selection, seeds from the more desirable plants in the field are collected and then planted the following season. By this method the more undesirable varieties in a mixed population are supposed to be eliminated and the more desirable ones perpetuated. In a later chapter we shall see that the appearance of an individual in the field may be very deceptive with respect to the kind of heredity it transmits to its progeny. In spite of this weakness of mass selection it has been very effective in increasing the average yield of many crops and is still considered a valuable practice.

The method of single-line selection has recently become preferable to

[2] Camerarius was fortunate in choosing for experimental study plants in which parthenocarpy occurred, but in which parthenogenesis did not occur. Had he chosen dandelion to study, his conclusions would have been different.

mass selection in the attempted improvement of many cultivated plants. This method may be illustrated by one example. David Fife of Canada secured a small sample of hard spring wheat from a friend in Scotland. When he planted the wheat in a small plot in Canada in the spring of the year, he discovered that this new wheat was a winter wheat and should have been planted in autumn. A single plant in the plot, however, developed as spring wheat. Seeds from this single plant were saved and planted. This one plant is the ancestor of all the Red Fife wheat now cultivated in Canada and the United States.

Red Fife, in turn, when crossed with Hard Red Calcutta wheat from Turkey, became one of the parents of the famous Marquis wheat, which for 20 years was regarded as the king of hard red spring wheats. In time it became surpassed by some of its more desirable progeny.

In contrast to corn, crops of close-pollinated plants, such as wheat, oats, and barley, are composed of inbred lines. The story of the search for new varieties of plants, as summarized in the 1936 and 1937 *Year Books of Agriculture*, portrays modern methods of securing new varieties of domesticated plants, and also the magnitude of this enterprise.

The work of botanists during the second half of the 19th century is remarkable for the number of important facts discovered about plants. In 1866 Gregor Johann Mendel, an abbot of Brünn, Austria, after eight years of experiments formulated certain general principles about hybrid variations in the garden pea that were later found to have general application to both plants and animals. In 1900 the principles formulated by Mendel and also his publication, which had been forgotten, were rediscovered independently by de Vries of Holland, Correns of Germany, and Tschermak of Austria.[3] These principles have been thoroughly tested by means of numerous experiments and they are now widely used as a scientific basis for further investigation and interpretation of heredity.

About the same time, de Vries began to emphasize the importance of another type of heritable variation in plants that is not dependent upon hybridization; it is known today as a mutation. Mutations had been noted earlier and referred to by various names, but their importance had not been recognized. The change of red to yellow sweet potatoes illustrated in Plate 4 is one example of a mutation. Another example on the

[3] After eight years of experiments with the progeny obtained by cross- and self-fertilization in the garden pea, Mendel published his data and conclusions in the *Proceedings of the Brünn Natural History Society* in 1866.

same plate is the red-flowered hibiscus plant, some branches of which regularly bear white flowers.

It thus became evident that three general types of variations should be recognized in plants. There are, first, those variations that are the direct results of the effect of environmental factors upon the conditions and rates of processes within the plant, without any changes in the hereditary make-up of the plant or its progeny. We have referred to many examples of this type of variation in previous chapters. Such variations are *non-heritable* and are referred to as *fluctuations*. In contrast to fluctuations are the two types of *heritable variations*: the *hybrid variations* resulting from cross-fertilization, and the *mutations* which are changes in heredity not dependent upon cross-fertilization, though they may be increased by it. Their rate of occurrence is also influenced by factors in the external environment, as we shall see later. The scientific recognition of the causes and consequences of these three different kinds of variations is largely a product of the research during the present century.

During all of this time, certain other botanists were interested in studying the detailed structures of cells. The cytoplasm and nucleus were clearly recognized and referred to as protoplasm about the middle of the 19th century. During the latter half of the century the chromosomes of the nucleus were seen, and their gross behavior during cell division in both vegetative and reproductive cells was recognized. During the present century it was discovered that nearly all of the known hereditary factors are definitely associated with the chromosomes.

While the 19th century is noted for the discovery of many important facts about plants, the final verification of many of those facts and of their several dependent relations was not accomplished until the present century. To those interested in plant and animal breeding, all these discoveries are of prime importance because they are the basis of a new science known as genetics. To us in general botany they will help explain many of our everyday observations; and as we proceed to amplify and clarify them in the next few chapters it will become evident that they constitute a basis of fact essential to any critical analysis of ideas about evolution, inheritance of acquired characters, relative importance of heredity and environment, adaptation, natural selection, and related phenomena.

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CHAPTER XXXVII

HEREDITY IN PLANTS

Many hereditary resemblances and differences among plants were mentioned in previous chapters, but the conditions and processes of which they are the results were not analyzed. In the study of plants and animals the terms "heredity," "inheritable," or "heritable" are used to indicate that something inherent in the parent is transmitted to its progeny, and influences, or conditions, individual development and behavior of the progeny. The distinctive characters of species, of varieties, and of either general or specific races reappear by development in succeeding generations over long periods of time. The modern species of elms and maples, for instance, still resemble their ancient ancestors that lived during the Cretaceous period many millions of years ago. The human race as a whole, or any one of the specific races of man, likewise exemplifies inheritance.

General Aspects of Heredity

The term heredity is quite properly used in several ways: (1) to refer to the resemblances of plants and animals to their progenitors, or (2) to designate what is obtained in the fertilized egg from the gametes, or (3) to indicate the whole range of biological processes underlying inheritance. The sequences of events in heredity that have been discovered and shown by experiment to recur in successive generations are often referred to as the laws of heredity. Many of the more fundamental laws of heredity in plants and animals are similar, but the related processes and structures involved in their operation may be quite different. Several examples of conditions in plants not met with in the study of heredity in animals are: the frequent occurrence of self-fertilization, the prevalence of vegetative multiplication, the differentiation of reproductive tissue from vegetative (somatic) cells throughout the life of the plant, the two-phase life cycle, and the development of endosperms in some seeds (Chapters XXXI, XXXIII, and XXXIV).

Heredity is not limited to parental resemblances. Among the progeny

of the same parents, or even of one plant, some of the individuals may differ greatly from others. All these variants among the progeny that develop in the same environment are the results of heredity, and they are referred to as heritable variations. Hereditary resemblances and dissimilarities reappear in succeeding generations. Maple leaves continue to reappear in opposite arrangement on maple trees growing in very different habitats; peach fruits develop from the flowers of peaches but not from apple blossoms; and white oaks grow only from the acorns of white oaks. Some of the progeny, however, may resemble a grandparent, or even a remote ancestor, more closely than the immediate parent.

On the other hand, if the individuals of the progeny differ from each other solely as a consequence of having developed in different kinds of environments, these differences will not reappear in subsequent generations unless equivalent environmental conditions are repeated. These differences are non-heritable, in contrast to those that are heritable. We have already learned to refer to non-heritable variations as fluctuations. They should also be recognized from now on as differences in degree of expression of certain hereditary properties, or potentialities, of the plant.

The expression of hereditary potentialities during the development of a plant is, of course, dependent upon external conditions. The potentiality of chlorophyll synthesis, for instance, is not expressed in most "green plants" growing in the dark. Many other examples may be recalled. Every plant has a great many hereditary potentialities, some of which are expressed more than others in a particular environment (Chapter XXXI). What any plant does during its lifetime depends, therefore, upon its environment as well as upon its heredity.

Now that we are familiar with the nature and causes of non-heritable variations and with the sequences of processes and structures in sexual reproduction and also in vegetative multiplication of plants, we may consider some of the fundamental processes of heredity and heritable variations. What, for instance, is actually transmitted from parent to progeny? Is it transmitted through cell division to all the cells of the roots, stems, leaves, and other organs of the plant? May it be transmitted by any cell of the plant? How is it transmitted? Is it a mysterious vital force, or is it a material mechanism composed of discrete units of matter? How does it become duplicated in new cells? What determines its constancy from generation to generation over long periods of time? Is it alterable?

These questions will appear even more significant if one begins to recall the numerous ways in which all the plants he knows differ from

one particular kind of plant. These thousands of differences are heritable and are determined by something that is transmitted from parent to offspring in each kind of plant. Then one may try to visualize some of the thousands of successive events that must occur in approximately the same manner and order every time an oak tree develops from an acorn. These repeated similarities also are dependent upon something that is transmitted from parent to offspring.

If we can first secure acceptable scientific answers to such questions as those listed above, we shall then have a much surer background of fact by which to explain why the progeny resembles the parents in some respects and differs from them in others, and why these resemblances and differences appear in the definite proportions first described by Mendel. The answers will also help us to understand why there are fewer variations when plants propagate only by vegetative means, why plants do not always "come true from seed," and why inbreeding does not always result in less desirable plants.

In addition we may wish to apply our knowledge to a consideration of questions of more general significance. What, for instance, is the explanation of the occurrence of new kinds of plants in successive geologic periods? How do new kinds of plants come to be? What are the causes of evolution, and in what ways is it limited?

In this and the next three chapters you will find a discussion of some of the more basic facts necessary to arrive at reasonable answers to the questions suggested above. For lack of space many interesting facts will have to be omitted. If the reader is interested in knowing more about some particular phenomenon, the books listed at the end of the chapter will be helpful as sources of data and further references.

Heredity in vegetative multiplication and cross-fertilization contrasted. We may begin with the familiar fact that when a desirable plant is obtained by means of cross-pollination it does not always reproduce true from seeds, but it may multiply unaltered by vegetative propagation for an indefinite period of time. In practice a large number of plants having the same heredity may be obtained by means of continued vegetative propagation, starting, of course, with cuttings all of which were taken from the same plant. The cuttings, however, may be taken from the roots, stems, leaves, or from any two or three of these organs. The individuals of a clone of plants obtained in this manner all have the same heredity (Chapter XXXV). This fact is evidence that all the cells of the

leaves, stems, and roots of a plant usually have the same hereditary properties, or potentialities. What exceptions do you know?

Properties, or potentialities, are merely the qualities or attributes of material objects and of their special arrangements in organized systems, or mechanisms. We may infer therefore that the individual cells of the several vegetative organs of a plant have within them exactly the same structural mechanism of inheritance. Furthermore, since cells multiply by cell division (two cells being formed from one), this hereditary mechanism must be exactly duplicated by some means every time cells divide.

This intrinsic mechanism by which the hereditary potentialities of the cells of the vegetative organs of a plant are preserved throughout its lifetime is surprisingly stable. In long-lived plants such as the redwood, and in plants that propagate vegetatively this mechanism may be perpetuated unaltered for centuries. Occasionally it becomes altered in some of the branches of a plant. Stable alterations in this mechanism are heritable, and are the means by which new kinds of plants are derived from preexisting ones. Seedless oranges and yellow roots of sweet potato, Plate 4, are examples of heritable variations that occurred in certain branches of the plant. Heritable variations that occur in this manner are known as mutations.

By cross-fertilization certain parts of the hereditary mechanism of the two parent plants are brought together in the fertilized egg. That is, the fertilized egg contains the hereditary mechanism that was in the sperm and also the one that was in the egg. The plant that develops from this fertilized egg thus possesses a hereditary mechanism partly like and partly unlike that of either parent. In certain characters it may resemble one or the other parent, while in other characters it may differ from both parents. Such individuals are called hybrids. When hybrids reproduce by seeds, their progeny usually are variable in appearance.

For example, when cross-fertilization occurs between red-flowered and white-flowered plants of snapdragon, the resultant progeny are hybrids and all of them are pink-flowered. This difference between parents and progeny is a hereditary difference. Cross-fertilization between the pink-flowered plants, or self-fertilization within any one of them, results in progeny in which approximately one-fourth of the plants are red-flowered like the original red-flowered plant, two-fourths are pink-flowered like the immediate hybrid parent, and one-fourth are white-flowered (Fig. 205).

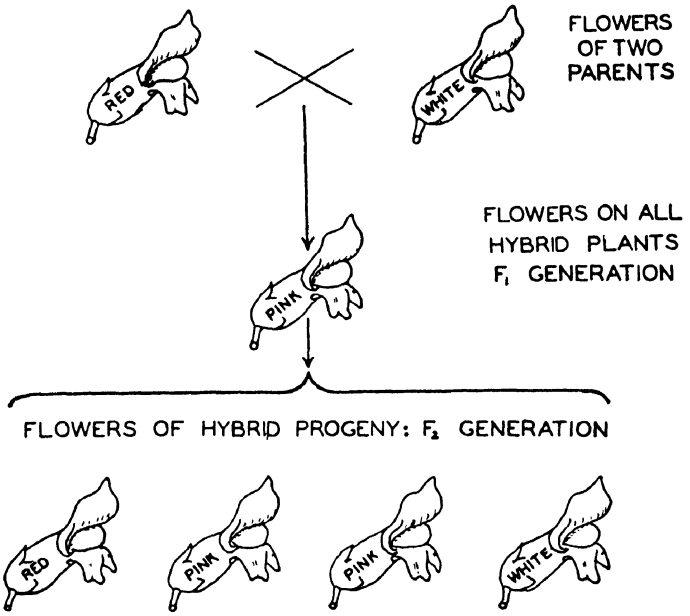

FIG. 205. A diagrammatic representation of the color of flowers on plants of snapdragon of the F_1 and F_2 generations following a cross between a red-flowered and a white-flowered variety.

If cross-fertilization occurs between the red-flowered and pink-flowered plants, one-half of the progeny are red-flowered, the others are pink-flowered. If cross-fertilization occurs between the white-flowered and pink-flowered plants, one-half of the progeny are white-flowered, the others are pink-flowered.

Self-fertilization in the red-flowered plants results only in red-flowered plants. Consequently all the red-flowered plants of this species of snapdragon are said to be a pure line with respect to flower color. Note, however, that our attention is only on flower color. The plants may or may not be a pure line with respect to certain other characters such as height, shape of leaf, and immunity to rust. Self-fertilization in the white-flowered plants results in only white-flowered plants. They constitute a pure line of white-flowered plants. The pink-flowered plants are hybrids with respect to flower color, but they may be pure-line plants with respect to other characters that we are ignoring at the present.

Red- and white-colored flowers are hereditary traits or characters in snapdragon, but the flowers and the pigments are not actually inherited. They develop as a result of something that is inherited. Anything that is directly inherited must be in the egg or in the sperm, since these two

gametes by their union form the fertilized egg, which is the first cell of each plant of the new generation. The gametes may be said to constitute the bridge by which the hereditary factors pass from one generation to the next one.

Since the microspore is the forerunner of the pollen, and the megaspore is the forerunner of the embryo sac (Figs. 165 and 166), these spores also constitute another single-celled bridge through which the hereditary factors must pass during the life cycle of a seed plant.

What is transmitted from parent to progeny? Hereditary potentialities are merely the properties of certain units of matter. Hence certain units of matter that pass from one generation to another in the sperm and egg must be determiners of the hereditary resemblances and differences that may be seen in plants. Any stable alterations of these units of matter that change their properties would result in the development of heritable variations, known as mutations. The differences in grouping of these units of matter that occur in sexual reproduction result in the kinds of hybrid variations exemplified by the flowers of snapdragon described above.

We may now ask whether we can see hereditary units of matter in cells. You have seen chromosomes in nuclei and plastids in cytoplasm. In specially prepared sections one can see in cytoplasm the very small bodies known as mitochondria. From recent experiments it appears that mitochondria may contain essential enzyme systems. All these units are reproducible and are inherited from cell to cell and from gametes to fertilized eggs. But we shall have to become aware of units so small that several thousands of them may be present in a single cell.

In microscope sections prepared for general classes chromosomes usually appear homogeneous, but they are far from being so. In certain stages of cell division slender threads can be seen in chromosomes, each extending from one end of a chromosome to the other (Figs. 207 and 209). The number of threads per chromosome ranges from one to four or more, depending on the stage of cell division and on the relative rates of duplication of threads and longitudinal separation of chromosomes. Because of their property of staining with dyes the threads have been called chromonemata (pl. of chromonema). They have also been called gene threads (genonemata) for contained in them are numerous submicroscopic structures known as genes.

For the present let us visualize a gene as being comparable to an enzyme, each consisting of a large complex molecule composed of differ-

ent kinds of smaller molecules chemically bound together, and having specifically active groups of atoms at a certain place or places. The specific action of these groups of atoms depends upon the particular arrangement of these groups with respect to other atoms in the molecule. A molecular structure of this type could become altered (mutate) with accompanying changes in potentialities without being destroyed.

The number of genes in a thread varies with the length of the thread and the distance between genes. The number may be very large, perhaps a few thousand in some threads. The genes are known to be arranged in a linear order in each thread. Furthermore, when a vegetative cell divides, its nucleus, each chromosome in the nucleus, each thread in a chromosome, and each gene in a thread become duplicated; and the

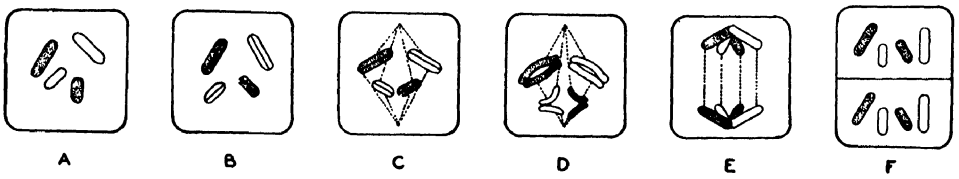

FIG. 206. A diagrammatic representation of certain stages of duplication and subsequent separation of chromosomes during ordinary cell division.

duplicates are qualitatively distributed in the two new cells (Figs. 206 and 207). Thus each chromosome in any vegetative cell of a plant has a duplicate in every other vegetative cell of that plant.

Besides being duplicated longitudinally a chromonema sometimes breaks crosswise. The fragments may rejoin, or join with fragments of another chromonema. These breaks result in complications we shall do well to disregard until we have sufficient background to visualize some of their effects upon heredity.

Plastids in the cytoplasm of plant cells may also pass bodily from the dividing cell to the two new cells formed. They are thus inherited bodily and continue to multiply in the newly formed cells by simple division. Any properties they possess are thus transmitted with them. Plastids in the egg become the first plastids in the fertilized egg.

Relatively little is known about cytoplasmic inheritance or about the influence of cytoplasm upon heredity. Enough has been discovered in recent years to demonstrate the presence of gene-like units of matter (plasmagenes) in the cytoplasm. A few discoveries have been made of the many dependent relations among chemical syntheses, enzymes, plasmagenes, and nuclear genes. The big problem is to discover how the

interactions among all these units result in an orderly development of a plant and all its parts. Since this is a relatively new field of research many tentative ideas are being proposed and tested.

It is important to remember that the whole hereditary mechanism of a plant is in its protoplasm, and that at one stage in the life cycle of a plant this mechanism is all contained in the fertilized egg. Differences in heredity must be the result of differences in this mechanism.

We have become accustomed to thinking of protoplasm as a living system composed of molecules of many kinds of substances which by themselves do not have the property of aliveness. It now becomes necessary to recognize chromosomes and genes as distinct components of this living system. In ways only partially understood, they influence various cell processes and thus impart certain properties to the cells which become evident as the plant develops. If some of these components of protoplasm are removed, the living system may survive, but its properties will be different. Even a change in the arrangement of the genes within a chromosome may be the cause of a change in the development of a plant. The relative location of the genes within a chromosome seems to be fairly constant.

The exact manner in which a gene may influence the development of a plant is as far from being understood today as is the manner in which small amounts of vitamins and hormones influence the development of an organism. All these compounds influence certain complicated chemical processes within the cells.

Later on we shall see that certain reproductive cells (spores, sperms, eggs) and also the cells of one whole phase of the life cycle of plants survive and grow with only one-half the number of chromosomes that are present in the cells of the other phase of the life cycle.

Heredity and Chromosome Behavior

Since each chromosome contains many genes and accordingly many hereditary potentialities, a knowledge of the behavior of chromosomes during the life cycle of a plant is essential to the understanding of the processes and consequences of heredity. Every cell that contains a particular chromosome also contains all its genes and their potentialities. If a chromosome becomes fragmented and a part of it is lost, then certain of its genes and potentialities are also lost. For the present we shall consider heredity only in relation to the longitudinal duplication and sub-

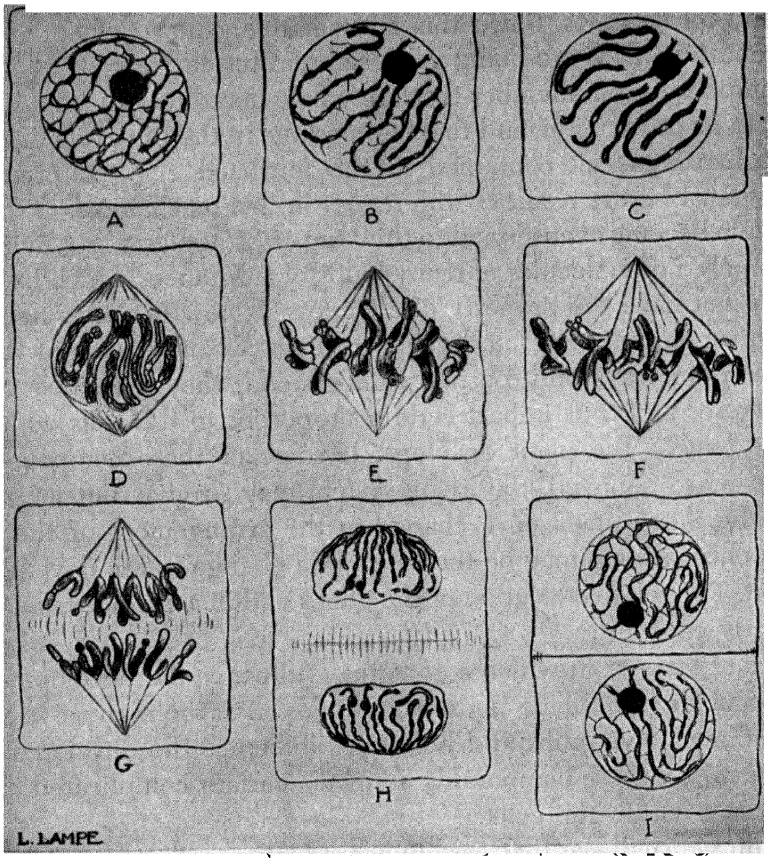

FIG. 207. A diagrammatic representation of chromosome behavior during ordinary cell division in the growing regions of plants.

A, non-dividing cell in which the thread-like chromonemata in the nucleus appear as a network (reticulum). B-C, early evidences of division: chromosomes become individually distinct, each consisting essentially of two coiled threads. D, the chromatids (the two longitudinal halves of a chromosome) become shorter and thicker, and the thread in each chromatid becomes duplicated; the nuclear membrane begins to disappear, and a spindle of "fibers" begins to form in the nucleus. E, each chromosome moves to the equator of the spindle where the spindle attachment of each of its chromatids becomes oriented in the spindle. F-G, the two chromatids of each chromosome separate as daughter chromosomes which move toward opposite poles of the spindle. H, chromosomes at the poles surrounded by a nuclear membrane; the cytoplasm of the cell has divided. I, chromosomes becoming reticulate; formation of a cell wall between the two new cells is under way. The two new cells are identical with each other and with the parent cell in chromosome complement.

Names that are often applied to different stages in ordinary cell division are: prophase, B-D; metaphase, E; anaphase, F-G; telophase, H-I. Drawn by Lois Lampe.

sequent distribution of chromosomes. In later chapters some of the results of crosswise breaks in chromosomes will be considered.

Cell division in vegetative cells: "mitosis." In Fig. 207 certain stages in the behavior of chromosomes in each cell division that occurs in all growing regions of plants are depicted. It should be easy to visualize the continuous behavior of chromosomes between the stages depicted. The

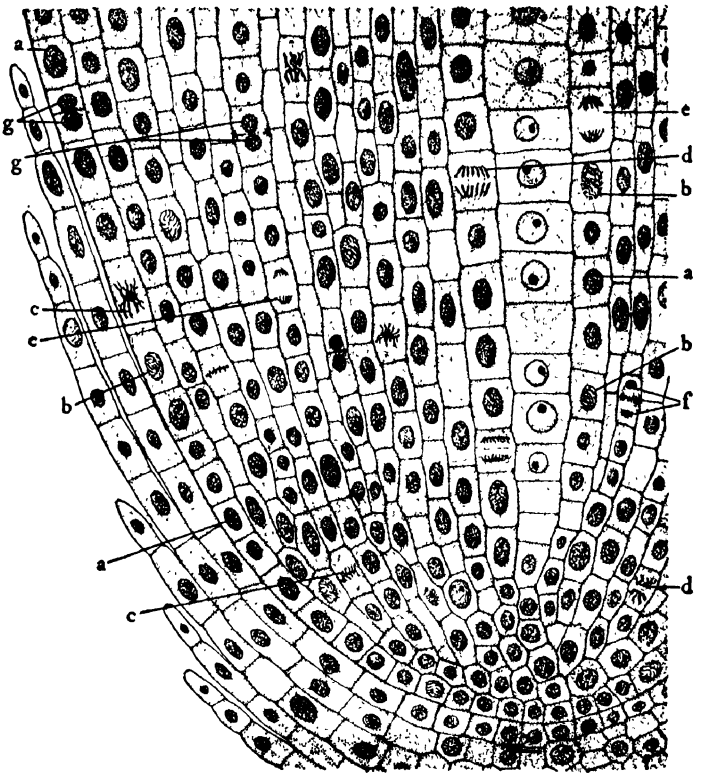

FIG. 208. Cell division and enlargement in a root tip of onion. A series of stages in the behavior of chromosomes during ordinary cell division is represented and labeled a to g. Courtesy of World Book Co.

whole process may be completed within thirty minutes or it may extend over a period of several hours. Cells in various stages of division may be seen in microscopic sections cut from some growing region of the plant (Fig. 208). Many facts about vegetative cell division ("somatic mitosis") are known; but for the present purpose of seeing the relation of chromosome behavior to the transmission of hereditary factors, it is necessary only to study the diagrams carefully. Then it will be seen that every time vegetative cells divide, each chromosome of a cell splits (divides)

longitudinally into two identical halves, or daughter chromosomes, which separate and migrate to opposite poles of the cell, resulting finally in two new cells identical with each other and with the parent cell in chromosome number and composition (chromosome complement). In other words, the important things to visualize as cells divide in the growing regions of a plant are (1) the exact duplication of each chromosome and of its included genes, and (2) the definite manner of the chromosome migration which results in the same chromosome complement in all the vegetative cells of the plant. Consequently all cells of the vegetative tissues of a plant have the same chromosome complement and hereditary potentialities that were present in the fertilized egg from which the plant developed.

These facts help us to understand why heredity remains unaltered when plants multiply vegetatively in nature or in cultivation. The cells of cuttings, for instance, all have the same chromosome complement, and it continues to be the same in the separate individuals that develop from the cuttings. If the chromosomes do not behave regularly as described above, mutations may occur in the vegetative tissues of the plant. For example, the occasional white branch that is found in plants must be the result of something that happened either in the plastids or in the part of a chromosome containing the genes that condition some of the processes involved in the synthesis of chlorophyll.

Since all the cells of the vegetative parts of a plant have the same chromosome complement and the same hereditary potentialities, one may well wonder why all the cells of the plant are not exactly alike in appearance. Their differentiation into the various tissues, such as epidermis, cambium, xylem, and phloem, must be dependent partly upon the influence of neighboring cells and partly upon an inheritance of tissue patterns about which little is known at present. Furthermore, certain hereditary potentialities are not expressed unless the plants attain certain stages of development. Hereditary potentialities that influence flower color and form, for instance, are expressed only when flowers develop; and potentialities that affect the color of endosperm of seeds are expressed only when the endosperm tissue develops from the triple-fusion nucleus.

Reduction division. The division of cells in the growing regions of plants is often referred to as ordinary cell division in contrast to a notable exception known as reduction division, which occurs in the life cycle of a seed plant only when the microspore mother cells and the

megaspore mother cells divide. This particular cell division is called reduction division because the two daughter cells formed have only one-half as many chromosomes as the mother cell. The cell divides, and a cell wall may be formed (Figs. 165 and 166), but the chromosomes do not split completely apart. This very unique cell division plays an equally unique part in the transmission of hereditary factors. It underlies the principle of heredity known as the "law of segregation of hereditary factors" with which we shall be concerned presently.

Some of the features of reduction division are depicted in Fig. 209. Obviously the facts depicted here were difficult to discover. Fortunately certain plants and animals have only a few chromosomes in each cell, and their chromosomes differ sufficiently in form that they may be recognized readily and watched during cell division. Here again many detailed facts are known; but for our present purposes it will be sufficient if we clearly understand and apply certain basic facts. In contrast to ordinary cell division, the chromosomes during reduction division do not separate longitudinally but assemble at the center of the spore mother cell in pairs, each paternal chromosome pairing with its homologous maternal chromosome. Later the mates of each pair of chromosomes separate and migrate to opposite poles of the cell, resulting finally in two new cells, each having only one-half as many chromosomes as the spore mother cell.

These two new cells divide completely, as in ordinary cell division, forming a tetrad of spores: a tetrad of microspores if the mother cell was a microsporocyte in the anther; a tetrad of megaspores if the mother cell was a megasporocyte in the ovule.

Chromosomes in the life cycle of a seed plant. Since the microspore is the forerunner of the pollen grain, and since the generative nucleus in the pollen grain is the forerunner of the two sperms in the pollen tube, the chromosome complement of these two sperms is identical, and it is also identical with that of the microspore from which the pollen grain developed. Hence in solving problems in heredity that involve the transmission of chromosomes by sperms, we can predict the chromosome complement of the sperms from that of the microspores.

Similarly a megaspore is the forerunner of an embryo sac; hence the chromosome complement of each of the eight nuclei in the embryo sac is the same, and it is identical with that of the megaspore. The fusion nucleus formed by the union of two of these nuclei has a double set of

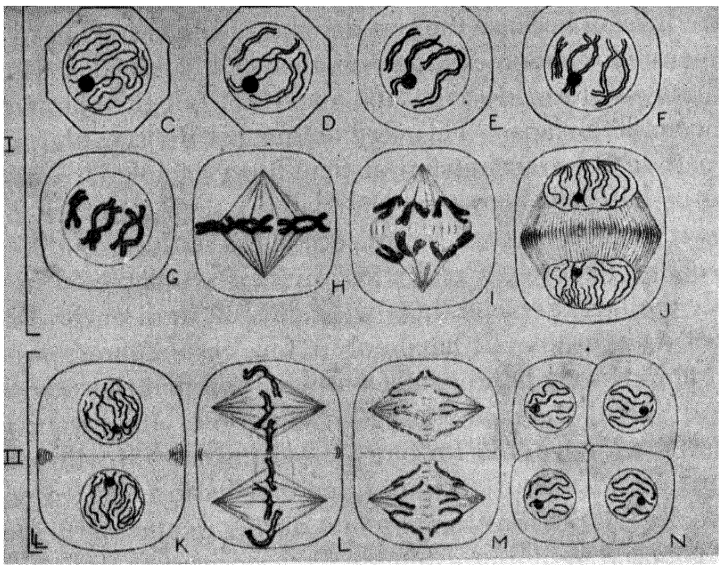

FIG. 209. A diagrammatic representation of chromosome behavior during reduction division and the formation of microspores and megaspores.

I, division of sporocytes (see also Figs. 165 and 166, pages 373 and 375) resulting in cells with a reduced number of chromosomes. C, six chromosomes in a sporocyte, each apparently with one thread. D, pairing of homologous chromosomes. E, the threads, closely coiled, become duplicated. F-G, each chromosome, now with two threads, has become separated from its pairing mate except at places where a thread of each has broken and reciprocally joined. H, paired chromosomes at the equator of spindle. I, the mates of each pair have separated and moved toward opposite poles; each mate has split apart lengthwise except in the spindle attachment region; the threads have become duplicated, resulting in four threads in each chromosome. J, three chromosomes at each pole; nuclear organization under way. Meanwhile the cytoplasm has divided; cell wall formation may or may not follow immediately.

II, K-N, the division of each of the two daughter cells with its chromosomes already partially split apart resembles ordinary cell division in most essentials. The result is a group of four spores. I and II together are often termed meiotic mitosis or meiosis. Drawn by Lois Lampe.

these chromosomes. When it unites with a sperm the resulting triple-fusion nucleus has three sets of chromosomes.

If we represent the number of chromosomes in the megaspore and in each of the eight nuclei of the embryo sac by n, then the number of chromosomes in the fusion nucleus is $2n$; but in the triple-fusion nucleus and in every cell of the endosperm of the seed it is $3n$. Since the fertilized egg has a set of chromosomes from the egg and another from the

sperm, it has the $2n$ number of chromosomes. Starting then with the fertilized egg, vegetative cell division (mitosis) results in an exact duplication of the $2n$ number of chromosomes in every cell of the embryo, root, stem, leaf, sepal, petal, stamen, anther (including microsporocytes), pistil, and ovule (including the megasporocyte). Thus the cycle is completed. Reduction division in the microsporocyte and megasporocyte initiates another cycle.

Unless some irregularity occurs, this chromosome cycle is repeated annually in all plants that reproduce once each season. The $2n$, or diploid, number of chromosomes occurs in all cells of the plant with two exceptions: (1) the microspores, pollen grains, pollen tubes, megaspores, and embryo sacs (previous to nuclear fusions) in all of which the nuclei have the n, or monoploid,[1] number of chromosomes; and (2) the cells of the endosperms of seeds which have the $3n$, or triploid, number of chromosomes.[2] Irregularities in the occurrence of the n and $2n$ number of chromosomes are described in Chapter XXXIX.

The pairing and segregation of chromosomes during reduction division. The pairing and subsequent distribution (separation and segregation) of chromosomes during reduction division are so important in the transmission of hereditary factors in sexual reproduction that they are singled out for further emphasis. The two chromosomes of each pair on the spindle of the cell are often referred to as homologs and as synaptic mates, and the pairing is called synapsis. One of these two chromosomes came from the sperm of the pollen parent, the other from the egg of the ovule parent. They are usually similar in appearance and contain many genes that influence the development of the same kinds of traits such as flower color and height.

These homologous chromosomes are all present in the fertilized egg, in each cell of the vegetative tissues of the plant, and in every microsporocyte and megasporocyte. They become segregated in separate cells following their migration to the opposite poles of the cell spindle during reduction division, and do not get together in the same cell again until fertilization occurs. Hence each microspore and sperm, and each megaspore and egg contains only one of the homologs of each pair.

The pairing of chromosomes is remarkably constant. That is, the same homologs pair during every reduction division in a plant, and in

[1] Also called haploid by many authors.

[2] In those plants in which the fusion nucleus is formed by the union of more than two nuclei, the number of chromosomes is correspondingly increased in it and in the subsequent triple-fusion nucleus and endosperm cells.

each subsequent generation. They seldom change mates. Irregularities in their mating usually result in recognizable mutations. In hybrids resulting from cross-fertilization of remotely related plants, the chromosomes brought together in the same cells may never have occurred together before. Sometimes they fail to mate or to mate regularly during reduction division, and very unusual sorts of progeny may be obtained, or the plant may fail to reproduce at all.

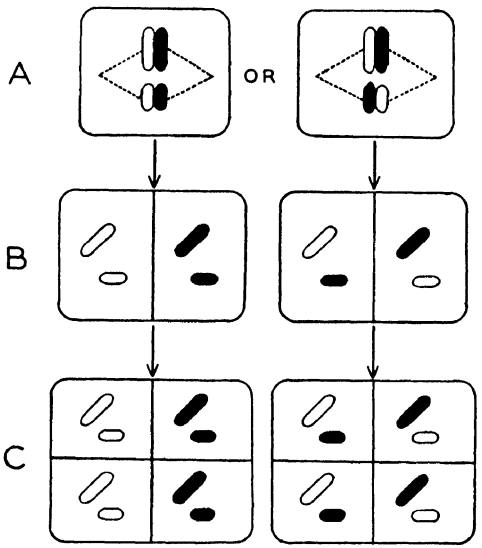

FIG. 210. A diagram of chromosome distribution during the formation of microspores from microsporocytes, or of megaspores from megasporocytes in a plant having two pairs of unlike chromosomes; all breaks disregarded.

The sperms formed in the pollen from this plant have the same chromosome complement as the microspores from which the pollen grains develop. Likewise, the eggs have the same chromosome complement as the megaspores from which the embryo sacs develop.

While the same chromosomes usually pair in all microsporocytes and in all megasporocytes of each generation of a plant, their orientation in the cell with respect to the poles of the spindle is a matter of chance. The two possible chances of orientation when only two pairs of unlike chromosomes are present are illustrated in Fig. 210. Evidently all the paternal chromosomes may go to one pole of the cell and all the maternal chromosomes to the other pole; or some maternal and some paternal chromosomes may go to the same pole.

This chance or random orientation of pairs of unlike chromosomes during reduction division becomes more interesting as the number of pairs of unlike chromosomes that are considered is increased. Thus if the megasporocyte or microsporocyte has three pairs of unlike chromosomes, there are four different ways in which the pairs may become oriented on the spindle, and consequently eight different kinds of megaspores or microspores with respect to chromosome complement may be formed (Fig. 211). On the other hand, if there are only one pair

[8] The term "like chromosomes" is somewhat of a misnomer in that the chromosomes are usually not alike with respect to all genes, but are alike with respect to those genes which are being considered.

of like chromosomes[3] and two pairs of unlike chromosomes, there are only two different ways in which the chromosomes may be oriented, and four different kinds of spores, eggs, or sperms may be formed. If there are two pairs of like chromosomes and only one pair of unlike chromosomes, there is but one possible orientation and two kinds of spores, sperms, or eggs. If there are 24 pairs of unlike chromosomes, there are

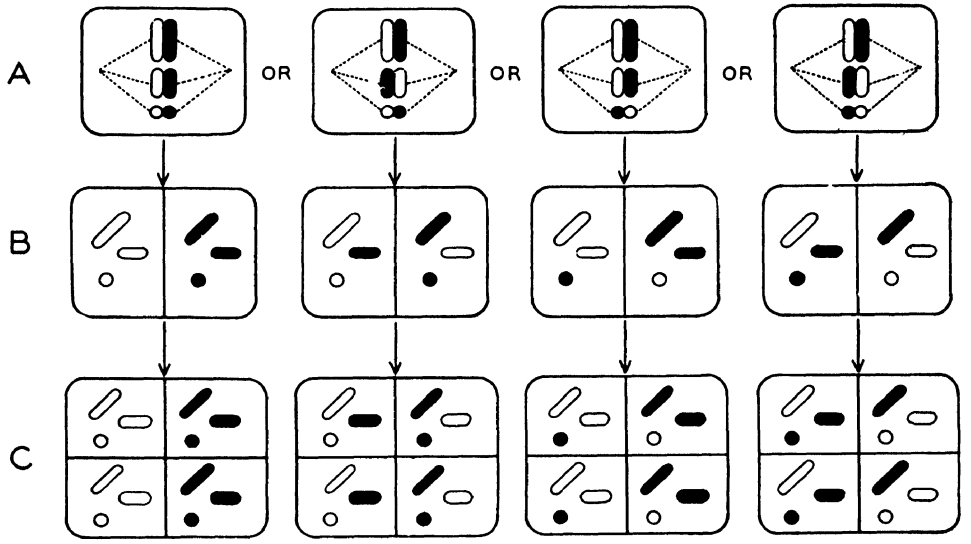

FIG. 211. A diagram of chromosome distribution during the formation of microspores from microsporocytes, or of megaspores from megasporocytes in a plant having three pairs of unlike chromosomes; all breaks disregarded.

8,388,608 different ways in which the chromosomes may become oriented and a possible 16,777,216 different kinds of spores, sperms, or eggs. Large as these numbers are, they are many times smaller than actually occur unless we reduce the problem to one gene in each chromosome. In speaking of whole chromosomes we have oversimplified the diagrams and calculations on these two pages in another way, namely, by disregarding breaks in chromonemata, especially those that occur during reduction division. This is not the time to consider them.

Chromosomes in cross-fertilization. Let us see if the facts we have learned about hereditary factors and chromosomes in relation to the life history of a plant are sufficient to explain the relative numbers of the different kinds of plants obtained by crossing and selfing in snapdragon, as described earlier in this chapter (Fig. 205). One of the eight chromosomes in the gametes of the red-flowered plant contained at least one gene with the potentiality of conditioning the formation of red pigment

in the flower; and its homolog, or synaptic mate, in the gametes of the white-flowered plant lacked this gene or contained a corresponding gene that lacked this particular potentiality. The zygotes formed by cross-fertilization contained both of these chromosomes and the plants that grew from them were pink-flowered.

We may for the present ignore all the other genes in these two chromosomes and also all the other chromosomes in these two kinds of plants, and fix our attention on these two chromosomes through two complete life cycles of snapdragon. This we may do by means of a diagram. We shall use the letter R as a symbol for the gene, or the potentiality, in the chromosome that conditions the formation of red pigment in the flower; and the letter *r* to indicate the potentiality in the homologous chromosome that conditions colorless flowers (Fig. 212).[4]

Owing to the behavior of chromosomes in reduction division, two kinds of sperms and two kinds of eggs with respect to flower color will be formed in the pink-flowered hybrid as shown in the diagram. The plants of the F_2 generation that obtain the chromosome containing the gene represented by R from both sperm and egg have red flowers. If they obtain this chromosome only from the egg or from the sperm and obtain its synaptic mate from the other gamete, the flowers are pink as in the F_1 generation. If the chromosomes from both sperm and egg lack the gene represented by R, the flowers are white. The different kinds of sperms and eggs unite at random. That is, their union is influenced not by the kinds of chromosomes and hereditary potentialities they contain, but by the chance of a sperm coming in contact with the egg.[5] Hence, if a large number of them unite, the progeny (F_2 generation) would consist of plants of which approximately 1/4 are red-flowered, 2/4 pink-flowered, and 1/4 white-flowered. Both the red- and the white-flowered plants, if selfed, would continue to breed true.

In order to check some of the inferences one might draw from this example, it will be necessary to consider another example of cross-fertilization in which one of the chromosomes in the sperm from a tall, smooth plant has a gene (T) that conditions height of plant and another gene (S) that conditions smooth epidermis; while one of the chromosomes in

[4] In preference to letters, small dots may be used to represent the genes in the chromosomes.

[5] In seed plants the kind of sperm that may come in contact with an egg depends upon the kinds of pollen grains that become attached to the pistil, and upon the subsequent growth of pollen tubes.

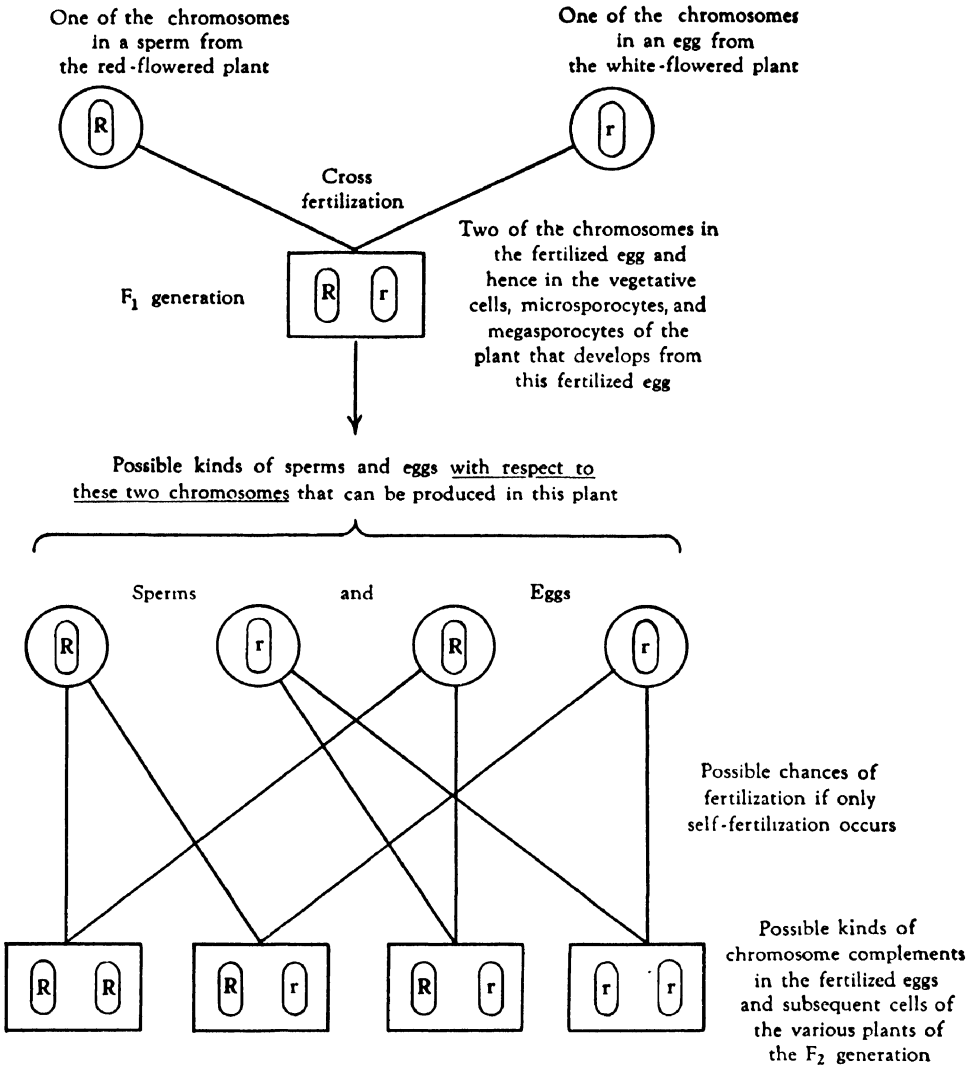

FIG. 212. A diagrammatic representation of the relation of chromosomes and factors of flower color in snapdragon.

the egg from a dwarf hairy plant has a gene (d) that conditions height and another gene (h) that conditions growth of hairs on the epidermis. If no breaks occur in the chromosomes between the genes that condition the development of these characters, we may represent the distribution of these two kinds of chromosomes in the plants of the F_1 and F_2 generations by a diagram (Fig. 213).

All the plants of the F_1 generation were tall and smooth like one of the parents, showing that the genes that condition the development of tall,

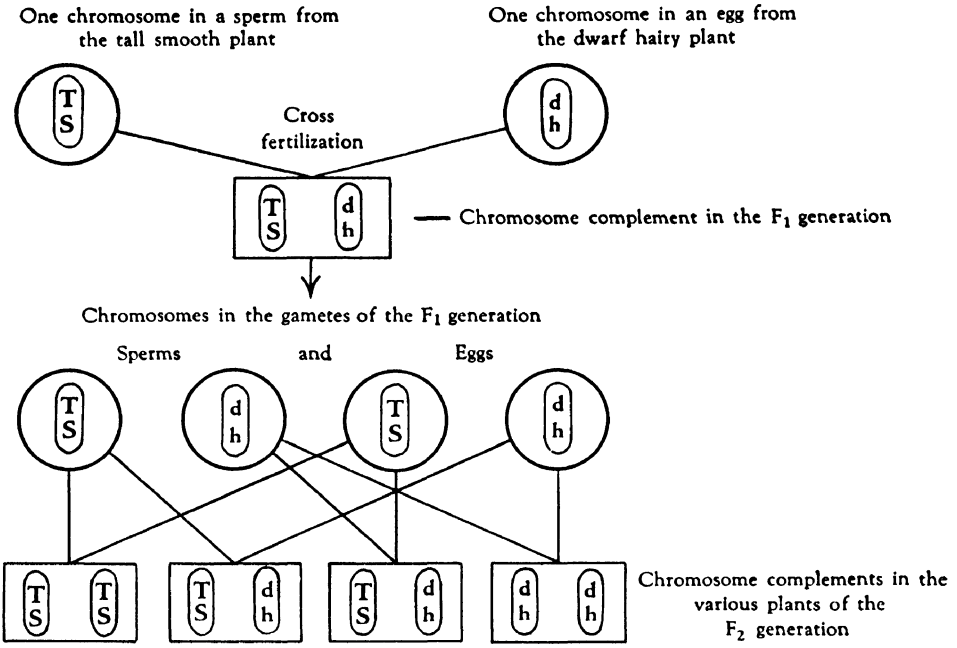

FIG. 213. Hereditary factors in the same chromosome are transmitted together from generation to generation unless a break occurs between them.

smooth plants completely dominated the effects of the genes that condition dwarfness and hairiness.[6] In the F_2 generation 1/4 of the plants were pure-line tall, smooth plants; 2/4 were hybrid tall, smooth plants; and 1/4 were pure-line dwarf, hairy plants. All the genes in one chromosome go with the chromosome. They appear, therefore, to be linked together. In this example all the dominant genes considered are in the same chromosome, but this condition should not be construed to be the general rule. The reader may be interested in solving a similar problem when the genes represented by T and h are in one chromosome, and those represented by d and S are in its synaptic mate.[7]

[6] Because of this fact we followed the convention of capitalizing the symbols for the dominant genes, but not those for the recessive genes. As symbols for the genes conditioning height we might also have chosen T and t, or D and d. These symbols are preferred in technical descriptions, and reference to the two genes as alleles is convenient.

[7] It is important to remember that chromosomes and genes are in the cells of the plant, and that the letters used as symbols for the genes are only on the printed page. Progress in understanding is made only when there is an effort to visualize the chromosomes and genes. Moreover, when each factor in which one is interested is in a different chromosome, as in Fig. 212, the factors may be represented in diagrams as letters without indicating their relation to chromosomes. But when two or more of these factors are in the same chromosome, the fact must be indicated in some way, as suggested in Fig. 213. That is, the letter symbols for the genes in any one chromosome should be kept together in the diagrams unless the chromosome breaks between them.

In the chapter on fat and protein synthesis one other amazing fact about chromosomes and genes was mentioned. Since the properties of chromosomes and genes remain constant through billions of cell divisions in each plant and from generation to generation, their chemical composition and internal organization must also remain constant. They are composed largely of protein substances. Since the chromosomes and genes are duplicated in number every time cells divide, the maintenance of their size must depend upon growth by the synthesis of new chromosomal substances from foods in the cell. The constancy of chromosomal synthesis peculiar to each species of plant and animal, and the constancy of chromosome behavior in cell division constitute an important part of the hereditary mechanism of cells. The persistence of species and races is dependent upon this constancy. A high degree of constancy accompanied by some irregularity results in a gradual evolution of varieties and of species of plants.

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CHAPTER XXXVIII

CROSS-FERTILIZATION AND HYBRID SEGREGATION

From the facts presented in the preceding chapter it must be evident that heredity is definitely related to several basic processes in cell division. The characters we see developing in a plant as it grows are conditioned by the hereditary factors that are transmitted from one generation to the next in the sperms and eggs. Many of these hereditary factors we now know to be the genes located in the different chromosomes. We have seen how the chromosomes with their particular hereditary factors assemble in pairs and then become separated during reduction division, and are still separated in the sperms and eggs; and how they are brought together again in different combinations in the fertilized egg.

As a consequence of this definite pairing, segregation, and recombination of chromosomes during sexual reproduction, the progeny of a hybrid plant are not all alike. When our attention is centered upon only one character, such as height of plant or flower color, the different kinds of hybrid progeny may appear in simple proportions such as 1:2:1, 3:1, and 1:1 as described in the preceding chapter. Since Mendel was the first to discover these definite ratios of the different progeny of hybrids they are often referred to as Mendelian ratios.

Owing to the fact that during reduction division the orientation of the pairs of chromosomes on the spindle of the dividing cell occurs at random, and the subsequent union of the different kinds of sperms and eggs also occurs at random, these ideal mathematical ratios are seldom obtained in experiments. One seldom obtains an exact 1:1 ratio of heads and tails when a penny is tossed several times, or an exact 1:2:1 ratio when two penines are tossed simultaneously a certain number of times. The ideal ratio, 5:5, is occasionally obtained when a penny is tossed 10 times, but sometimes deviations as great as 9:1 or 1:9 occur. As the number of tosses is increased, the magnitude of deviation from the ideal ratio decreases.

In the study of heredity we must recognize the role of chance during reduction division and fertilization. Many other processes in chromo-

somes and heredity, such as the duplication of chromosomes and genes in ordinary cell division and pairing of synaptic mates in reduction division, are much too definite to be regarded as the results of chance.

The basic facts of segregation and recombination of hereditary factors as distinct units in the sperms and eggs, and the consequent ratios of hybrid progeny were discovered by Mendel before chromosomes had been clearly recognized. The subsequent discovery of chromosomes and of their definite behavior, however, furnished a basis of fact that enabled biologists of this century to explain the principles of hybrid segregation formulated by Mendel, and to extend and clarify our knowledge of hybridization. It was difficult, for instance, to understand why certain factors seemed to be "linked together" until it was discovered that they were in the same chromosome, and would be present wherever that particular chromosome was present. Similarly, other techniques necessary for devising critical experiments and evaluating inferences pertaining to the results were discovered from time to time. Thus through a slow accumulation of facts and the discovery of their dependent relations, the subject of hybridization has been removed from the realm of mystery and speculation and has become an understandable science.

Mendel's experiments. Mendel investigated the results of cross-fertilization in several kinds of plants, and also in mice and bees. From several seedsmen he obtained seeds of more than thirty varieties of peas, mostly of one species (*Pisum sativum*), and planted them in a small garden at his monastery. He noted that certain distinctive characters of each variety remained constant from year to year. Since some of these characters were easy to detect, he decided that peas would be admirable plants with which to test experimentally the various ideas about hybrids that were current at the time. His success in discovering fundamental laws of heredity when all others had failed depended in part on his choice of suitable experimental material, and in part on his persistence in keeping exact records of all the progeny of his plants through a series of several generations.

To appreciate Mendel's experiments one should imagine him at work in his garden among peas some of which were slightly taller than he was; others were dwarfs less than knee-high. Some were white flowered; others were violet-red flowered. On some plants the flowers and pods developed only in terminal clusters at the top of the stem; on others they appeared in the axils of the leaves along the stem. The pods on some plants were yellow; on others they were green. Some pods were

inflated; others were constricted between the seeds. The seeds within the pods were either all green or all yellow, depending upon the pigments in the cotyledons of the embryo. In some pods the seeds were rough; in others they were smooth.

Peas are naturally close-pollinated, and unless they have been artificially cross-pollinated they may be considered pure-line plants with respect to all of their characters. After studying his plants carefully for two years, Mendel became assured that each of the fourteen varieties named above bred true to type, but he continued to test them for purity throughout the period of experimentation.

By means of cross-pollination Mendel began to obtain hybrids among these plants. We can imagine him with a pair of forceps removing the young anthers from some of the flowers, placing pollen upon the stigmas by hand, and carefully labeling each one with a description of the ovule and pollen parent. Later he collected the ripened pods and seeds, kept them separate, and planted the seeds the following season.

During this second season he kept a record of the appearance of all the hybrid plants, i.e., the F_1 generation. No matter which way the crosses were made between any two of the pure-line plants described above, the influence of certain hereditary factors was found to dominate the influence of others completely. In these peas the factors that severally conditioned the development of tall plants, red flowers, axillary flowers, green pods, inflated pods, smooth seeds, and yellow seeds completely dominated the effect of the factors that conditioned the contrasting characters of dwarfness, white flowers, terminal flowers, yellow pods, constricted pods, rough seeds, and green seeds. Mendel, however, was not the first person to note the complete dominance of some factors in hybrids, and the lack of complete dominance of others.

When the F_1 plants bloomed during this second season, Mendel allowed them to self-pollinate naturally. Again he kept careful records, and planted the seeds the following season. From the embryos of these seeds the mature plants of the F_2 generation developed. During this third season he obtained an accurate record of more than 5000 progeny of the F_1 generation. He continued the experiments for eight years, testing and retesting his data and conclusions. Aided by the young men at the monastery he obtained data about many thousands of progeny.

Mendel had several reasons for choosing the garden pea for his experiments. The plants are easily cultivated, they have a short period of

growth, all types of hybrids are fertile, the plants do not have to be prevented from cross-pollinating, the characters chosen are easily recognizable and may be combined and separated in different plants as if each depended upon a single hereditary factor. Because of this simplicity some phases of the experiment were relatively easy and the results were not difficult to analyze. For the same reason most students in elementary botany learn something about Mendel and his hybrid peas. They also learn something about Hugo de Vries and mutation, but very little about his evening primroses, for the heredity of primroses is peculiarly complex and not the sort of thing one enjoys during his first approach to the study of heredity.

Some explanations. We now know that the garden pea has *seven pairs* of chromosomes. Consequently each sperm and egg has but seven chromosomes, while each cell of the vegetative body of the plant has fourteen chromosomes. The genes that specifically condition the fourteen characters listed earlier occur separately in these fourteen chromosomes. Thus they appear to be unit factors, and the characters they condition appear to be independent unit characters. In one chromosome is the factor of tallness; in its homolog, or synaptic mate, is the factor of dwarfness. During reduction division these two chromosomes become separated. Consequently each sperm or egg of a hybrid pea will have but one of these two height factors—a fact often referred to as the *purity of gametes*, or as Mendel's law of the segregation of hereditary factors. Half of the total number of microspores and resultant sperms will have one of these height factors, and half will have the other height factor. A similar distribution of height factors also occurs in the megaspores and in the resultant eggs and fusion nuclei in the embryo sac.

Similarly in another pair of homologous chromosomes are the factors that condition flower color; in another pair are the factors that condition seed form, and so on for each of the seven pairs of homologous chromosomes and seven pairs of contrasting factors. Furthermore, one factor of each pair of contrasting factors completely dominates the influence of the other.

Evidently, if either height of plant, flower color, flower position, seed form, seed color, pod form, or pod color is considered separately without regard to the other characters, the results of hybridization in the garden pea are as simple and as easy to decipher as were the two examples described in the previous chapter.

Anyone who is familiar with the facts discussed in the section on the pairing and segregation of chromosomes in the previous chapter can use the foregoing facts about peas and predict what Mendel must have obtained in each of his experiments. Before going further, the reader will find it profitable to predict what Mendel must have obtained in the F_1, F_2, and F_3 generations after crossing (1) a pure-line tall plant with a pure-line dwarf plant, (2) a pure-line red-flowered plant with a pure-line white-flowered plant, (3) a pure-line yellow-seeded plant with a pure-line green-seeded plant; and so on for each of the other pairs of contrasting factors.

Such predictions may be shown diagrammatically by means of conventional symbols for the different hereditary factors as described in the previous chapter. Any kind of symbols may be chosen for the factors if one indicates what factors they represent.[1] It is important to remember that these symbols indicate only the genes, or hereditary factors, in the chromosomes. Words should always be used to describe the visible characters which develop as a result of the presence of these genes. Hence the symbols TT and Td each represent a pair of genes either of which, when present in the cells of a plant, influences its growth in height. They represent the hereditary make-up, or *genotype*, of the plants with respect to height. If these plants are peas, both of them will be tall plants.

[1] For the hereditary factors in the garden pea discussed in this chapter we have chosen the following letter symbols. The dominant factors are indicated by capital letters.

Visible Characters in the Plant	Symbols Used for Hereditary Factors in the Cells	Visible Characters in the Plant	Symbols Used for Hereditary Factors in the Cells
Height of plant	T and d	Form of pods	I and c
Tall	TT and Td	Inflated	II and Ic
Dwarf	dd	Constricted	cc
Color of flowers	R and w	Surface of seeds	S and r
Red	RR and Rw	Smooth	SS and Sr
White	ww	Rough	rr
Position of flowers	A and t	Color of seeds	Y and g
Axillary	AA and At	Yellow	YY and Yg
Terminal	tt	Green	gg
Color of pods	G and y		
Green	GG and Gy		
Yellow	yy		

The visible character that develops is referred to as the *phenotype.* For example, if 400 progeny of a hybrid plant of genotype Td are found to differ from each other in the proportion of 100TT:200Td:100dd, the genotypic ratio is 1:2:1; but the phenotypic ratio—what one sees in the field or garden—is 3:1. These ratios are often called monohybrid ratios because they represent the progeny with respect to a single character.

All the plants that have the factors TT are pure-line tall plants; the eggs and sperms formed in the pollen and embryo sacs in these plants each contain the factor T. If only self-fertilization occurs, each individual in the progeny will have the factors TT, since one height factor is obtained from the egg and the other from the sperm. Similarly, the sperms and eggs formed in the pure-line dwarf plants of the genotype dd each contain the factor d, and all the progeny obtained by selfing have the factors dd. When plants having the factors TT and dd are crossed, each individual in the progeny has the factors Td, because the fertilized egg from which it develops has the factor T from one gamete and the factor d from the other one.

For convenience in representing the proportions of the different kinds of progeny of hybrids, the checkerboard diagram is often used. If the height factors in a plant are represented by Td, then half of the sperms will have the factor T, the other half will have the factor d. Half of the eggs also will have the factor T, the others will have the factor d. Similarly, in a plant having the factors of flower color, Rw, half of the sperms will have the factor R; the other half the factor w. Half of the eggs will have the factor R; the other half will have the factor w. Now if we indicate the factors in the eggs on one side of a checkerboard diagram and the factors in the sperms along a side at right angles, we can indicate quickly (1) the possible chances of union of the different kinds of sperms and eggs, and (2) the proportion of the different kinds of progeny.

	T	d
T	TT	Td
d	Td	dd

Genotypes of F_2 generation

	R	w
R	RR	Rw
w	Rw	ww

Genotypes of F_2 generation

Within the checkerboard diagrams are represented the genotypes of all the different kinds of progeny of each of the hybrid parents having the genotypes Td and Rw, and also the ideal proportion in which they may be expected to occur, especially if the total number of progeny in

the field is very large. In predicting the F_3 generation no new problems arise.[2]

Two characters considered simultaneously. If we wish to understand the inheritance of factors when two characters are considered simultaneously, we have only to apply the same principles previously used for a single character and the facts we know about the behavior of chromosomes during reduction division. The ratios that result from a cross when two independent characters are considered are called dihybrid ratios.

Suppose we cross a plant whose genotype is TTRR with a plant whose genotype is ddww. All individuals of the F_1 hybrids will have the genotype TdRw, for they will have obtained one height factor and one flower-color factor from each of the two pure-line parents. Since the factors T and d are in separate homologous chromosomes (one from the pollen parent, the other from the ovule parent) and the factors R and w are likewise in another pair of homologous chromosomes, the hybrid with the genotype TdRw can have four kinds of sperms and four kinds of eggs with respect to height and flower color (Fig. 210). We may represent the factors in these sperms and eggs as follows: TR, Tw, dR, and dw.[3] If the homologous chromosomes that pair during reduction division always separate and migrate to opposite poles of the spindle, then the factors T and d would not occur in the same sperm or in the same egg;

[2] Mendel, of course, seldom obtained ideal ratios of hybrid progeny in the F_2 and F_3 generations. Some phenotypic ratios actually obtained by him from the F_1 hybrids are given below.

Number of Parents. All were F_1 Hybrids. The genotype is indicated in parentheses.	Number of Progeny of the F_1 Hybrids. The F_2 generation.
1064 tall plants (Td)	787 tall and 277 dwarf plants. 2.84:1.
929 red-flowered plants (Rw)	705 red- and 222 white-flowered plants. 3.15:1.
258 plants from yellow seeds (Yg)	6002 yellow and 2001 green seeds. 3.01:1.
253 plants from smooth seeds (Ss)	5474 smooth and 1850 rough seeds. 2.96:1.
1181 plants with inflated pods (Ic)	882 plants with inflated pods and 299 plants with constricted pods. 2.95:1.
580 plants with green pods (Gy)	428 plants with green pods and 152 plants with yellow pods. 2.82:1.
858 plants with axillary flowers (At)	657 plants with axillary flowers and 201 plants with terminal flowers. 3.14:1.

Hereditary factors that conditioned red flowers were "linked" with those that conditioned grayish-brown seed coats, and those that conditioned white flowers and white seed coats were "linked."

[3] See footnote, p. 456.

neither would the factors R and w. We may now represent all these facts briefly, including also the union of the different eggs and sperms, and the resultant genotypes of the progeny.

Genotypes of Parents	TTRR	×	ddww
Factors in Gametes	TR	↓	dw
Genotype of All F_1 Hybrids	TdRw		
Factors in Gametes of Hybrids	TR, Tw, dR, dw (Factors in Sperms)		TR, Tw, dR, dw (Factors in Eggs)

(Selfing)

	TR	Tw	dR	dw
TR	TTRR	TTRw	TdRR	TdRw
Tw	TTRw	TTww	TdRw	Tdww
dR	TdRR	TdRw	ddRR	ddRw
dw	TdRw	Tdww	ddRw	ddww

Genotypes of F_2 generation

Within the diagram are represented the genotypes of all the different kinds of progeny with respect to height and flower color that may be obtained from the hybrid pea having the genotype TdRw, and also the ideal proportion in which they may be expected to occur in the field if the total number of plants is very large. Note that many of the plants that would appear to be similar in the field differ from each other in their hereditary constitution.

By using the same principles, one may predict the probable progeny of crosses between other pure lines of peas, such as (TTYY) × (ddgg) and (TTgg) × (ddYY). Mendel experimentally proved that each of the fourteen factors which he studied in peas segregated in the same manner.

Three characters considered simultaneously. No new problems arise when three characters, such as Mendel studied in peas, are considered simultaneously. Thus F_1 hybrids of the pure lines that have the genotypes TTRRgg and ddwwYY would all have the factors TdRwYg, and considering these three characters alone there would be eight different

kinds of sperms and eggs. One merely needs to visualize the chances of orientation of the three pairs of chromosomes (Fig. 211) and their contained factors during the process of reduction division to see that the factors in the sperms and eggs of this hybrid would be distributed as follows: TRY, TRg, TwY, dRY, Twg, dRg, dwY, and dwg. In this case the checkerboard diagram is very large.

Other problems with hybrids. It is, of course, possible to consider two or more characters simultaneously even though the parents are pure lines for some of them. For example, if the genotype of the parent were TTRwgg the checkerboard would be very small, for there would be only two different kinds of sperms and eggs, with respect to these particular hereditary factors. The paired chromosomes containing height factors contain the same height factor, and the paired chromosomes containing seed-color factors have the same seed-color factor. But the paired chromosomes containing flower-color factors have unlike flower-color factors, and these are the only ones that differ in the sperms and eggs.

What kind of progeny would be obtained by crossing a plant of genotype TTRw with a plant of genotype Tdww? Since it does not matter which way the cross is made, one merely decides for convenience that one of these plants is the pollen parent; the other one the ovule parent. If we decide that the plant of genotype TTRw is the pollen parent, the sperms will have the factors TR and Tw, and the eggs from the ovule parent will have the factors Tw and dw. Hence the progeny have the genotypes TTRw, TTww, TdRw, and Tdww, as shown in the diagram:

	TR	Tw
Tw	TTRw	TTww
dw	TdRw	Tdww

To predict the proportion of the resultant kinds of progeny after either selfing or crossing, one merely applies the foregoing principles to decide (1) what kinds of sperms and eggs may be formed in the parents, and (2) the possible chances of fertilization. It will be excellent practice for the student similarly to predict the nature of the progeny that would be obtained by selfing any one, or by crossing any two, of the types of plants represented in the preceding diagrams.

Interpreting the progeny represented by the checkerboard diagrams. There is no value in being able to construct checkerboard diagrams that represent the progeny of a plant, or of two kinds of plants, unless one can read them and visualize what they represent, after they are constructed. Since they are made to be read, one should always follow certain accepted conventions in making them, so that he may see almost at a glance both the phenotypic and the genotypic ratios of the progeny.

From what we know of the relation of phenotypes to genotypes we can predict from the diagrams on page 463 that in one field about 3/4 of the plants are tall and 1/4 are dwarf; in the other field 3/4 are red-flowered and 1/4 are white-flowered. Similarly from data in the diagram on page 465 we can predict the relative percentage of tall and dwarf plants in the field, and also of those that are red- and white-flowered. From this same diagram one may also learn that 9/16 of the plants in the field are tall red-flowered, 3/16 are tall white-flowered, 3/16 are dwarf red-flowered, and 1/16 are dwarf white-flowered. All these ratios refer to phenotypes, not to genotypes. It should always be remembered that the checkerboard diagram represents the proportion of different genotypes of plants in a field and not the actual number of plants in the field, and these diagrams should be read accordingly.

Much more can be learned by looking at the genotypic ratios, and also the genotypes of particular individuals in the progeny. For instance in the diagram of the progeny of the plant of genotype Td, it is obvious that 1/3 of the tall plants in the garden are pure tall plants, and 2/3 of them are hybrid tall plants; also that all the dwarf plants are pure dwarf plants. The term *homozygous* is often used to refer to any character for which the plant is a pure line, that is, contains a pair of like factors, of which one factor was obtained from the sperm and the other from the egg. The plants of genotypes TT and dd are homozygous with respect to height, while the plants of genotype Td are all *heterozygous* with respect to height. A completely pure-line plant would be homozygous with respect to all its factors.

In the diagram of the progeny of the plant of genotype TdRw, 1/4 of the plants are homozygous with respect to both height and flower color; another 1/4 are heterozygous with respect to both height and flower color. Still another 1/4 are homozygous with respect to height but heterozygous with respect to flower color, while the remaining 1/4 are just the opposite.

In the field one can see only four kinds of plants: tall red-flowered,

tall white-flowered, dwarf red-flowered, and dwarf white-flowered. But from the diagram we may learn that of the tall red-flowered plants in the field only 1/9 are pure tall red-flowered, 4/9 are hybrid tall red-flowered, 2/9 are homozygous with respect to height and heterozygous with respect to flower color, and the remaining 2/9 are just the converse of the preceding. Of the tall white-flowered plants, 1/3 are pure tall white-flowered. One third of the dwarf red-flowered plants are homozygous with respect to height and flower color. All the dwarf white-flowered plants in the field are pure dwarf white-flowered.

Ascertaining the genotype of parents. If one were told that a dwarf white-flowered pea plant was crossed with a tall red-flowered one, and that all the progeny were tall but some of them were white-flowered, he should be able to state at once the genotypes of the two parents.

Disregarding the progeny for a moment, we know that the genotype of the dwarf white-flowered parent was ddww, and that the tall red-flowered parent contained the factors T and R. Since all the progeny are tall, we are sure that the other height factor in it was also T. Since some of the progeny are white-flowered, we can be sure that the other flower-color factor was not R, and must have been w. Hence the genotypes of the two parents were ddww and TTRw.

Inbreeding. Attention has already been called to the fact that continued inbreeding of hybrids and their progeny results in a number of inbred lines that are homozygous with respect to many of their hereditary factors. A hint of this fact is evident in the checkerboard diagram of the progeny of the plant of genotype TdRw, since 1/4 of the plants of the F_2 generation are homozygous with respect to height and flower color. A much better idea of the effect of inbreeding may be obtained by working out a diagram for several successive generations, beginning with three characters in a hybrid. Of course, the making of these diagrams becomes increasingly tedious as the number of characters represented increases. If all the fourteen characters discussed in this chapter were considered, the number of different eggs and sperms would be equal to the seventh power of 2, or 128.

Obviously, inbreeding may be undesirable when it increases the homozygosity of undesirable factors, or when it decreases the number of desirable factors one wishes to have in one plant. Following inbreeding, these desirable factors may be brought into one plant by crossing inbred lines from which the undesirable factors have been eliminated. On the other hand, inbred lines that are homozygous for several desired

factors may be very important as economic plants. Many of our best varieties of close pollinated plants are inbred lines, namely, wheat, oats, barley, peas, and beans.

Inbreeding without selection will not entirely eliminate hybrids. This fact may be discovered by starting with a plant of genotype Td and noting the percentage of pure-line plants and hybrids in each successive generation obtained by selfing all individuals. In the first generation the hybrids constitute 1/2 of the progeny, 1/4 of the next, 1/8 in the next, and so on. In the nth generation the proportion of hybrids to pure lines may be represented by the equation $(2^n - 1)$ TT : 2Td : $(2^n - 1)$ dd. Thus in the 8th generation it would be 255TT : 2Td : 255dd.

Hybrid endosperms. Inheritance in the endosperm is a unique feature limited to certain seed plants because the endosperm is a unique tissue that develops from the triple-fusion nucleus only in the seeds of some plants (Chapter XXXIII). Hybrid characters in the endosperm are always evident the same season that cross-fertilization occurs, for the endosperm grows to maturity during that season. We have already seen that hybrid characters of the embryo, such as the green and yellow cotyledons of pea seeds, are also evident the same season that cross-

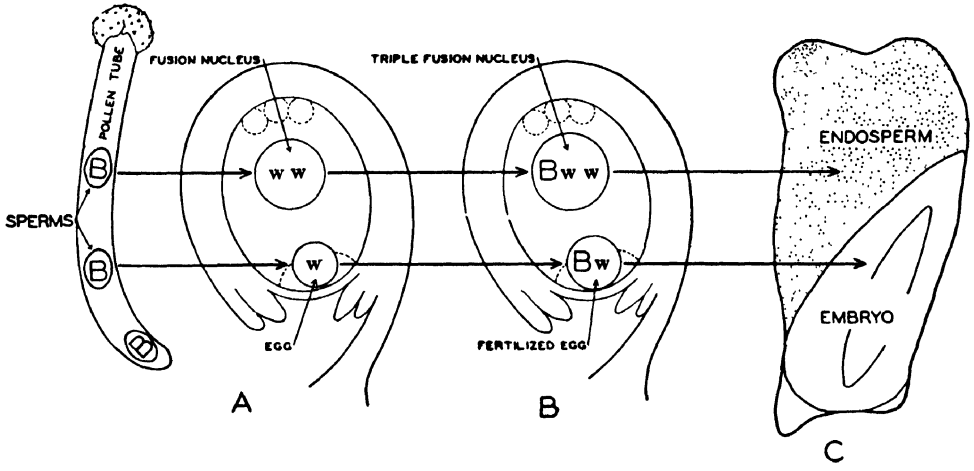

FIG. 214. A diagram of the derivation of the gene complement of the triple fusion nucleus and endosperm cells resulting in xenia.

fertilization occurs; but they are dependent upon factors inherited through the fertilized egg, whereas endosperm characters are dependent upon factors inherited through the triple-fusion nucleus (Fig. 214).

To understand hybridization in endosperms it is necessary only to remember (1) that the two sperms in the pollen tube have the same

complement of chromosomes and the same hereditary factors, and (2) that the egg and the fusion nucleus in the embryo sac have the same complement of chromosomes and hereditary factors, except that the fusion nucleus has a double set of these chromosomes. With this one exception, the fertilized egg and triple-fusion nucleus in the same embryo sac have the same chromosome complement.

Some of the factors in these chromosomes specifically affect the processes in the endosperms, such as the formation of starch, dextrin, protein, and pigment. It is often observed that when brown, blue, or yellow-grained corn is growing near white-grained corn, a few colored grains of corn appear on the ears of white corn, but white grains do not appear on the ears of colored corn in the same season (Fig. 215). Similarly,

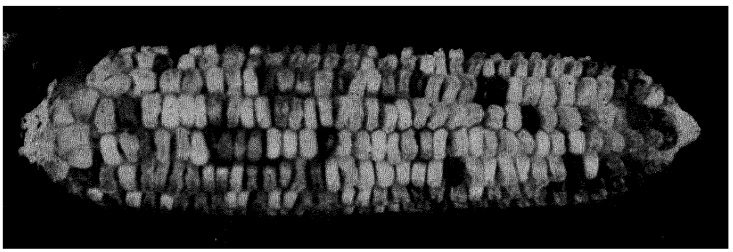

FIG. 215. Ear of Stowell's Evergreen sweet corn from an open pollinated plant. The development of the endosperm of some of the grains was influenced by sperms from waxy corn, and black Mexican sweet corn growing nearby. Photo by G. W. Blaydes.

grains of starchy corn appear on the ears of sweet corn, and grains of field corn appear on the ears of pop corn.

Long before the processes of fertilization and triple fusion were known in plants, this phenomenon was called xenia, a term that means hospitality. It was thought that the white corn, sweet corn, and pop corn were being hospitable to the other kinds of corn—unreciprocated hospitality. The Indians who wanted to keep their ceremonial corn "pure" looked upon it as contamination. We now know that it is the result of cross-pollination, triple fusion, and the dominance of certain hereditary factors in the endosperm, as indicated in Fig. 214. The pollen grain came from a variety of blue-grained corn; the ovule grew in a variety of white-grained corn.

Xenia is the evident result of the influence of the pollen parent on the endosperm of the ovule parent the same season that cross-pollina-

tion occurs. Hence, it will occur only in seeds in which an endosperm develops from the triple-fusion nucleus. Furthermore, the sperm must contain a dominant endosperm factor, and the fusion nucleus the contrasting recessive endosperm factor.

If seed "C" in Fig. 214 is planted and only self-fertilization occurs, in the mature plant that develops from the embryo there will be two kinds of pollen grains, two kinds of embryo sacs, four kinds of triple-fusion nuclei, and an ear of corn on which 3/4 of the grains will be blue and 1/4 will be white, as shown in Fig. 216. See also Fig. 217.

The fact that the ovule in a grain of corn is enclosed in the closely

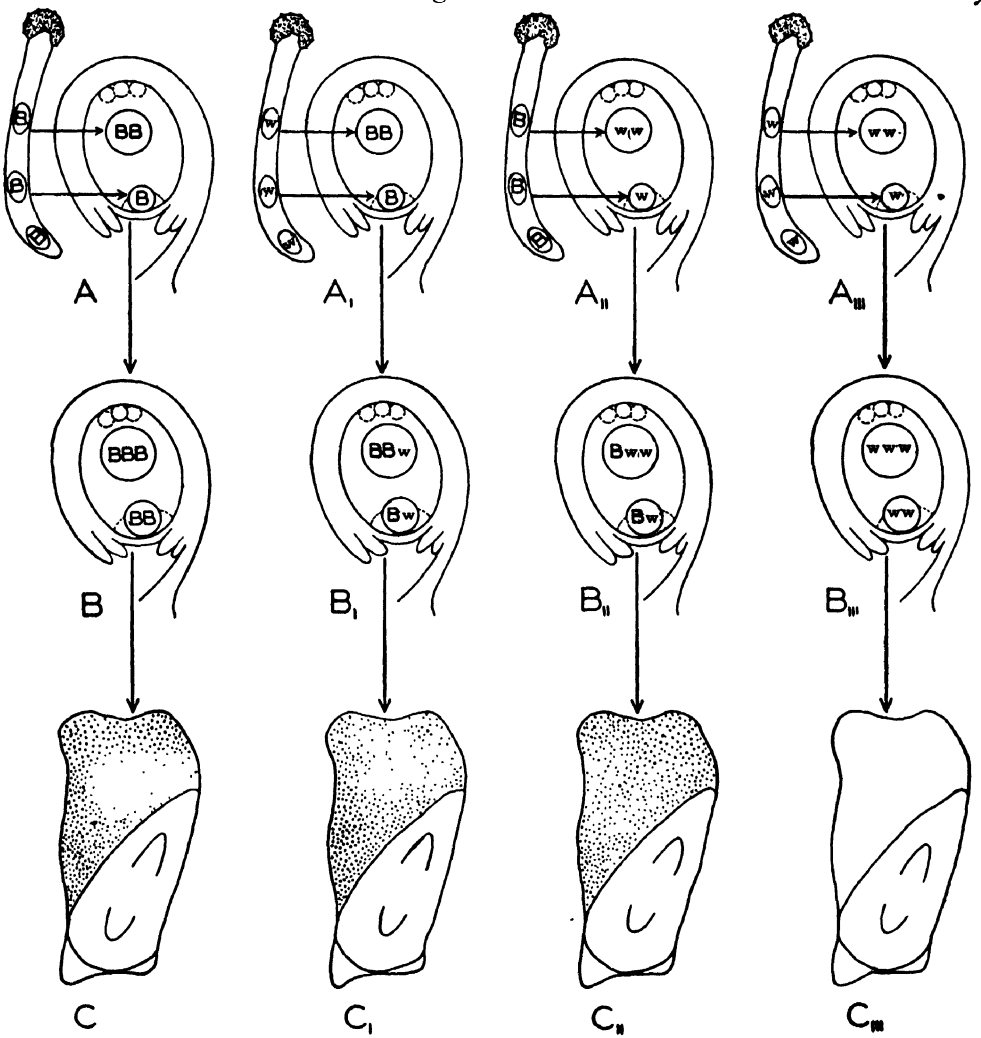

FIG. 216. Diagram illustrating the results of inheritance in the endosperm following selfing of a hybrid plant from a seed like seed C in Fig. 214.

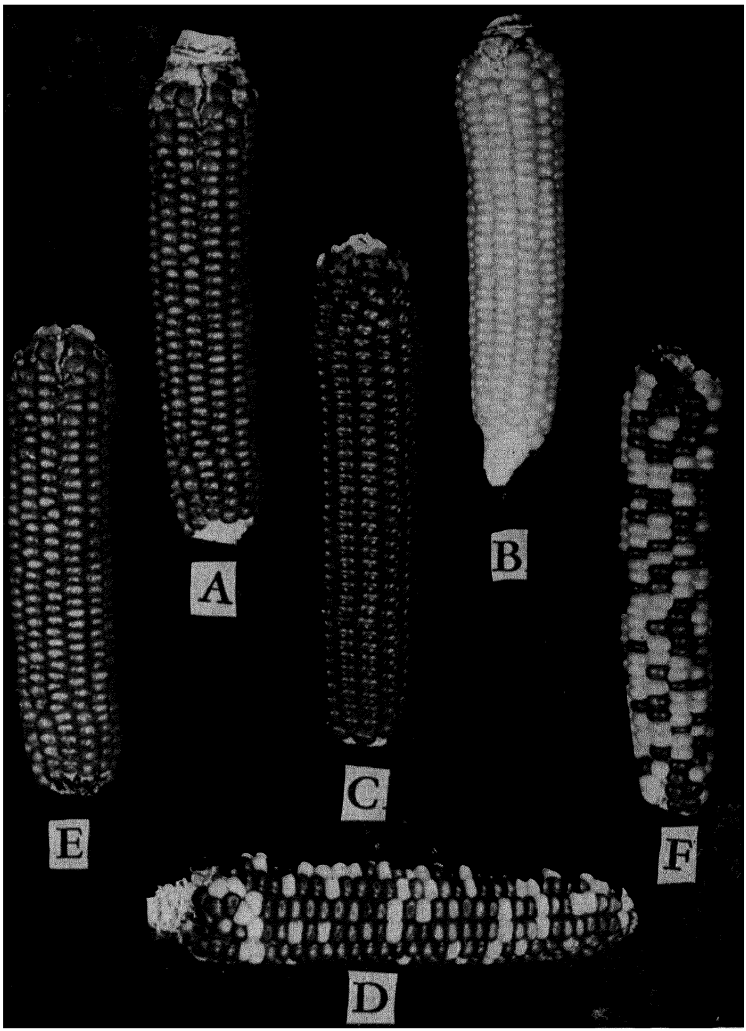

FIG. 217. Photograph of a demonstration. A and B represent ears of corn from two pure lines of plants one of which has grains with pigmented endosperms. C represents the grains on ears of corn when plants from A and B are crossed. D represents ears of corn on plants from C when selfed the following season—a 3 : 1 ratio. E represents ears of corn obtained when plants from C and B are crossed. F represents ears of corn obtained when plants from C and B are crossed—a 1 : 1 ratio. Endosperms grow to maturity the same season pollination occurs. The intensity of color of these pigmented endosperms was altered by the environment in which the individual plants grew and by exposure to light after the ears were harvested. Photos from G. W. Blaydes.

adhering ovulary is not shown in the diagram. Some of the colors in grains of corn are due to pigments in the grain coats. Xenia, however, is strictly an endosperm phenomenon.

We have described here a simple example of hybrid endosperms. Other examples, some of which are complicated because of partial dominance, linkage, crossing over, or multiple factors, have been analyzed and explained in the literature.

Other Problems. With one exception (page 456) the foregoing discussion of chromosomes and heredity has been limited to simple cases in which the several genes considered were in different chromosomes. As we have already seen, this limitation enables us to consider certain general principles of heredity in relation to the longitudinal duplication of chromosomes without being much concerned about crosswise breaks that might occur.

These breaks must be considered, however, if we want to understand certain visible differences in heredity. This is particularly true if our attention is centered on the distribution of two or more genes located in the same chromosome. You will learn presently that the chart on page 456 represents only one of two probable outcomes.

During ordinary cell division in the growing regions of plants the genes in each duplicated chromonema usually remain together as if they were permanently linked. One would of course expect them to remain together as long as the chromonema remains intact, since they constitute a part of its physico-chemical structure. If a break occurs, each fragment of chromonema contains the portion of linked genes it had previous to the break. These occasional breaks in chromonemata in vegetative cells are discussed in Chapter XXXIX.

But in reduction division, breaks in chromonemata or chromatids are of common occurrence, particularly when the chromonemata of two synaptic mates are coiled about each other. Localized stresses in the coils are thought to be the causes of the breaks. The chief point of interest for us here is the reciprocal rejoining of breaks, for it results in an exchange of corresponding segments between a chromonema of one synaptic mate and a chromonema of the other mate. Each of these two chromonemata will then consist of one or more segments of a paternal and maternal chromonema. They continue this way as chromosomes in the dyads, spores, gametes, and in the cells of the following generation of plants. This exchange of corresponding parts of homologous chromosomes is known as *crossing over,* and usually occurs at some place, or places, in

each pair of chromosomes during each reduction division in every generation.

The end result of a single crossover is easy enough to visualize, but the story of the events that lead to it seems complicated without visual aid. Let us turn to F in Fig. 209. Represented here are three pairs of synaptic mates. The chromonemata have become duplicated in each mate, and the mates have separated except where they are held together at the regions (chiasmata) of crossing over. Note that each crossover is between only one chromonema of the paternal and only one of the maternal chromosome, and that it occurs at the same level in the two chromosomes. Since the chromosomes pair gene to corresponding gene (or allele to allele), crossing over results in an exchange of groups of corresponding genes.

For an example of the effect that crossing over would have on Mendelian ratios let us turn again to the chart on page 456. If a crossover were to occur occasionally at some point between the locations of genes (T) and (S), and between genes (d) and (h), some of the gametes of the F_1 generation would have chromosomes containing genes (T) and (h), or genes (d) and (S). Thus instead of the two kinds of gametes represented in the chart there would be four. What differences would there be in the progeny?

Since a crossover may occur in any one of many places along the two threads, the probable number of arrangements of genes in a pair of synaptic mates from generation to generation is amazing. The general form of the mates, however, continues to be recognizable because the exchanged segments are equal.

An exchange of segments between non-homologous chromosomes is referred to as reciprocal translocation. Both translocations and crossovers may occur between genes any place along the chromosome. They have been studied with interest as a means of discovering the relative locations of the genes within a chromosome. The transferred segments of a chromosome may contain genes whose presence can be detected by the appearance or absence of certain characters in the plant. By comparing the effects of different pieces of the same chromosome in different individual plants, the relative positions of the different genes in a chromosome may be closely estimated.

The discussion of the numerous variations that may occur in crossing over and the other complicated processes of Mendelian inheritance lies beyond the scope of this book.

CHAPTER XXXIX

MUTATIONS

We have been emphasizing the individuality, stability, and regularity of chromosomes and the smaller hereditary units of matter in the protoplasm, particularly the genes. It is the stability and orderly behavior of these hereditary units of matter that maintain the constancy of the different kinds of plants during their lifetime, and during succeeding generations. This constancy in organization and processes is, however, only relative. Changes in both chromosomes and genes are known to occur, and departures from the orderly splitting, pairing, and migration of chromosomes have been observed many times. When these changes in the hereditary units of matter in the cell are relatively stable, they are initial steps in the evolution of new kinds of plants. Their effects may become evident in the appearance of new characters or in the modification of preexisting ones, and in the consequent formation of new varieties of plants.

We have already learned that all that is inherited is within the protoplasm of the sperm and the egg, and hence in the resultant fertilized egg. The hereditary units of matter in these cells, and the physiological processes they condition are the precursors of all the characters we see in the growing plant. The inherent differences in plants we see about us, therefore, are dependent upon the composition and arrangement of the microscopic and submicroscopic units of matter of which protoplasm is composed. Likewise the heritable changes that occur in the visible characters, through time, must be dependent upon certain alterations in these small heritable units of matter. In them may be found the origin of all heritable differences and of all the initial steps of evolution. If we wish to understand the gross phenomena of living organisms we must first try to understand some of the microscopic and submicroscopic structures and processes of which these gross features are the consequences.

A change in a single gene may result in a very striking change in the development of some visible character. In such cases the relation of the character to the gene is easily detected by the study of Mendelian ratios

as described in the preceding chapter. Among the characters that appear to be results of changes in single genes are red-flowered snapdragons and fuzzless peaches, or nectarines. The relationship is not so easily detected when the development of the character depends specifically upon the interaction of several genes.

We should not be misled into attributing the development of a particular character solely to the influence of a single gene, even though it appears, or fails to appear, when the particular gene is present or absent. The total development of a plant, or of any part of it, is dependent upon the collective influences of numerous genes. When a plant having all of its genes is compared with a plant in which one gene is lacking, we may be able to detect one or more effects of this one gene on the development of the plant. The number of different kinds of influences a particular gene may have has never been fully discovered.

Thus far we have emphasized the orderliness of the numerous processes that occur every time cells divide, and when plants reproduce sexually. It is time now to turn our attention to some of the irregularities, or aberrations, that sometimes occur, and to try to visualize their relation to the changes that are occurring in plants today and have been occurring in plants for a billion years or more.

Mutations in the vegetative cells of plants. We have seen that the exact duplication of the hereditary mechanism when a cell divides in the growing regions of the vegetative body of a plant depends upon an exact duplication of all its chromosomes and genes, and also upon a very definite distribution and assemblage of these daughter chromosomes in the nuclei of the two new cells.

When we are able to visualize the usual orderly procedure of events in cell division, we can begin to appreciate some of the irregularities which occur occasionally, and with a little scientific imagination we can even predict what some of them will be. For example, the chromosomes may divide without further division of the nucleus or of the cell, resulting in a cell with a tetraploid ($4n$) number of chromosomes. Some or all of the chromosomes on their way to the poles of a cell might divide a second time before a new cell wall is formed, resulting in cells with an increase in number of chromosomes. Some of the chromosomes might fail to divide, and one of the new cells would lack one or more chromosomes. The two halves of a divided chromosome might go to the same pole of the spindle, resulting in two new cells, one of which has $2n + 1$, the other $2n - 1$ chromosomes. A chromonema might become

broken in two or more places. The fragment with the spindle-attachment region might continue as a chromosome. The remaining fragments might become lost in the cytoplasm; or they might become reattached in a different order, or joined to fragments of other chromosomes.

Having predicted that such irregularities might occur in chromosomes during ordinary cell division in plant meristems, one has only to turn to cytological literature to learn that all of them, and others, actually do occur. Classified detailed descriptions of them are available in the books cited in Chapter XXXVII. These chromosomal aberrations and gene mutations alter the heredity of individual cells.

If the altered cell survives, it may become the forerunner of a sector of tissue, a whole branch, a leaf, a root, or a part of a flower that differs from other corresponding organs of the same plant. Some of the colors and patterns of variegated leaves, the white branches of plants, and the yellow sweet potato roots (Plate 4) are easily observed results of such changes in the vegetative cells of plants. In similar fashion the branches bearing seedless oranges originate. The nectarine and the Stark Delicious apple are the results of mutations in vegetative cells. Many varieties of sugar cane, potatoes, and other plants that propagate mainly by vegetative means are known to have originated by aberrations in ordinary cell division. If the aberration occurs in the fertilized egg, the whole plant will be different, since the fertilized egg is the forerunner of all the other cells of a plant.

When such a change occurs in the body cells of the higher animals after they have developed beyond a very early embryonic stage, it perishes with the individual in which it occurs. The reproductive tissues in these animals soon become differentiated from the body (somatic) tissues. In plants the situation is quite different. If the aberration occurs in the growing tip of a stem, flowers may later develop from cells containing the aberrant chromosomes. Or if it occurs in some organ of a plant which propagates vegetatively, a whole plant containing the aberrant chromosomes may be obtained by this means, and all its flowers would develop from altered cells. In either case, if the alteration in chromosomes is a stable one, it is perpetuated in plants by sexual reproduction. The white flower of hibiscus shown in Plate 4 is borne on a branch that grew from the stem base of a red-flowered plant. White-flowered branches have developed from this side of the stem base annually for the past 9 years. This aberration in the hereditary units must

have occurred in the meristem of the seedling, and has been perpetuated in all branches from that part of the meristem.

We may consider a case in which the division of the chromosomes was not followed by further cell division and wall formation, resulting in a cell with the tetraploid ($4n$) number of chromosomes. This aberration is known to occur under natural conditions. The frequency of its occurrence has been increased experimentally by exposing certain plants to high or low temperature, by wounding them, or by treating them with various chemicals, especially anesthetics and alkaloids. Examples are the increased frequency of occurrence of $4n$ number of chromosomes in the first cells formed from the zygotes of corn, wheat, barley, and sweet clover when the flowers have been exposed to 40°-45° C. for a half hour while the zygotes are dividing. Similar results were obtained with low temperatures in Jimson weeds, and in some of the adventitious branches that developed from *wound surfaces* in tomato stems. A weak solution of chloral hydrate was one of the first chemical agents used to increase the rate of chromosome doubling. In cells treated with this reagent some or all of the chromosomes divided a second time while they were migrating toward the poles of the spindle in the dividing cells.

All these external factors are known to alter the polarity of cells and the viscosity, permeability, surface tension, and streaming of protoplasm. It is probably through such indirect means that they influence the regular behavior of chromosomes. Spindle formation and the migration of chromosomes are certainly influenced by all of these internal conditions in the protoplasm, except permeability.

Recently it was discovered that an alkaloid, colchicine, from the autumn crocus is very effective in preventing spindle formation and subsequent cell wall formation in dividing cells, thus stopping the process with the separation of the chromatids. These treated cells contain the tetraploid ($4n$) number of chromosomes. The plant, or some part of it, may be soaked in a very dilute solution of colchicine, or the solution may be sprayed upon the plant. How far botanists may go in increasing the number of chromosomes in plant cells by this method will have to be decided by future experiments.

Even before the discovery of colchicine and other means of increasing the number of chromosomes in a cell, it was known that tetraploid ($4n$) cells would survive and grow, and that whole plants bearing flowers could be obtained from them as described above. They had been found in the wild state. In such plants the gametes contain the diploid ($2n$)

number of chromosomes when compared with gametes of the ancestor of the tetraploid plant. If they unite they form a zygote with the $4n$ number of chromosomes and thus the tetraploid condition is perpetuated. But if a diploid ($2n$) gamete unites with a monoploid (n) gamete, a triploid ($3n$) zygote is obtained. Certain irregularities, however, may occur during reduction division, and some of the progeny may not have exactly $4n$ or $3n$ number of chromosomes.

Tetraploid plants that have been obtained by experimental methods usually have larger cells, stems, leaves, flowers, and seeds than their diploid ancestors, though this increase in size does not always occur. A slower growth and a longer vegetative period are more generally characteristic of them than increase in size. Many irregularities and various degrees of sterility occur.

Monoploid tomato plants and Jimson weeds that develop from monoploid unfertilized eggs (parthenogenesis) are smaller and less vigorous than the parent diploid plant. Those that have been studied are sterile unless gamete formation occurs without reduction division. All such gametes have the same chromosome complement and it is identical with that of the vegetative cells of the plant. If self-fertilization were to occur, completely homozygous individuals would be obtained and perpetuated until some change occurred in a gene of one or more of the chromosomes. In later chapters we shall see that the formation of completely homozygous individuals is common in some species of mosses and ferns.

Other aberrations of chromosomes noted above, such as a gain or a loss of a chromosome or of a fragment of a chromosome, are of course accompanied by changes in the development of the plant, depending upon whether the cells gained or lost certain genes and their potentialities. These changes may be more striking than those that are merely the result of the doubling of the number of similar chromosomes.

It is now known that species of many genera of plants differ from each other by multiples of some basic number of chromosomes. For instance, the different species of wheat have either 7, 14, or 21 pairs of chromosomes. Similar series of multiples of seven also occur in the different species of oats, cinquefoil, tall meadow rue, and certain other genera of plants. These facts are sufficient evidence that the number of chromosomes alone is not enough to have been the cause of the origin of these different species and genera. Species of other genera differ by multiples of other basic numbers, such as 6, 8, 9, and several others. The different

species of chrysanthemum have 9, 18, 27, 36, and 45 pairs of chromosomes.

Apparently these species originated in part by a doubling of chromosomes; but there have been certain changes within the chromosomes themselves, such as fragmentation or even changes in the genes. If a gene consists of a few molecules closely bound in a group, then changes in a gene might occur from (1) a gain or a loss in molecules, or (2) a rearrangement, a gain, or a loss of atoms within the molecules. On the other hand, if a gene consists of only one molecule, then alterations within it would be limited to rearrangement, gain, or loss of atoms or groups of atoms.

What are mutations? In a broad sense any of the irregularities in the composition and arrangement of chromosomes and genes and in the consequent changes in development that cannot be ascribed to the direct effects of cross-fertilization (hybridization and subsequent hybrid segregation) may be called mutations. The term mutation was first used to refer to the occurrence of observable differences in hereditary characters not traceable to the direct results of cross-fertilization. It was later discovered that these visible mutant characters were the results of differences in the composition, behavior, and arrangement of both chromosomes and genes. Some authors use the expressions "chromosomal aberrations" and "gene mutation," preferring to limit the term mutation to changes that occur only in the genes, whenever such a distinction can be made. For convenience we shall use the term mutation in these chapters to include an aberrant condition in either chromosomes or genes, or any hereditary variation that is not the direct result of cross-fertilization.

Mutations during reduction division. We have seen that the pairing and segregation of chromosomes during reduction division are very regular processes, and that the Mendelian ratios among hybrid segregates are the consequences of this regularity. But here again, with a little scientific imagination we may visualize the possible occurrence of certain irregularities. Reduction division might fail to occur, with the result that the spores and gametes formed would have the diploid ($2n$) number of chromosomes, just like the cells of the vegetative body of the plant. The synaptic mates, instead of separating and moving to opposite poles of the cell, might continue to adhere to each other and move to the same pole of the cell. This might happen in one or in several pairs of chromosomes. Sometimes when chromosomes of two different species

are brought together in the cells of a hybrid by means of cross-fertilization they fail to mate regularly in reduction division, and many irregularities occur. As shown by the literature of cytology, these suspected irregularities, and many others, actually do occur. Each of them will be considered briefly.

When the chromosomes fail to undergo reduction division, the resulting spores, sperms, and eggs not only have the diploid ($2n$) number of chromosomes but they also have the same chromosome complement, which is identical with that of the cells of the vegetative body of the plant. This is the usual process in dandelion. Fertilization does not occur in dandelion. The parthenogenic embryo develops directly from diploid ($2n$) eggs. These eggs are one-celled vegetative propagules, and the progeny of a dandelion plant is a clone. Seeds of many species of plants may contain embryos that did not develop from fertilized eggs. The broad term for this phenomenon is *apomixis* (without mingling).

The type of irregularity in which the members of one or more pairs of homologous chromosomes fail to separate during reduction division results in a change in chromosome number and complement. If the chromosomes of one pair fail to separate, both of them migrate to the same pole of the spindle. As a result, some of the spores, sperms, and eggs have $n + 1$ chromosomes; others have $n - 1$ chromosomes. If two of the pairs of chromosomes fail to separate, the gametes have $n + 2$ and $n - 2$ chromosomes. Hence some fertilized eggs lack one or more chromosomes, and others have one or more extra chromosomes with all their genes and potentialities.

Such changes in chromosome behavior may be the initial steps in the formation of new varieties and species. Within certain genera of plants we may arrange several of the species in a series, such that each species in the series differs from the preceding one and the next one following it by only one or two chromosomes. A similar situation may be found among the varieties of a species. The usual diploid ($2n$) number of chromosomes in corn is 20. The number of chromosomes that have been found in different varieties of corn are 21, 22, 23, 24, 25, 26, 27, and 28.

Irregularities in reduction division in hybrids may be obtained (1) by crossing remotely related plants having the same number of chromosomes, but chromosomes which previously have not been together in the same cell, or (2) by crossing plants differing in chromosome number. The irregularities that may occur in the pairing, or lack of pairing, of the chromosomes in such hybrids are numerous, and only a few examples

will be mentioned here. These irregularities of chromosomes, though indirectly the result of cross-fertilization, should be distinguished from the hybrid effects of cross-fertilization that are directly dependent upon the mixing of chromosomes of two kinds of plants, described in the preceding chapter.

Of the eighteen recognized species of wheat, three have 7 pairs of chromosomes, nine have 14 pairs, and six have 21 pairs. Self-fertile hybrids are readily obtained from crosses between species having the same number of chromosomes. Hybrids are less readily obtained by crosses between species with different numbers of chromosomes, and they are often self-sterile. Hybrids obtained by crossing species with 14 and 21 pairs of chromosomes are sometimes self-fertile. Hybrids between species with 7 and 14 pairs of chromosomes or between those with 7 and 21 pairs are self-sterile; but they may be successfully back-crossed with parents, or crossed with certain other species. Obviously several new kinds of chromosome combinations may be obtained by such means.

Hybrids have also been obtained between species of different genera of plants, such as wheat and rye, wheat and couch grass, radish and cabbage. Here again there is often a high degree of sterility and many peculiar irregularities are obtained. Radish and cabbage each have 9 pairs of chromosomes and their F_1 hybrid has 9 cabbage chromosomes and 9 radish chromosomes. Among the F_2 hybrid segregates was a hybrid containing 18 cabbage chromosomes and 18 radish chromosomes, which must have been obtained from gametes formed without reduction division. Subsequent generations of this particular hybrid also contained 9 pairs of radish chromosomes and 9 pairs of cabbage chromosomes. Apparently the cabbage and radish chromosomes did not pair with each other during reduction division. This new hybrid has all the characteristics of a distinct species. Recognized species are sometimes formed in this way in the wild state.

Influence of environment. The above summary of some of the better-known types of aberrations in chromosomes and genes is barely more than an introduction to this particular phase of natural phenomena. But perhaps it is sufficient to indicate some of the research that is being done and to supply a basis of understanding as to how visible hereditary differences originate. All such differences begin as changes in the composition and arrangement of units of matter in the protoplasm of cells. For example, the molecules of which genes are composed may undergo change in composition. We have already seen that changes in the com-

position of molecules may be the result of a change in the arrangement of atoms, or of a loss or gain of certain atoms. In an earlier chapter it was shown that a rearrangement of a few atoms in a molecule of glucose resulted in the formation of fructose, and vice versa; and that the composition of molecules is altered by oxidation-reduction processes.

Next in order are changes in chromosome structure, such as changes in the arrangement of genes within the chromosomes; and among the larger units are changes in the arrangement of chromosomes themselves. Changes in the composition of the molecules of the genes are often regarded as the most fundamental ones. They are chemical changes, whereas the others appear to be physical changes. But this difference may be regarded as one of degree rather than of kind. Each of these changes is the first step in the development of the type of heritable variant known as a mutant. In brief, a mutation may occur among the chromosomes as a whole, among the genes within a chromosome, or among the molecules and atoms within a gene.

Moreover, mutations may occur in an apparently uniform environment, or the same kinds of changes may occur in different kinds of environments, and their frequency of occurrence may be increased or decreased by a change in environment. To illustrate these points we shall begin with a simple analogy.

Glucose, fructose, and mannose are all distinct sugars of the formula $C_6H_{12}O_6$. If one of them is placed in a bottle of water, the other two will be slowly formed from it even if the bottle is kept in a uniform environment. But the rate of change from one kind of sugar to another varies with the intensity of certain factors in the environment, such as temperature and the presence or absence of barium hydroxide or other chemicals. Geochemists calculate the age of rocks on the basis of the rate at which uranium changes to lead and helium. Even the rate of this process is unaffected by ordinary changes in the environment on the surface of the earth.

These simple examples are cited as a reminder that within a system (molecule, gene, chromosome, and cell) there may be intrinsic conditions that result in change, and that the effects of the environment on these intrinsic conditions may result only in altering the rate of change. That is, the effects of the environment may not result in any new compound or structure.

By special laboratory methods chemists are able to make 16 kinds of sugars of the formula $C_6H_{12}O_6$. Only about one-third of these have ever

been found in plants. This fact should keep us from inferring that just anything may happen in a living organism. The number of kinds of changes that *may* occur in any system is dependent upon conditions within the system. The number that *does* occur may depend in part upon the environment. Of those that do occur, only certain ones are sufficiently stable to persist. Obviously if all heritable changes in living cells depended upon the conversion of one hexose sugar to another, only a few kinds of heritable differences could occur.

The changes that occur in the composition of the molecules of the genes are not changes in sugar molecules, but changes in the much more complex molecules of proteins, or protein-like substances. The kinds of changes in protein molecules, however, are probably as independent of changes in the external environment as are those in the molecules of sugar. Likewise, the rate of change may be influenced by changes in certain factors of the environment. We should not, therefore, overemphasize environment and underemphasize the intrinsic nature of change in hereditary units of matter. If differences in environment are important in causing heritable change, we would expect that artificial environments, such as X-rays, would cause new kinds of variations, whereas they merely increase the frequency of those that occur in nature.

This point is further illustrated by the mutations that have occurred in the Boston fern and its varieties growing in greenhouses where the environment is comparatively uniform, though not as uniform as that in a tropical rain forest. The sword fern (*Nephrolepis exaltata*), a native of Florida and the American tropics, has been cultivated in greenhouses and as a house plant for more than a century. In 1895, a florist near Boston discovered among his sword ferns a mutant which became known as the Boston fern (*Nephrolepis exaltata bostoniensis*), and also as the best fern among house plants. Since 1895 more than 200 mutant varieties of the Boston fern are known to have come into existence. Only one of these new varieties has spores that germinate. One variety reproduces by viviparous budding of the leaves. Some of the varieties survive when exposed continuously to the dry air of our homes, which in winter is usually drier than desert air; others can be kept alive only in a saturated atmosphere. The leaves differ greatly in size and form (Fig. 218). Some varieties have leaves several feet long; the smallest variety has leaves scarcely more than an inch in length. The simplest leaves are once-pinnate and plain. The more complex leaves are 5- to 6-pinnate

with variously crested leaflets. These plants also exemplify the fact that mutations occur in vegetative organs, for these mutations occur when the ferns propagate vegetatively from rhizomes and runners.

Although the kinds of mutations are apparently independent of changes in the environment, the rate at which they occur is influenced by the environment. Very little is known about the comparative increase in frequency of the several kinds of mutations. If the rate of certain mutations is consistently increased more than that of others in a given environment, we might expect that certain variations will accumulate



FIG. 218. The cultivated Boston fern (upper left) and five of its many mutant varieties, all of which originated from mutations in vegetative cells.

more abundantly than others in certain habitats, provided, of course, that they are not eliminated more rapidly.

Experimental means of speeding up mutations by decreasing or increasing the temperature, by treating the plant with chemicals, or with ultra-violet light, X-rays, and radium emanations have enabled investigators to obtain data about mutations much more readily. The idea that mutations under natural conditions may depend upon cosmic rays has already been discredited. It is interesting to note that plants from old seeds, like those from seeds treated with X-rays, have more mutations than plants that grow from freshly harvested seeds. Apparently X-rays speed up deleterious changes in seeds similar to those that occur natu-

rally with age. The effects of X-rays are the result of chromosomal aberrations and of the destruction of hereditary units of matter.

Some genes are much more stable than others. When the colors of variegated leaves, flowers, and grain coats are the visible effects of local mutation, the various sizes of the pigmented areas are evidences of the amount of tissue that developed from the cells in which the mutation occurred. The occurrence, shape, and location of the white and pigmented areas in the leaves of coleus, however, are seldom due to local mutations in the leaves. These patterns are as definitely heritable through genes in the gametes as are the pigments. There are pure lines of coleus with respect to these patterns; and when they are crossed with each other, the patterns recur in the usual Mendelian ratios in the progeny of the hybrids.

The idea that only the best or "fittest" mutations survive has been abandoned by most students of plant physiology and heredity. So, also, have the notions that a heitable variation must have some adaptive value to survive, that the variation occurred to meet some need, and that the variation was selected by nature. Numerous heritable variations that neither interfere with nor contribute to the life of the plant occur and survive, and their mode of origin is precisely the same as in the case of those that are beneficial or those that are lethal. Only a few of the numerous heritable differences that we see in plants are life and death differences.

To one who tries to classify the plants of the world, the most fundamental heritable differences among them appear to be those that differentiate the major groups, such as bacteria, fungi, algae, mosses, ferns, and seed plants. Members of all these different groups of plants may be found growing near each other in any natural forest, grassland, and desert, or even in water. Since they occur in most environments, the great groups of plants became differentiated by heritable mutations that have no survival value. Within each of these great groups, however, species differ from each other by gene complements that have survival value in some habitats. These points will be amplified in the next chapter.

Many mutations are of such a nature that the mutants cannot survive in *any* environment. These are called lethal mutations. Because of them some of the several fundamental processes, such as chlorophyll synthesis and photosynthesis, fail to occur. If the lethal mutation is dominant, the plant perishes. But if it is recessive, it may survive in the race indefi-

nitely, if there is sufficient cross-fertilization to keep it associated in hybrids with the alternative dominant factor. Individuals that become homozygous for the lethal mutation perish.

Mutations that occur when plants are exposed to X-rays, extreme temperatures, or other special conditions are reported to be of the same kind as those that ordinarily occur in fairly uniform environments. It appears, therefore, that the influence of environment is limited to changes in rate of mutation and to the survival and distribution of the new types of plants formed.

Importance of scientific evidence. In view of the facts discussed in the last four chapters it should be evident that the present generation is aware of numerous botanical facts and principles that were unknown in earlier times; many of them were unknown or but vaguely glimpsed before the beginning of the present century. These chapters could not have been written today except for numerous recent discoveries in the fields of physics, chemistry, and geology, and in the specialized fields of botany: physiology, morphology, cytology, genetics, and ecology. The present points of view are the results of more knowledge about the fundamental nature of chemical stability and chemical change, a better understanding of plant processes and development in relation to environment, and the integration of the facts of sexual reproduction, chromosome behavior, and the transmission of hereditary factors during the life cycles of plants.

For all these advances in knowledge civilization is indebted to the scientific method of procedure in experimentation and observation. It is by this procedure that man has learned what to believe about his environment, and how to manipulate a portion of it to his own advantage. In the absence of data, he observes the obvious phenomena about him and speculates about their origin. Dependable decisions come only through intelligent experimentation and observation, and by the repeated subjecting of the inferences drawn to the test of new situations and additional data. The discovery of basic principles ("laws") of nature enable us to infer with greater precision what has occurred in the past and what is most likely to occur in the future. We can be reasonably sure, for instance, that every person in the world older than we are, was once an infant who developed from a fertilized egg. We can be equally certain that if there are new species of oak trees a million years from now, they will have been derived from oak species now living. The number of such inferences one may draw about living organisms depends

upon the number and kind of scientific principles which he fully appreciates.

You may remember that Camerarius and other investigators during the 18th century fully confirmed the fact that sexual reproduction occurs in plants. But the discovery that fertilization is the actual union of sperm and egg, and that the embryo develops from a fertilized egg, is the product of the experiments of the second half of the 19th century. All sorts of fantastic ideas about sex had prevailed before that time. Each of the other major ideas discussed in these chapters passed through a similar history. We need, therefore, to distinguish clearly these early guesses, which have been passed on to most of us by tradition, from the conclusions that may be drawn today from more extensive and more critical data.

Darwin did not know how to evaluate the various ideas current in his time concerning evolution. He therefore began to collect facts that might help him reach some reasonable conclusions. At the end of twenty years of investigation he concluded that species are mutable, that by variation new species originate from preexisting ones, and that by innumerable slight variations the plants and animals of the present have descended from only a few primordial progenitors of early geologic time. The numerous discoveries since Darwin's time have reasonably confirmed his conclusions that species are mutable, and that the plants and animals of today are the modified descendants of preexisting ones, and so on back through millions of years. Darwin, of course, tried to explain how all these changes in living organisms may have occurred. We may not agree with all his explanations today, for at that time (the middle of 19th century) nothing was known about chromosomes or their relations to hereditary factors, and there was no clear distinction between heritable and non-heritable variations.

Mendel did not know what to believe about the various ideas concerning hybrids that were current in his time. Two years before Darwin published his book, *Origin of Species*, Mendel began his famous experiments with peas. We are already familiar with the definite ratios he discovered through his experiments. Even more important, however, is his inference that hereditary factors must be discrete units that may be combined in cells and later separated without loss of their individuality. At the turn of the century, Bateson of England and de Vries of Holland came to the conclusion, on the basis of experiments, that all hereditary variations occur as if they were the result of abrupt (discontinuous)

changes in the cells. The clear recognition of chromosomes in 1884, and the subsequent discovery of their regular behavior, of their relation to the transmission of hereditary factors, and of their occasional aberrations furnished a background of fact adequate to confirm the conclusion of Bateson and de Vries.

This conclusion is quite distinct from Darwin's earlier idea that changes in organisms come about by the accumulation of slight continuous changes occurring in the same direction and surviving because they are of some "advantage" or of "adaptive value." We have already shown that mutations may be beneficial, harmful, or inconsequential, and that their survival does not depend upon their being beneficial to the plant.

In the quest for knowledge and understanding of living organisms, if we cannot make pertinent observations and perform critical experiments ourselves, we can at least base our thinking upon the well-attested data discovered by others.

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CHAPTER XL

TYPES OF VARIATIONS AND DIVERSITY OF ORGANISMS

In all his attempts to arrive at a scientific basis of improving plants and animals by selection and controlled breeding, and in his efforts to interpret the diversity of living organisms in the world about him, man has been confronted with the problem of understanding the nature of organic variation. His various answers to the problem are voluminously illustrated throughout recorded history, as are also the various social implications he attached to any particular answer. For a long time the answers were based upon casual observations accompanied by philosophical and metaphysical speculation. As a consequence we have socially inherited all sorts of contradictory explanations and their associated phrases and slogans.

It is most important for us today, therefore, to try to recognize established facts and see what inferences may reasonably be drawn from them. The numerous experimentally established facts included in previous chapters may be used as a basis for (1) distinguishing types of variations, (2) considering the causes and consequences of the different types, and (3) understanding the uses one may make of a knowledge of these variations. Other data will be included in the chapters on the great groups of plants; but we shall have a better appreciation of certain features of the different types of plants in the world today if we can approach a study of them with certain basic ideas about how they came to be.

Solely on the basis of heredity, and without any reference to causes, the variations in living organisms may be classified as either heritable or non-heritable. Having made such a classification of variations, one may then attempt to distinguish their underlying causes and consequences, as we have tried to do in many of the foregoing chapters.

The first part of this chapter is primarily a review and summary of several previously described facts about variations. Some of the uses that may be made of these facts in evaluating various ideas about evolution and adaptation are briefly outlined in the remainder of the chapter.

Non-heritable variations. Non-heritable variations, or *fluctuations*, are merely differences in the expression of hereditary potentialities in individuals of similar heredity growing in different kinds of environments. They are the kinds of variations in the development of a plant that man is trying to obtain when he adds water and fertilizers to the soil, or otherwise tries to change the environment in a way that will be most favorable to the growth of a particular kind of plant. Any one of several environmental factors may greatly alter the development and appearance of a plant by affecting the rate of such processes as photosynthesis, respiration, and transpiration, or by affecting the permeability or other physical conditions of the protoplasm. In fluctuations, therefore, the hereditary mechanism of the plant remains unchanged, and the heredity of the progeny is not influenced by the environment of the parent plant.

This fact is most easily tested experimentally with pure-line plants. One example will be cited. In Norway a pure line of oats was cultivated in experimental plots in several different types of soil and climate in different parts of the country. When the growth and development of the plants in the various plots were compared, several differences in yield and other characters were evident. A careful record of all these differences was made in an experiment which was continued for 7 years. At the end of that time seeds from five of the plots in different parts of the country were planted in one plot in the same conditions of soil and climate. The resulting plants were all alike. That is, there were no lasting effects of the variations in development that occurred in the plants of the preceding seven generations in the diverse environments to which they had been exposed. In all, seven different pure lines of oats and two pure lines of barley were similarly tested and no changes occurred in the heredity of the progeny.

Experiments of this sort do not prove that a change in environment never causes a heritable change in a plant. But they do show that the variations we have called fluctuations are non-heritable, that they have no influence on subsequent progeny, and that they are not the means by which improved varieties were obtained through domestication, or by which evolution occurs. Incidentally, these experiments also show some of the fallacies in the popular belief in the inheritance of acquired characters.

Fluctuations are, however, of great economic importance. It is to secure the best possible expressions of the hereditary potentialities in our present crop plants that so much labor is annually expended in cultivat-

ing them, and that concerted efforts are now being made to check the rapid deterioration of one important part of their environment, the soil. New kinds of plants are obtained only by changes in hereditary factors, not through fluctuations.

Heritable variations. Heritable variations may be further distinguished as *hybrid variations* and *mutant variations*. Further illustrations of mutants are given in Plates 5, 6, and 7.



PLATE 5. Double and crested flowers of cosmos (right) from mutations in the parent stock (left).

The cause of hybrid variations is easily recognized. Cross-fertilization results in combining a part of the hereditary mechanism and potentialities of two genetically different plants. The chromosomes and their contained genes are brought together in the fertilized egg during cross-fertilization and become segregated in subsequent generations of the hybrid.

The causes of mutations are not as easy to recognize as are the causes of fluctuations and hybrid variations. In spite of the prevalent popular



PLATE 6. *Trillium grandiflorum* above and a mutant variety (*Trillium grandiflorum plenum album*) below.



PLATE 7. The red sunflower, a mutant from the common yellow-flowered ancestor (*Helianthus annuus*).

idea that environment is responsible for about everything a living organism does, it appears, on the basis of experimental evidence, that the causes of mutations are wholly or mainly intrinsic. The effects of the environmental factors appear to be limited largely to changes in the rates of mutation rather than changes in the kinds of mutation.

Perhaps the popular belief in the omnipotence of the environment is

due to the acceptance and retention of a too literal version of the fiction with which we were entertained in childhood. The fantastic but entertaining *Just So Stories* in which Kipling tells us how the elephant got its trunk and the leopard got its spots; or the equally fantastic stories in supposedly more serious literature that tell us how the giraffe got its long neck and why certain reptiles have no legs, should be read and remembered as interesting flights of fancy, but not allowed to interfere with scientific thinking. They admirably illustrate the traditional belief in the inheritance of acquired characters.

If environment does change the heredity of a plant it must cause an alteration in the composition or in the arrangement of the hereditary units of matter. Furthermore, any change that is inherited through sexual reproduction must occur either in the reproductive cells, or in cells that are the forerunners of reproductive cells.

Changes in the forerunners of reproductive cells which later become inherited are much more likely to occur in plants than in animals because the reproductive tissue becomes differentiated from body tissue much earlier in the development of an animal. Neither the reproductive cells nor any forerunners of them are in the neck of the giraffe, in the legs of a reptile, or in the trunk of an elephant. In a seed plant, however, cells in the growing stem tips are remote forerunners of the reproductive cells, which develop in the stamens and pistils of flowers after the plant has passed through a vegetative phase of growth. Beginning with a fertilized egg, or with a vegetative propagule, cells follow each other in regular sequence by billions of cell divisions up to the immediate forerunners of the reproductive cells. Hereditary changes that occur in these vegetative (body) cells previous to or during their division may be transmitted by subsequent cell divisions to the reproductive cells. Even this condition does not exemplify the traditional belief in the inheritance of acquired characters, for that belief is based upon the assumption that changes—including fluctuations—in mature body cells that are not forerunners of reproductive cells may be transmitted to the offspring.

The origin of new kinds of plants by evolution. There are two very different methods of approaching a study of evolution. One method is descriptive; the other is interpretative. The interpretative method will be noted first. The fundamental processes in living organisms may be studied until those that inevitably result in evolution are recognized. This is the method of approach we have been using throughout most of this book.

Not much more need be said to emphasize this point of view or to review the initial processes of evolution enumerated in the preceding chapter.

Heredity and heritable variations in living organisms must depend upon small heritable units of matter, such as chromosomes and genes, in the protoplasm. These units of matter are in the fertilized egg, and are transmitted from cell to cell during cell division throughout the life cycle of a plant. The smallest plants, such as the blue-green algae and bacteria, have no sex, no organized nuclei and chromosomes, and yet there are distinct species of them just as there are of other plants. In these smaller plants the hereditary units of matter appear to be distributed throughout the protoplasm of the cell. In other plants these units of matter, so far as known, are mostly concentrated in the chromosomes within the nuclei.

Changes in one or more of these units of matter may result in the formation of new varieties. Further changes may result in what are called new species. New species, then, are primarily the old species with certain changes in chromosome and gene complements and their consequent effects on visible characters. Whenever the accumulation of aberrant changes in chromosomes and genes in a particular variety of plant reaches the point where the individuals of that variety in nature no longer cross freely with individuals of the ancestral stock, or with individuals of other varieties, it is well on the way to being a new species: the kind of species we recognize when we speak of red oaks, black oaks, and white oaks. So long as the individuals of a variety cross freely with those of other varieties of the ancestral stock, the variety fails to acquire that individuality we recognize in most species, and we refer to it merely as a hybrid variety. It is not always easy to decide when a variety has enough individuality to be called a species.

The origin of a new species from an old one may come about by a series of changes over a long period of time, or it may occur rather abruptly perhaps by a single basic mutation or a rare kind of cross-fertilization exemplified by the new radish-cabbage species mentioned in the preceding chapter. The doubling of chromosomes may also be a rather abrupt beginning of a new species, particularly if the progeny with the increased number of chromosomes grow in a wider range of habitats. If there is no crossing with the parent stock, a few more changes in the chromosomes and genes may make the variety with the double number of chromosomes sufficiently different to be considered a new species.

It is important to remember that a new species is primarily the old one with a few differences in chromosomes and genes. These hereditary changes in plants and animals on the earth have been occurring for a

billion years or more, and they are the fundamental underlying steps of the great diversity of plants and animals on the earth today. Geologically, the most recent kind of plants are the seed plants, and the most recent animals are the mammals. Since they were formed by changes in a comparatively few of the hereditary units of their ancestors, we may expect to find them fundamentally much more like than unlike their ancestors. In fact, we may expect to find in them certain basic features that were in their remote ancestors many hundreds of millions of years ago. These basic features are, of course, the fundamental physiological processes that are essential to all living organisms. Variations in hereditary factors that inhibit, or unbalance, any one of these fundamental processes are lethal, and they result in the extinction of organisms when not annulled by alternative dominant factors.

The initial steps in the formation of a new species, then, may be visualized somewhat as follows: origin of heritable differences by such changes in chromosomes and genes as those described in the preceding chapter; segregation of these differences in certain individuals; a decrease in cross-fertility, or a decrease in cross-fertilization because of geographic isolation; and an increase in homozygosity and distinct individuality.

The descriptive method of approach to the study of evolution was the one followed by our forefathers before chromosomes and Mendel's law of hybrid segregation were known. This method includes the study of the visible characters of organisms; their methods of development and reproduction; and their fundamental similarities, differences, and relationships, including those of fossils. Some of these facts will be evident in subsequent chapters.

The study of evolution from this point of view led to the discovery of several fundamental principles about living organisms. A few of those upon which there is general agreement are briefly stated below. They will be of greater interest if each one is considered with reference (1) to the probability of its being explained on the basis of the facts you know about chromosomes and genes, and (2) to the extent to which any preconceived ideas you have held about the subject are incorrect.

The kinship of organisms, both living and fossil, is interpretable only on the basis of descent by modification (evolution) through a long period of time.

Diversity of organisms is the result of evolution. That is, species are not specially created, unchangeable units.

Within a group of related organisms, such as the species in a genus, the different ones may be arranged in series such that some particular character appears in ascending or descending order of magnitude. This fact does not imply that the different species necessarily evolved in this order, but it does imply that intrinsic conditions limit evolution.

Evolution of organisms is limited in direction. That is, it does not proceed in all conceivable directions.

The same general trends of evolution occur in organisms living in very diverse habitats—for instance, in water and on land.

Similar trends of evolution occur in different taxonomic groups of organisms.

Divergent trends of evolution occur in organisms living in similar environments.

Evolution may continue in a definite direction in a race of organisms until it results in processes and structures that are handicaps to the race and bring about its extinction. That is, "adaptation" is not the end of evolution.

Evolution may result in the development of useful organs and in the subsequent deterioration of such organs to vestigial structures.

Species formation is increased by geographic isolation, and by other means that eliminate cross-fertilization.

Adaptation. In an earlier chapter attention was called to the desirability of periodically considering the appropriateness of terms used in biology. The term adaptation was in the list cited at that time. It is often stated that plants, and also animals, may become "acclimated" or "adapted" to new conditions. One even hears that they adapt, or acclimate, themselves to new conditions. If this latter statement is true, there is no need to discuss the matter, for there is no evidence that plants can plan and direct changes within themselves to meet new conditions. To say that they *become* acclimated, or adapted, states a condition that can be experimentally investigated. We may arrive at an answer as to how they become adapted, if they do.

It may be untrue, however, to say that a plant becomes adapted to a new condition. When we say that a plant is adapted to a certain condition we are merely saying that it can live, grow, and reproduce in that condition. If it cannot live there—is not adapted—and we place it there, it dies. It neither adapts itself nor becomes adapted. To do so, it would suddenly have to become another kind of plant by an abrupt change in its heredity.

One often hears that plants are well adapted to the environments in which they grow. Any serious ecological study of a plant will most probably show that it may be found in some of the habitats in which it grows well—is well adapted—that it also occurs in other habitats in which it barely survives, but that it does not occur in habitats in which it cannot survive. All this merely means that some plants grow better in some environments than others do because they are different kinds of plants. It will become clearer later on that a distinction should be made between the popular idea that an *individual plant* becomes adapted, and the botanist's idea that a *species of plant* becomes adapted.

In one sense, however, it is true that an individual plant becomes adapted, or better adapted, to a certain environmental condition. This fact may be easily illustrated with seedlings, say of cabbage. If seeds of cabbage are planted in three different plots, one of which is kept warm and moist, another warm and comparatively dry, and the third cool and either moist or dry, the seedlings will grow in all three plots. A few weeks later, if the seedlings are exposed to a freezing temperature for a few hours, those in the warm plot will be killed, while those in the dry and cool plots may survive. They have become physiologically different. The gardener says they have become "hardened." This physiological conditioning of a plant, however, is not what is usually meant by the terms acclimated and adapted. It is merely a fluctuation that is not transmitted to the progeny.

One usually refers to the acclimation and adaptation of a mixed population of plants rather than to a single kind of plant. A few examples will be discussed briefly because of the principles they exemplify. A population composed entirely of the same kind of homozygous close pollinated plants would behave like a single individual, provided, of course, that no mutations occurred in any of the individuals. If there were mutations in some of the individuals then we would no longer have a homogeneous population of plants, but a mixed one of different kinds of plants. In a population composed of different kinds of plants, some plants behave differently than others when the environment changes.

Examples of mixed populations of plants are: a bluegrass lawn in which there are also other kinds of grasses, clover, and weeds; a forest; or a field of crop plants composed of closely related species and varieties of plants.

Several kinds of changes may occur in a mixed population, but it is a question whether any of them is correctly referred to as becoming ac-

climated, or adapted. From your own experience with lawns, you know that new kinds of plants may come in through seed dispersal, some plants present may die during a hot dry summer, and following the proper application of water and certain fertilizers bluegrass may grow so luxuriantly that many other plants become overshaded and die.

Experimental studies of the so-called acclimation of crop plants that have been introduced from one country into another show that some of the species and varieties in the mixed crop simply grew better than others in the new country. These varieties had more viable seed than those that did not grow so well. Hence as the farmer harvested the seeds each year he obtained a greater and greater percentage of seeds of those plants that were already well adapted to the conditions in the new country.

The above example refers to experimental studies of a mixed population of close pollinated plants such as wheat, oats, and barley. If, however, the mixed crop consists of hybrids, or of open pollinated plants that are cross-fertile, various combinations and segregations of factors would occur each year. Here again man, by selecting seeds, would be an additional factor in the final outcome.

The influence of man is exemplified by our great array of domesticated plants, most of which would become extinct within a few years if he were suddenly to disappear from the face of the earth. Exclusive of modern methods of controlling plant breeding, he has been a factor in the evolution of domesticated plants for many thousands of years (1) by placing the plants close together in his fields and gardens, thus facilitating cross-fertilization, (2) by introducing plants from other parts of the world that would interbreed, (3) by cultivating in a way that eliminated ecological influences of one plant upon another ("competition"), (4) by preserving the plant during seasons of the year in which it might otherwise perish, and (5) by selecting certain varieties and eliminating others.

In the wild state all plants grow in mixed populations. In what ways do these mixed populations, when not interfered with by man, differ from those of crop plants under the conditions of cultivation? In the first place, all their interrelations are dependent solely upon the "laws" of nature. No conscious selecting, preserving, protecting, and distributing takes place. Instead, random (chance) survival, random natural elimination (destruction) by physical factors and by other organisms, and random dispersal checked by geographic barriers are paramount.

Ever since Darwin adopted the terms "natural selection" and "sur-

vival of the fittest," they have been accepted and used freely with a variety of implications by some biologists, adversely criticized or rejected by others. Those who object to the terms regard them as slogans that are used without an adequate analysis of the conditions from which they are inferred or to which they are applied. Such scientists think the terms "random survival" and "random elimination" are more in accord with the established facts.

For example, in a natural climax forest undisturbed by man, the area is fully occupied by the plants already growing there. Countless numbers of seedlings may be found in such forests, but the survival and growth of any one of them to maturity depend upon the death of some established plant. Even these innumerable seedlings are but a small percentage of the seeds that began to develop, because many of them are eaten by animals and others are destroyed by fungi and bacteria, or by other means.

Since the embryo in the seed develops from a fertilized egg, there are hazards that precede the formation of embryos. Out of the cloud of pollen grains containing sperms, or the generative nucleus from which sperms are formed, perhaps not more than one potential sperm in a trillion, or several trillions, ever unites with an egg. If any one of the rare sperms that unites with an egg, or any one of the relatively few seeds that germinate, or of the seedlings that grow to maturity happens to be the "fittest" of the lot, would it be a case of "natural selection" or of random survival?

Before the advent of man, biological conditions in the natural vegetation throughout the world were comparable to those in the forest described above. Erosion, flooding, fires started by lightning, volcanic eruptions, aridity, and glaciation occasionally destroyed some of the vegetation locally and increased the areas in which seedlings might develop to maturity.

Many structures that have survived are of no particular value to the plant. You have learned to distinguish several different kinds of trees by distinctive hereditary characters, such as leaf form, leaf arrangement, type of venation, and kind of leaf margin. Not one of these characters is of any survival value to the plant, yet each of them is an external expression of hereditary changes that occurred and have in some instances survived for millions of years.

When we distinguish families of plants on the basis of such differences as the number of carpels in the pistil, the arrangement of the floral parts in spirals or cycles, and the number of stamens and petals, we are again

recognizing hereditary differences that have occurred and survived, yet they cannot possibly be of any consequence in the survival of the species. In view of the fact that innumerable hereditary characters that are of no survival value to the plant have originated by exactly the same kind of processes that initiate valuable characters, "survival of the fittest," if it does occur, must be limited to very special cases. The term "valuable" in the above sentence refers to those characteristics that are essential to existence, or to those that enable plants to grow in different kinds of environments.

Finally, a species, as generally conceived, is a mixed population of very similar individuals, differing slightly from each other in gene complement. If different individuals of a species become separated, or isolated, in places where they no longer interbreed, they may in time become sufficiently different to be regarded as different races or varieties. Such race differences as have been intensively studied seem to bear no relation whatever to survival, for they occurred in various local areas having similar environments. Yet this differentiation of races is undoubtedly an initial step in the evolution of new species. The decisive fact is that the indivduals became isolated from each other, and the different kinds of mutations that occurred remained segregated in the local areas because of the absence of cross-fertilization.

Some of these racial differences do influence fundamental processes such as photosynthesis and respiration; and if the environment changes, some of the races may survive better than others, and some may be completely eliminated. One may refer to the races that survive as examples of the "survival of the fittest." Which of the races will be the fittest, however, depends upon the nature of the changes in the environment. The races that are destroyed by one kind of change in the environment might be the fittest of the population if some other kind of change had occurred. There seems to be no serious objection to the use of the expression "survival of the fittest" in this specific sense. One may rightly object, however, to the idea that the heritable changes by which the different races originated "occurred to meet a change in environment," or that they were actually "selected by nature." To accept this last idea, one would have to assume that the environment changed in order to favor certain races and exterminate others.

Another interesting point about the development of these isolated races is the fact that some of the heritable changes that occur in them are similar, or parallel, while others are divergent. Since the individuals that became isolated in different regional areas belonged to the same species,

their gene complements were largely alike but somewhat unlike. If heritable variations are dependent primarily upon intrinsic conditions, there should be both parallel and divergent evolution, regardless of whether the environments in the isolated areas are similar or dissimilar.

In the chapter on plants of the past, we shall see that various kinds of plants evolved, flourished for a time, and then became extinct. The redwoods, ginkgo, and stinking cedar as well as numerous other species of plants that were once widely distributed became extinct everywhere except in a few local areas. Yet they grow well today when planted in other parts of the world. They do not reproduce naturally in all these new environments. Within the first third of the present century the American chestnut was almost exterminated by a parasitic fungus. Other species of plants are being eliminated by insects, bacteria, viruses, and fungi. By destroying natural habitats, man is also exterminating species. Similar phenomena also occur in the animal kingdom. Toward the close of the glacial period several kinds of animals became extinct on the American continent. Among them were species of elephant, horse, camel, rhinoceros, and tiger. The causes of their failure to survive are not known, but among probable eliminating factors are diseases, changes in physical environment, failure to reproduce, development of detrimental structures, and the accumulation of lethal genes.

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CHAPTER XLI

NON-GREEN PLANTS

The term "non-green plants" is ordinarily used by botanists to refer to all species of plants that lack the inherent potentiality of synthesizing chlorophyll. It is a hereditary characteristic of species. For example, no chlorophyll is synthesized in any individual plant of the meadow mushroom, or of the common bread mold, under any environmental conditions. On the other hand, chlorophyll is synthesized in most corn plants in the light, but not in the dark. The meadow mushroom is a species of the non-green plants. Corn is a species of the green plants, even though some individual corn plants are albinos. These albinos cannot survive and reproduce in nature as non-green plants. Likewise coleus is a species of the green plants, though certain varieties of it contain so much anthocyan that the plants appear purple. Green-colored molds are not species of green plants because the pigment in them is not chlorophyll. The green color of frogs, snakes, insects, and birds is due to other kinds of pigments or to the refraction of light. Some of the flatworms and smaller animals are green because green algae live within their bodies. The terms chlorophyllous plants and non-chlorophyllous plants may be used in preference to green plants and non-green plants.

Nearly 80 per cent of the known species of plants are green, but there are fewer individual green plants on the earth than non-green ones. Most non-green plants are small and inconspicuous. Many of them are one-celled plants which cannot be seen unless they are magnified by means of a microscope. Among the larger fungi are the familiar molds, puffballs, mushrooms, toadstools, and bracket fungi. Most non-green plants are either fungi or bacteria, but there are also a few species of non-green algae and several dozen species of non-green seed plants. Among them are Indian pipe, dodder (Fig. 219), beechdrop, snow plant (Plate 3), squaw-root (Fig. 220), "pine sap" and broom-rape (Fig. 221).

Certain species of algae can live in the light as green plants, and also in the dark as non-green plants if an external supply of sugar or of some of its derivatives is available.



FIG. 219. Species of dodder (*Cuscuta*) grow as parasites on numerous green plants. The slender yellow stems of the one pictured here form a loose net among the broad leaves of the host (*Abronia*). Photo by W. S. Cooper.



FIG. 220. Squaw-root or cancer-root (*Conopholis*), parasitic on roots of oak. Flowers are present on the plants pictured on the right. Photo by G. S. Crowl.

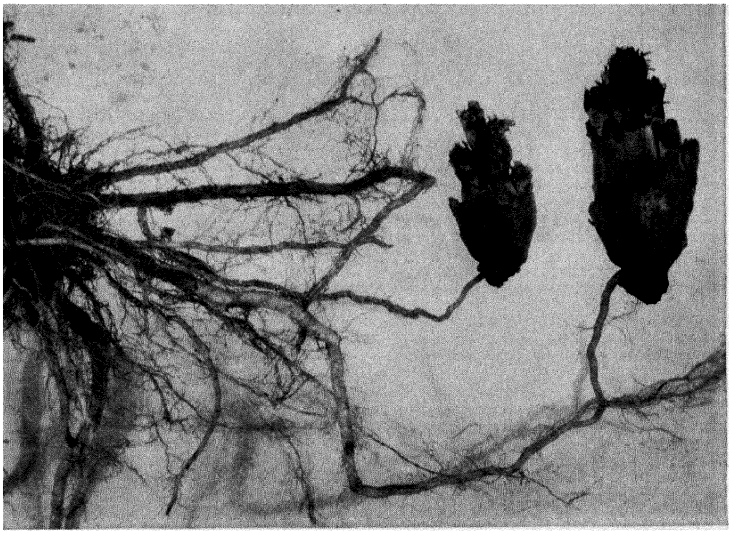


FIG. 221. Two parasitic plants of Louisiana broom-rape (*Orobanche*) attached by haustoria to roots of a tobacco plant. Photo by A. L. Pierstorff.

Non-green plants live in all sorts of habitats in water and soil, and also within and on the bodies of plants and animals. Those that grow within or on the living tissues of plants and animals and obtain food from them are *parasites*. Those that obtain food from the dead bodies of plants and animals, from their products, or from their non-living parts, such as the dead bark and heartwood of trees, are *saprophytes*. If they can grow only within living tissues they are called *obligate parasites*. If they cannot grow within living tissues, they are said to be *obligate saprophytes*. But if they can grow either as parasites or as saprophytes, they are referred to as *facultative species*. There are all sorts of gradations between saprophytic and parasitic plants.

With the exception of a few special groups of bacteria, non-green plants cannot synthesize sugar. Some of them, such as yeast, when supplied with an external source of sugar, inorganic salts, and water, can make the rest of the foods necessary for growth and reproduction. Others are dependent upon an external source of amino acids, or of proteins also. Plants that can synthesize sugar are sometimes called *autophytes* in contrast to parasites and saprophytes. In addition to food, non-green plants may also be dependent upon an external supply of certain vitamins and hormones, as well as inorganic salts.

We may apply at once all that we know about the physiology and heredity of green plants toward an understanding of non-green plants, for the living part of a non-green plant is protoplasm and there are definite species of them just as there are of green plants. The principal differences between these two types of plants lie in the processes by which they obtain food and in the consequences of these processes. Some of these consequences are beneficial to other plants and to animals, and some of them are harmful and destructive.

Parasitic plants. When a plant grows within or on, and also subsists upon food from the living parts of another organism, it is a parasite. The parasitized organism is the *host*. It may or may not be injured by the parasite. If it is injured, it is said to be diseased. Some parasitic plants are beneficial to the host. The nitrogen-fixing bacteria in the roots of clover, for example, are beneficial to their host, since upon their death their chemically bound nitrogen becomes available to the clover plant.

All sorts of gradations may be found from extreme parasitism to a total lack of it. Some parasites grow only within certain organs of one kind of host. Others grow within or on numerous kinds of hosts. Still others are but partial parasites. Sometimes both host and parasite are benefited rather than harmed by their relationship.

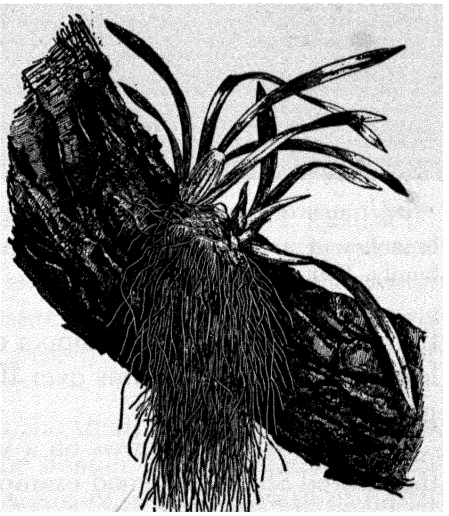


FIG. 222. An epiphytic orchid the roots of which merely hold the plant on the branch of the tree. After Kerner.

Some plants are merely perched upon or attached to others, but obtain no food from them (Fig. 222). These plants are known as *epiphytes*, in contrast to parasites. Examples of epiphytes are Spanish moss hanging on the branches of a tree (Fig. 223), and the mosses and lichens attached to the bark of trees wherever trees grow. In deciding whether a plant is a parasite, it is necessary to consider both its position and its source of food. It may be even more difficult to decide when an animal is a parasite. A protozoan may live within the cells of a plant. Roundworms burrow into roots and survive on the food within the root. Aphids obtain food by sucking the "juice"



FIG. 223. Festoons of Spanish moss (*Tillandsia usneoides*) pendant on the branches of a live oak in Florida. Spanish moss is a member of the pineapple family. Photo by G. W. Blaydes.

from living plants. A grasshopper climbs upon a plant and eats its young leaves, while a cow roams over the pasture and eats the live leaves of grasses.

A mistletoe which grows on a variety of trees in the southern half of the United States is a good example of a partial parasite (Fig. 224). Its sticky seeds adhere to the branches of trees; and when one of them germinates, a root-like haustorium grows through the bark to the conductive tissues of the host. The stems and leaves of this mistletoe contain chlorophyll, and some sugar is synthesized in them. Water and salts are of course obtained from the soil through the host. No one knows at present what percentage of the food of the mistletoe is obtained from the host, or whether it can develop under experimental conditions in the absence of a host. The relation of such plants as the mistletoe to their hosts is similar to that of a grafted scion to the stock.

An analogous partial parasitism occurs when the root tips of green plants penetrate the roots of other green plants and become haustoria.



FIG. 224. The evergreen mistletoe is conspicuous on deciduous trees during the winter months. Photo by Tillman Johnson, University of Oklahoma.

How frequently this process occurs is unknown. The roots of some plants, such as those of bastard toad flax of the eastern states, and of the desert shrub, *Krameria,* of the southwestern states, habitually form haustorial unions with the roots of many other plants. It is well known that unions occur among the roots of adjoining forest trees. Whether they are of any value to the trees is not known.

Some non-green seed plants, such as the small purple beechdrops attached to the roots of beech trees and the slender climbing dodder which becomes attached by haustoria to the stems of a great variety of hosts, obtain food directly from green plants. The Indian pipe, when casually observed, appears to be a saprophyte living on the litter of decaying leaves on the forest floor, but it apparently obtains all its food from fungi which digest the fallen leaves, and also live in and on its roots. Several layers of fungal filaments completely invest each of its many short roots, and numerous branching filaments of the fungus permeate the surrounding layer of decaying leaves and humus. Owing to the surrounding sheath of fungal filaments, the cells of the roots of Indian pipe are not in direct contact with the soil.

Fungi that live in such intimate relation with the roots of plants are

called *mycorhizal fungi*. They may live wholly external to the root, merely forming a sheath around it; the fungal filaments may grow into the cells of the root; or the entire fungus may grow within the cells of the root (Fig. 225). Such mycorhizal fungi are habitually present on the roots of

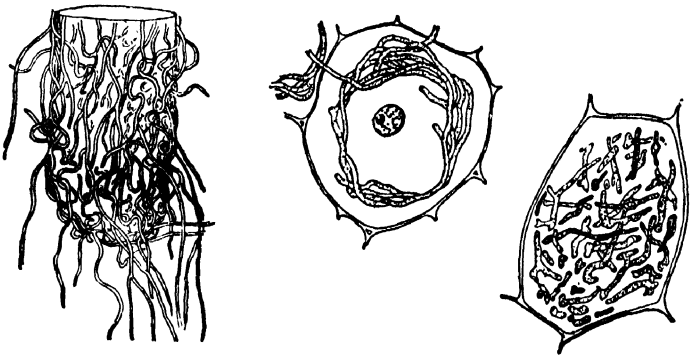


FIG. 225. External and internal mycorhizal fungi. After Frank and Magnus.

most green plants in forests. Some of them have been reported as harmful to certain trees, others as beneficial, or even essential to them. Under natural conditions, pines (Fig. 226), heath plants, and beeches are ap-

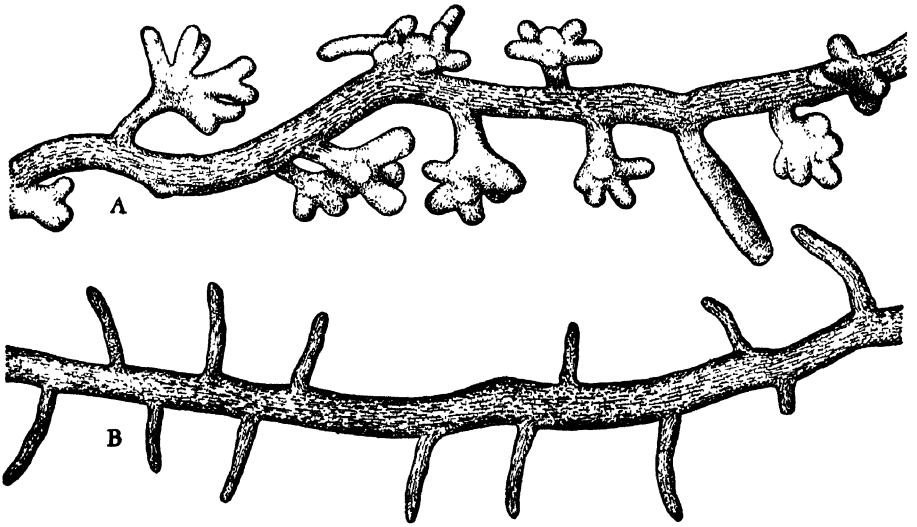


FIG. 226. Eastern white pine mycorhiza (A), and root (B) not infected by fungi. Drawn from photo in *Black Rock Forest Papers*, 1:66, 1937.

parently dependent upon mycorhizal fungi, for their seedlings live but a few years if deprived of them under experimental conditions.

Diversity among the non-green plants. There are all sorts of gradations

between saprophytes and parasites, and also between these two groups and the autophytes. Many terms have been proposed to designate these intergradations.[1] Some of this diversity is related to (1) the kinds of substances the organism can digest and utilize as food, (2) the method of securing food, and (3) the kind of substance oxidized during respiration.

In the cells of all animals, of all green plants, and of most non-green plants also, respiration involves the oxidation of reduced carbon atoms in sugar, or in organic compounds derived from sugar. When this oxidation is complete, one of the end products is carbon dioxide. A few groups of bacteria, however, are unique in that they oxidize reduced nitrogen, reduced sulfur, or reduced iron. Consequently nitrates, sulfates, and oxidized iron in the soil are among the end products of respiration of these bacteria. The oxidized compounds are essential to green plants, which are therefore partly dependent upon the activities of these bacteria. The bacteria in turn are partly dependent upon the activities of green plants for reduced nitrogen, and upon both green plants and other kinds of bacteria for reduced sulfur and iron.

These special groups of bacteria are unique in one other way. Although they are non-green and are underground, they synthesize sugar from carbon dioxide and water. The energy necessary for this synthesis is obtained from the oxidation of reduced nitrogen, sulfur, and iron. They are as truly autophytes as the green plants. The synthesis of sugar in these bacteria in the absence of light is often referred to as *chemosynthesis* in contrast to photosynthesis. Similarly, certain bacteria may oxidize reduced manganese and synthesize sugar.

The green and some purple bacteria (Plate 3) contain pigments similar to chlorophyll; and when they are exposed to light, photosynthesis occurs within them.

Autophytes. All plants, whether green or non-green, in which sugar is synthesized from carbon dioxide and water are called autophytes in contrast to parasites and saprophytes. Perhaps the term should be limited to those in which the synthesis of amino acids and proteins also occurs. Most autophytes, however, are *not* independent plants. They could not continue to live in a world devoid of all non-green plants. The non-green plants are dependent upon certain reduced compounds made in the

[1] J. M. Coulter, C. R. Barnes, and H. C. Cowles, *A Textbook of Botany*, American Book Company, 1931, Vol. 3.

green plants.[2] The green plants in turn are dependent upon certain oxidized compounds from the non-green plants. Dependent relations between green and non-green plants briefly outlined above are indicated in

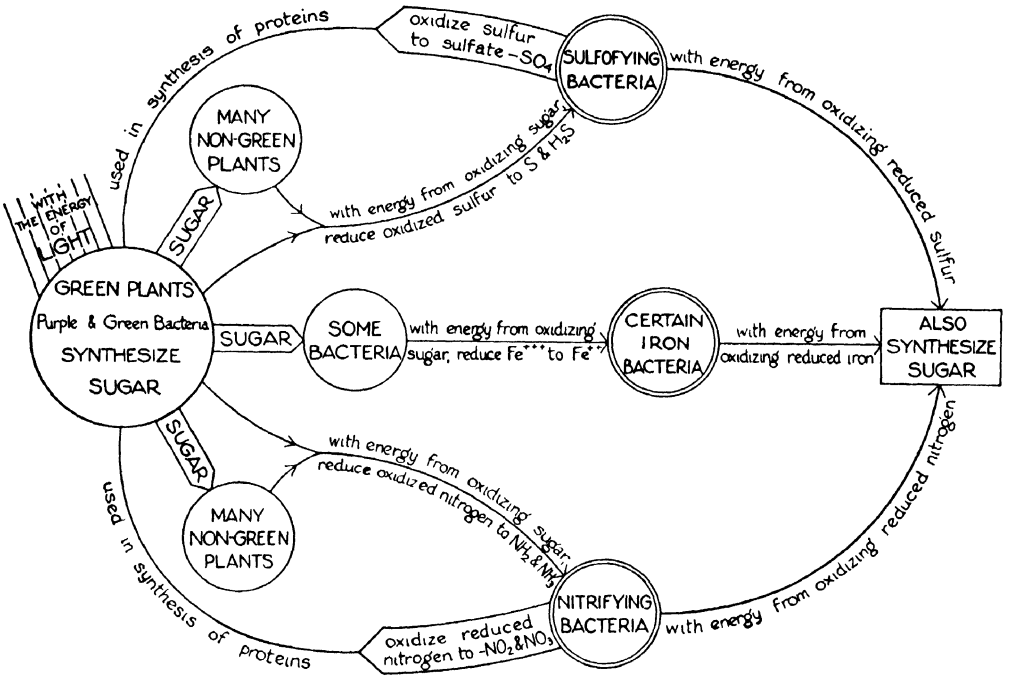


FIG. 227. Diagram of some dependent relations among green and non-green plants.

Figs. 227, 228, and 233. Others will be indicated in later chapters. In the absence of adequate data we have assumed that the first food made from carbon dioxide by autophytic bacteria is some kind of sugar, as it is in green plants.

Saprophytic plants. These are the organisms that cause most of the decay of organic matter. They live upon and obtain food from the dead bodies of plants and animals, and also from the products of all living organisms. Some of them have enzymes that digest cellulose, pectic compounds, and even kerosene and coal. Digestion of these substances occurs outside the body of the plant. Their enzymes, therefore, must diffuse from the living cells where they are synthesized into the surrounding media.

[2] Probable exceptions are the sulfur bacteria. Although they utilize the sulfur reduced by other plants, it is possible that sulfofying bacteria could survive independently by utilizing the sulfur and sulfur compounds (SO_2 and H_2S) emitted by volcanoes. The iron bacteria also have possibilities of living independently of other plants.

External digestion and the digestion of substances that cannot be digested by most other organisms are outstanding features of this group of plants. Among the animals there are a few protozoans, such as those in the alimentary tract of termites, that can digest cellulose. External digestion, however, is a common characteristic of animals, for the food within the alimentary tract is still outside the cells of the body. The processes that occur in the digestion of bread in the alimentary tract of an animal are no different fundamentally from those that occur when bread is decomposed by mold. The plant may digest certain substances the animal cannot, but saprophytic plants are present in the alimentary tracts of animals and they may digest certain substances there. Some wood-boring beetles can chew the wood, but their internal fungi digest it.

Without the saprophytic plants the surface of the earth would soon become encumbered with the undigested remains of plants and animals.

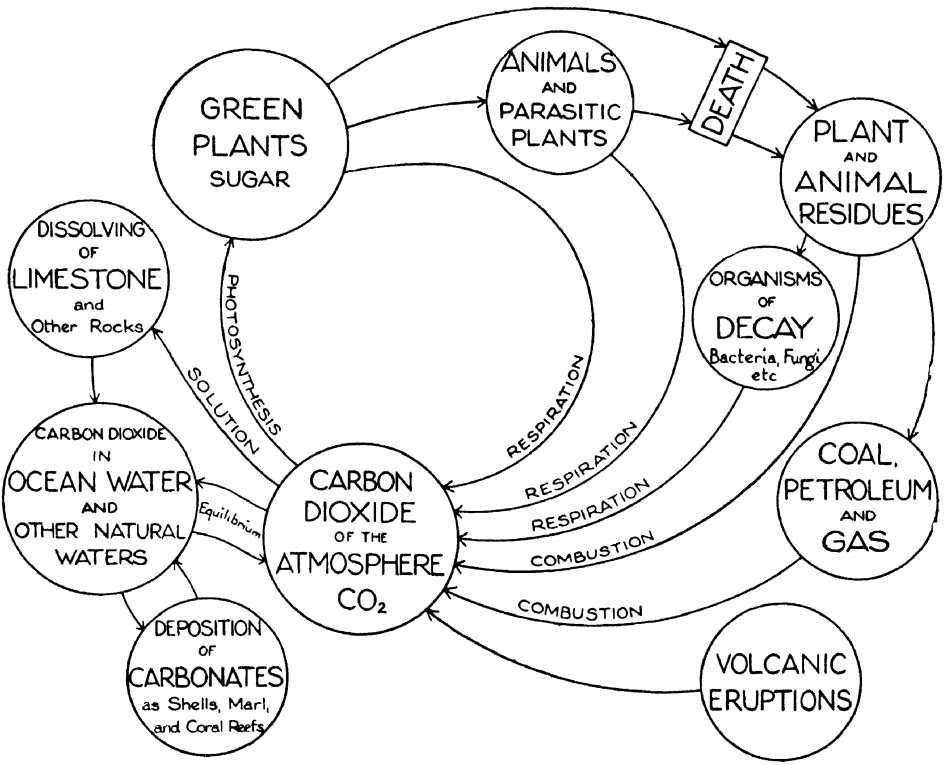


FIG. 228. The carbon cycle in nature.

Except in bogs where the growth of saprophytes is comparatively slow, only a thin surface layer of humus has accumulated in all of geological

time. Moreover, without a comparatively rapid digestion of cellulose and the subsequent oxidation of the products of digestion, the supply of carbon dioxide in the air would gradually become depleted (Fig. 228).

During decay not only is carbon dioxide formed and liberated to the air, but inorganic ions are liberated from their organic union and are again available to green plants.

Some saprophytic plants are valued in industry because they do not completely oxidize certain compounds, but leave a residue which man values for certain purposes. These residues are often referred to as products of fermentation. The complete oxidation of a substance in saprophytic plants usually consists of a series of steps, each of which is the result of the activity of successively different organisms. Sugar is oxidized to alcohol by yeast. Acetic acid bacteria oxidize the alcohol to acetic acid. Other organisms then oxidize the acetic acid to simpler compounds and finally all are oxidized to carbon dioxide and water. After insoluble substances are digested, many intermediate and successively simpler compounds may be formed before oxidation is complete. Moreover, the kinds of intermediate products formed vary with the species of organism that oxidizes each of them. The industries producing beer, wine, vinegar, glycerin, alcohol, and cheese all depend upon the fermentation products of carefully cultivated species of saprophytes. The quantity and quality of the products vary with the kinds of fungi and bacteria present.

The unpleasant odors of decaying matter likewise are due to the intermediate products of oxidation-reduction which are formed during the growth of certain bacteria and fungi.

Saprophytes are ever-present agents of destruction, and are the organisms that make cold storage and refrigeration necessary in our modern civilization. The freezing, canning, drying, and preserving industries are based on methods of eliminating saprophytes. Buildings and other wood structures are protected from them by means of metal, paint, tar, and creosote. As agents of decay they dissipate more of the energy chemically bound in sugar during photosynthesis than all other living organisms combined. On the other hand their very destructiveness is valued as a means of removing sewage and other undesired organic products. Saprophytes, then, are as intimately associated with our daily lives as are the green plants and parasites.

CHAPTER XLII

THE BIOLOGY OF BACTERIA

Of all the groups of non-green plants, the ever-present bacteria and their effects are most often discussed among educated people everywhere. Although the great majority of the human race has never seen bacteria, every individual has had both direct and indirect contacts with them. Characteristics of some bacteria are indicated in Figs. 229A, B, C. They are the causes of many diseases and of much of the decay of organic substances. Certain pleasant and unpleasant flavors of foods such as cheese, milk, butter, and eggs result from bacterial action, and bacteria influence our lives in many other ways. As a matter of fact, household sanitation, sewage disposal, refrigeration, quarantine, vaccination, aseptic surgery, personal hygiene, and all of our splendidly organized and vitally necessary methods of guarding and purifying water have developed as we have learned how and where bacteria live and how they affect plants and animals, including ourselves.

Some bacteria manufacture their own food; others obtain it from living or non-living sources. A few species are unique in that they can synthesize sugar and other foods from water, carbon dioxide, and inorganic salts. Most species, however, depend upon an external source of sugar, and sometimes of protein also. At one end of the scale are the bacteria that derive energy from light, or from compounds containing reduced nitrogen, iron or sulfur, and synthesize sugars and other foods. Such organisms are independent of other living plants except for the sources of reduced nitrogen and sulfur. At the other extreme is the obligate parasite that grows only in the living tissues of another organism. Between these two extremes are the various kinds of saprophytes that live and multiply upon the dead tissues and products of other organisms.

The autophytes among bacteria include the nitrifying bacteria that oxidize ammonia to nitrates and nitrites; the iron bacteria which oxidize ferrous to ferric salts; and some sulfur bacteria that oxidize reduced sulfur. These are extremely important in soil development and will be

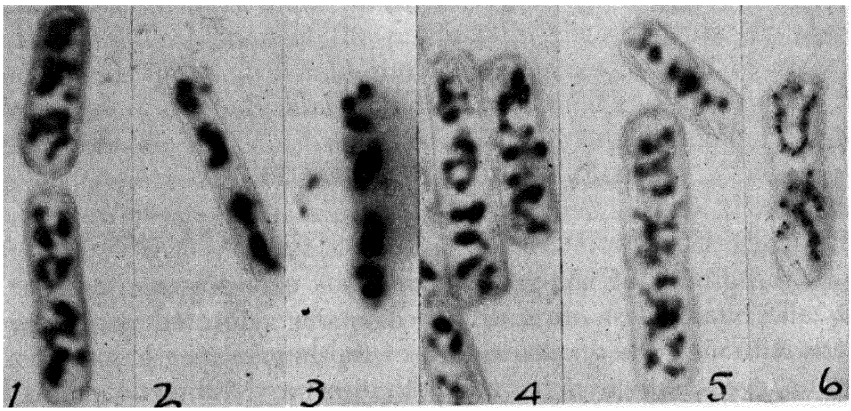
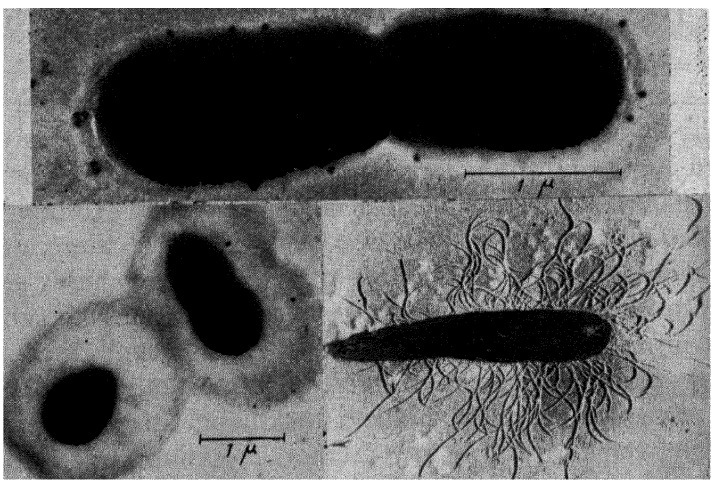


FIG. 229A. Nuclear division in *Bacillus megatherium*. 1, polar view of 3 chromosomes in bottom nucleus of upper cell; 3, spindle formation in second nucleus from top; 4, 5, nuclear membranes; 6, chromosomes as long beaded threads (all × 4850). Original from E. D. DeLamater.



(bacteriophage) (after Luria, Delbruch, and Anderson). Lower left: *Diplococcus pneumoniae* (Type I) with a slimy sheath, or capsule, after exposure to type I antiserum (after Mudd, Heinmets and Anderson). Lower right: a giant bacterium with many flagella (× 4500) (modified after Crowe and Robinow). All from Henrici and Ordal, *The Biology of Bacteria*, 3rd ed. Courtesy of D. C. Heath and Company.

discussed in more detail in the following chapter. The energy released by these oxidations is utilized in the synthesis of sugar and other foods. The other autophytes are the green and purple sulfur bacteria, the first of which utilize the energy of light and the second the energy of reduced sulfur in making sugar.[1]

Most species of bacteria are obligate saprophytes or parasites, but some of them may grow either as parasites or as saprophytes.

External factors and bacteria. The environments in which bacteria and their allied organisms live and reproduce are so different from those of larger plants that some of the effects of environmental factors need to be considered, especially those of light, water, oxygen, and temperature.

Light. Most bacteria, because of their location in soil, in foods, in decaying matter, and within other living organisms are rarely exposed to the direct rays of light. Most species live only a few hours when exposed to full sunlight. Sunlight, therefore, is a destructive factor in the development of most bacteria and of great importance in the purification of rivers polluted with sewage, and in the elimination of bacteria from all exposed surfaces.

The rapidity with which certain bacteria are killed by direct light depends upon the intensity and quality of the light. Although the evidence is extremely difficult to obtain and the results are often conflicting, it appears that the rays of the blue and violet end of the visible spectrum are most injurious to bacteria, particularly the pathogenic species. The intensity of the light used must always be kept in mind in comparing the destructive effects of various radiations. Near infra-red rays through their heating and drying effects may be germicidal. The ultra-violet rays are very destructive and have proved to be very important in hospitals and in water purification. Bacteria are destroyed by short rays of light apparently through the coagulation of the protoplasm, or the formation of some toxic substance in the medium.

Water. Bacteria cannot grow and multiply in the absence of water, although some may remain alive for months or years in an arid environment.

About 85 per cent of the weight of active bacteria is water. Spores are

[1] In the green sulfur bacteria hydrogen sulfide replaces water in the process of photosynthesis and sugar, sulfur and water are the end products. The purple sulfur bacteria utilize the energy from oxidation of sulfur to sulfates in the synthesis of sugar. Generalized equations representing these chemical changes are:

$$6CO_2 + 12H_2S \longrightarrow C_6H_{12}O_6 + 6H_2O + 12S$$

$$3H_2S + 6CO_2 + 12H_2O \longrightarrow C_6H_{12}O_6 + 6H_2O + 3H_2SO_4$$

supposed to contain much less water than the vegetative cells. Diffusion of foods and other materials into the bacterial cell is impossible unless the cell is surrounded by at least a film of water. Current statements that living bacteria have persisted inside rocks since the time of their formation a million years ago have not been generally accepted, because of the almost insurmountable difficulties in proving that these microorganisms may not have been carried into the minute pores of the rocks with the movements of underground water and gases.

The solution or substrate in which bacteria grow is commonly called the *medium* (pl., *media*). The properties of a medium are determined by the substances it contains. For example, sugar and salts may be in solution in the medium, thus determining its concentration. When the concentration of water in the medium is less than in the bacterial cells, water diffuses out of the cells and the bacteria may become inactive. Consequently jellies keep more readily than preserves, preserves more readily than canned fruits, and canned fruits more readily than fruit juices to which no sugar has been added. Jellies have a high concentration of sugar and a comparatively low concentration of water. In the fruit juices the converse is true.

In the laboratory bacteria are often placed in gelatin or agar media. When the water content of gelatin falls below 50 per cent, bacteria develop very slowly. When the gelatin dries out, the vegetative cells become inactive and eventually die. As noted above, however, many bacteria, especially those found in the soil, may live—but not grow—for months or years in a desiccated state. Since most of the bacteria that are causes of disease cannot survive desiccation, there is little danger of living ones being carried long distances by air currents.

Oxygen. Molecular oxygen is essential to nearly all living organisms. A few kinds of bacteria, however, can live without it. Most organisms use free oxygen in the respiratory processes and are known as *aerobes*. Some bacteria, such as those that are the causative agents of lockjaw and those that cause butter to become rancid, grow only when the free oxygen content of the medium is extremely low, and when organic substances containing combined oxygen are available. These bacteria are known as *anaerobes*. Anaerobic bacteria occur especially in poorly drained soils, in deep waters of lakes and seas, and in all sorts of media from which oxygen has been removed or excluded.

Bacteria are exposed only to the oxygen that is dissolved in the medium surrounding them. At room temperature this is ordinarily a very dilute

solution equivalent to dissolving 1 cc. of free oxygen in 100 liters of water. If the oxygen content of the medium is increased to 30 times this amount, most bacteria die. In other words, oxygen at such concentrations has the same effect on bacteria as a solution of formaldehyde, or bichloride of mercury, two of our commonly used antiseptics. Even pronouncedly aerobic bacteria cannot withstand very high concentrations of oxygen. If the oxygen content of the air above the nutrient medium is increased to 4 times the usual amount, the growth of some strains of *Streptococcus* is stopped. Even the same strain of bacteria differs in its susceptibility to oxygen according to the medium in which it is growing. Anaerobic bacteria grow better within liquid media or below the surface of agar media because of the decreased oxygen content. Among the bacteria there is a marked diversity in their endurance of molecular oxygen.

Hydrogen peroxide (H_2O_2) is toxic to bacteria because it changes readily to water and atomic oxygen which is very active chemically. In the presence of molecular oxygen, hydrogen peroxide may be formed in the medium in which the bacteria are growing. The hydrogen peroxide may in turn be toxic to the bacteria.

Temperature. When compared with other plants, bacteria as a group can live under a very wide range of temperature conditions. In this respect they are perhaps equaled only by the blue-green algae. The temperature of the bacteria is of course the same as that of the media in which they grow. Within a limited range, high temperatures accelerate life processes and low temperatures retard them. Food is used less rapidly at lower temperatures, and bacteria with a limited food supply live longer under such conditions.

Some of the bacteria that thrive in hay infusions multiply at temperatures as low as 40° F. or as high as 110° F. The minimum temperature at which some species can grow may be higher than the maximum temperature at which others can survive. The optimum temperature for most bacteria lies between 70° and 100° F. Few species continue vegetative development at temperatures higher than 115° F. Some bacteria, however, that bring about the rapid decay of organic matter, such as silage, may live at temperatures as high as 175° F. Living bacteria have also been found in hot springs at temperatures but little below this figure. This endurance of high temperature is remarkable in view of the fact that many proteins begin to coagulate and some fats begin to liquefy and separate at 145° F.

Although bacteria are often distinguished as aerobes and anaerobes as

noted above, certain species may grow as aerobes at one temperature and as anaerobes at another. Many of the high-temperature bacteria, for example, will not grow at temperatures below 110° F. when exposed to air, but will grow under anaerobic conditions at 95° F.

At temperatures near the freezing point bacteria grow very slowly, but may survive for weeks or even months. When freezing occurs and the medium becomes solid, diffusion is extremely slow and life processes are reduced to a minimum. Typhoid bacteria are known to have lived four months in ice cream and for about five years when kept frozen. Streptococcus bacteria that cause sore throat may also live in ice cream. Certain pathogenic bacteria and some of the common microorganisms of the soil are known to survive for a few days when exposed to the temperature of liquid air (about −310° F.). Cultures of certain bacteria have been exposed to the temperature of liquid hydrogen (about −425° F. or about 35° above absolute zero) for short intervals with no apparent harm to the organisms.

What are bacteria? Bacteria are at once the simplest in structure, the smallest in size, the most abundant, and the most generally distributed of all plants, both green and non-green. Only the blue-green algae are comparable in these respects. Although one-celled organisms, bacteria often cohere in distinct groups more or less heritable in form. The cells have gelatinous sheaths; and when many of the sheaths coalesce, the bacterial scums often seen on water and on damp objects are formed.

The cells of bacteria are so small that their exact structure is difficult to ascertain. Definite cell walls exist in most bacteria, but relatively little is known about their chemical composition. Nucleo-proteins containing nucleic acids characteristic of those present in chromosomes have been obtained from some bacteria by chemical analyses. Nuclei, chromosomes, and mitotic-like figures have been noted in a few bacteria after special treatments of the cells (Fig. 229A). Whether or not nuclei and chromosomes are present in all bacteria, the occurrence of species and races of bacteria is good evidence that the hereditary mechanism in them is as definite as it is in other organisms. One would expect genes in bacteria to mutate as they do in other organisms, and there is evidence that new races of bacteria originate in this way. Certain observations are interpreted by some investigators as evidence of sexuality in bacteria, but this interpretation is regarded as inconclusive by others.

A few bacteria move about by a gliding movement not understood

at present. Many species are not motile at all; but in others protoplasmic threads known as *flagella* (sing., *flagellum*) extend through the cell wall and are organs of locomotion. A single flagellum may be several times the length of the cell. Locomotion results from a rotary or whip-like movement of the flagella. The flagellate forms are active for a time but later become stationary and lose their flagella. Brownian movement of both living and dead bacteria is a common phenomenon.

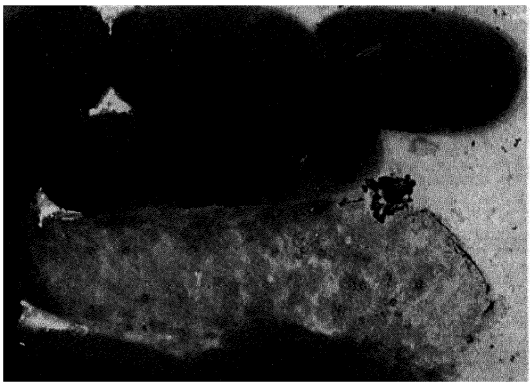


FIG. 229C. Micrograph of *Escherichia coli* 30 minutes after virus inoculation of bacterial colony. Note a single lysed cell (× 15,200). Original from Stuart Mudd.

Bacterial cells are slightly heavier than water (sp. gr. 1.038 to 1.065). The largest bacillus studied is from 3 to 6 microns in diameter and 40-60 μ in length. The coccus forms may vary from 0.15 μ to more than 1 micron in diameter. It requires several billions of such cells to weigh a milligram.

Destruction of bacteria by viruses. In some cultures of bacteria certain particles much smaller than bacteria appear. These particles are known as *viruses,* or virus-like *bacteriophages.* They may become adsorbed on the surfaces of bacteria (Fig. 229B). Soon after this adsorption, often less than a half-hour, the bacterial cells swell and finally burst, leaving only scattered debris and virus particles, or remains that are referred to as "ghost cells." Such disintegration is known as *lysis.* See Fig. 229C.

Do bacteria cause disease? A century ago so little was known about bacteria that this question could not be answered with certainty. The techniques necessary to ascertain the definite connection between a certain bacterium and a particular disease had not yet been discovered. Today some people have the mistaken notion that all bacteria are harmful. Bacteriologists know that only a very small percentage of the species of bacteria cause disease.

Cell division and reproduction. Bacteria multiply by simple cell division, and the resulting halves form two new individuals. Under favorable conditions these individuals in turn divide, and there are four

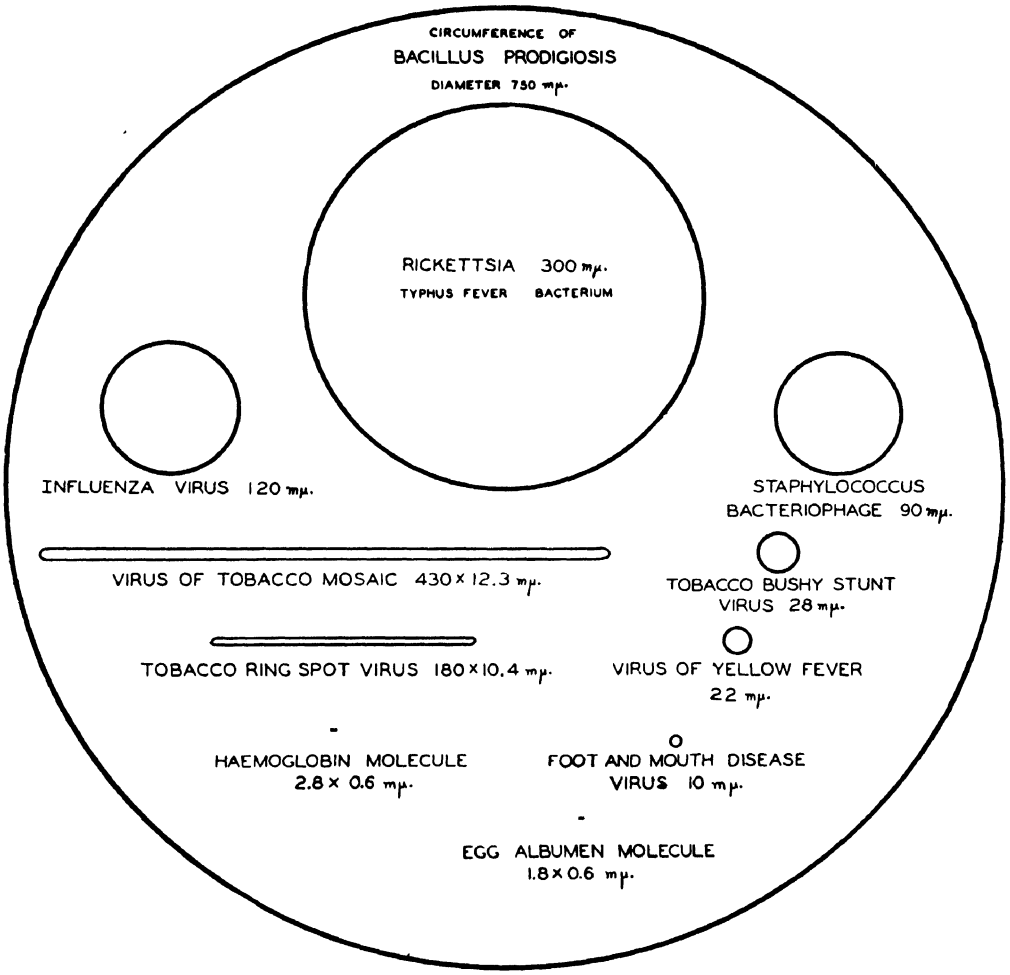


FIG. 230. Diagram of the relative sizes of several viruses compared with those of certain bacteria, bacteriophage, and protein molecules. On the same scale the diameter of a human red blood corpuscle would be 3.5 feet. Data from W. M. Stanley.

individuals. This process may continue indefinitely. At suitable temperatures divisions may occur as often as every 20 minutes, which is the same as saying that an individual may exist but 20 minutes. A little computation will show that within a day the number of such rapidly dividing bacteria becomes enormous. If division occurred every 30 minutes, starting with one bacterium, we would have: At the end of 24 hours, 281 million million bacteria = 1 pint in volume. At the end of 48 hours, 281 million million pints = about 32 cubic miles of bacteria.

Such rapid increases of bacteria are limited to very short periods of

time. Toxic substances that inhibit growth of bacteria often appear in the medium. Their food, water, oxygen, and salt supply is limited to the film immediately surrounding them. Colonies of bacteria cannot become very large because the movements of substances through the mass is limited by the rate of diffusion. In nature other environmental factors such as light, moisture, and temperature rarely remain favorable for long periods. Bacteria are also consumed by many microscopic animals.

The protoplasm of a bacterial cell may contract into a rounded mass at one end, or in the middle, with the formation of a secondary wall; this mass is termed a *spore*. It contains less water, is less likely to be injured by drying, and will endure greater extremes of temperature and greater concentrations of poisons than the ordinary bacterial cell. It is because the spores of certain bacteria can withstand a temperature of boiling water that steam pressure is used in sterilizing cans of corn, beans, peas, and other vegetables. Most of the bacteria that cause diseases do not form spores. Those that cause botulism and tetanus are exceptions.

Bacteria and sanitation. We often go to considerable trouble to prevent decay; but we owe our continued existence on the earth to the fact that bacteria (and fungi) remove the dead bodies of plants and animals that would otherwise have accumulated on the earth. Together with the fungi they secrete enzymes which digest the highly complex organic substances composing the bodies of plants and animals into simpler substances. By repeated oxidations these substances are ultimately changed into carbon dioxide, water, and inorganic salts. These are again available to green plants.

The sewage that is drained into rivers is digested and oxidized by bacteria to simple harmless compounds. Our great cities, where thousands and sometimes millions of people are crowded into a small area, must have enormous sewage-disposal works in which aeration and other conditions are made favorable for a more rapid growth of the bacteria of decay, and the quick destruction of the sewage. This prevents the pollution of streams, lakes, and harbors into which the sewage would otherwise be carried.

The modern processes of filtering and purifying the water supplies of cities not only remove sediment, but also eliminate the bacteria of disease. The processes include adding minute quantities of alum and chloride of lime to the water, and then filtering it through sand. For

many years the water-borne organism causing typhoid fever took a large annual toll in human lives. Cities are now practically free of this disease; most typhoid cases originate from polluted well water in rural communities. To eliminate the contamination of surface wells requires merely careful location and construction of the wells with reference to surface drainage which often contains large numbers of bacteria.

Sanitary practices, such as quarantine, disinfection, admitting direct sunlight into living rooms, cleanliness, cooking foods, pasteurizing milk, and keeping foods in refrigerators, are all related to the elimination or the reduction of the number and kinds of bacteria with which we come into contact.

Bacteria and disease. While most bacteria are not causes of disease, some are, and these are known as pathogenic bacteria. The invasion of the body tissues by bacteria is known as *infection*. The severity of the disease depends upon the ability of the organisms to invade the tissues, multiply rapidly, and cause injury. The injury to the body is due to the destruction of tissues and the formation by the bacteria of certain poisonous substances called *toxins*. When the body is invaded, *antitoxins*, or *antibodies*, are formed that neutralize the effects of the toxins either by combining with them chemically, or otherwise rendering the cells immune. In this way the body is protected until the bacteria are destroyed by the colorless blood cells (leucocytes), or until the bacteria are made harmless by other means.

The term *immunity* denotes the qualities of a plant or animal by which the invasion or growth of pathogenic organisms is prevented, or their products are rendered harmless. A plant or animal is *susceptible* to an infectious disease when such qualities are absent, or inadequately developed. Not all persons are equally susceptible to certain diseases, and susceptibility may vary in the same individual from time to time. A person is usually immune to a disease if his blood contains the corresponding antibody, or is able to produce it. Some of the more common bacterial diseases of the human body are tuberculosis, pneumonia, diphtheria, typhoid fever, and tetanus.

Diseases of plants. Although most of the diseases of plants are caused by fungi, the destruction of plants by bacteria is often sufficient to present a serious economic problem. Bacteria may be present in the healthy tissues of some plants. They may, however, penetrate the host through wounds or natural openings and then spread throughout the plant or remain localized within certain tissues. They are carried from

plant to plant by insects, by man, and by other animals. Bacteria are less frequently dispersed by rain and wind.

Bacteria in milk. Among the natural media in which bacteria grow, milk is ideal for most bacteria of decay and some pathogenic organisms (pathogens). Milk, then, must be handled carefully if it is to be used as food. The cows, the stable, the vessels in which the milk is placed, the persons who handle it are all possible sources of bacterial contamination. It is of paramount importance that attention be paid to cleanliness and to the retardation of bacterial growth by immediate refrigeration.

In spite of all precautions, bacteria do occur in milk. To check their multiplication, particularly after shipment from the dairy farm to the cities, the milk is heated. This process, which is known as *pasteurization,* destroys nearly all the active pathogens. Such heating, however, does not kill spores; but if the milk is kept cool, their subsequent germination and growth are largely prevented. Milk may be heated to 165-175° F., held a few seconds, and immediately cooled again.[2]

The bacteria of natural waters are discussed in Chapter XLVI.

The science of bacteriology. The study of bacteria has made great strides since Leeuwenhoek in 1676 first saw through his crude magnifier the "animalcules" from his teeth. Many years elapsed and many investigations were made before the biological significance of these microorganisms was established. Even now a large portion of the world's population has never heard of bacteria, a larger number is indifferent to their importance, and too many people still like to believe that disease results from mysterious influences rather than from bacterial infection.

Spontaneous generation. Since earliest times man has probably been interested in the question of the origin of living organisms on the earth, and has tried to formulate answers on the basis of what he imagined or what he observed. Some of these observations, and also the inferences drawn from them, we now know were erroneous. It was believed, for example, that mice came from rags and meal, that mud produced frogs, that putrid meat changed to bees and flies, and that water in some manner gave rise suddenly to all sorts of *fully formed* aquatic organisms. Although many people ardently subscribed to a special creation of each kind of plant and animal, they at the same time accepted the idea of the spontaneous production of such organisms from inorganic matter. It required, of course, only simple experiments to show that screened

[2] This is the so-called *flash* method. The *holding* process of pasteurization consists in heating the milk to 140-150° F. for 30 minutes.

meats produce no maggots, that rags and meal inside stoppered bottles never give rise to mice, and that frogs develop from frog eggs and not from mud. Although a few individuals as early as the 17th century definitely expressed the opinion that organisms arise only from preexisting organisms, it was not until after the middle of the 19th century that the theory of spontaneous generation was shown to be utterly false as an explanation of the origin of fully formed plants and animals.

Speculation. Early Greek philosophers, including Aristotle (384-322 B.C.), all subscribed in their writings to the idea of spontaneous development of living organisms. Their statements were copied and enlarged upon by nearly all the medieval scholars of Europe. For example, there was then a widespread belief in the "goose tree" and the "vegetable lamb." Geese and ducks were thought to be formed either directly from the fruit of certain trees, or from sea shells borne by these trees. Current also were the so-called observations that certain trees bore melon-like fruits containing fully formed lambs. Such incredible accounts as these were widely accepted until early in the 18th century.

Early experimentation. During the 16th century a few investigators with a desire to experiment for themselves showed that spontaneous generation of some organisms was clearly erroneous. Van Helmont (1577-1644), although he thought his experiment proved that mice came from wheat grains, was troubled because these mice were just like those borne by a female mouse.

The Italian physician Redi (1626-1697) proved experimentally that "worms" in meat are fly larvae. He further showed that if the flies are kept from depositing eggs on meat, no larvae develop in it. Redi did not, however, draw the inference that this experiment disproved spontaneous generation. Indeed, he suspected that "worms" in plant galls arose spontaneously from plant juices. Vallisneri (1661-1730) soon afterward proved that these "worms" likewise developed from the eggs of insects.

Leeuwenhoek and his microscopes. The early Dutch student of microscopy, Leeuwenhoek (1632-1723), looking through his simple magnifiers, saw organisms invisible to the unaided eye. He examined all sorts of infusions containing microorganisms, and left accurate descriptions, and many remarkable figures of bacteria, yeasts, algae, and many other organisms. Leeuwenhoek did not subscribe to the theory of spontaneous generation, but insisted that the tiny organisms he saw grew from similar organisms that got into his infusions from the air.

Sterilization by heat and chemicals. In 1776 Spallanzani (1729-1799), an Italian, proved that if meat broth is heated for an hour or two in hermetically sealed flasks, no microorganisms develop in the broth. The methods employed in this simple experiment were used by Appert in 1810 to exclude bacteria and molds from foods, and are the basis of our canning industry. The objection was immediately made, in the case of Spallanzani's experiment, that the heating had spoiled the air inside the flask so that no organism could live there, and therefore that spontaneous generation had not been disproved. Upon exposure to air the broth was soon teeming with organisms. For this objection Spallanzani's experiments provided no explanation.

Schultze in 1836 obtained similar results, although he admitted air to his previously heated flasks of broth through tubes containing strong acids and other chemical compounds. Schwann (1810-1882) the same year allowed the air to enter the flasks through intensely heated tubes. It was argued by opponents that both the heat and the chemicals had altered the air. Von Schroeder and von Dusch in 1854 filtered air entering the flasks through cotton or wool plugs, and no organisms developed in the flasks of broth. These experiments are the forerunners of the modern use of cotton plugs in culture flasks in all pathology and bacteriology laboratories.

The chemical theory of fermentation. Owing to poor techniques, other investigators often failed to confirm the results of these experiments or to secure consistent results, and the belief in spontaneous generation continued. About this time the so-called *chemical theory of fermentation* was current, and this indirectly gave comfort to the proponents of spontaneous generation. This theory, supported by Liebig (1803-1873) and others, assumed that in decay, or in fermentation, large molecules simply disintegrated into smaller ones, and that fresh meat spoiled because it came into contact with other spoiled meat which initiated the breaking up of the molecules. In other words, this theory would imply that microorganisms, though they may accompany decay and fermentation, are not the causes of these putrefactive processes.

Louis Pasteur. A few people had suggested as early as the 18th century that bacteria, or certain microscopic agents, are the causes of fermentation and disease. But it was not until the latter half of the 19th century that Louis Pasteur (1822-1895) with a series of brilliantly planned and expertly conducted experiments finally eliminated the idea of spontaneous generation as a correct explanation for these phenomena.

Pasteur's first conviction that microorganisms are the *cause* and not the *result* of fermentation came when he was investigating the troubles in the beet-sugar distilleries at Lille, France. Besides the normal fermentation resulting in alcohol, the vats frequently contained lactic acid, a product for which there was no market. Pasteur found that when yeasts were present alone in the vats, alcohol was formed. When certain rod-shaped bacteria were present, however, lactic acid appeared also. By properly transferring the two organisms to sugar solutions he was able to secure either alcohol or lactic acid at will, depending upon whether the yeast or the bacterium was present in the solutions.

The proponents of spontaneous generation were still not convinced and demanded more proof. Pasteur felt certain that bacteria are present in the air and set about to verify his conviction. He prepared numerous flasks of various sterilized media, sealed the sterilized flasks, and later opened them at various places, such as in rural districts, on busy street corners, and on mountain tops. The results indicated clearly that bacteria are much more abundant in some areas, such as dusty streets, than in quiet countrysides or mountain tops. Even then the skeptics were unconvinced: they insisted that the sealing of the flasks had brought about an unnatural condition.

Pasteur soon afterward utilized an experimental idea that did away with the necessity of sealing the flask. Sterile media were placed in sterile flasks the necks of which had been drawn out into long, narrow S-shaped tubes having very small openings at the outer ends. In this experiment the flasks were not sealed, and the culture media were given free access to the air. No matter where the flasks were placed or how long they were kept, bacteria did not develop in the media. But when the flasks were opened so that the media became exposed to air in the usual way, they soon became contaminated. The results of these experiments were clear, but there was a lack of unanimity in the inferences drawn from them. Pasteur was so sure of the completeness of his demonstration that in a public lecture at the Sorbonne in 1864 he closed his address with these prophetic words: "Never will the doctrine of spontaneous generation recover from the mortal blow of this simple experiment." Nearly all thinking people now accept the fact that organisms arise only from preexisting organisms and not by spontaneous generation. Some of the flasks prepared by Pasteur have been kept to the present time, and no living organisms have appeared in them.

Two centuries earlier, Redi had proved experimentally that worms

do not arise spontaneously from meat. From the time of Redi to that of Pasteur many critical experiments were performed. One result of these experiments was the gradual abandonment of the idea that plants and animals like those on the earth today arise by spontaneous generation. Progress in understanding the origin of living organisms, and in following certain practices, such as those of sanitation, personal hygiene, aseptic surgery, and the preservation of food, was seen to depend upon other ideas and upon further discoveries.

Even more impressive than all these early experiments are the facts known today about the composition, organization, and correlations of the parts of living cells, and of multicellular organisms. That such highly organized structures could arise suddenly from either inorganic or organic masses of matter appears quite untenable. Even if non-living colloidal masses of organic matter ever attain the state of being alive, escape destruction, and multiply, a very long geological period of time would elapse before highly organized cells capable of exact duplication by reproduction could evolve. After considering pertinent data from all fields of science for 25 years, Oparin came to certain conclusions about the probable origin of living organisms on the earth, and clearly summarized the data and conclusions in a small book which is cited at the end of this chapter.

Pasteur's experiments were not limited to the question of spontaneous generation. He studied vinegar-making, silkworm diseases, rabies, and diseases of sheep and cattle. He not only showed that bacteria and other microorganisms cause diseases, but he developed methods of vaccination that made man and other animals immune or at least less susceptible to certain diseases. Perhaps one of the most touching stories in all biology is that of Pasteur's treatment of the little boy who was bitten by a mad dog.

Modern bacteriology. Out of the experiments of Pasteur and equally significant ones by Koch (1843-1910), Lister (1827-1912), and many others, the modern techniques used in the control of pathogenic organisms have developed. Bacteriology is now an important biological science with many specialized phases of research in medicine, dentistry, veterinary medicine, agriculture, dairy technique, plant pathology, and many industrial processes.

Methods of killing and controlling bacteria. It was known long before bacteria were discovered that certain practices are valuable in the preservation of foods, caring for wounds, and the prevention of disease.

Most of these methods were found out accidentally because the true nature of putrefaction and diseases was unknown for many centuries, and these methods are consequently crude and often not dissociated from magic. There is now a great body of experimentally established facts about the control of bacteria. In the references below, further information may be secured about the effectiveness and uses of the following means of controlling bacteria: cleanliness, ventilation, sunlight, drying, refrigeration, antiseptics, brine and sugar solutions, sterilization, fumigation, pasteurization, canning, precipitation by chemicals, isolation, vaccination, antitoxins, and serum treatment.

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CHAPTER XLIII

BACTERIA OF THE SOIL

Bacteria of many kinds—both harmful and beneficial—live and grow in the soil. They are often incredibly numerous, sometimes numbering as high as a billion individuals in a gram of fertile garden soil. Some of the relations of bacteria to decay and disease were described in the preceding chapter. We shall now consider the importance of soil bacteria to cultivated plants and soil formation. Many soil bacteria are important in the maintenance and improvement of fertility; some have quite the opposite effect.

Distribution. Most soil bacteria occur in the upper two to ten inches of the soil where the supply of organic compounds is usually greater. In the surface inch of soil, bacteria are not so numerous because of the destructive effects of light and of frequent desiccation. Relatively few bacteria are found below a depth of two or three feet in humid regions. In well-aerated soils, such as those of irrigated semi-deserts, bacteria grow at greater depths. They are probably always present as far down as the roots of plants extend.

Nitrogen sources of green plants. Since nitrogen makes up such a large part of the atmosphere of the earth, it was early assumed that green plants obtain nitrogen from the air. The noted chemist, Liebig, was convinced that this must be so, for he believed that the ammonia of the air was a sufficient source of nitrogen for plants. A long time and many experiments were needed to show that nitrates and ammonium salts in the soil are the usual sources of nitrogen in plants. Although this fact was surmised in 1838 by Boussingault of France, and in 1847 by Lawes and Gilbert of the Rothamsted Experimental Farms in England, nearly a half century elapsed before final proof was obtained. The various methods by which atmospheric nitrogen is combined in compounds which green plants can utilize began to be understood just before the beginning of the present century.[1]

[1] For a discussion of the experiments of some of the most important contributors to our knowledge of how green plants obtain nitrogen, consult any good text on soil microbiology.

The occurrence of nitrogen compounds usable by green plants is due almost entirely to the action of certain bacteria. Such bacteria may be referred to as *nitrogen bacteria*, and several groups are known to play an important part in the nitrogen cycle in nature. The importance of such microorganisms is recognized when we recall that every time a crop is harvested, the nitrogen within the plant is removed from the field. In the course of a few years this practice, along with the natural leaching by water, would seriously deplete the nitrogen content of the soil. To maintain soil fertility the nitrogen compounds lost in this way must be constantly renewed. The nitrogen bacteria are very important in this renewal.

The three groups of bacteria that form nitrogen compounds usable by green plants are the *ammonifying bacteria*, the *nitrifying bacteria*, and the *nitrogen-fixing bacteria*. A fourth group, the *denitrifying bacteria*, by releasing nitrogen from these compounds, have the opposite effect and decrease the nitrogen content of soils.

Ammonifying and nitrifying bacteria. Although millions of dollars are spent every year in adding commercial fertilizers containing nitrogen compounds to soils, our immediate interest is how the combined nitrogen in natural organic compounds is again made usable to green plants. These compounds include the undecayed remains of plants and animals. The ammonifying and nitrifying bacteria bring about a chain of chemical and physical processes by which the nitrogenous substances are transformed into simpler and more soluble compounds. These are really processes of decay, and the nitrogen bacteria are among the saprophytes that bring this about.

Ammonification. The disintegration and digestion of the large protein molecules of organic bodies in the soil are activated by *proteolytic* (protein-dissolving) enzymes. The resulting products, largely urea, peptones, and amino acids, undergo additional chemical changes by which ammonia (NH_3) is released. In so far as nitrogen is involved, this is a reduction process known as *ammonification*, and it takes place only through the agency of microorganisms. Some of the chemical reactions may be represented as follows:

$$\begin{array}{lll} \text{Urea} + \text{Water} & \longrightarrow & \text{Ammonium carbonate} \\ CO(NH_2)_2 + 2H_2O & \longrightarrow & (NH_4)_2CO_3 \end{array}$$

$$\begin{array}{lll} \text{Ammonium carbonate} & \longrightarrow & \text{Carbon dioxide} + \text{Ammonia} + \text{Water} \\ (NH_4)_2CO_3 & \longrightarrow & CO_2 + 2NH_3 + H_2O \end{array}$$

In addition to the investigators named above, Berthelot, Hellriegel, Wilfarth, Beijerinck, and Winogradski should be mentioned.

Nitrification. Ammonia in turn becomes the compound transformed in nitrate formation. Only a few species of soil bacteria activate this process; they may be classified into two groups. The first group oxidizes ammonia to nitrous acid.

$$\begin{array}{cccccc} \text{Ammonia} & + & \text{Oxygen} & \longrightarrow & \text{Nitrous acid} & + \text{ Water} \\ 2NH_3 & + & 3O_2 & \longrightarrow & 2HNO_2 & + 2H_2O \end{array}$$

The nitrous acid may form salts with basic ions in the soil.

$$\begin{array}{cccccccc} \text{Nitrous acid} & + & \text{Potassium carbonate} & \longrightarrow & \text{Potassium nitrite} & + & \text{Carbon dioxide} & + \text{ Water} \\ 2HNO_2 & + & K_2CO_3 & \longrightarrow & 2KNO_2 & + & CO_2 & + H_2O \end{array}$$

The formation of nitrous acid and nitrites from ammonia occurs in soils in America and Australia primarily in the presence of species of *Nitrosococcus*; in the soils of Europe, Asia and Africa species of *Nitrosomonas* are the nitrite formers.

The last stage in nitrification is the oxidation of nitrous acid and nitrites to nitric acid and nitrates.

$$\begin{array}{ccccc} \text{Nitrous acid} & + & \text{Oxygen} & \longrightarrow & \text{Nitric acid} \\ 2HNO_2 & + & O_2 & \longrightarrow & 2HNO_3 \end{array}$$

The nitric acid may form salts with basic ions in the soil.

$$\begin{array}{cccccccc} \text{Nitric acid} & + & \text{Potassium carbonate} & \longrightarrow & \text{Potassium nitrate} & + & \text{Carbon dioxide} & + \text{ Water} \\ 2HNO_3 & + & K_2CO_3 & \longrightarrow & 2KNO_3 & + & CO_2 & + H_2O \end{array}$$

Nitrous acid and nitrites seldom accumulate in soils, for as rapidly as they are formed other nitrifying bacteria of the genus *Nitrobacter* oxidize them to nitrates.

Thus the process of nitrification includes the oxidation of ammonia to nitrites, and the further oxidation of nitrites to nitrates. Each step in the process from proteins to ammonia, from ammonia to nitrites, nitrites to nitrates, is dependent upon the presence of appropriate bacteria. Nitrification is an oxidation process and the energy released is used by the bacteria in the synthesis of sugar from carbon dioxide and water, and also in the further elaboration of sugar and certain inorganic salts into proteins and other cell compounds of the bacteria. These microorganisms, then, are autophytes.

The conditions necessary for natural nitrification include moderate moisture, warm temperatures of the soil, good aeration, and fairly

neutral reaction, in addition to the raw materials necessary for certain food syntheses in the bacteria. The bacteria involved in ammonification are common and widespread in most soils, but the nitrifying bacteria are largely restricted to well-aerated, moist, nearly neutral soils.

Denitrification. The nitrates accumulated in soils through the agency of bacteria may disappear in several ways. They may be used by green plants, carried away by water, or changed into insoluble substances. They may also be reduced by other organisms to nitrous acid and ammonia, or to molecular nitrogen. This reduction of nitrates to gaseous nitrogen is referred to as *denitrification*. It occurs under certain conditions and decreases the nitrogen content of the soil. Some of the chemical reactions involved in the reduction of nitrates may be indicated as follows:

$$\begin{array}{lll} \text{Nitric acid} & \longrightarrow & \text{Nitrous acid} + \text{Oxygen} \\ 2HNO_3 & \longrightarrow & 2HNO_2 + O_2 \end{array}$$

$$\begin{array}{lll} \text{Nitrous acid} & \longrightarrow & \text{Water} + \text{Nitrogen} + \text{Oxygen} \\ 4HNO_2 & \longrightarrow & 2H_2O + 2N_2 + 3O_2 \end{array}$$

The organisms that bring about the reduction of nitrates are principally anaerobic bacteria, known collectively as *denitrifying bacteria*. Since denitrification is a reduction process and may occur in the absence of light, the organisms must obtain energy by oxidizing carbohydrates and other organic compounds.

Denitrification is likely to occur in any soil containing nitrates under anaerobic conditions. It is characteristic of poorly drained soils, and of soils periodically flooded, as in rice fields. In certain regions denitrification may so deplete the soil of available nitrogen compounds that plant growth is restricted.

Nitrogen-fixation. Nitrogen constitutes nearly 80 per cent of the earth's atmosphere; the combined nitrogen in all plants is relatively so small that if plants could directly use the free nitrogen of the air the supply would be inexhaustible. Over every acre of land surface the air contains nearly 300 million pounds of nitrogen. It has been calculated that the earth's atmosphere contains the prodigious total of over 5000 million million tons of nitrogen. In spite of this, nitrogen is the most expensive component of fertilizers.

Certain bacteria together with a few other organisms directly utilize the free nitrogen of the air. These bacteria transform this free nitrogen

into compounds usable by all plants. The chain of processes in this transformation is termed *nitrogen-fixation.*

It has been known for more than 20 centuries that certain legumes, such as clover, beans, and peas, enrich the soil. For this reason legumes have long been used in crop rotations because farmers have known that other crop plants grow better and yield more following the plowing under of legumes.

It was not definitely known that nitrogen compounds accumulate in legumes through the agency of nitrogen-fixing bacteria until 1886-1888.[2] Since that time the life cycles of these organisms have been thoroughly studied. These bacteria occur as microscopic motile rods free in the soil. When legumes are planted and roots form, the bacteria invade the cells of the roots by way of the root hairs. The root becomes infected and enlarges locally in the form of *nodules* (Fig. 231). These nodules

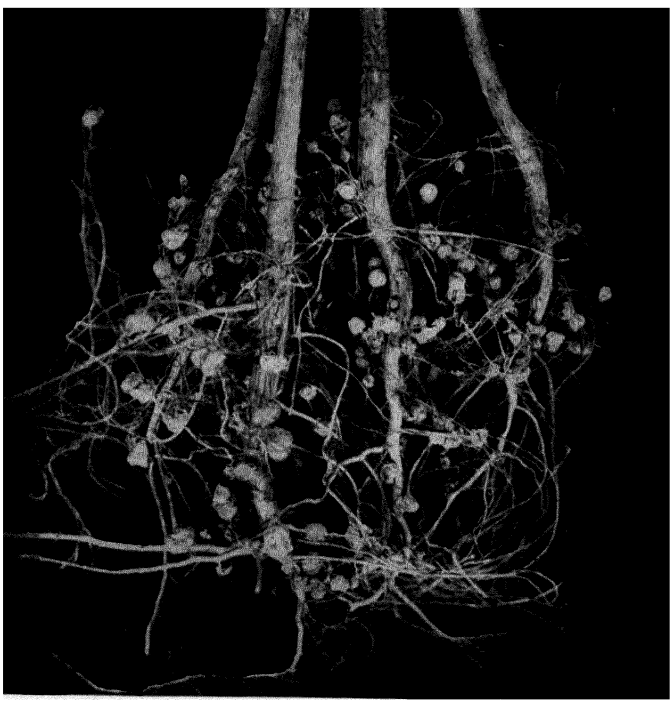

FIG. 231. Nodules containing nitrogen-fixing bacteria on the roots of soybean. Photo from Agricultural Extension Department, Ohio State University.

[2] First shown by Hellriegel and Wilfarth. Pure cultures of these bacteria were first isolated by Beijerinck in 1888.

contain millions of bacteria, which become somewhat enlarged and branched (Fig. 232).

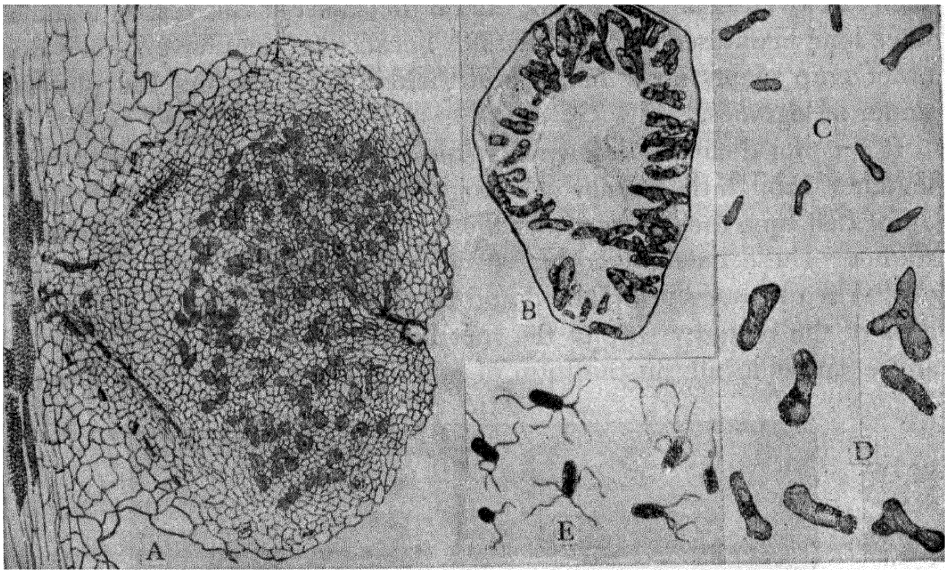

FIG. 232. Nitrogen-fixing bacteria: A, section of a nodule of bean root in which bacteria were present in many cells; B, one of the cells containing bacteria much enlarged; C-E, forms of nitrogen-fixing bacteria from nodules of different host plants: C, from soybean, D, from alfalfa, E, from common bean. From E. B. Fred, I. L. Baldwin, and E. McCoy, Univ. of Wisconsin, 1932.

The bacteria are dependent on the carbohydrates in the legume roots. Unless there is an abundance of sugar in the roots of the host plant, few or no nodules develop, because the bacteria do not invade the root hairs.

Although several species of bacteria infect legumes, there may be considerable specificity in their relations to the host. Some investigators have classified legumes on the basis of the bacteria to which they are most susceptible. The red, white, and alsike clovers, for example, constitute one group; alfalfa, sweet clover, and yellow trefoil another group; certain peas a third group; and cowpeas, peanuts, lima beans, and Japan clover still another group. Recent experiments indicate that the specificity of the nitrogen-fixing bacteria may not be as pronounced as earlier experiments seemed to show.

Although the series of events in "fixing" nitrogen are not well known, the important process is the combining of free nitrogen with other

elements, resulting in a nitrogenous compound, perhaps an amino compound. The formation of these complex compounds is a reduction process and requires the energy made available through the oxidation of sugars made by the leguminous plant. The bacteria multiply, mature, and die within the nodules, and the nitrogen compounds are used or accumulate within the legume. At the death of any part of the roots of the legume these compounds enter the soil.

Still another group of bacteria fix nitrogen without being associated with higher green plants. These organisms are saprophytes and make possible a series of processes sometimes called *non-symbiotic nitrogen-fixation*, in contrast to the nitrogen-fixation in legumes, which is called *symbiotic*. They live especially in humous soils and derive their energy by the oxidation of such organic compounds as carbohydrates, organic acids, and other products of fermentation. In addition to energy, the fixation of nitrogen by the bacteria is affected by many other conditions in the soil. Dark prairie soils are ideal media for these bacteria and under natural conditions have the highest nitrogen content.

Non-symbiotic nitrogen-fixing bacteria may be classified into two groups: those using free oxygen (*aerobic*), largely species of the genus *Azotobacter*; and *anaerobic* species belonging to the genus *Clostridium*. The species of *Azotobacter* are coccus forms and non-motile; those of *Clostridium* are rod-shaped and spore-forming.

Summary: the nitrogen cycle. We have now discussed the origin of nitrogenous compounds in soils through the agency of bacteria. Neither nitrification nor nitrogen-fixation in soils occurs in the absence of certain microorganisms, chiefly bacteria. We may now summarize the complete cycle of events in the origin and transformation of nitrogen compounds. In the green plants, amino acids are made from carbohydrates and nitrogen salts and are used by both plants and animals in the synthesis of proteins. The death of plants and animals results in a residue of substances, some of which are proteins. Through the agency of bacteria the proteins are digested to simpler compounds such as amino acids. Then through further chemical change ammonia is formed from water and the NH_2^- ions. *Ammonification* is the name applied to this series of processes.

Ammonia is then oxidized to nitrites and to nitrates through the agency of nitrifying bacteria. These processes are *nitrification*. The nitrates may be used by green plants and by most non-green plants in the synthesis of proteins, and we are back where we started. Certain

other groups of bacteria may reduce the nitrates and nitrites to gaseous nitrogen. This is *denitrification.*

Other groups of bacteria bring about the transformation of free nitrogen of the air to amino compounds which accumulate in the organisms. This is known as *nitrogen-fixation.* Nitrogen-fixing bacteria are of two

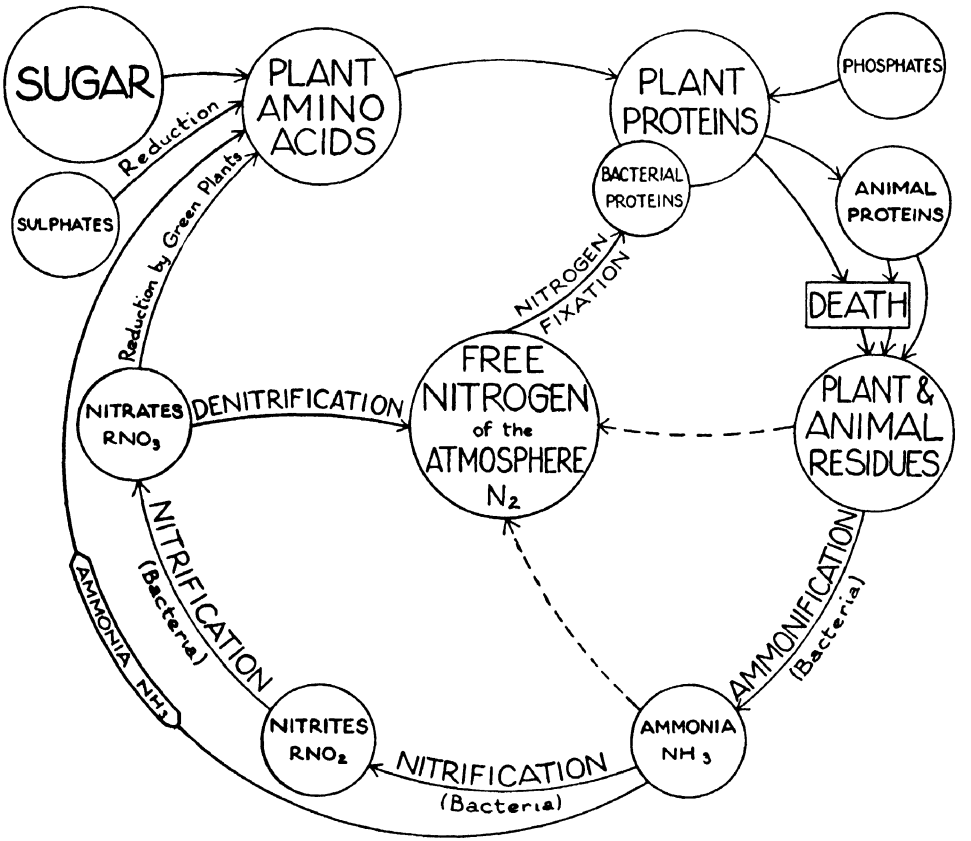

FIG. 233. Diagram of the nitrogen cycle in nature. Broken arrows indicate escape of ammonia and other volatile nitrogen compounds to the air.

kinds: those living symbiotically in legume roots, and those living free in the soil. Upon their death the nitrogen compounds become available.

All the processes having to do with nitrogen in its relation to green plants may be grouped together into what has generally been known as the *nitrogen cycle* (Fig. 233).

Sulfur bacteria. We have seen earlier that sulfur is a part of the molecule of some amino acids and proteins. Green plants in general obtain

sulfur from sulfates of the soil. Upon the death of the plant the proteins containing sulfur are acted upon by bacteria, with the formation of hydrogen sulfide. The hydrogen sulfide is oxidized through the agency of *sulfur bacteria* to elemental sulfur and sulfur dioxide. The latter is further oxidized to sulfuric acid which may react with a salt, such as calcium carbonate, and form calcium sulfate. This formation of sulfates is known as *sulfofication*, and takes place through the agency of the bacteria. The sulfates are then available to green plants and the cycle is complete.

Sulfates in the soil may be depleted through the action of another group of bacteria, forming hydrogen sulfide. Reduction of elemental sulfur may also result in the formation of sulfides. This reduction process is known as *desulfofication*.

Sulfofication is an oxidation process through which sulfofying bacteria obtain energy that is used by them in the synthesis of sugar and other foods. Such microorganisms are thus autophytes, and in this respect resemble the nitrifying bacteria. See footnote, page 517, and Fig. 227.

Bacteria and phosphates. Organic compounds of phosphorus are present in plant and animal residues. Before the phosphorus is usable by green plants, these complex compounds must be resolved by soil microorganisms. Such decomposition involves a number of reactions; phosphoric acid is finally formed, it accumulates in the soil as phosphates of calcium, magnesium, iron, and aluminum.

Iron bacteria. Bacteria are associated with the transformation of iron compounds in the soil through oxidation-reduction reactions. Certain iron bacteria are able to bring about the oxidation of ferrous to ferric iron, thereby obtaining energy by which they synthesize their sugars and other foods; thus they are autophytes. Under anaerobic conditions ferric iron may be reduced to ferrous iron by other iron bacteria. Although it is rarely necessary to add iron to soils, iron deficiencies sometimes occur in alkaline regions owing to the formation of insoluble compounds of iron both by colloidal aggregation and by bacterial action.

Compounds toxic to some bacteria have been isolated from certain species of soil bacteria. It had been known for many years that pathogenic organisms are rapidly destroyed when added to the soil, and it had been early suggested that products of certain soil bacteria might indeed be toxic to others. Scientific research in recent years on microorganisms of the soil has resulted in the isolation of antibiotic substances, such as gramicidin and tyrocidine from *Bacillus brevis*. Numerous bacteria are

now known to inhibit the growth of other bacteria. See Chapter XLIV for additional data on antibiotics.

If we could review all the activities of the many kinds of bacteria we would appreciate still more their fundamental importance in our biological world. Parasitic bacteria may cause the death of living organisms. Numerous saprophytic bacteria in turn digest the organic compounds in the dead bodies, and oxidize the carbon compounds in respiration. Through these disintegrative processes the inorganic ions, such as those of phosphorus, iron, and magnesium, that are chemically bound in the compounds of living cells are liberated; and ammonia and carbon dioxide are formed. A few special groups of bacteria through these unique respiratory processes oxidize the reduced nitrogen and sulfur of body compounds to nitrates and sulfates, which may again be reduced by bacteria or by green plants. Thus by numerous activities of groups of bacteria following each other in definite succession the body compounds indigestible by animals and green plants become converted into simpler compounds that are usable by green plants. In the grand "passing show" of nature, green plants and the larger animals play the easily visible roles; but their action would soon cease were it not for the bacteria and their associates, the fungi, most of whose activities are off-stage, unseen, and even unsuspected a century ago (Fig. 227).

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CHAPTER XLIV

THE FUNGI

Slightly moist bread in a warm room soon becomes covered with filamentous molds. Clothing, leather, and books left in moist rooms are soon "musty" because of the development of other kinds of molds. The flavors of some kinds of cheese are due to the growth of blue and green molds. Around old stumps in meadows, and within forests where organic matter is abundant, puff balls, mushrooms, and toadstools may be found (Fig. 234). From decaying logs and even from standing trees bracket mushrooms often protrude (Fig. 247). Field and garden crops are often infected with *mildews, rusts,* and *smuts.* In the process of bread-making yeast causes the dough to "rise." Many animals, including man, suffer discomfort through skin invasions of molds which cause, among other diseases, "ringworm" and "athlete's foot." Certain molds are the sources of chemicals having great medicinal and industrial value. Some of these plants are saprophytes, some are parasites, and some live as both saprophytes and parasites. All these plants collectively are called *fungi* (sing. *fungus*).

The name fungus is the old Latin word for mushroom. Just as it is hard to tell whether some organisms are plants or animals, the great diversity among fungi makes it equally difficult to distinguish clearly certain fungi from certain bacteria and algae. The most common characteristic of fungi is a vegetative body of either a loose web or a compact mass of filaments none of which contains chlorophyll (Fig. 235). The fruiting and reproductive bodies of numerous fungi are readily recognized, but the reproductive bodies of many common fungi are seldom found; hence some fungi must be recognized without them.

Vegetative parts of a fungus. A toadstool among the leaves on the forest floor, or a bracket fungus on a fallen tree trunk is but a small part of the fungous plant. The part not readily seen consists of a widely dispersed mass of filaments (Fig. 235). In describing fungi these filaments are called *hyphae* (sing. *hypha*). Hyphae are either continuous tubular structures, or divided by cross walls into cell-like segments containing

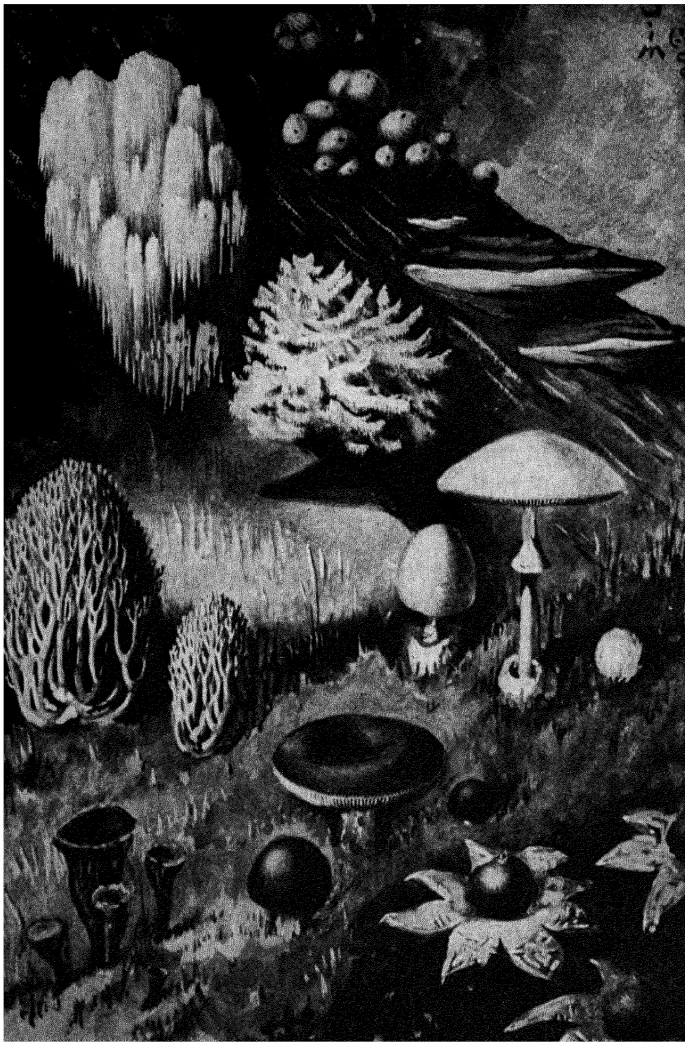

FIG. 234. Mushrooms, toadstools, and puffballs. On the log: two hydnums, puffballs, and bracket fungi. On the ground: coral fungus (*Clavaria*), poisonous amanita, red russula, cornucopia fungus (*Craterellus*), earthstars (*Geaster*).

one to many nuclei. Usually they are highly branched and form loose cottony masses, such as may be readily seen in the bread mold. The common meadow mushroom has colorless hyphae that spread in all directions through a large mass of soil and are usually unseen unless one digs carefully around the fruiting bodies that appear above the soil. The "mushroom" is formed by the growing together and coalescence of

numerous hyphae into a compact characteristic structure. The whole aggregate of hyphae growing on, or within, the substrate is called the *mycelium* (Greek for *fungus*). The underground hyphae of some species grow in small compact masses, forming tuber-like bodies. Those of some other species form compact hard strands of many hyphae that grow as a collective unit and push their way through firm substrates.



FIG. 235. Stages in the development of the common edible pink-gilled mushroom (*Agaricus campestris*). Note the underground vegetative body of the plant.

The cell walls of hyphae are composed of such substances as cellulose, pectose, callose, and chitin. The foods found in fungi are carbohydrates (including sugars and glycogen), fats, and proteins. Various kinds of enzymes are synthesized in the fungi, and are important in transforming substances not only within the fungous cells, but outside in the host or in the substrate. Fungous hyphae may grow into the tissues of the host or other substrate by mechanical pressure similar to that of growing roots, or the substrate may be digested by enzymes from the hyphae.

Fungi may be found wherever the environment is not inimical to the establishment of a mycelium, and where there are substances they can digest and use as food. They are found on land and in water, growing free as saprophytes or as parasites within, or upon, many different hosts. Aquatic fungi are not as numerous as terrestrial ones, and are far less abundant than the algae and bacteria. The aquatic species live as parasites on fresh-water and marine organisms, or as saprophytes on the dead bodies and residues of such organisms. They are most numerous in well-

lighted and well-aerated water where there is the largest number of host plants and animals. Any aquatic organism may be invaded, injured, or destroyed by parasitic fungi at some stage of its life cycle. The growth of aquatic fungi may be checked by epidemics of bacteria.

Terrestrial fungi occur everywhere on, or in, most kinds of plants and many animals, as well as on their dead bodies. It would be difficult to find a twig lying on the ground in a forest that is not being invaded and disintegrated by some fungus, and one may easily discover the cobwebby fungous hyphae among the fallen leaves on the forest floor. Soil fungi are most abundant in the upper foot of soil. Fungi digest the woody tissue by enzyme action. They injure the living hosts largely through the destruction of tissues, through the formation of toxic substances, through the consumption of food, and through interference with physiological processes.

There are some 100,000 species of fungi and thousands of chemically different substrates; hence some fungi grow where others cannot. Fungi are most numerous and grow best in moist warm situations, but they may be found also on the desert, in refrigerators, and on the arctic tundra.

Millions of bushels of fruits and vegetables in storage are destroyed each year by fungi. Most of the apples, for example, that spoil in storage are destroyed by a single fungus, a blue mold which causes a soft rot. In northern states where snow covers the ground throughout the winter, much of the grass on golf greens is killed at the soil surface by another fungus, the so-called "snow mold." The spores and other dormant structures of fungi often survive the natural extremes of temperature and drought for long periods.

We shall now consider in more detail a few of the common species of fungi, in order to secure a better understanding of their structures, growth, and reproduction, and also of their biological significance.

Bread mold. If a moist piece of bread is placed under a bell jar for a few days, a tangle of colorless hyphae may cover the bread and even fill the jar. This is the mycelium of the bread mold, *Rhizopus nigricans*. Its hyphae are much branched and have no cross walls; some of them (rhizoids—root-like hyphae) penetrate the bread for short distances, while others form the visible web. Bread mold, of course, grows on many other substrates. Enzymes from the mold digest the bread. The resulting soluble food diffuses into the hyphae of the mold. Decay is nothing

more than the digestion and oxidation of organic substances. Growth of the fungus may continue until the food is exhausted.

The mycelium starts from a spore as a single hypha and spreads over the bread by terminal growth of its multitudinous branches. At node-like points on the spreading hyphae upright branches and several rhizoids develop. These nodes also become new centers from which radiating horizontal hyphae extend and increase the complexity and density of the mycelium.

The tips of the upright hyphae enlarge and form globular spore cases, *sporangia*, which eventually contain many vegetative spores (Fig. 236).

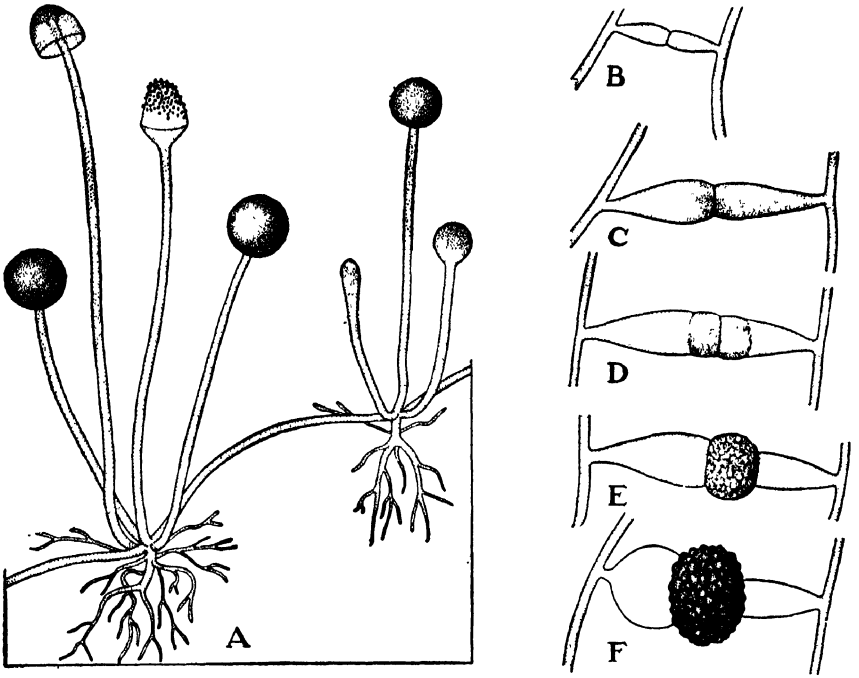

FIG. 236. Bread mold (*Rhizopus*): A, general habit of growth and reproduction by asexually formed spores; B, C, D, E, and F, stages in the fusion of hyphae of male and female mycelia and the formation of a zygote.

Many sporangia usually develop at about the same time, and upon their rupture millions of black spores are liberated from them. The spores are so light that they float in the air for long periods; hence it is easy to see why moist bread when exposed to the air for even a short time and then placed in a closed container soon becomes "moldy." When spores come to rest on a moist organic substrate, they germinate almost immediately, and from them new mycelia originate. When bread is

wrapped in waxed paper while still warm from the oven, mold spores are more likely to be kept out, and the bread keeps in good condition for a much longer period.

Sexual reproduction can be observed between mycelia of bread mold started from different spores on the same culture plate. Where hyphae of the two mycelia come in contact, the adjoining walls dissolve and the contents of the two "cells" fuse. The union of the two protoplasts, or gametes, results in a heavy-walled black zygote. Upon germination of a zygote, a short hypha develops which terminates in a globular sporangium containing spores. From these spores branching hyphae grow, and the development of a new mycelium begins.

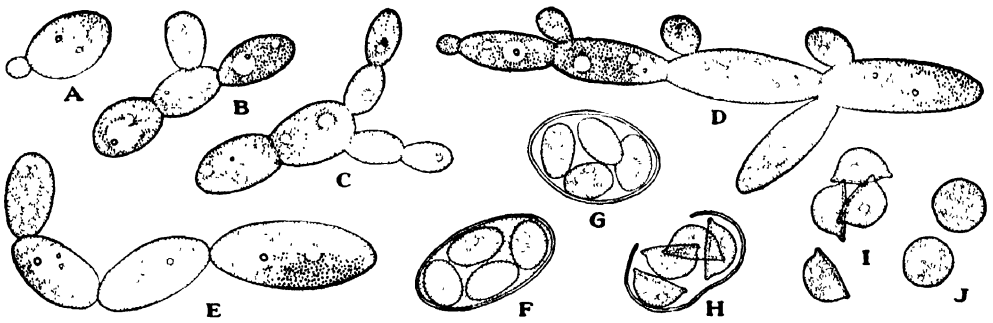

FIG. 237. Yeast from fermenting sauerkraut, A-D, vegetative growth of diploid cells by budding. F-J, monoploid ascospores formed after reduction division of a diploid cell. A-G, *Saccharomyces;* H-J, *Hansenula.*

Yeasts. In the discussion of respiration it was noted that the formation of alcohol and carbon dioxide from a sugar solution may be brought about in oxygen-free containers if certain yeasts are present. When yeasts are thoroughly mixed with flour and water, their activities bring about the "rising" of bread dough. The carbon dioxide resulting from the oxidation of sugar accumulates in bubbles throughout the dough and makes it porous. While the bread is baking, the alcohol vaporizes and with the carbon dioxide passes from the bread into the air.

The yeasts are generally microscopic one-celled plants more or less ellipsoid in form. Although a single yeast cell is microscopic, the enormous numbers that develop in a sugar solution soon make it cloudy, and eventually sediment collects at the bottom of the vessel. The yeast cakes sold by commercial firms consist of starch grains and yeast cells pressed together into a compact mass.

New cells develop vegetatively in yeasts either by simple division

or by "budding" accompanied by the usual duplication of chromosomes. If there is not an immediate separation of the "bud" from the parent cell, short, fragile, branched or unbranched chains of cells develop (Fig. 237A-E). Reduction division in diploid cells is followed by the develop-

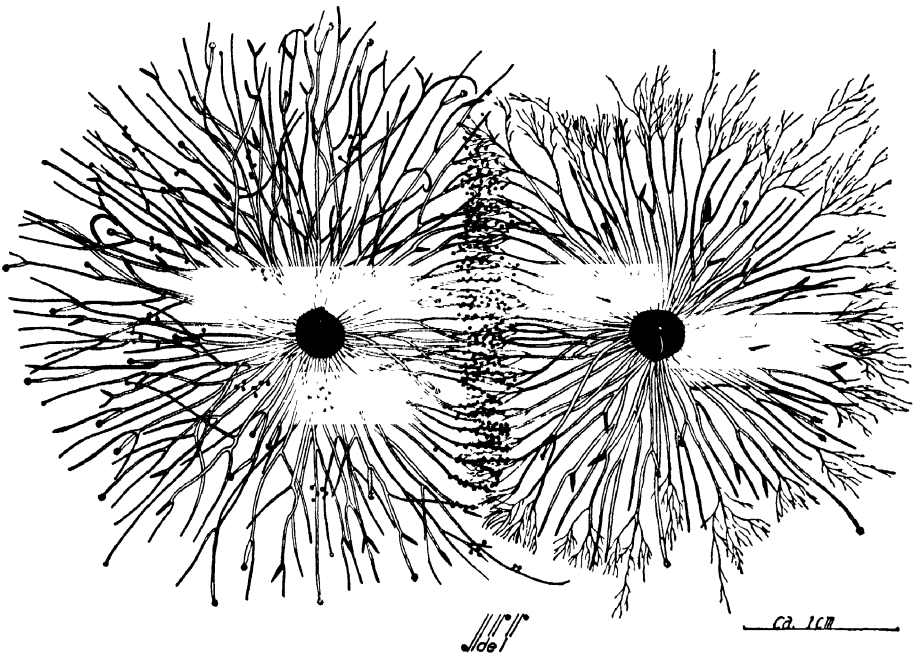

FIG. 238. Diagrammatic representation of zygotes formed in the water mold, *Achlya*, when hyphae of a female mycelium (left) come in contact with those of a male mycelium (right). The numerous small branching hyphae around the periphery of the male mycelium are antheridial branches on which the male organs (antheridia) containing male nuclei develop. The scattered small darkened spheres on the female mycelium represent immature egg cases (oogonial initials). The darkened awl-shaped hyphae and spherical masses of spores at the apexes of certain hyphae in both mycelia are vegetative propagules. For further details of the sexual processes, see Fig. 239. From J. R. Raper.

ment of monoploid *ascospores* (Fig. 237F-J). These spores may fuse in pairs forming diploid cells or they may "bud" and form monoploid vegetative cells which may increase in number by budding and also fuse in pairs and form zygotes. Thus the vegetative cells of yeasts may be diploid or monoploid. In some species of yeast, such as the pressed yeasts of commerce, most of the vegetative cells are diploid.

Water molds. In temperate latitudes in early spring dead fish and other aquatic animals may be found in ponds and streams, completely covered with a colorless slimy mass of fungous hyphae. The same

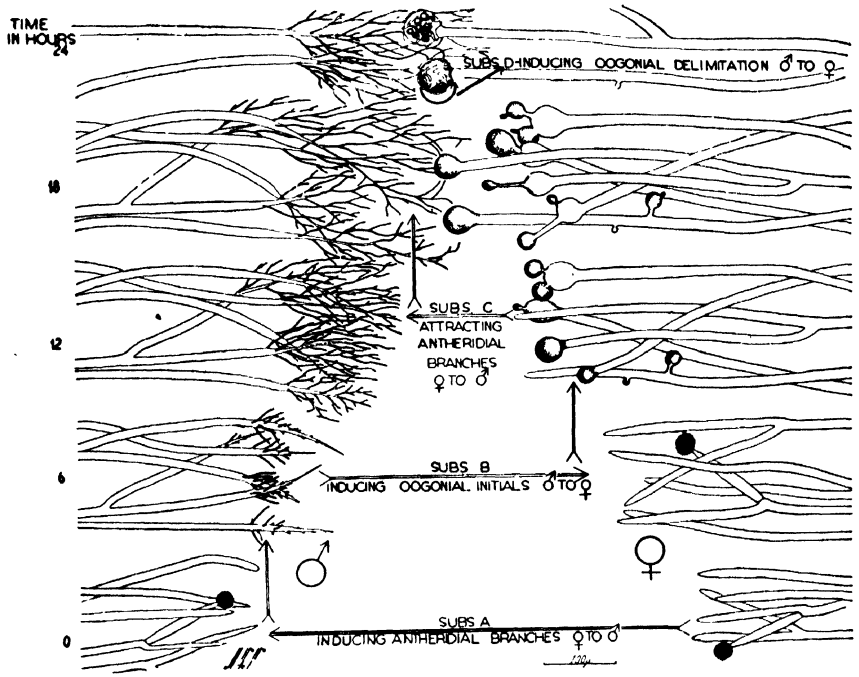

FIG. 239. Diagrammatic representation of the sex organs of the water mold, *Achlya*, and of their hormonal relations as indicated by arrows; an elaboration of Fig. 238. Hormone A from the female mycelium (right) is essential to the formation of antheridial branches on the male mycelium (left). Hormone B from the antheridial branches is essential to the formation of oogonial initials on the female mycelium. Hormone C from the oogonial initials is essential to the formation of antheridia on the antheridial branches. The direction of growth of the antheridial branches is also influenced by this hormone. Hormone D from the antheridia is essential to the further development of the oogonia and the formation of eggs within them. Finally sexual fusions result in the formation of zygotes. From J. R. Raper.

fungus, or other species of water molds, may also grow on living animals, and on decaying plant and animal remains. They are at times very destructive to fish eggs and young fish. Water molds were so named before it was generally known that many species of them grow in moist soils. The vegetative phase consists of tubular branching hyphae within the host or the substrate.

The slimy mass of filaments on the outside of the animal is largely made up of hyphae that terminate in club-shaped sporangia, within which the protoplasts divide into many motile spores. After liberation from the sporangium, the motile spores may undergo various changes in appearance; from them new hyphae develop. Sexual reproduction begins by the formation of egg cases, or *oogonia*, each containing from one to

twenty egg cells, and by the development of *antheridia* containing sperm nuclei. The union of a sperm nucleus and an egg nucleus results in a *zygote*. Upon germination the zygote divides internally and motile spores result. From these motile spores new hyphae may develop under favorable conditions. Hyphae may develop, however, from unfertilized eggs—another example of parthenogenesis in plants. It has been discovered that at least four hormones are necessary in sexual reproduction in one of the water molds (Figs. 238 and 239).

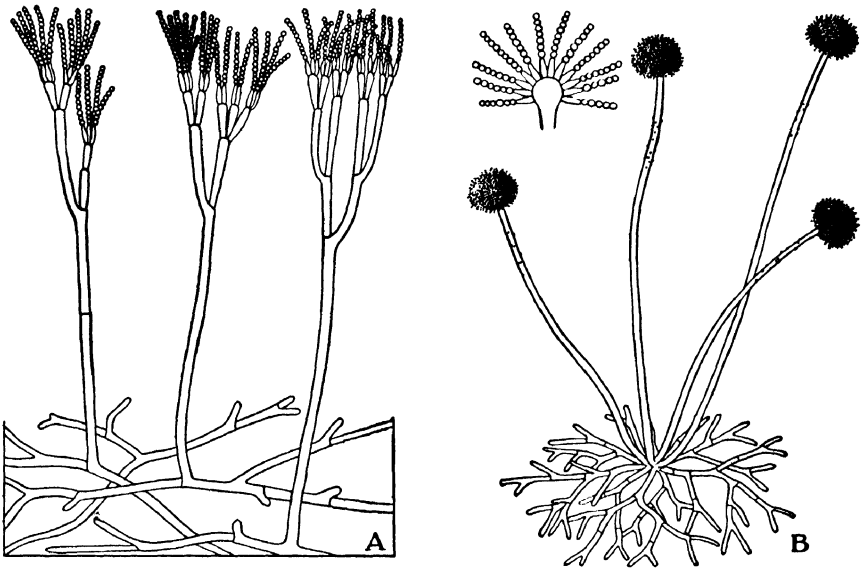

FIG 240. A, blue mold (*Penicillium*); B, green mold (*Aspergillus*). The spores (conidia) are formed by successive abstrictions of the tips of the upright hyphae (conidiophores) that develop from a felt-like meshwork of mycelium on the substrate. These one-celled vegetative spores develop in enormous numbers and are readily carried everywhere by air currents or by rain water, especially in the summer months.

Blue and green molds. These molds were named on the basis of spore color in some common species. Some blue molds impart flavor and color to certain varieties of cheese, such as Camembert and Roquefort. These fungi and others are the causes of the decay of vegetables, fruits, and meats both in storage and during transportation, and they occasion enormous monetary losses. They are aerobic and during warm periods of high humidity may grow luxuriantly on many household articles. In tropical and semi-tropical climates electrical and optical equipment may be much damaged by these and other molds. The main structural features of blue and green molds are shown in Fig. 240.

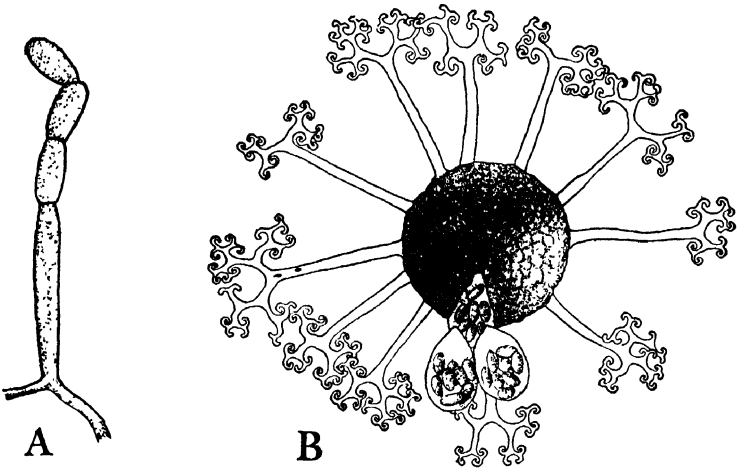

FIG. 241. Reproductive structures of a powdery mildew: A, conidia formed during the summer months; B, an ascocarp, which lives through the winter and within which the asci and ascospores develop. They can be forced out of the ascocarp by a slight pressure as indicated in the drawing. B from C. J. Chamberlain, *Elements of Plant Science*, McGraw-Hill Book Company, Inc.

Two species of blue mold (*Penicillium notatum* and *P. chrysogenum*) are sources of penicillin, a compound having definite bactericidal properties. It is especially effective against certain pathogenic cocci, as well as one of the spirochaetes causing syphilis. Similar compounds synthesized in smaller mold fungi are streptomycin and chloromycetin. Such substances are known as *antibiotics*. Aureomycin is another recently discovered antibiotic. The lethal effects of some of these antibiotics on the causal agents of prevalent human diseases are summarized in Fig. 242.

Mildews. During summer and early autumn cobwebby mycelia may be seen on the leaves of such plants as ragweed, knotweed, red clover, lilac, crimson rambler, sunflowers, and willows. The hyphae of these fungi also have cross walls. When in contact with a leaf, some of the branches of the hyphae become haustoria or rhizoids which penetrate the epidermal cells of the host tissue. The mycelia of these fungi are on the surface of the host. Other hyphae grow upright from the surface mycelium and bear at their tips chains of colorless conidia in a manner similar to that of the blue molds noted above. The conidia, or summer spores, are carried about by air currents from leaf to leaf, and many plants thus become infected during the growing season. These fungi are called *powdery mildews* because of the appearance of the conidia.

Causative Agents:→	Bacteria									Rickettsiae			Viruses				Spirochaetes
Diseases:→	Dysentery*	Gonorrhea	Pneumonia*	Scarlet Fever	Tetanus	Tonsillitis	Tuberculosis	Typhoid Fever	Whooping Cough	Typhus Fevers	Spotted Fevers	"Viral" Pneumonia	Common Cold	Influenza	Measles	Poliomyelitis	Syphilis
Penicillin	−	+	+	+	−	+	−	−	−	−	−	−	−	−	−	−	+
Streptomycin	+	+	+	−	−	?	+	?	+	−	−	−	−	−	−	−	+
Chloromycetin	+	+	+	?	?	?	?	+	+	+	+	+	−	−	?	?	+
Aureomycin	?	+	+	+	?	+	?	+	+	+	+	+	−	−	−	−	+

* Some kinds.

FIG. 242. Tabular representation of the effectiveness of four well-known antibiotics on the causal agents of some diseases common to man. Molds or mold-like plants are sources of such antibiotics. (+, effective; −, not effective; ?, effect unknown.)

In late summer small black dots may appear among the hyphae on the infected leaves. The dots are reproductive bodies and under the microscope are seen to be spherical and thick-walled, with curiously branched transparent appendages. These fruiting bodies, or *ascocarps,* are the result of the growth of coalescent hyphae, following the fusion of the protoplasts of an oogonium and an antheridium. Each ascocarp contains several sac-like structures termed *asci* (sing. *ascus*) (Fig. 241). Within each ascus are usually 8 *ascospores,* although the number may vary from 2 to many. The germination of an ascospore the following spring results in a hypha which may grow upon other plants and start a new life cycle of the fungus. Sexual union preceding the formation of ascocarps and reduction division during the formation of ascospores make possible many kinds of hybrids and hybrid segregates.

The *downy mildews* have tubular non-septate hyphae similar to those of bread molds and water molds (Fig. 243). They are internal obligate parasites that are very destructive to many plants, such as potato, onion, tobacco, and grape. More than 1000 such fungi belong in a group called

Phycomycetes. One especially interesting group of Phycomycetes is the *Entomophthorales,* internal parasites of insects.

The powdery mildews, on the other hand, have septate hyphae and

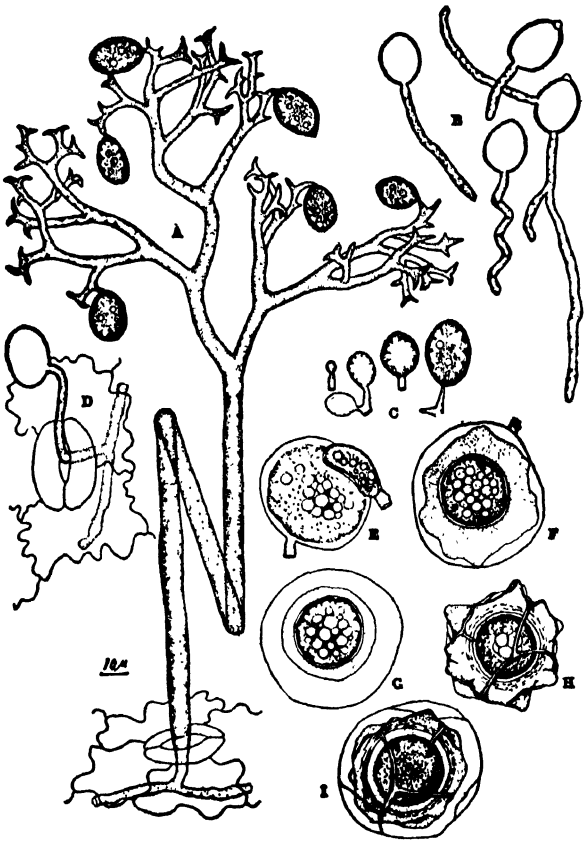

FIG. 243. Enlarged drawings of the reproductive structures of a downy mildew parasitic within tobacco, tomato, eggplant, and pepper. The mycelium is intercellular. A, a branched conidia-bearing hypha protruding from a leaf through one of the stomates; B, germination of conidia; C, stages in the development of a conidium at the tip of a hypha; D, the hypha from a germinating conidium has grown into a leaf through a stomate; E-I, stages in the development of a zygote by sexual reproduction. From North Carolina Agricultural Extension Service.

special reproductive structures (ascocarp, ascus, ascospore) not found in the downy mildews. Asci and ascospores develop in more than 12,000 species of fungi. All of these fungi are called *Ascomycetes.* Other representatives of this group are yeast, blue and green molds, cup fungi, morels, and truffles. Numerous conidia develop on upright hyphae of some of the Ascomycetes during the growing season.

The life cycle of a downy mildew is so unlike that of a powdery mildew that different methods of eradication are needed. The mycelium of the downy mildew parasitic on potatoes may over-winter in the tuber and the next spring grow into the tissues of the new potato plant developing from that tuber. Branched conidiophores grow outward through the stomates, and conidia are formed from the terminal branches. The conidia may be carried by wind or water to other parts of the plant or to other plants. Motile spores develop within each conidium. When the leaves are wet, the motile spores emerge from the conidia and germinate almost immediately. The resulting hyphae penetrate the host, and new internal mycelia develop. Sexual reproduction may take place when the fungus is growing in culture, but apparently does not occur when the fungus is growing in the potato plant.[1] The reproductive structures of the downy mildew of tobacco are illustrated in Fig. 243.

Cup fungi, morels, and truffles. The cup fungi are usually found growing on soil and on decaying wood. The vegetative body, or mycelium,

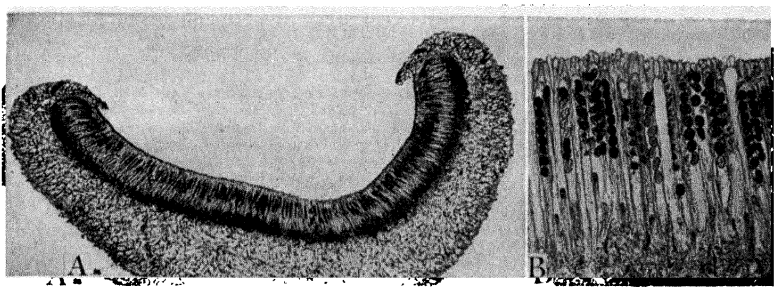

FIG. 244. Photomicrographs of reproductive structures of a cup fungus (*Peziza*): A, section through the cup which is lined with a layer (hymenium) of asci and intermingled sterile hyphae; B, a portion of the hymenium further magnified to show asci and ascospores in more detail.

is largely underground or near the surface. The part usually visible, the fruiting body, is cup-shaped and lined with a layer of parallel asci and sterile hyphae. Each ascus generally contains 8 ascospores (Fig. 244). The morel, prized for its flavor, is related to the cup fungi, but has a hollow reproductive body covered above with a layer of asci. The fungus is not edible after the spores have matured and should be eaten only when immature.

[1] It is of historical interest to recall that this so-called "potato blight" caused a serious famine in Ireland in 1843-46 and led to the repeal of the Corn Laws. These laws had imposed severe restrictions on the importation of wheat and other small grains. Previous to this date the annual consumption of potatoes in Ireland was 25 bushels per person.

A related group of fungi are the truffles, which are widespread in Europe and are also found in several places in the United States. Truffles are considered a delicacy and gathering them is an industry in France. The plants, which generally grow from 3 to 12 inches below the surface of the soil, have a peculiar odor which is not evident to most people. Pigs and dogs have been trained to locate the plants. The fruiting body of the truffle is a globose, warty structure enclosing the spore-bearing tissues. This fungus is disseminated by rodents that eat the truffles and scatter the undigested spores.

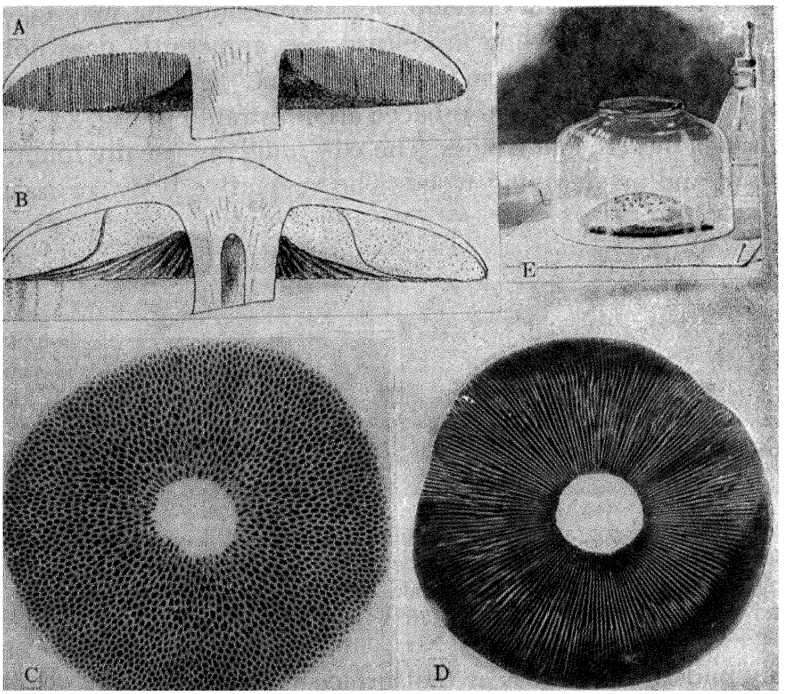

FIG. 245. Spore prints may be used to identify spore color and the arrangement of spore-bearing surfaces of mushrooms. C is a spore print of a pore fungus represented by A. D is a spore print of a gill fungus represented by B. The method of obtaining spore prints is represented by E. The inverted vessel is used to prevent air currents from scattering the spores as they fall on the paper from the cap of the mushroom. The cap should be carefully lifted as soon as enough spores have fallen to form a distinct print. Permanent mounts can be made if the spores fall on a paper covered with a thin coating of mucilage; this may then be moistened enough to hold the spores in place by carefully placing the paper on a wet towel until the moisture has penetrated through the paper to the mucilage. From W. Hamilton Gibson.

Mushrooms, toadstools, and puffballs. These are popular terms and do not correspond to any technical classification of fungi. To many people the term "mushroom" means an edible fungus while "toadstool" refers to a poisonous or inedible one. No such distinctions can be made on the basis of the form, color, structure, or place where they grow. A few species may be safely eaten by some persons, but not by others. Beside the edible species, others are woody or unpalatable, and a number of species are deadly poisonous to all of us. The term "puffball" refers to a fungus that emits clouds of spores when stepped on. Puffballs are inedible when mature, but many of them are edible when young. Perhaps the best advice to would-be mushroom hunters is to learn to identify positively a few of the common edible species and avoid all others.

The vegetative parts of all these fungi are in the soil, wood, or other substrate on which the reproductive bodies appear. These bodies, varying from a fraction of an inch to more than two feet in height or diameter, are compact masses of hyphae. The vegetative hyphae of some toadstools are the cause of destructive wood-rots in timber and in wooden buildings. When mature, the reproductive structures may contain almost countless numbers of spores (Figs. 245 and 246).

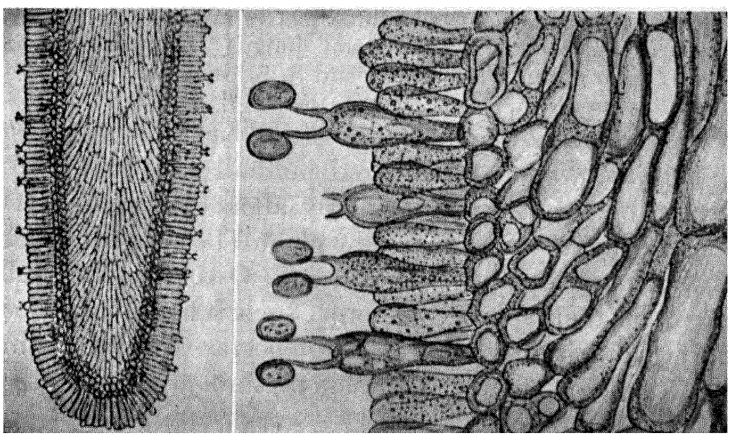

FIG. 246. Arrangement of spores on the gills of the cultivated mushroom: at the left a vertical section of one gill as it appears when magnified enough for one to see the continuous external layer of basidia; on the right a highly magnified section of a small portion of a gill including several club-shaped hyphae (basidia), three of which bear two basidiospores each. In our wild species of this mushroom, as well as in most toadstools, each basidium bears four basidiospores. Modified from Julius von Sachs.

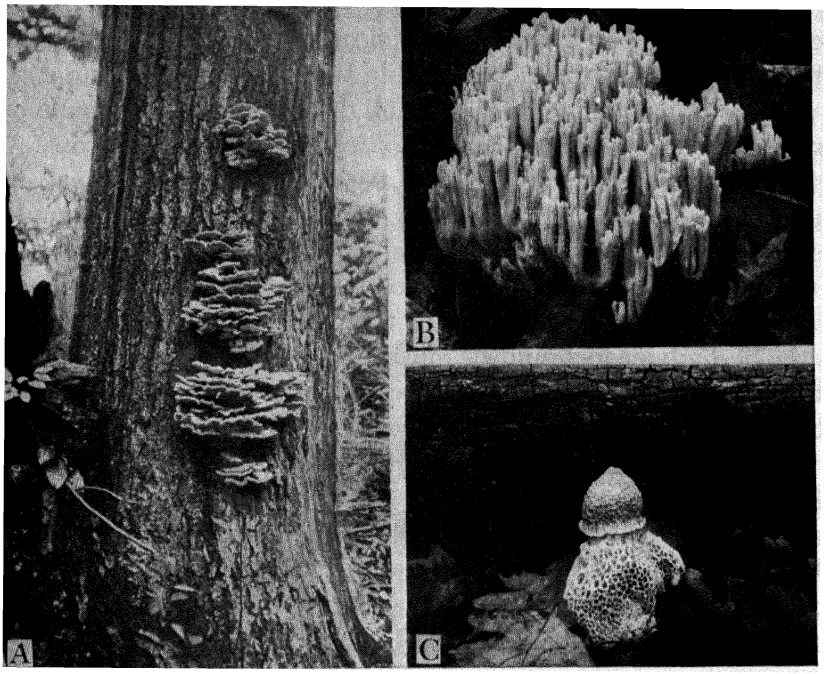

FIG. 247. Reproductive structures of three species of fungi: A, the sulfur mushroom (*Polyporus sulphureus*); B, a coral fungus (*Clavaria*); C, stink-horn (*Dictyophora*). Photos from W. G. Stover and R. B. Gordon.

The common meadow mushroom often bears 2 billion spores, a polypore 10 billion, and a good-sized puffball may have 7000 billion spores. It has been estimated that only about one spore out of each trillion spores ever develops into a new plant. The appearance of fruiting bodies is illustrated in Figs. 234 and 247. Owing to the club-shaped hypha on which their spores are borne, such fungi as toadstools, puffballs, smuts, and rusts are called *Basidiomycetes*. There are some 13,000 known species of basidiomycetes. Some mushrooms are basidiomycetes, but others are ascomycetes.

The culture of the common meadow mushroom is an important industry in scattered localities, where it is carried on in specially constructed buildings with insulated walls, in caves, or in old mine tunnels where the temperature and humidity can be controlled. Light is not harmful, but it is not necessary; and it increases the difficulty of controlling other conditions. After the beds of soil rich in organic matter are prepared and sterilized, they are inoculated with pieces of mycelia of pure races. These

mycelia develop from spores sown on boiled grain in sterilized culture bottles.

Fairy rings. When growth conditions are favorable in lawns and pastures, the fruiting bodies of the common meadow mushroom often occur in so-called "fairy rings" (Fig. 248). The rings were thought in ancient

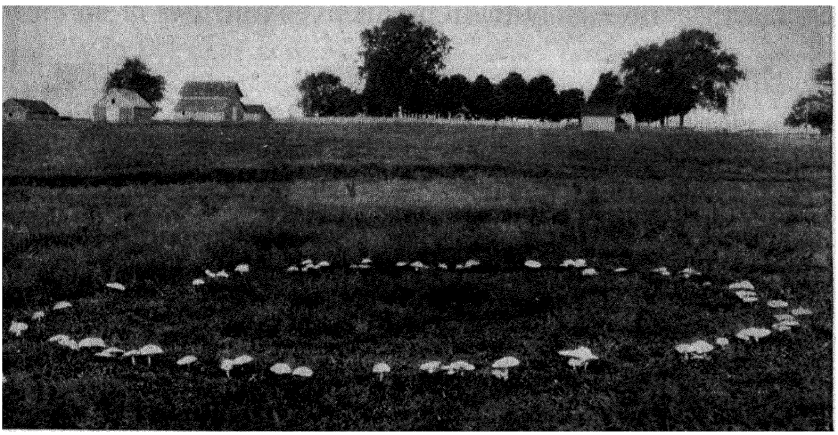

FIG. 248. A fairy ring of a common mushroom (*Lepiota*) on a ranch in Colorado. Photo from the New York Botanical Garden.

times to represent the paths traversed by dancing fairies. The circular appearance is due to the outward growth of the underground mycelium from the original center. The hyphae are perennial, and their radial extension is accompanied each year by the death of the older portions of the hyphae in the central areas. The fruiting bodies thus appear in circles which increase in diameter from year to year. Nearly perfect rings of this mushroom 160 feet in diameter have been reported, but the diameter is usually less than 20 feet. Similar rings are developed by many other fungi, including morels and puffballs. Some have attained diameters of nearly a quarter of a mile and could have resulted only after hundreds of years of outward extension of the mycelium from the original center of growth. These largest rings are usually irregular, and occur in incomplete circles.

An eruptive skin disease of man and other mammals, known as "ringworm," is caused by a fungus. Pustules appear in irregular circles about the point of infection because of the radial growth of the hyphae in the skin. The lesions are caused by the fruiting bodies of the fungus as they break the skin, and thus appear as miniature fairy rings.

Smuts. Seed plants of many kinds, particularly many of the grasses, are infected by parasitic fungi that are unlike those just described. Owing to their appearance, some of them are referred to as *smuts,* others as *rusts.* The vegetative and floral parts of oats, wheat, rye, corn, rice, and onions sometimes contain black or dark-brown masses of fungous spores (Fig. 249). These masses are generally regarded as the smut plants, but they are merely the reproductive structures of an extensive

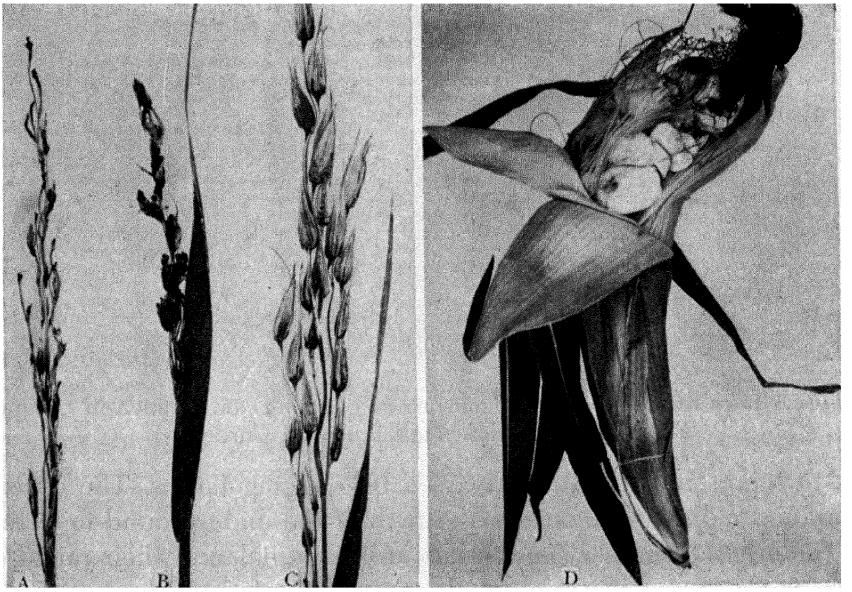

FIG. 249. Effects of smuts of cereals: A and B, loose smut of oats; C, covered smut of oats; D, enlarged and distorted "corn grains" filled with smut. Photos from U. S. Department of Agriculture.

mycelium in the host. Several types of smuts may be exemplified by the loose and covered smuts of oats and barley, the loose and stinking smuts of wheat, and by the corn smut.

At threshing time the mature spores of *bunt,* or the *stinking smut of wheat,* may stick to the surface of the wheat grains and remain there until the grains are planted.[2] At that time the spores germinate in the soil. The resulting short basidium-like hyphae bear basidiospore-like spores called "sporidia." These spores fuse in pairs and germinate, or they may germinate without fusion. The resulting hyphae penetrate the

[2] The spores may also fall to the ground, germinate, and grow saphrophytically in the soil for a short time only.

young wheat seedling. The internal mycelium grows to the stem tip, keeps pace with the growing wheat plant, and finally enters the ovularies of the inflorescence. The floral parts are greatly distended by harvest time. Masses of smut spores have replaced the embryo and endosperm of the seeds. During the threshing of the wheat these spores are released and scattered among the other grains of wheat. Unless these grains are disinfested before they are planted, another generation of bunt fungus will grow in the next crop of wheat.

The spores of the *loose smut of wheat*, appearing as dark-brown or black masses in the inflorescences at flowering time, may be blown to the stigmas of other wheat plants. There they germinate and the resulting hyphae penetrate the ovularies. The mycelium remains dormant within the embryo until the seed is planted and starts to grow. It is not possible by superficial examination of the seed to ascertain the presence or absence of the internal mycelium. Following the germination of these seeds the mycelium grows within the developing host plant, and masses of spores appear just before flowering time, replacing the destroyed flower parts. Thus the life cycle is complete. The methods of control of this fungus must evidently be different from those used in the elimination of the stinking smut of wheat. The loose smut of barley is similar.

Masses of *corn smut* may also be seen on any part of an infected mature corn plant. The infection, however, always takes place when the tissue is young. The corn smut fungus does not spread throughout the host from the point of infection but remains more or less localized. The smut galls and their masses of spores appear one to three weeks after infection. The spores may remain alive in the soil or in plant litter for many months, and consequently the fungus is difficult to eliminate.

Rusts. One of the most complex life cycles in the entire plant kingdom is that of the *black stem rust* of cereals and grasses.[3] The *stem rust* of wheat is important commercially because during some years it decreases the yield of the American wheat crop by an estimated 120 million bushels. The life cycle of this rust illustrates so well how difficult may be the problems encountered in attempting to control the fungi that cause diseases of economic plants, that it will be described in more detail than would otherwise be justified in this textbook (Fig. 250).

[3] There are at least 8 varieties of the black stem rust fungus, *Puccinia graminis*, but only 3 infect cereals: *P. graminis tritici*, infecting wheat, barley, and many wild grasses; *P. graminis avenae*, on oats and some wild grasses; and *P. graminis secalis*, on rye, barley, and wild grasses. Among the varieties of rust there are hundreds of genetically different races, and each race of rust affects only certain genetic races of host plants.

During the summer the fungus is first apparent on the surface of stems and leaf sheaths as patches of innumerable red spores (*uredospores*). These spores are blown about by the wind and the hyphae from them infect other wheat plants. New mycelia develop, and the spores from them may be blown to other wheat plants. This process may be

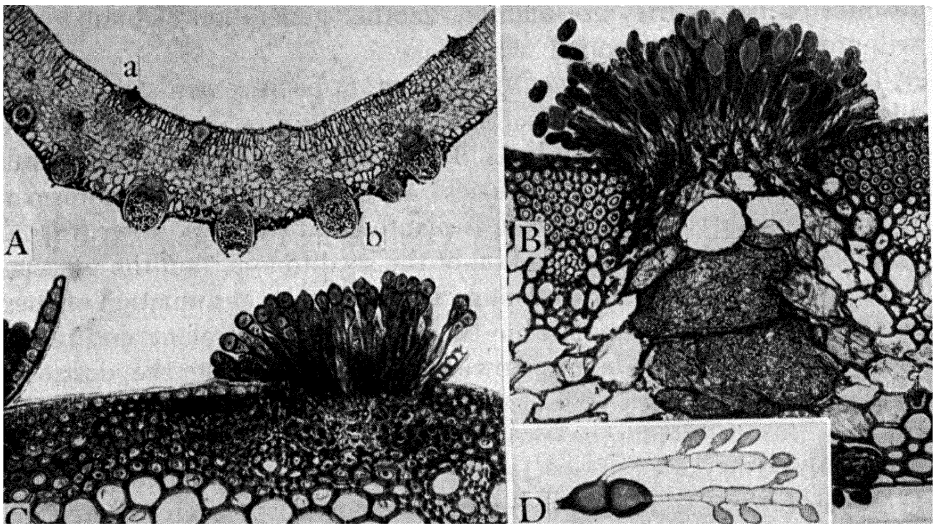

FIG. 250. Photomicrographs of the reproductive structures of stem rust (*Puccinia graminis*) of wheat: A, cross section of a leaf of common barberry with aecia containing aeciospores (b) on the lower side and spermagonia (a) on the upper; B, a pustule of red summer spores (uredospores) that has broken through the epidermis of a wheat stem; C, a pustule of teliospores in a wheat stem a little later in the season; D, the following spring, a basidium bearing 4 basidiospores has developed from each of the two cells of a teliospore. Hyphae from the basidiospores infect leaves of the common barberry and the cycle is repeated.

repeated every week or ten days during the spring, thus spreading the fungus rapidly over large areas.

These same internal mycelia a little later produce many two-celled, thick-walled black spores (*teliospores*). These second spores in the life cycle begin to appear before the wheat plant is mature, and they live over the winter on the stubble and straw. After winter dormancy they germinate, and a short club-shaped hypha (*basidium*) develops from each of the two cells. The basidium is four-celled, and from each of its cells a third kind of spore (*basidiospore*) forms. Reduction division occurs just previous to the formation of basidiospores; hence there will be

genetic differences among the basidiospores and the mycelia that grow from them.

During the remainder of the life cycle of this rust certain remarkable phenomena occur. The basidiospores are blown about by the wind. Hyphae from these spores do not infect wheat plants, but they do infect the common barberry plant and a few of its relatives.[4] The hyphae penetrate the leaves of barberry. In a short time there appear on the upper surfaces of the leaves pustules of flask-shaped masses of hyphae, *spermagonia*, which produce a fourth type of reproductive body, *spermatium*. The spermatia may unite with receptive hyphae of the internal mycelium and result in binucleate hyphae. Since the different spermatia in a leaf may have originated from various races of the rust, such a union makes possible hybrids between different races. Such hybrids and the resulting hybrid segregates still further complicate measures of control.

Further growth of these binucleate hyphae within the barberry leaf results in a mycelium and pustules of cluster cups (*aecia*, sing. *aecium*) on the lower surface of the barberry leaf. Within these cups, a fifth reproductive body, the cluster cup spore, or *aeciospore*, develops. Aeciospores in turn continue the life cycle only when they lodge and germinate on young wheat plants and a limited number of other grasses. The mycelium from them grows within the tissues of the wheat plant, and first the red spores, and later the black spores, develop—thus completing the life cycle.

Here, then, is a parasitic rust that lives successively on two totally unrelated host plants during a *complete* life cycle. It has several kinds of spores, which are morphologically and physiologically different from each other. Curious as it may seem, the first definite proof that diseases may be caused by parasites was obtained when Anton de Bary discovered many of the facts of the life history of wheat rust in 1865.

It is interesting to note the possible variations in the life cycle of the stem rust of wheat, as given above. Red spores cannot survive the winters of the North Central States. They may, however, be blown many miles southward and there cause infection of growing wheat or other grasses in the fall. Red spores borne in the South cannot survive the hot dry summers and so do not cause infection of the young wheat plants there in the following fall. In the early spring red spores from southern

[4] *Berberis vulgaris* is very susceptible to this rust. The green and red varieties of the cultivated Japanese barberry, *Berberis thunbergii*, are immune to it. Certain other species, such as the American barberry (*B. canadensis*) and some species of *Mahonia*, are susceptible.

wheat are blown northward and successively lead to infection of the growing wheat of higher and higher latitudes. This cycle of infection by means of red spores alone, makes possible widespread epidemics of wheat rust in the absence of barberry plants. Such a condition can be controlled only by procuring immune races of wheat. These general epidemics, however, occur more rarely than the local epidemics in regions in which the common barberry is growing.

The problem of crossing and selecting varieties of wheat immune to stem rust is further complicated by the fact that there are more than 180 races of the fungus which pass one stage of their life cycle in barberry. A variety of wheat may be immune to most of these races, but a few races may infect and injure it so much that cultivation of it is unprofitable except in the limited areas where these particular races do not occur.

It thus becomes evident that continuous research and experimentation will be necessary to combat the organisms causing the rusts.

Other interesting examples of two-host rusts are the white pine blister rust (white pine stem, and currant or gooseberry leaves), and apple rust (apple leaves and fruits and red cedar shoots). However, not all rusts involve two host plants, and many of them do not infect crop plants.

Slime molds. A rather curious group of non-green organisms are the slime molds. They are frequently classified as plants, sometimes as animals, and may be discussed in connection with the fungi. The vegetative part of the plant is a multinucleate mass of naked protoplasm with about the consistency of mayonnaise, called a *plasmodium*. The plasmodium lives in moist places and streams through and over the substrate and finally comes to rest on the surface of plants and other objects. The different species of slime molds have characteristically colored plasmodia and variously shaped sporangia bearing many spores (Fig. 251).

Lichens. Certain fungi and certain algae live together, forming the compound plant structures called *lichens* (Figs. 252-254, and Plate 3). These plants grow in a great diversity of habitats, such as on exposed rocks, on tree trunks, and on the ground. They grow and survive in the most extreme habitats on the earth, from the mountains of the antarctic where the temperatures are rarely above freezing, to the deserts of southern California where midsummer temperatures of rocks on which they grow may be as high as 175° F. Some kinds of lichens appear almost structureless, forming a thin coating on the rock surface and on soil (crustose); others are somewhat leaf-like in appearance (foliose); and

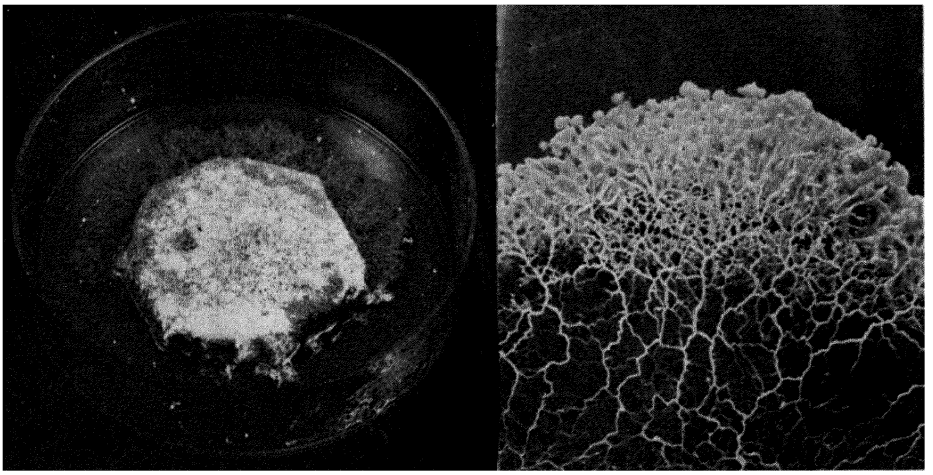

FIG. 251. Slime molds. Left: Moist-chamber culture of *Physarum polycephalum.* Smaller dish is covered with filter paper which extends into shallow layer of water in larger dish. A small amount of dry oatmeal and a bit of slime mold are placed on the paper. In a few days rapid growth of mold results in beautiful plasmodium, lemon-colored due to flavo-protein. The mold, dried on the filter paper, remains viable for a long time as a source of inoculum. Right: More highly magnified view of plasmodium of *Physarella oblonga* growing on glass. Photos and data from W. D. Gray.

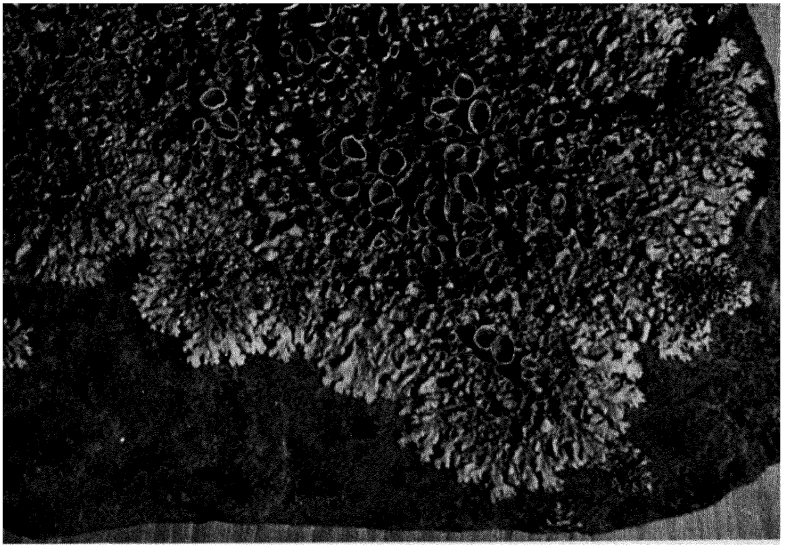

FIG. 252. Photograph of a foliose lichen (above) and a crustose lichen (below) on a rock substrate. Several cup-shaped ascocarps of the fungus in the foliose lichen are evident. Photo by G. S. Crowl.



FIG. 253. Rock tripe (*Gyrophora*) a foliose lichen on a sandstone cliff. The smaller lichen (lower left) is the toad-skin lichen (*Umbilicaria*). Photo by R. T. Wareham.



FIG. 254. A plant community of lichens, mosses, and other small plants; pioneer vegetation with consequent soil formation and accumulation on rock substrates. Photo by C. H. Jones.

still others are much branched and cushion-like (fruticose). The latter are represented by the so-called "reindeer moss" (*Cladonia*) of north temperate and tundra regions. Lichens are usually grayish-green in color, but many species are bright yellow, red, brown, or black.

A lichen is sometimes considered to be merely a fungus that is parasitic on certain algae, just as fungi are parasites on wheat, corn, and potatoes (Fig. 255). Experiments have shown that the lichen fungus,

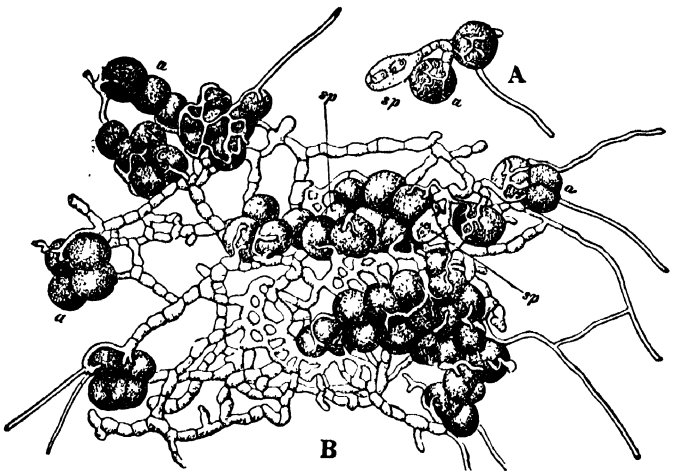

FIG. 255. Early stages in the development of a lichen. The hyphae surround and penetrate the cells of the alga. After Bonnier.

when growing alone on culture media, usually does not develop a body structure resembling that of the lichen; nor does the alga in pure culture. Nevertheless, the form of the lichen is heritable and reproduced from one generation to another. For this reason it seems desirable to regard the lichens as distinct compound plants and to classify them as a separate group. There can be no doubt that the fungus derives most of its food from the algae enclosed by it. The alga in turn may have a more constant water supply because of its covering of fungous hyphae. The algae have a much longer photosynthetic season inside the lichen than if they grew directly on the same substrate.

The species of fungi of the lichens usually belong to the group that bear asci and ascospores. A few species of basidiomycetes are also known to form a part of the lichen body. The alga is either a green or a blue-green; one of the commonest is *Protococcus* (see Chapter XLVII). Vegetative propagation is exceedingly common among lichens, and takes

place through the dissemination of minute isolated fragments containing both the fungous hyphae and the algae.

Groups of fungi. The four groups of fungi recognized by many botanists are the *Myxomycetes* (slime molds), *Phycomycetes, Ascomycetes,* and *Basidiomycetes* (see also page 692). The bacteria are often included with the fungi, certain slime molds may be associated with animal groups, and the lichens are a special problem because of their "dual" nature. There are in addition many fungi in which zygotes, ascospores, or basidiospores either are not formed or have not yet been discovered. Here belong, for example, fungi causing leaf spot of beets, "athlete's foot," and early blight of potato. These fungi are known as *Fungi Imperfecti.*

Fungi and research. Research and experimentation with fungi have gone on for many years, resulting in a vast store of knowledge regarding their growth, life cycles, occurrence, and value as synthesizers of organic chemicals, as well as better methods of control.

In recent years some fungi have been used as experimental organisms in elucidating fundamental aspects of heredity and sex. We have already referred to *Achlya.* Certain vitamins and amino acids may be synthesized in some races of the pink bread mold (*Neurospora*), for example, but not in others. Each failure in a synthesis is due to a single gene mutation. From this mold we get important information on chemical mechanisms by which certain gene actions result in the formation of known characteristics. Much fundamental research today deals with molds and other fungi, together with certain bacteria and algae.

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CHAPTER XLV

PLANT DISEASES

Among the earliest records of cultivated plants occur references to plant diseases, but for centuries the causes were thought to be mysterious and supernatural. The ancient Hebrew, Greek, and Roman writers frequently mentioned smuts and rusts, and diseases of the olive, the vine, and the fig. From the fall of the Roman empire (476 A.D.) until the 19th century, however, little was added to the knowledge of plant diseases. Even in modern times explanations of the causes of diseases of plants were impossible as long as people subscribed to the doctrine of spontaneous generation of living organisms. As late as the first quarter of the 19th century many fungi were regarded even by scientific men as merely transformations of the cellular structure of the plant upon which they grew. Plant diseases were thought to be due to internal disturbances resulting in the auto-degeneration of the tissues.

About the middle of the 19th century the recognition of fungi as causes of plant diseases came about through the researches of certain mycologists, the most famous of whom was Anton de Bary, who discovered the true nature of rusts in 1853 and published an account of the life history of stem rust of wheat in 1865.[1] The idea that some diseases are caused by parasites had often been expressed, but de Bary proved it beyond any doubt.

About this time the researches of Louis Pasteur and others were forming the foundations of the science of bacteriology. These investigations soon led to the rejection of the belief that fungi and bacteria, associated with diseased parts of plants, were produced in the lesions by the tissues of the diseased plants. That bacteria may cause diseases of plants was first proved definitely in 1880 when Burrill of Illinois discovered that bacteria cause fire blight of pears and apples (Fig. 256). Proof of in-

[1] Farmers had long believed the barberry to be associated in some mysterious way with rust epidemics. As early as 1660 planting the barberry was prohibited in certain sections of France. Massachusetts in 1760 decreed that all barberry plants in the colony must be removed.

fectious diseases in both plants and animals was established at about the same time.

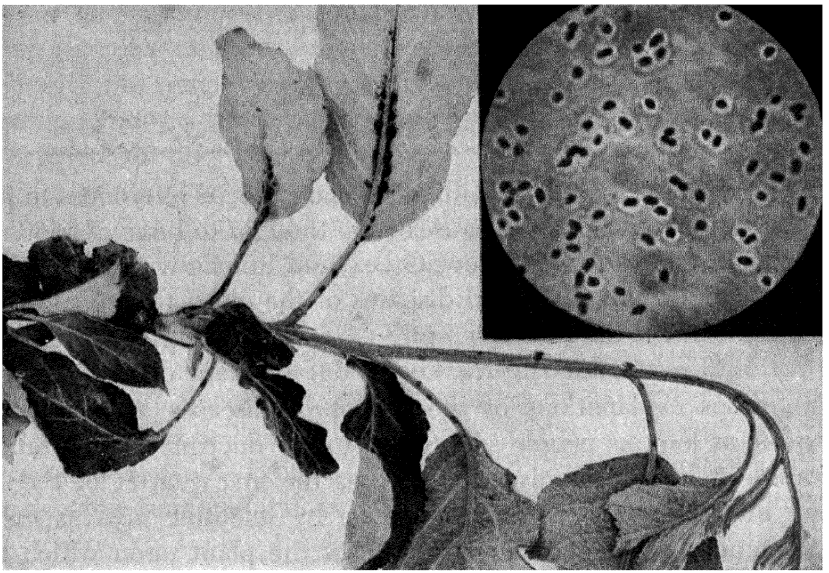

FIG. 256. Fire blight of apple. Gelatinization of the cell walls results in a slime which oozes to the surface of the host, and in the above pictures appears as dark blotches on the leaf blades, petioles, and twig. At right a photomicrograph of bacteria in ooze as seen when magnified about 2000 times. Photos from U. S. Department of Agriculture.

While the early contributions to our knowledge of plant diseases were mostly by European workers, the study of plant diseases and their control is now progressing most rapidly in America. Research in plant pathology is being carried forward not only by the universities and colleges but also by the United States Department of Agriculture and by every state agricultural experiment station, as well as by several privately endowed institutions and industrial laboratories.

Plant diseases are so diversified that no single statement satisfactorily defines them as a distinct group of phenomena. When parasites partially or wholly invade and infect a host, the resulting injuries or alterations in development, behavior, and well-being may be referred to as "infectious diseases." Agents, such as fungi, bacteria, viruses, nematodes, and certain insects, which cause infectious diseases are called *pathogens*. Examples of easily observable symptoms of plant diseases are galls,

blights, leaf spots, and wilts. These symptoms are just as "normal" to an infected plant as their absence is to an uninfected plant. Indeed, a well-trained pathologist can often tell which pathogen is present in a host by the characteristic appearance of the symptom.

One may wish to use the term "plant disease" to include physiological conditions that result from a deficiency of food, water, oxygen, light, or inorganic salts. Such diseases have been called "deficiency diseases." The observable symptoms when such deficiencies exist are a characteristic, or "normal," development of the plant under such conditions. They are often sufficiently specific that by studying their appearance one may learn to decide correctly which particular condition is deficient (Chapter XXX).

Likewise, wounding results in plant development *peculiar* to wounding but unusual in an unwounded plant. Yet the effects of many kinds of wounds are not considered to be diseases. Gnawing insects and grazing animals, as well as lawn mowers and pruning knives used by man, injure plant tissues, but such wounds in themselves are not diseases.



FIG. 257. Head of rye in which two large black ergot sclerotia have developed. From Luerssen.

Economic aspects of plant diseases. One needs only to examine the records of modern history to realize the extent of human misery and distress, as well as the starvation of millions of other animals, brought about by plant diseases. When rye is infected by the ergot fungus, large purple to black bodies replace many of the rye grains (Fig. 257). These structures are poisonous to man and other animals. From the 17th to the 19th century there were about 45 epidemics of ergot poisoning in Germany and about 20 in France and Spain. The Irish famine was brought about by the destruction of most of the potato crop by a blight fungus during the years 1843 to 1846. This blight resulted in the death of a quarter of a million people and the migration of a million and a half persons from Ireland to America.

The increasing occurrence of plant diseases is undoubtedly the result of increased concentration of crops, continuity of areas devoted to single crops, more rapid systems of transportation, and greater transfer of

plants and plant products from one part of the world to another. When a new plant is introduced into a country great care must be exercised to prevent the simultaneous introduction of its associated parasitic organisms. When certain plants of a given area are badly infected with pathogenic organisms, the government sometimes prohibits the transportation of such plants, or plant parts, into other sections of the country. This is known as "plant quarantine."

In spite of our ever-increasing knowledge about plant diseases, they continue to cause enormous losses every year throughout the world (Table 16). Farmers, orchardists, and nurserymen frequently cultivate a crop at a loss instead of a profit because of diseases or unfavorable weather conditions.

TABLE 16. Average Annual Reduction in Yield Due to Diseases, in the United States for the Years 1933 to 1937 Inclusive. Estimates by U. S. Dept. of Agriculture.

Crop	Percentage Reduction in Yield	Actual Reduction in Yield
Field corn	14.66	266,947,000 bu.
Wheat	12.64	89,227,000 bu.
Irish potato	18.12	58,031,000 bu.
Peach	10.82	7,639,000 bu.
Apple	13.62	18,331,000 bu.
Tomato (manufacture)	14.86	186,000 tons
Tomato (market)	19.64	2,687,000 bu.
Tobacco[a]	23.20	379,249,000 lb.
Cotton	15.46	1,881,000 bales

[a] Estimates reported for 1937 only.

Environmental conditions and plant diseases. We are aware that the existence of any plant depends upon its environment. Some of us have seen whole crops destroyed by unusual environmental conditions, such as flood, drought, tornadoes, and fires. As might be expected, plant pathogens are influenced by the environmental factors of the soil and the atmosphere. Whatever affects the host, such as temperature, light, oxygen supply, and the water content of the soil, will also directly or indirectly influence the organism causing the disease. Considerable information

has been accumulated in recent years regarding the direct relationship between the prevalence or rarity of certain diseases and certain environmental factors. A few illustrations will be cited. It should be noted also that environment alone may cause injuries, some of which, such as bitter pit of apples and blossom-end rot of tomatoes, have been referred to as "diseases" (Fig. 258).

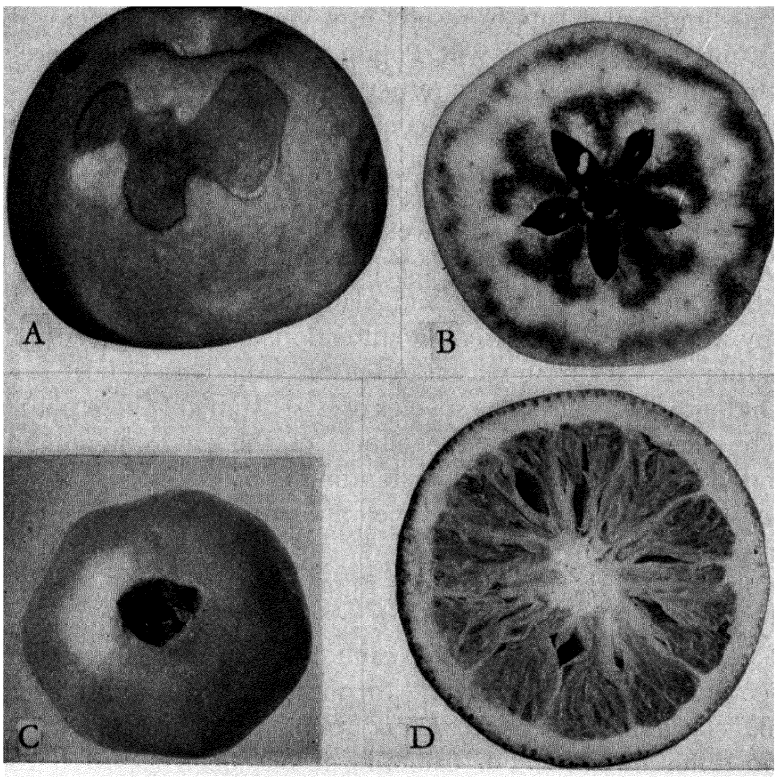

FIG. 258. Injuries to fruit caused by environmental conditions such as temperature and drought. A, apple soft scald; B, apple brown core; C, tomato blossom end rot; D, freezing injury of orange. Photos from U. S. Department of Agriculture.

The potato scab fungus causes more lesions on tubers growing in an alkaline soil, whereas the growth of the organism causing clubroot of cabbage is favored by an acid soil. The organism causing tobacco root rot is practically eliminated from soils of very high acidity.

The weather influences the abundance or scarcity of plant diseases largely through the effects of temperature and moisture either on the hosts or on the parasitic organisms.

Peach leaf curl is generally more widespread in years having cold wet spring seasons. Potato scab lesions are usually most abundant at a temperature of about 70° F. The fusarium-wilt organism which infects tomatoes growing in greenhouses makes little progress at soil temperatures of 63° F. and 95° F., but develops rapidly at temperatures midway between these extremes. When growing in soils of either low or high water content, the tomato plant is not affected much by the wilt organism. A medium water supply results in a vigorous and succulent plant which is quite susceptible to wilt. Potato scab appears to be more severe on potato tubers growing in dry rather than in moist soil.

Apple scab develops rapidly in cool, moist weather. Rainy periods between the time of opening buds and petal fall increase the prevalence of the disease. Discharge of ascospores from the asci in fallen leaves occurs only when they are thoroughly wet. The new leaves on the tree will become infected only when they are continuously wet for several hours.

Variations in hosts, parasites, and plant diseases. It has been known for many years that the extent of infection and the susceptibility to plant pathogens vary from season to season, from host to host, and even among individuals of the same species of host. Many of these phenomena cannot be accounted for by the effects of the environmental factors enumerated above. A better understanding is possible today because of increased knowledge of the genetic complexity both of host plants and of plant pathogens.

Varying degrees of infection and injury may occur even under apparently similar field environments. A species of fungus causing disease may be composed of several races, each differing from the others in its virulence on specific hosts. Owing to population shifts, some of these races may be more abundant or less abundant than others at various times on different hosts. For example, it has been reported that the species of fungus (*Puccinia graminis*) which causes stem rust of wheat is a mixed population of at least 180 races, each of which can be distinguished by its relative virulence in different varieties of wheat. Through a period of time the relative abundance of the different races in a given area fluctuates, with corresponding changes in infection and destructiveness of the disease.

Both mutation and hybridization must be considered. They may occur in the host, or in the pathogen when it is growing either in pure culture or inside the host. From a highly mutating pathogen several new mutant races, differing in virulence in various hosts, may appear within a few

generations. These new races may remain constant or continue the variability of the species through further mutations.

In those fungi where nuclear fusions occur, recombinations of heritable factors due to hybridization of different races may result in hybrids varying in degree of virulence. For example, investigators at the University of Minnesota crossed two monoploid races of the corn smut species and from the resulting hybrid obtained nearly 40 segregates, no two of which were alike.

In 1928 "Race 56" made up only 0.5 per cent of all the varieties of the wheat stem rust fungus isolated from rusted wheat in the United States, and was found only in three states. By 1938 this race was found in 66 per cent of the tests made and had extended over large areas in the United States, Mexico, and Canada. Evidently wind was a very efficient agent in scattering spores of this new genetic race. Moreover, Race 56 was the primary cause of the elimination of Ceres wheat, which had been one of the least rust-susceptible wheat varieties in the country. New races of such pathogens are possible at any time, and thus the fight against the causal agents of such diseases must be waged continually.

Newly introduced varieties of wheat less susceptible to wheat rust than varieties formerly harvested may also differ in characteristics important to millers and bakers. Each new variety has to be tested for flour composition and quality, important factors in making bread, cake, and other well-standardized food products.

Symptoms of plant diseases. The external symptoms of plant diseases are of many kinds, and only a few of the commoner ones will be summarized here.

1. *Pustules* are fruiting bodies or spore masses of parasitic fungi which have ruptured the outer tissues of the host. Rusts and smuts are common examples (Figs. 249, 250).

2. *Scabs and blotches* are surface lesions caused by local growth of fungi. Apple scab is a common example (Fig. 260).

3. *Mycelia* may be prominent, such as the external mycelia of powdery mildew, the compact masses of mycelia of ergot of rye (Fig. 257), and the black "tar-spots" on leaves of willow and maple.

4. *Overgrowths* of host tissues result in malformations of leaves, stems, and roots. Crown gall of apple, raspberry, and grape; black wart of potato; black knot of cherry and plum; clubroot of cabbage; root nodules of legumes; nematode galls on roots of tomato and cotton; insect galls on

leaves and stems of various plants; and "witches' brooms" on hackberry are some common examples (Figs. 231, 264, 265, 709).

5. *Leaf spots* are dead spots caused by the local growth of parasites in the leaf tissues of the host. They occur frequently on leaves of cherry, tomato, rose, and many other plants.

6. *Wilts* include various diseases that are first noticeable by the sudden wilting of leaves or of the whole plant. Bacterial wilts of cucumber and cantaloupe are rather common. Damping-off of seedlings and cuttings is a type of wilt disease caused by local infection and weakening of stems near the surface of the soil.

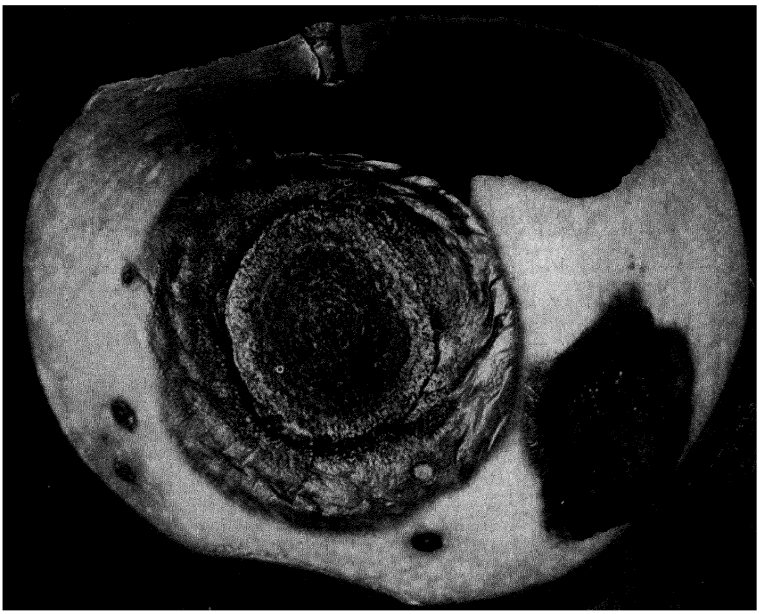

FIG. 259. Apple infected by the fungus which causes bitter rot of apples. Photo from Ohio Agricultural Extension Service.

7. *Rots* are the result of the decomposition of the cell walls of affected tissues, such as the soft rot of sweet potatoes, bitter rot of apples (Fig. 259), and brown rot of stone fruits (Fig. 261).

8. *Blight* is the term applied to the sudden dying of leaves, shoots, and blossoms. The fire blight of apple and pear is common wherever these trees grow in America (Fig. 256).

9. *Cankers* are sunken dead areas on stems in which the bark is

killed. Fire-blight cankers are caused by bacteria. The nailhead canker on stems of apple trees is caused by a fungus. Similar dead areas may be caused by low temperatures and by sun scald.

10. *Yellowing or chlorosis* of leaves is caused by viruses, by some fungi and bacteria, by low temperatures, or by a deficiency of certain salts.

Control of plant diseases. In recent years it has become increasingly evident that really efficient measures for controlling plant diseases must depend on an accurate and detailed knowledge of the life cycle of the pathogen. The acquisition of this knowledge is sometimes a laborious and technical procedure. Special training and well-equipped laboratories are essential to progress in acquiring the necessary facts.

When the life cycle of the causal organism is known, experience has shown that there is usually some point in the cycle that is subject to attack by methods of control. Spores or young hyphae outside the plant are often easily destroyed by chemicals or heat; but it may be impossible to eliminate an internal mycelium that develops from them without injuring the host. For example, a spore or hypha of the apple scab fungus may be destroyed by a suitable fungicide on an apple leaf before the first hypha has grown into the leaf. After the hypha is once inside the leaf it is difficult to kill it without destroying the leaf. Similarly it is much more economical to try to eradicate the black stem rust of wheat by removing barberry plants than by attempting to spray the wheat.

Numerous plant diseases are known, and many control measures have been devised and applied with varying success. Even when a partially efficient control measure has been worked out, it has been found by bitter experience that the application is not a rule-of-thumb matter. No single procedure will give the same results in all kinds of weather, with all varieties of plants, or at all times of the year. In other words, the successful application of such treatments as sprays, dusts, and hot water depends on the condition both of the host and of the parasite; and such measures must be used with keen discrimination if the results are to be effective.

With these general considerations in mind, representative diseases caused by fungi, bacteria, slime molds, nematodes, and viruses will now be considered.

Apple scab. In the United States as a whole, scab is the most destructive of apple diseases. The olive-brown areas of "scab" are quite notice-

able on the leaves, fruits, and flower pedicels (Fig. 260). These spots not only lessen the commercial value of the fruit, but also decrease photosynthesis, cause early abscission of fruits and leaves, and check the growth of the remaining apples. The mature ascospores in the old dead leaves on the ground are projected into the air from the bursting asci during rainy weather in the spring and are blown about by the wind to

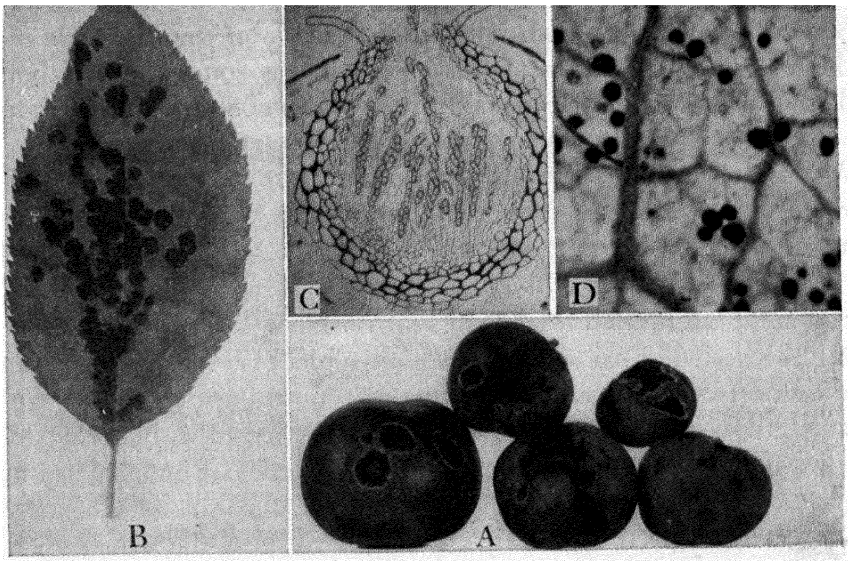

FIG. 260. Apple scab: A, on the fruit; B, on a leaf in which the fungus lives throughout the winter; C, magnified section of an ascocarp with asci and ascospores from an over-wintered leaf; D, ascocarps visible in an old leaf after it has been cleared in hot potassium hydroxide. Adapted in part from A. L. Pierstorff and Ohio Agricultural Extension Service.

the apple trees. The spores germinate almost immediately on the living tissues of opening buds, young leaves, and flowers if a film of water is present. Sprays of lime sulfur, or wettable sulfur, must be applied before extended periods of rain to prevent infection by the hyphae from the germinated ascospores. After infection and growth of an internal mycelium, conidia develop and are distributed to other parts of the tree by rain water.

It is extremely desirable that all pre-blossom infections of apple scab be prevented, since conidia may be produced all summer long from hyphae of mycelia if the early infection by ascospores is allowed to

occur. Sprays are applied often enough to protect all young growing parts from invasion. This protection is generally secured by some such program as the following: (1) a delayed dormant spray is applied as soon as the leaves which surround the young flowers have emerged about 1/4 inch; (2) a pre-pink spray before the slightly emerged petals have become colored; (3) the pink spray before the flowers are in full bloom; (4) the calyx spray just after petal fall and before the blossom end of the fruit has been covered by the calyx; (5) another spray ten days after the calyx spray; and (6) later sprays applied when necessary.

A well-informed plant pathologist, with the aid of weather forecasts and information from orchardists concerning the condition of the buds, can intelligently modify the above spray program according to weather conditions. In some states pertinent information concerning spray programs is broadcast daily by radio for all sections of the state during the spring months.

Damping-off. Seedlings of plants often are infected at the surface of the ground in such a way as to cause the killing of the stem and consequent death of the whole plant. Gardeners and nurserymen are especially troubled by this damping-off disease in seedbeds. Several species of fungi cause damping-off, and they have been reported from all parts of the world. Practically all species of plants are susceptible to these fungi. Sometimes the plant is destroyed before the seedling emerges from the ground; in other cases the disease may not be apparent until after the seedlings or cuttings are transplanted. The fungi may live for long periods of time in the soil as saprophytes. It is doubtful if highly organic soils are ever free from such organisms. Abundant moisture on the plant or in the soil, and a fairly high temperature are favorable to the growth of these fungi and their invasion of green plants.

Control measures for damping-off lie largely in soil disinfection and the proper regulation of temperature and humidity. Hot water, steam, sulfuric acid, and formaldehyde have all been found effective means of disinfecting soils. Dusting seeds with copper or mercury compounds is also an efficient control.

Downy mildew of grapes. This disease is probably native to North America, having been reported in the United States in 1834. It was not known in Europe until 1875. The presence of the downy mildew on grapes in France led more or less accidentally to the discovery about

1881 of an important fungicide known as Bordeaux mixture. A disease caused by the root louse (*Phylloxera*) had become a serious menace to the vineyards of France, and in order to combat this disease the French imported some American grapes which are immune to the root louse. The American stock, however, was infected with the downy mildew fungus which then spread all over Europe. Apparently at least one vineyard-keeper customarily sprinkled a copper sulfate-lime mixture on the vines along the highways to discourage theft of the grapes. The French pathologist, Millardet, observed that where such a mixture was sprinkled on the vines, the ravages of mildew were reduced. He began experiments which led to the general use of Bordeaux mixture as a spray for the successful control of this and other diseases.

The fungus invades all green parts of the grape plant and appears as whitish patches of mildew. The fungous hyphae enter the plant largely through the stomates. The presence of the mycelium within the plant may result in loss of leaves, dwarfing of young twigs, and destruction of fruit. Since the fungus winters over as spores in fallen leaves, the disease may be combated by getting rid of the leaves (sanitation), and by spraying the plants with Bordeaux mixture before the young hyphae from the spores invade the young leaves and flowers.

The powdery mildews. The powdery mildews occur everywhere in temperate and tropical regions and on a large variety of hosts. These fungi are visible on the surface of the affected plant, and sometimes the parasitized tissues of the host become malformed. They are either whitish to grayish, powdery or mealy depending upon whether the visible structure is the mycelium, the summer spores, or the blackish fruiting bodies. The powdery mildews are always superficial parasites and in this way differ sharply from the downy mildews considered above. The methods recommended for the control of powdery mildews include removing the infected parts, or using an appropriate spray or a sulfur dust.

Brown rot of stone fruits. This disease is important in the United States and Europe because it destroys the fruit of such orchard crops as peaches, plums, cherries, and apricots (Fig 261). Among the pome fruits the apple may also be affected. The disease is usually recognized by the rotting of fruits, blasting of flowers, and the killing of young stems. A brown spot appears on the fruit and may enlarge until the whole fruit is decayed. In later stages the fruit dries and shrivels to a

condition that has given rise to the term "mummified fruit." When the flowers are infected, "blossom blight" occurs and results in the death of the flowers. The fungus may grow from the blossoms into the twigs, and there cause cankers and death of the twig.

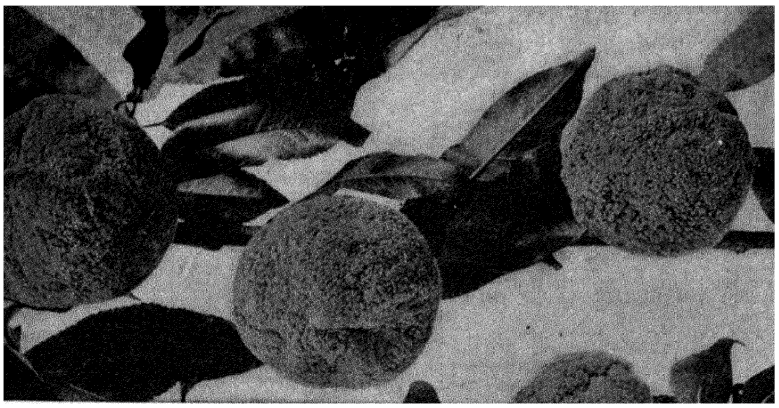

FIG. 261. Brown rot of peaches. Photo by J. A. McClintock, Georgia Experiment Station.

New infections may occur from the time of early flowering until the fruit is mature. Insects and winds are the principal means of spore dispersal. The fungus may overwinter in mummified fruits and in twig cankers. Control of the disease may be accomplished by thorough pruning accompanied by removal of mummies and diseased twigs and the application of the appropriate sulfur sprays or dusts throughout the growing season.

Peach leaf curl. Typical symptoms of peach leaf curl are pinkish, puckered, and thickened leaves or parts of leaves. Infection of peach leaves is most frequent when a cold wet period follows the parting of the bud scales in spring. The mycelium invades the tissues and in a few weeks a layer of asci forms on the upper surface of the leaves. This disease causes the early abscission of the leaves. Young shoots and flowers are also infected and killed. The disease is easily controlled by one application of a lime-sulfur or Bordeaux spray *during* the dormant period *before* the buds begin to swell.

Wood rots. Trees, fence posts, telephone poles, railroad ties, and bridge timbers sooner or later decay, as the result of the activities of certain wood-rotting fungi. These fungi nearly all belong to the groups

of "fleshy" fungi. They may destroy the heartwood, the sapwood, or both (Fig. 262). Changes in the color and texture of the wood usually accompany the growth of the fungi. The internal mycelium is of course the destructive agent through its formation of wood-digesting enzymes.

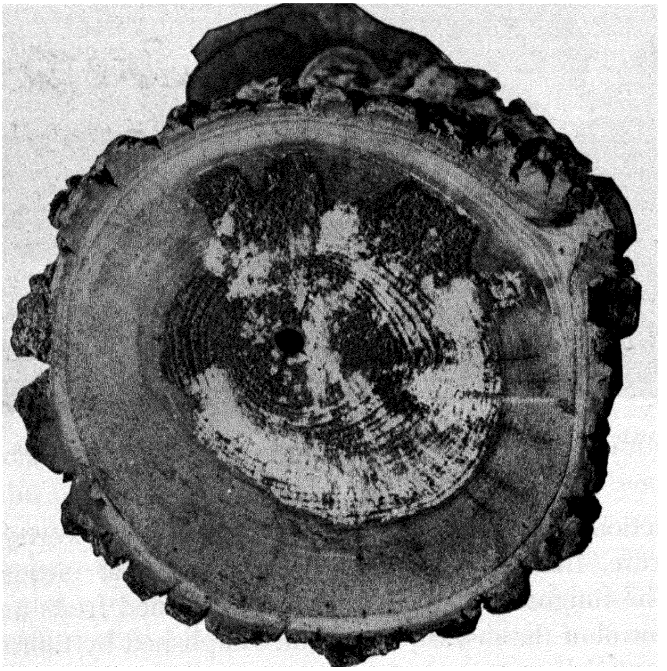

FIG. 262. Cross section of a stem of white ash in which a saprophytic fungus has destroyed a part of the heartwood. The obvious mycelium pictured on the cut surface grew after the section was removed from the tree and placed in a moist chamber. From U. S. Department of Agriculture.

The external fruiting bodies (Fig. 247), popularly known as "conks," produce numerous spores, which are carried to other trees primarily by wind. Living trees are infected through wounds, as well as by the direct growth of the fungus from infected stumps into the heartwood of trees in sprout forests.

It is practically impossible to control wood rot in forests. The infection of orchard trees may be avoided by careful treatment of wounded trees, and by the eradication of all infected ones. Telephone poles, railroad ties, and other timbers in contact with soil may be protected for long periods of time by appropriate treatment with coal-tar creosote, tar, crude oil, or certain salts of zinc.

When fox-fire is traced to its source it is usually found coming from saprophytic fungi (Fig. 263) living in partially decayed wood or bark. Some of the energy set free in respiration in these fungi is light energy.

The smuts. The smuts described in the preceding chapter are destructive to cereals, but effective measures of controlling some species have been discovered. The importance of knowing exact life cycles of fungi that cause disease before one attempts to formulate methods of

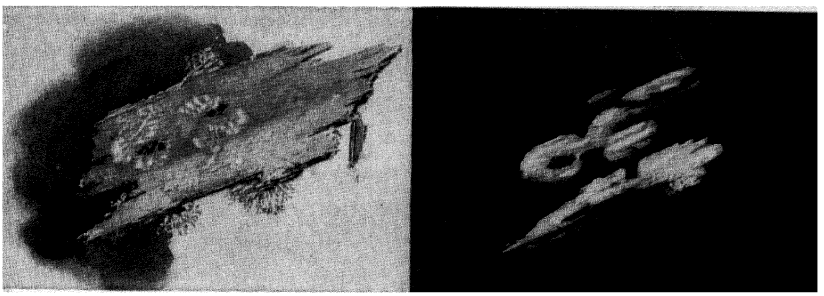

FIG. 263. Fox-fire. Fungous mycelium in a piece of wet bark as seen in light and in darkness. After W. Hamilton Gibson.

control is shown by a study of three kinds of smuts: corn smut, loose smut of oats, and loose smut of wheat and barley (see Chapter XLIV).

The spores from the black masses or lesions on the corn plant fall on the ground, remain there over the winter, and may be the source of infection of young plants if carried to wounds during the following spring. The most effective methods of control are selection of seed from healthy plants, selection of hybrids immune to the disease, and crop rotation.

The mycelium of the fungus which causes the disease known as loose smut of oats grows within the oat plant and produces millions of spores in the young flower panicle. These spores are blown about by the wind and some of them lodge in the flowers of healthy oat plants. There they germinate; and the mycelium may grow among the glumes, or beneath the epidermis of the grain coat. Some spores may not germinate but remain attached to the outer portion of the glumes. The fungus overwinters in either of these three places, and when the oats are sowed may cause infection of the seedling and eventually a smutted head at or before harvest time. The fungus is killed by treating the seed with formaldehyde or with ethyl mercury phosphate before planting.

The fungi causing loose smut of wheat and barley live through the

winter as mycelia inside the grain. Spores may also survive the winter on the seed. The spores on the surface are easily killed, but it is difficult to kill the hyphae inside the seed without injuring the embryo. The fungous hyphae in the wheat seed are killed when the seeds are immersed in water at a temperature of 129° F. for ten minutes; the hyphae in barley seeds may be killed by similar treatment at 127° F. Neither the wheat nor the barley embryos are injured if these directions are accurately followed.

Plant diseases caused by bacteria. It is sometimes difficult to discover whether a disease is caused by bacteria or by fungi since both are often present in the same lesion. It is of course necessary that this discovery be made before effective remedial measures can be worked out. Most bacterial diseases of plants are very difficult to control. Among the better measures of control are: rotation of crops, use of disinfected seed, prompt and complete destruction of diseased plants or parts of plants, proper care of wounds made by storms and pruning, seed sterilization, and the planting of less susceptible varieties. The fire blight of pear is probably the best known of these diseases, and the methods suggested for its control will be discussed.

Fire blight. Fire blight is one of the most destructive of the diseases of pome fruits. Its most frequent symptoms appear as blighted twigs, flowers, and leaves. Infection takes place in the flowers, young shoots, and leaves. Any diseased part of the plant may exude a sticky fluid containing the bacteria. Rain may distribute the bacteria to other parts of the plant. Insects, however, are the most important carriers of the bacteria from one plant to others.

Fire blight is difficult to control. To decrease the possibilities of infection of apple and pear trees, tender sprouts should be kept removed from the trunk and larger branches during the early part of the growing season. In addition, all blighted twigs should be removed from the pear orchard at least twice weekly during the active blight season. Blighted branches found in the fall of the year should also be removed. Other suggested methods of control include the application of sprays at blossoming time and the planting of varieties of pears and apples less susceptible to the disease.

Clubroot of cabbage. The organism which causes this disease in certain members of the mustard family, such as cabbage, turnips, and radishes, is a very primitive mold. Deformed, and club-shaped roots are evidence of the progress of the disease. The organism enters through root hairs or through wounds, and digests the tissues of the host as the

plasmodium grows. If the cambium is invaded, further development of the tissues of the root is very irregular (Fig. 264A). The disease is most prevalent in warm, wet, acid soils. Control methods recommended are: use of disease-free plants, application of hydrated lime (from one to two tons per acre), planting of less susceptible varieties, avoidance of planting cabbage in infected fields.

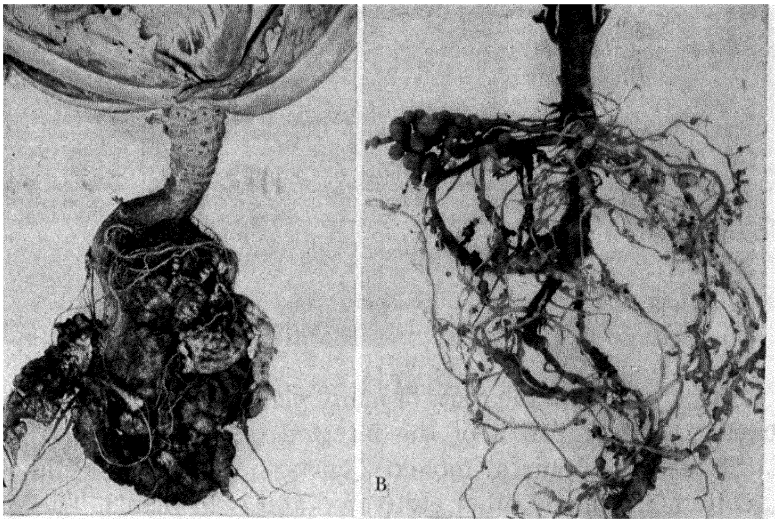

FIG. 264. A, clubroot of cabbage; B, nematode galls on roots of tomato. Photos from U. S. Department of Agriculture.

Galls. The development of galls on leaves, stems, and other parts of plants is induced by insects,[2] bacteria, and fungi. The greater variety of galls are caused by insects. Galls may be formed on many kinds of plants and are readily seen on oaks, hackberries, willows, goldenrods, asters, and roses. In some way, perhaps primarily by means of hormones, the organisms living in these plants initiate peculiar overgrowths of certain local tissues, with the ultimate formation of a gall having a specific form and pattern. Leaves and young twigs are the parts usually affected. The different forms and patterns of galls are correlated with the causal insects, rather than with the plants on which they occur. In many instances the insects can be identified from the characteristics of the galls (Fig. 265).

Nematode galls. The nematodes, sometimes called roundworms, may live either as parasites or free in moist soil containing organic matter.

[2] These insects include gall-wasps, gnats, aphids, and mites.

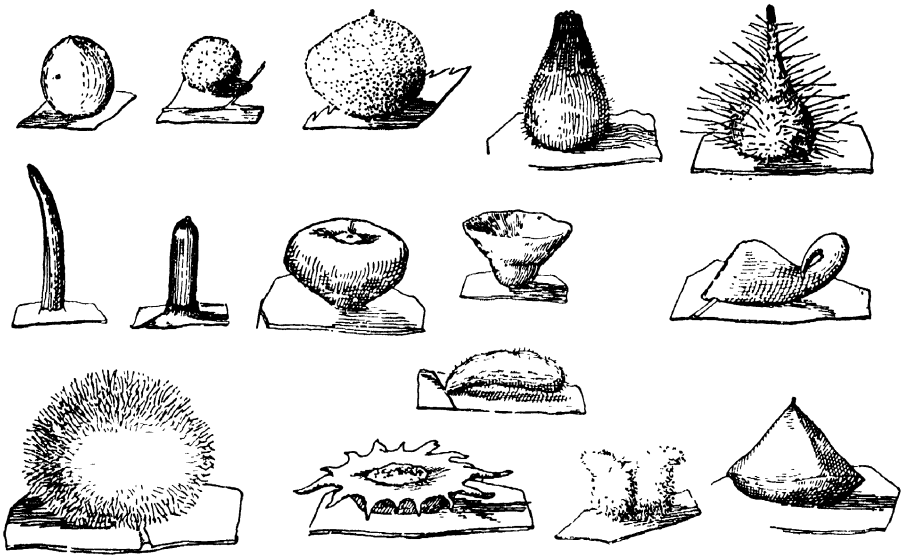

FIG. 265. Fifteen different galls on hickory leaves caused by as many different species of insects. Drawings by B. W. Wells.

They eat their way into the roots of many plants, feeding upon the juices, and cause the overgrowth of the infested organs (Fig. 264B). They infest the roots of tomato, tobacco, cucumber, lettuce, peony, strawberry, cotton, and many other cultivated and wild plants. The so-called nematode disease of wheat affects the flowering parts, transforming the grains into galls. Stems and leaves of rye, clover, alfalfa, begonia, and many bulbous plants become distorted, swollen, and variously colored because of infestation by leaf and stem nematodes. An excessive development of fibrous roots of sugar beet is also caused by nematodes. The chief methods of control are soil disinfestation and crop rotation.

Virus-diseases of plants. Among the diseases recognized in relatively recent times as being caused by viruses are tobacco mosaic, curly top of sugar beet, peach yellows, yellow dwarfing of onions, tomato streak, leaf roll of potatoes, virus gall of sugar cane, and witches' broom of sandalwood tree. Viruses also affect animals and cause such diseases as infantile paralysis, smallpox, influenza, common colds, measles, and rabies. There are many viruses, each of which has characteristic effects on a plant (Fig. 266). Some viruses have been found to cause diseases in many more varieties of plants than have others. Viruses have been detected in more than a thousand species of plants growing in all

parts of the world. The tobacco mosaic virus has been shown to be a protein of a high molecular weight, which may be purified by repeated recrystallization without losing its property of causing the disease. This causal agent increases in number in contact with the protoplasm of the plant. It cannot be cultivated in any known non-living culture medium.

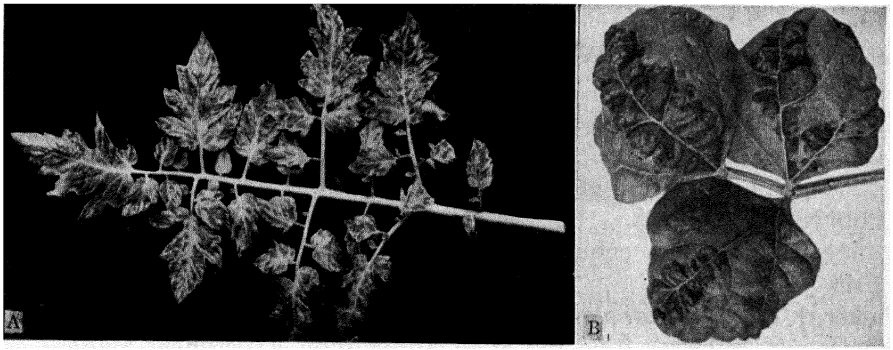

FIG. 266. Symptoms of mosaic disease on leaves of tomato and bean. Photos: A, by J. D. Wilson; B, by U. S. Department of Agriculture.

One kind of virus is lethal only to certain species of plants. Even these plants may survive for a long time if the concentration of the virus in their cells remains low. They may, however, fail to grow as well or yield as much as plants free of viruses. Viruses are usually not localized in certain tissues and organs, but permeate all living parts of the plant. Herbaceous plants are apparently more susceptible to viruses than woody species, although lethal virus diseases of elm, plum, and peach are well known. Viruses are transmitted from diseased to healthy plants by insects, such as leaf hoppers, aphids, and flea beetles, and sometimes on the tools used in cultivating, pruning, and grafting. Certain viruses are transmitted through the seed, while others are not. Some viruses may be carried over from one season to the next in other plants such as weeds and wild plants which grow nearby. Control has been accomplished by the removal of such additional plants.

Other control measures include the eradication of diseased plants, control of the insects that transmit viruses, use of virus-free seeds, the avoidance of inoculating wounded parts of plants in grafting and vegetative propagation, and the selection of less susceptible varieties.

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CHAPTER XLVI

UNDER-WATER ENVIRONMENTS

Numerous kinds of plants live continuously under water. Many epiphytes, on the other hand, grow in a medium of air and are in contact with water only during rains or when covered with dew. Even a rooted plant in dry uplands grows almost entirely in the atmosphere which surrounds its tops and fills the spaces between the particles of the soil. Except for short intervals after rains, its root system in summer is in contact only with thin films of water held by the soil particles, and much of it is exposed to the soil air.

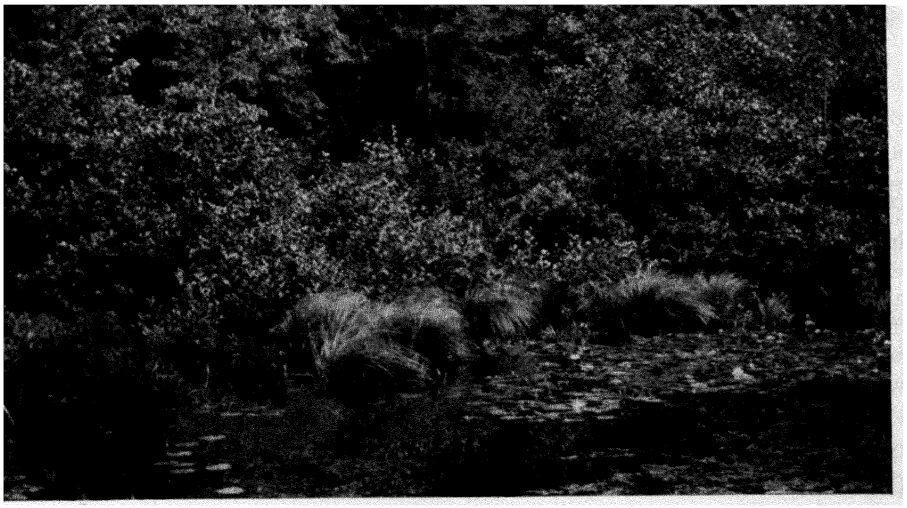

FIG. 267. An abrupt transition in habitats and vegetation.

Other species of plants live partially submerged in the shallow water of marshes and swamps between uplands and near the borders of oceans, lakes, and streams (Fig. 267). Some of them are limited to areas in which the water level fluctuates with the rains and tides. Many plants can endure partial submergence for limited periods of time, and many

others thrive with their roots and rhizomes in soil continuously below the water surface. The erect stems of such plants extend above the water surface, or because of long petioles their leaf blades are exposed to the air above the water. Among the plants of the world there appear to be all gradations between those limited to land and those limited to water habitats (Fig. 268). Those on land can endure varying degrees

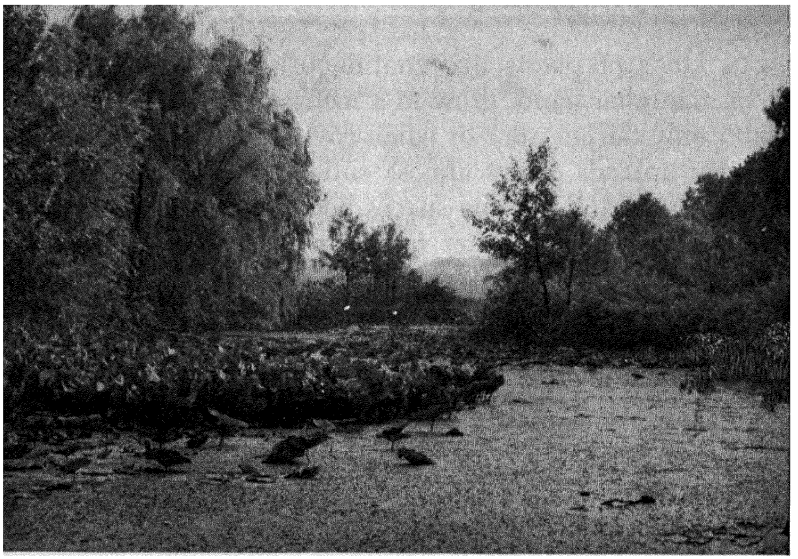

FIG. 268. Plants in various degrees of submergence. Many plants not evident in the picture are wholly submerged. Water milfoils, hornwort, elodeas, pondweeds, and many others may be wholly submerged or with their tips slightly above the surface (foreground). Leaf blades of water lily and pond lily may be floating or raised above the surface. The leaves of cat-tail and bulrush are mostly aerial, and all but the root systems or parts of root systems of dogwood, alder, and willow are above the water. Photo by E. S. Thomas, Ohio State Museum.

of exposure to the air and to water loss by exaporation. Those below the water surface can endure low concentrations of oxygen.

Some submerged plants live wholly suspended in water. Others have roots in the underlying substrate. The general processes of nutrition and growth in submerged plants are the same as those in land plants, and they are dependent upon the same external factors. These factors, however, are not similarly distributed or equally available in air and in water media. A few of the conditions in land habitats and in water habitats are compared in the accompanying summary.

The Land Habitat	*The Water Habitat*
Plants and animals with high water content living in a medium of air.	Plants and animals with high water content living in a medium of water.
The medium: the atmosphere above soil always in motion, and its molecules always in rapid motion; rarely saturated with water vapor; compressible, hence rarely destructive when in motion; air and water movement in soil restricted by soil particles.	*The medium:* the hydrosphere relatively quiescent, except surface layers of large bodies of water and rapid streams; molecular motion comparatively slow; incompressible, hence offers great resistance to movement within it, and when in rapid motion very destructive.
Carbon dioxide: always available above and below soil surface.	*Carbon dioxide:* in solution, both free and bound in bicarbonates; concentration variable, often high in water containing organic matter and in soil beneath water.
Oxygen: always available above soil surface, not always available below soil surface.	*Oxygen:* in solution; concentration highest in surface layer, often deficient in deep water and in soil beneath water.
Temperature: large daily and seasonal fluctuations of air temperature; smaller variations of soil temperature, except where relatively dry soil surface is exposed to the sun, where the daily and seasonal extremes commonly exceed those of the air.	*Temperature:* smaller daily and seasonal fluctuations even in upper layers; temperature very constant in deeper water; temperatures of water and underlying soil not very different.
Soil: stability, penetrability, porosity, gas content, and water content important in root development. Inorganic salts in soil and dust available when in solution or in direct contact; concentration sometimes very low; in arid regions more concentrated and sometimes toxic.	*Soil:* stability, porosity important. Inorganic salts obtained from medium by suspended plants, from soil by rooted plants; salt concentration sometimes very low; usually higher in oceans than in moist soils; in closed basins salts may accumulate to toxic concentrations.
Light: usually abundant at upper vegetation surface; decreased at lower levels by taller plants.	*Light:* abundant at water surface except for clouds, fogs, and shade of plants above surface; rapidly decreases below surface. Rough surfaces and turbidity increase reflection, decrease light penetration.

It is evident that an aquatic environment includes most of the factors of a land environment, but the intensity or quantity of any factor is very different. Certain conditions essential to green plants, such as light, carbon dioxide, and oxygen, are more often at a minimum in water than in air. Rates of diffusion also are so much slower in water that, in the absence of currents, the movement of dissolved gases to plants may be so slow that both photosynthesis and respiration are limited. On land transpiration often becomes destructive. Because of these effects of the medium, some kinds of plants survive only in certain places on land, others only in certain places in water. Plants that can live both in water and on land are either microscopic plants or those larger plants which have emergent leaves when growing in water. The vertical spread of plants on the earth is diagrammatically represented in Fig. 269.

Under-water habitats are roughly of two kinds: fresh water, including lakes and ponds, rivers and streams; and marine, such as oceans, seas, gulfs, and bays. There are also inland bodies of water of high salt content in the plains, semi-deserts, and deserts.

The Fresh-water Environment

The fresh-water environment includes all non-saline lakes and ponds, rivers and smaller streams, swamps, marshes, and bogs. Each of these types of habitat is considered separately.

LAKES AND PONDS

Lakes and ponds differ from each other chiefly in area, depth of water, permanence, effects of winds and temperature changes, and depth of light penetration. They represent the so-called standing water, in contrast to the flowing water of streams, although there may be surface movements due to winds, changes in temperature, and deep springs.

Light. The intensity of light at the surface of a lake is dependent primarily on the latitude and the time of day. It may be modified locally by clouds, fog, smoke, dust, and marginal shade. It is not, however, the intensity of the light at the surface that is of importance in the growth of submerged plants, but the light that actually penetrates the water to the depth at which they live.

The amount of direct sunlight that is reflected from a smooth water surface ranges from 2 per cent when the sun is directly overhead to nearly 100 per cent when the sun is near the horizon. Of the total

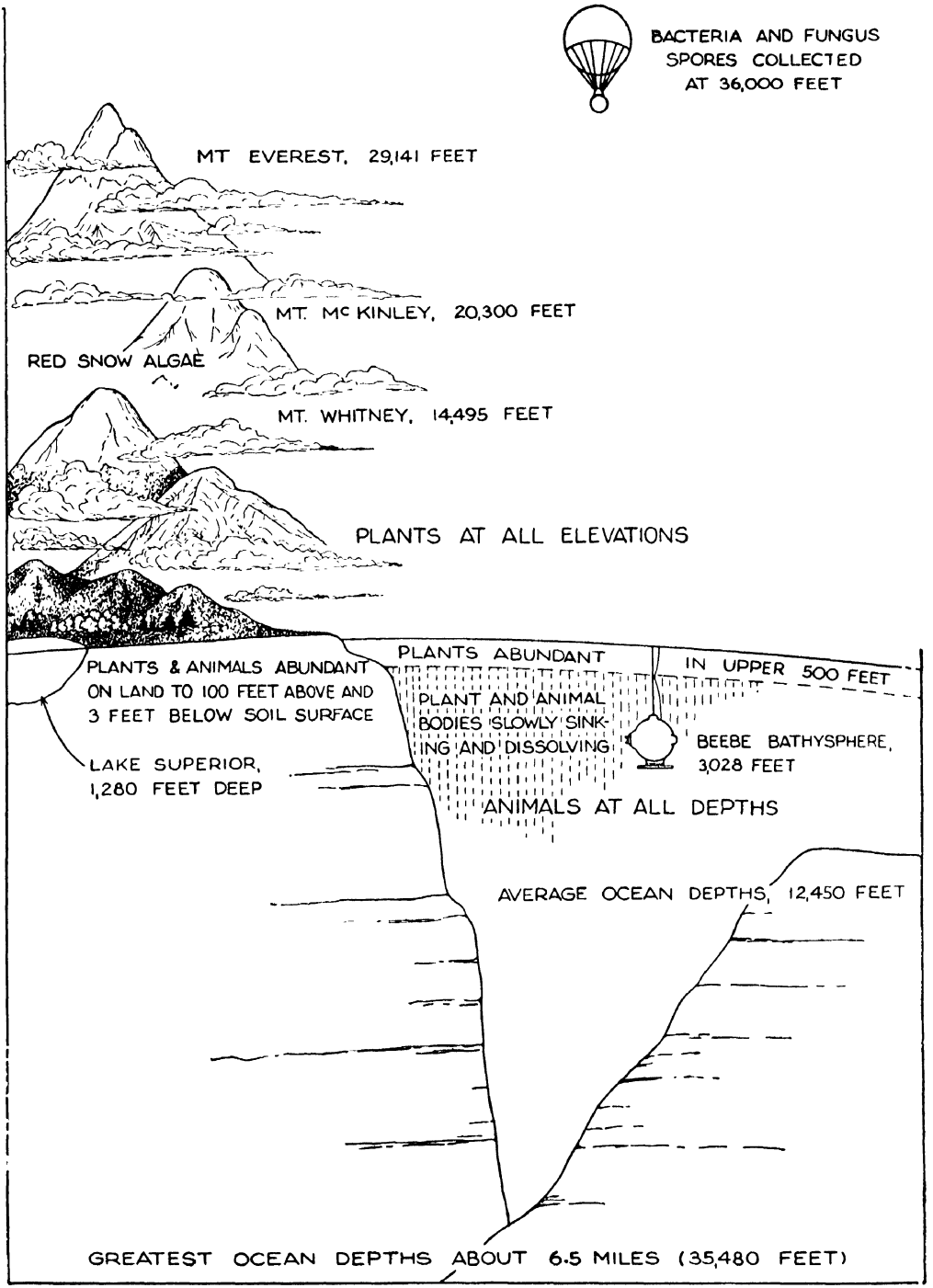

FIG. 269. The vertical distribution of living plants on the earth.

radiation from the sun and sky during a day, 7 per cent is reflected from a smooth water surface; but when the water surface is rough, as much as 25 per cent may be reflected. The light below the water surface is thus always less than that above.

Natural bodies of water are usually colored or turbid with suspended colloidal particles and microorganisms. These minute objects reflect and refract the light in all directions. They also absorb it and are highly effective in reducing light intensity in the water below them. About 40 per cent of the light that enters the water is usually absorbed in the first meter. Not more than 5 to 10 per cent of the visible rays penetrate to a depth of 10 meters; and at depths of 50 meters the light is negligible and consists only of certain green, blue, and violet rays.

As a result of the reflection and absorption of light at the surface of the water, the length of the daylight period in deep water is relatively short and is limited to the middle of the day, when the sun's rays are near the vertical. Radiation from the sky is insufficient to illuminate the depths.

Photosynthesis. In clear-water lakes the layer of water in which effective photosynthesis occurs rarely exceeds a depth of 10 meters. In turbid or colored water it is much less. It is therefore readily seen why the bulk of the suspended and rooted plant populations of lakes is confined to the upper layers of open water and shallow margins. Only in the extremely clear water of high mountain lakes is photosynthesis adequate at greater depths. There are a few very slow-growing green plants that exist at depths of 15 and even 30 meters, where photosynthesis in them is evidently just above the compensation point. The maximum depth of most rooted aquatics in the lakes of the United States is 6 to 7 meters. At this depth the plants are exposed to about 2 per cent of total sunlight.

Oxygen. Oxygen enters lake and pond water primarily from the atmosphere. It diffuses into the water more rapidly when the surface is agitated and increased by wind. Additional dissolved oxygen is brought into lakes from the atmosphere by rain water and by rapid tributary streams, particularly if they flow over falls and riffles. Oxygen is also added during the daylight period by photosynthesis in submerged green plants.

The oxygen concentration is decreased through the respiration of both plants and animals. It is also dissipated by high temperature of the water. Indeed, in shallow ponds containing an abundance of both

plants and animals, the oxygen content may become so reduced during hot weather that fish and other submerged animals suffocate. The death of submerged plants in shallow water may likewise occur from suffocation.

Carbon dioxide. The sources of CO_2 in the water of ponds and lakes are diffusion from the atmosphere, oxidation of organic matter by bacteria and also the respiration of all other organisms, inflowing streams, and the release of CO_2 when the soluble bicarbonates of calcium and magnesium are changed to insoluble carbonates and accumulate as marl (Fig. 228, page 513).

When carbon dioxide dissolves in natural bodies of water, more than half of it combines with the water, forming carbonic acid: $CO_2 + H_2O \rightarrow H_2CO_3$. The remainder exists as free carbon dioxide. Submerged green plants utilize in photosynthesis not only the free CO_2 but also the CO_2 in carbonic acid and the so-called "bound" CO_2 in bicarbonates, such as those of calcium, magnesium, sodium, and iron.[1]

There is about one-third of a cubic centimeter of CO_2 in a liter of air, and it is constantly available at the surface of land plants because of continuous air currents. In lakes the CO_2 concentration is highly variable. It may be unavailable at times, particularly in bog lakes, and at other times it may accumulate to the equivalent of 20 cubic centimeters per liter of water. Apparently the death of submerged vegetation in warm shallow water in midsummer may result from starvation, from suffocation, or from some other indirect effect of high temperature. In spring and autumn carbon dioxide is quite uniformly distributed from the top to the bottom of deep lakes, but in summer and winter it may be either abundant or nearly absent at different depths.

Nitrogen. The nitrogen (N_2) in solution in water is no more usable in aquatic plants than is the nitrogen of the atmosphere in land plants. However, as on land, nitrogen may be combined by microorganisms into such usable substances as ammonia, nitrates, and organic nitrogen

[1] The bicarbonates are metal hydrogen carbonates: $Ca(HCO_3)_2$, $Mg(HCO_3)_2$, $Fe(HCO_3)_2$, and $NaHCO_3$. When carbon dioxide is released from these bicarbonates, the carbonates $CaCO_3$, $MgCO_3$, and $FeCO_3$ are formed. These carbonates, with the exception of sodium, are relatively insoluble and accumulate on plant surfaces; eventually they form layers of marl on lake bottoms in limestone regions. Some of the limestones of the Middle Western States originated in fresh-water lakes.

compounds. Since so small a portion of it is transformed in biological processes in lakes, its concentration is rather constant and uniform.

Inorganic salts. The chemical elements essential to fresh-water plants are the same as those essential to land plants. Rooted aquatics obtain the salts containing these elements primarily from the underlying soil. A much smaller amount enters the plants from the water surrounding their green shoots. Suspended and floating plants are dependent on the salts in solution in the water. The concentration of these inorganic salts in lake water is lower on the average than in soil water. Extensive sand areas in lakes may be as barren of rooted vegetation as similar areas on land, even though the lake water contains sufficient salts for the growth of large numbers of suspended and floating plants.

Seasonal stratification of water. For a period of time in spring and autumn the temperature of the water at different depths in lakes becomes nearly uniform (about 4° C.). This is the temperature at which water reaches its greatest density. It becomes lighter whether cooled below or warmed above 4° C. As these uniform temperatures develop, convection currents are formed by the lighter water moving upward and the heavier water moving downward. Wind storms at these seasons result in mixing and stirring the water to great depths. These are the spring and autumn "overturns."

During the summer the surface water becomes warmer and lighter, with the result that layers of warm water float on the colder and denser water beneath. Winds then usually disturb only these upper layers of warm water, and there is little vertical mixing of water. This condition prevails until autumn. As the water at the surface is cooled to 4° C. (39.2° F.) convection currents carry the water downward until the lake becomes uniformly dense and the autumnal overturn occurs.

With the coming of winter the density of the surface water is decreased again as it is cooled below 4° C. These upper layers of colder and lighter water float on the denser water below. If ice is formed it also floats, because its density is about nine-tenths that of water. Under these conditions the water is quite stagnant, and there is little or no mixing.

During both summer and winter the water in deep lakes may become stratified. In summer, when there are the greatest differences in temperature between the upper and lower layers of water, there is an intermediate layer in which the records of temperature on a thermometer change as much as 3° to 5° C. per foot as the thermometer is raised or

lowered through the water. This layer in which differences in temperature are comparatively abrupt is known as the *thermocline.*

Since many organisms, both plant and animal, move about only within certain temperature limits, and since their growth is also limited by the available CO_2 and O_2, it must be evident that these organisms in deep lakes are distributed in strata in summer, and to a less extent in winter. During an exceptionally warm winter in a mild temperate climate the surface water may not be cooled below 4° C.; no spring overturn occurs, and there is no renewal of oxygen in the lower layers of water. During the following summer those fish that can live only in layers of cold water may suffocate. Similar consequences may also follow whenever there is insufficient wind to cause the spring overturn.

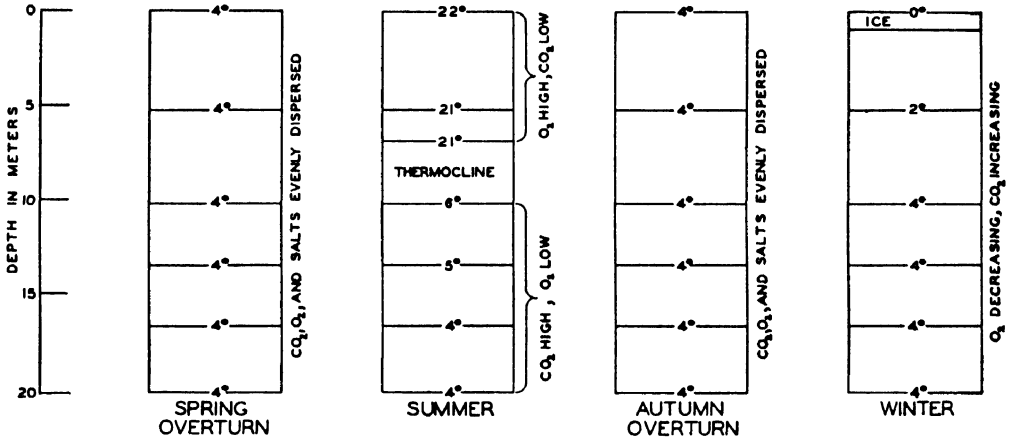

FIG. 270. Diagram of seasonal changes in temperature and stratification in certain deep lakes. Also usual effects on distribution of oxygen and carbon dioxide. Data from Paul Welch.

The data given in Fig. 270 should help one to understand (1) why in some lakes the thermocline in summer is a potent barrier between the many organisms that live above and below it; (2) why the densest population of plankton, both plant and animal, occurs in the spring and autumn; (3) why certain fishes in the summer time live only in deep water and others only in shallow water.

Violent winds may at any time cause the mixing of water to considerable depths. When the mixing results in carrying oxygen to greater depths, it may be followed by an enormous increase of certain species. Violent winds may also increase wave action and destroy the plants in shallow water or wash them up on land. Wave action may also stir

up mud; and with the increased turbidity of the water resulting in decreased light penetration, the algal population may decrease.

Plant population. Most flowering plants cannot survive complete submergence, and only a limited number can thrive with their roots and lower stems permanently covered with water. Besides the rooted seed plants along the shore, the aquatic plant population includes the countless numbers of minute floating and submerged algae which are described in the next chapter.

All bodies of fresh water contain bacteria and lesser numbers of parasitic and saprophytic fungi. Bacteria are known to occur in the open water of lakes and ponds at all depths, and are often exceedingly abundant on the bottom deposits. They are usually not harmful to man. There are bacteria of decay, of nitrification, and of nitrogen-fixation as well as those truly parasitic within other plants and animals. Their abundance is influenced by light, by sudden changes in temperature, by the amount of sedimentation, and by certain animals, such as the protozoa and rotifers, that feed on them. Direct counts have shown that there may be from a few thousand to several million bacteria in a cubic centimeter of lake water. By way of comparison, a cubic centimeter of a moist, fertile soil may contain several billion bacteria.

RIVERS AND STREAMS

The temperature of the water in rivers and streams is fairly uniform from top to bottom. The greatest extremes of turbidity occur, varying from the muddy Missouri and Yangtze rivers to the nearly transparent water of "spring-fed" mountain brooks. Light penetration is diminished greatly in muddy waters. Suspended silt may decrease the light in the first inch of water to 10 per cent of that at the surface. Oxygen deficiency does not usually limit the growth of aquatic plants in unobstructed streams. The oxygen content varies between day and night and may at times even exceed the saturation point in streams with abundant submerged plants.

Stream water is usually moderately alkaline or neutral; only rarely is it as acid as the water in bog lakes, unless there is seepage from coal mines or other mineral deposits. Free carbon dioxide does not accumulate in running water but may increase in deep quiet stream pools.

In swift streams seed plants are not conspicuous, except for a few well-rooted species on the margins. Sluggish waters may, however, become completely choked by the luxuriant growth of submerged and

floating plants, such as elodea, eel grass, pond weeds, water hyacinth, water cress, and willow herb. The margins of rivers rarely have permanent plant communities because of deposition or erosion and ever-changing water levels. The flora and fauna most characteristic of streams and rivers are the suspended microscopic or near-microscopic organisms known as plankton. The plant constituents of the plankton are largely diatoms and other minute algae. The plankton "harvest" of rivers and streams is surprisingly large. The total mass of plankton organisms of the Illinois River at Havana, Illinois—where it flows slowly—amounted in one year to 200,000 tons live weight, or about 10,000 tons of dry matter. In other parts of the same river the tonnage may be greater or much less.

Plankton develops in the more sluggish and deeper pools of streams, and these areas become the feeding grounds of innumerable animals. Plankton is not to be looked upon as a mass of living organisms floating downstream as fast as the stream flows. It is decidedly localized. Neither is it true that plankton increases in variety and abundance downsteam. Flash floods in small tributaries may increase the plankton in the master stream. Great floods temporarily decrease the plankton in the whole stream system. Compared with lakes, running water is a distinctly different environmental complex. Temperatures are more uniform, and no periods of winter and summer stagnation occur. In general the concentration of inorganic salts is higher in streams than in most lakes. Effects of pollution with manufacturing and municipal wastes may be much more evident and destructive. Spores and seeds are less likely to lodge on stream bottoms; hence the establishment of new plants by this means is less frequent in streams than in still water.

MARSHES, SWAMPS, AND BOGS

As lakes and ponds are gradually filled by partially decayed organic matter and by silt washed from the uplands, rooted vegetation encroaches upon the area. This filling gradually brings about changes in the nature of the environment. The effects of winds become less, and there is no overturn of water caused by winds in spring and fall. Shading by rooted aquatics becomes important, and organic matter accumulates rapidly. In fact, all stages of transition from a typically acquatic habitat to a land environment may occur as lakes and ponds become bogs, marshes, or swamps through increased drought, through drainage, or through the accumulation of organic matter and soil.

A marsh is dominated by cattails, grasses, sedges, and rushes, and may be found in either temperate or tropical regions. A swamp is usually regarded as an area where the water never covers the soil deeply but is never far below the surface, and where the vegetation is dominated by shrubs and trees, such as buttonbush, low willows, alders, and swamp trees.

Bogs differ from marshes and swamps in that mosses form an important part of the vegetation; they and the other aquatic plants become enmeshed in a floating substrate which rises and falls with the water level and upon which sedges, grasses, low and tall shrubs, and even trees may subsequently grow. Many northern lakes have open areas of water surrounded by floating marginal mats of herbs, bog mosses, and shrubs. As peat accumulates below the mat the bog may become more or less solid and support a forest of conifers, such as black spruce, tamarack, and arbor vitae.

Bogs may be either acid or alkaline. If alkaline, the water is generally clear, and shrubby cinquefoil occurs among the shrubs; if acid, the water may be brown in color, and sphagnum moss is usually present in the substrate. Bog water is usually lower in dissolved oxygen, free carbon dioxide, and the salts of potassium and nitrogen than that of the more open type of lake. Likewise, the plant and animal population in bog lakes is comparatively low, and there are fewer species. In the Great Lakes region and northward, a peat substrate may accumulate on valley bottoms from bog plants that grew there.

The term "bog" is frequently applied in the Southern States to wet, acid sand flats on which many characteristic bog plants grow, as well as to areas having a peat and muck substrate. Some typical bog plants associated with the grasses, sedges, and mosses of acid bogs are cranberry, blueberry, snowberry, leatherleaf, pitcher plant, sundew, and dwarf birch.

The Salt-water Environment

The oceans, bays, gulfs, and a few inland bodies of salt water are also habitats of aquatic plants and animals. These marine habitats differ from the fresh-water environment principally in being saline. The salinity is due largely to chlorides and sulfates with smaller percentages of carbonates. Few species of plants can grow both in the sea and in fresh water. The salinity is essential to the marine species and toxic to the fresh-water species.

Our largest bodies of water are the oceans, with a combined surface area of nearly 140 million square miles, or about 70 per cent of the earth's surface. In contrast to this, the surface of all bodies of fresh water taken together is scarcely one million square miles. The vast expanse and diverse conditions of oceans constitute enormous possibilities of development of marine plant and animal populations. Ocean water is practically a continuous medium, in sharp contrast to the more isolated bodies of fresh water.

The oceans vary in depth from a few feet of water along the coasts to nearly 6 miles in the so-called "deeps." On the ocean floor are plains, hills, valleys, and mountain ranges.

Pressure varies from 15 pounds to the square inch at the surface to nearly 8 tons at the greatest depths. Such enormous pressures would seem to preclude the possibility of living organims, but the effects of this pressure are annulled by an equivalent pressure inside the body. Equalization of pressure within the body, however, does not take place rapidly; consequently, vertical migration of living plants and animals under these conditions is somewhat restricted. Except along the coast, the influence of the land on the ocean is much less than it is on bodies of fresh water.

The specific gravity of sea water with a salinity of 3.5 per cent is about 1.028 at 0° C. The density of the aerial environment of land plants is much less than that of their protoplasm, while the density of the living parts of marine organisms is about the same as that of the medium in which they live. Most marine plants are slightly heavier than the water, but their small size and proportionally large surface areas, as well as occasional gas bladders and fat globules, contribute to their floating capacity. Dead bodies of marine plants and animals eventually sink to the bottom, unless devoured or dissolved, although the rate of sinking is extremely low. Below depths of 5000 meters none of the parts of most of the smaller plants and animals can be found, for the whole body has gone into solution.

The solar energy actually available to plants is decreased in the ocean by the same factors that decrease it in fresh water: absorption, reflection, suspended matter, wave action. Where suspended matter and minute organisms are abundant, the water is apparently green because of the scattering of the short blue and violet rays and the absorption of the red and yellow. Blue water contains little or no suspended matter.

Photosynthesis in plants of the ocean generally occurs above a depth

of 150 meters, although a few living green plants have been found at 300 meters. Beebe reports the disappearance of all but the blue and violet rays at depths of 250 meters in the clear water near the Bermuda Islands. Below 500 meters almost complete darkness prevails, except for the feeble light emitted by certain deep-sea fishes and other animals.

The gases of the air are absorbed directly from the atmosphere, although carbon dioxide and oxygen are subject to local variation because of photosynthesis and various oxidations. Gases are carried to great depths through the action of storm waves and ocean currents.

Sea water is a dilute solution of salts, with some dissolved gases and traces of many organic compounds, containing more than half of the known elements. Some elements are in marine organisms but have not as yet been recognized in the water itself because of their extremely low concentrations. The relative amount of an element may be far greater in a plant or an animal than in the medium in which it lives. Large quantities of potassium and small amounts of sodium, for example, accumulate in some marine plants, even though sodium salts are very abundant in the ocean and potassium salts relatively scarce. The relative amount of any element that accumulates in the different species of plants may vary greatly even though the plants are growing in the same environment.

The relative proportions of salts in the main body of the ocean are fairly constant at all latitudes. The relative percentages of the different elements in the salt after the water has evaporated do not vary much from the following: chlorine, 54 per cent; sodium, 31 per cent; magnesium, 4 per cent; calcium, 1 per cent; bromine, 0.2 of 1 per cent; sulfate radicals, 8 per cent; and carbonate radicals, 0.2 of 1 per cent.

Surface temperatures of the ocean vary greatly with latitude and with the time of year. However, surface variations between winter and summer are much less than those encountered on land. Sea water becomes heavier as it is cooled until its freezing point is reached. As a result, temperatures below 0° C. may occur, in contrast to the rather constant 4° C. of most deep-lake bottoms. The bottom temperatures of the oceans in temperate regions are around 2° C. Seasonal variations in temperature are unusual below 500 feet. At depths of a mile or more the temperature is near the freezing point at all times.

The effects of temperature are so closely tied up with those of other factors that its influence has been frequently exaggerated. Temperature apparently often determines the range of plant distribution both vertically and latitudinally. Some species of plants grow and reproduce at or

below the freezing point, such for example as the marine algae of arctic and antarctic regions. The destructive effects of temperature, however, are much less in the ocean than on land because of the absence of extremes and rapid changes. Indirectly temperature is important in another way since carbon dioxide is much more soluble in cold than in warm water; in the tropics the warm water may become almost depleted of this gas. Likewise the population of plant and animal plankton is less in the warmer water of tropical oceans than in the cooler water of temperate regions. Other factors that reduce plankton population in the tropics are the increased rate of respiration, and deficiency in compounds of nitrogen and phosphorus.

PLANTS AND ANIMALS IN THE OCEAN

Water environments, both fresh and marine, are populated with great numbers and many kinds of plants and animals. The largest as well as the smallest known organisms live in the ocean. In the sea are whales, large fishes, crustaceans, and squids, as well as myriads of microscopic species. The largest plants in the sea are the brown kelps (Fig. 271)

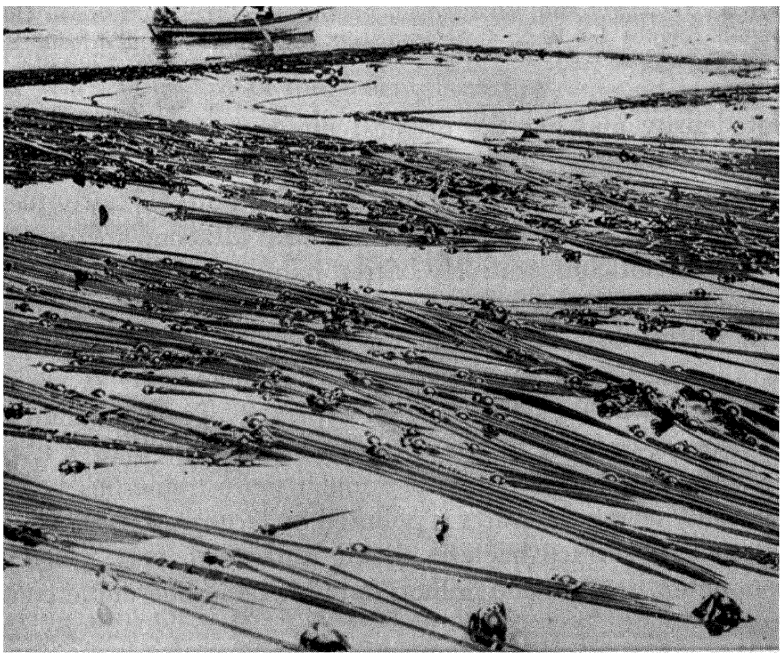

FIG. 271. One of the brown algae (*Nereocystis*) along the western coast of North America. Only a part of the plant is visible at the surface of the water at low tide. See Fig. 287F. Photo from Helen Brown Bromley.

some of which are 70 meters long. Among the smaller plants are the one-celled diatoms (Fig. 272) and the bacteria. Animals probably exist at all depths and over the entire ocean floor; but living green plants are rare below 300 meters because of inadequate light. The plant population consists of both suspended and bottom species. It reaches its

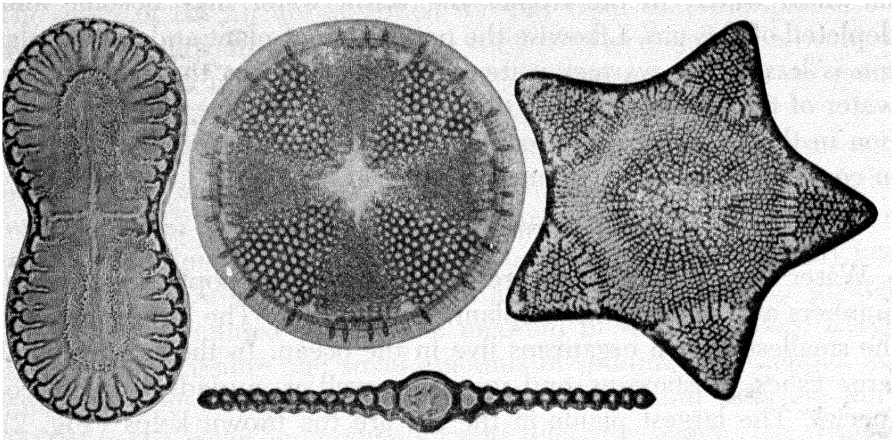

FIG. 272. Diatoms. The names of these species and others may be found in papers by P. S. Conger and Albert Mann published by the Smithsonian Institution, Washington. Photos by P. S. Conger, except the middle upper from Bausch & Lomb Optical Co.

greatest density and has the greatest number of species in shallower water near shore where inorganic salts are more abundant and there is more adequate light from top to bottom. Mud bottoms fairly teem with organisms, and many plants and animals are attached to rocky shores, whereas sand is a comparatively barren habitat.

The bacteria of the sea vary greatly in abundance depending upon depth of water, distance from shore, availability of suspended or dissolved organic matter, and the presence of other plants as well as animals. The sea water itself is not an especially good medium for the growth of most bacteria unless considerable organic matter is present. As might be expected, bacteria are much more numerous near shore, and especially where the water is polluted by large centers of population. The number of surface bacteria, living and dead, may range from a few or none up to some 300 million individuals in one cubic centimeter of water.

In bodies of water less than 200 meters deep the bacteria are much more numerous in the mud bottoms than in the water above. These

bacteria are largely anaerobic and spore-forming, as compared with the aerobic and non-spore-forming bacteria floating in the water. The bottom bacteria include the nitrifying, the nitrogen-fixing, and the humus-decomposing types. Certain bacteria of the sea are of interest because they obtain energy by the oxidation of such substances as hydrogen sulfide, sulfur, ammonia, nitrites, and methane, and use the energy in the synthesis of cell substances.

An accurate quantitative comparison between organisms on land and in the ocean is difficult to make. Krogh has estimated that the entire life zone on land is rarely more than 30 meters thick, from tree tops to root tips inclusive, in contrast to the 4000 meters of ocean in which animals live, and the 300 meters populated by green plants. For every tree in a forest there may be nearly a half million animals large enough to be seen by the naked eye. When the microscopic animals, bacteria, and algae are added to this, the total number is prodigious. Under a square meter of ocean water near the equator, down to a depth of 200 meters, there may be a billion or more scarcely visible or microscopic plants and a million animals of various sizes, mostly microscopic. But the mass of these organisms is surprisingly small, perhaps aggregating only about 1/100 of a corresponding volume in a forest. Forest trees stand for years, but many of the ocean plants are renewed several times a year. The total biological productivity in the ocean, however, probably never equals that in the forest, though locally it may be of comparable magnitude.

In sharp contrast to the land, no seed plants, no ferns, no mosses, no liverworts ever grow in the open sea. The plants characteristic of the ocean are limited to algae, bacteria, and a few fungi. The species of plants characteristic of the ocean rarely occur in fresh water. On the land the larger plants are the chief sources of food of the animal populations. In the water microscopic plants are the initial links in the food chains of nearly all the animals. Enormous numbers of these plants grow every year, but directly they constitute only a small part of the food of the largest animals (Fig. 273).

The food chain from green plants to the larger animals ("producer" to "consumer") may become greatly extended because the smallest animals, having consumed the plankton, may become the food of crustaceans and small fishes. The latter in turn may be eaten by still larger fishes (Fig. 274). It is evident that much of the energy value of the food originally made in green plants is never realized by the "ultimate con-

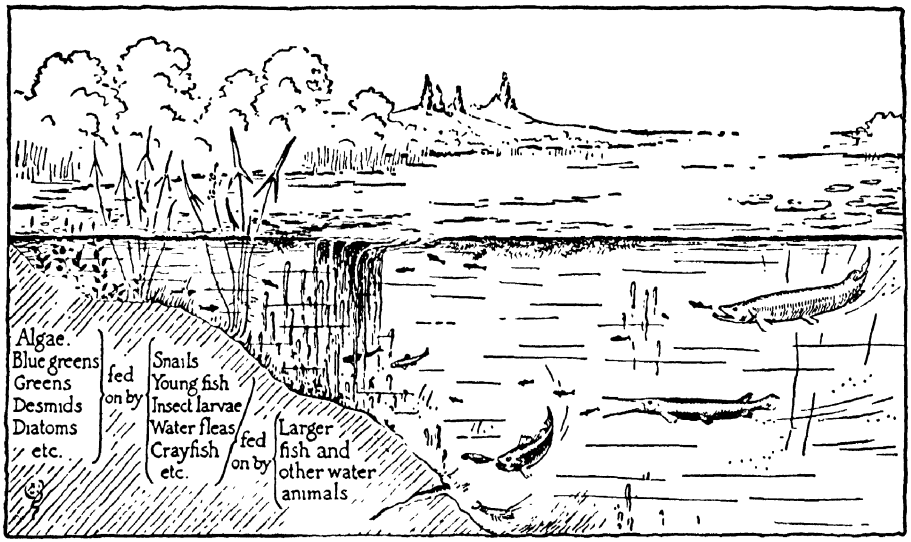

FIG. 273. Food relations of some aquatics. No matter how long the chain of animals is from algae to fish, the fundamental food organisms are the algae that transform inorganic materials into foods. Courtesy of World Book Co.

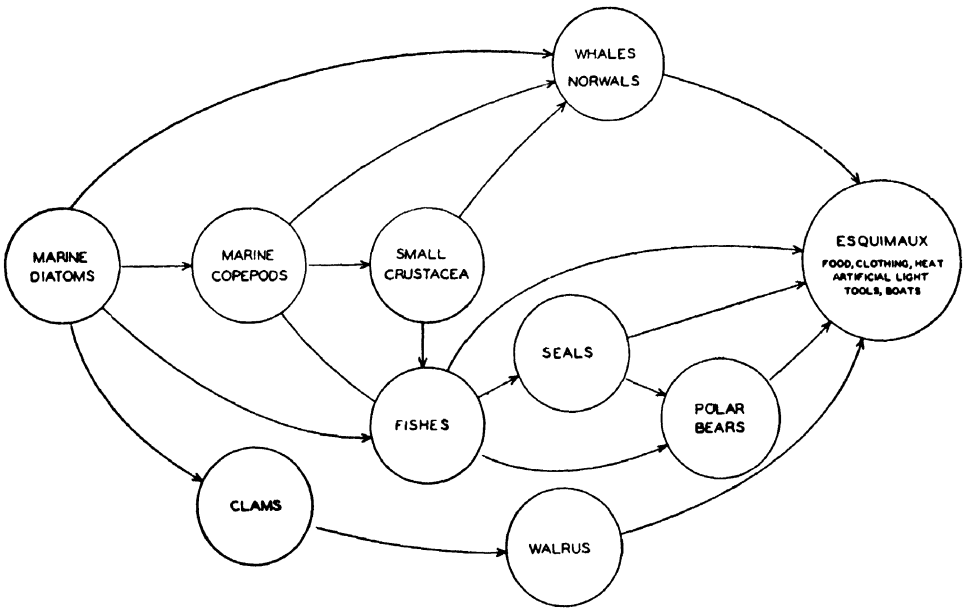

FIG. 274. A diagrammatic representation of the dependence of Esquimaux on diatoms. Assume that each organism obtains only 10 per cent of the food consumed by the preceding one in the chain, and compute the amount of diatoms necessary for a gain in weight of 1 pound in an Esquimau boy.

sumer" because of the necessary respiratory and assimilatory processes of the often numerous "middlemen." Each "middleman" may use in these processes up to 90 per cent of the initial energy value of the food.

In spite of the small size of most marine organisms, a rapidly moving feeder can get large amounts of food in the sea. This is evident in the growth of the blue whale calf. At birth it is 7 meters long and weighs 2 tons, but may become 23 meters long and weigh up to 60 tons in two years. Food of the blue whale consists entirely of plant and animal plankton which passes into the whale through the so-called "whale-bone sieve." As much as 2 tons of plankton have been found in the stomach of a mature blue whale at one time. If there are only three links in the food chain of the whale, the gain of 58 tons in weight implies consumption of food equivalent to 58,000 tons of algae in a two-year period. Whalers often locate the places where whales may be found by the presence of large quantities of plankton on the surface of the water. Biologically algae and bacteria are the most important aquatic plants.

Artificial Environments

Many algae will grow and reproduce in artificial environments, called culture media, if these media are similar in composition to the environments in which the algae grow naturally. The culture may contain a single species (pure culture); a single species of algae, although bacteria may be present (uni-algal culture); or several species of algae (mixed culture). Such cultures of algae are of value in studying life cycles, in understanding physiological and genetic processes, in estimating possible maximal large-scale yields of "algal crops," and in doing controlled experiments with such environmental factors as light, temperature, salts, and gases. Such algae are available for further analyses for pigments, other cell constituents, and possible antibiotics.

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CHAPTER XLVII

THE ALGAE

Of all the plants in the biological communities of both fresh and salt water the *algae* (sing. *alga*) are the most important synthesizers of food. They are commonly called pond scums and seaweeds. Algae, however, are not confined to water habitats. In the rainy tropics and subtropics they grow on moist surfaces everywhere, and even within the leaves of many plants. Some can grow in snow, as is often evident in the pink color of polar and high alpine snowfields (Plate I). The trunks of many woody plants of the moist temperate zone have green patches of algae, usually located on the shaded side. The algae of the soil are so numerous that one gram of earth from a heavily fertilized field may contain as many as a million individuals. A few algae grow in intimate association with certain fungi, forming compound plants known as *lichens*. Algae grow within the aerial roots of cycads and in the hair follicles of the three-toed sloth. They are attached to the appendages of crustaceans and to the backs of turtles. They live within the bodies of many minute animals, and even in the intestines of some mammals, including man.

The algae, moreover, exhibit as much variation in color, in size, in form, and in method of reproduction as any of the other groups of plants. They may be red, orange, brown, yellow, yellow-green, green, blue-green, purple, and violet. Rarely are they colorless. Some algae are so minute that their form is just discernible with a microscope. The giant kelps of the Pacific, on the other hand, attain lengths of more than 200 feet. In form algae may be globular, disk-shaped, thread-like, sheet-like, leaf-like, or large and paddle-shaped; branched or unbranched; attached or free-floating.

The structures associated with sexual reproduction in some species are comparatively simple; in others, they are remarkably complex. Among the various species of algae, vegetative propagation may result from the division and separation of cells, from the breaking of filaments, from specialized thick-walled dormant cells, or from motile spores

that develop directly from vegetative cells. In one large group of algae no sexual reproduction occurs.

Algae are economically important both directly and indirectly. Commercial transactions involving the collection, processing, and sale of algae amount annually to several million dollars. The animals of the oceans, lakes, and streams are ultimately dependent upon various kinds of algae.

What are algae? First of all, algae are plants. Some consist of only a single cell, a single filament, or branched filaments. Even the more complex ones have no organs exactly comparable to those of seed plants. They contain chlorophyll, although other pigments may partly or entirely mask the green color. The presence of these pigments usually enables one to distinguish algae from fungi, bacteria, and small animals. Many of them are easily distinguished from other green plants by the number, size, and form of their chloroplasts. Many species are capable of self-locomotion by twisting, bending, gliding, and swimming; and motile spores and gametes develop in many species.

The occurrence of motile algal plants and cells may require us to change one of our notions about plants if we have been accustomed to associate independent movement only with animals. It should be remembered that the names "plants" and "animals" are very old and were used long before microscopes were made. It is easy to separate plants from animals when we are thinking of oaks and horses or corn and mice. Now that the microscope has enabled us to see minute living organisms not even suspected before, it is not surprising to find that the criteria we are accustomed to use in separating plants and animals will not apply to many of these smaller organisms.

Among the many organisms having flagella some are more plant-like than others. When exposed to light, some of them are green and synthesize both sugar and amino acids; others remain colorless and obtain food only from external sources. Even within a single genus, such as *Euglena*, some species are more plant-like than others. For example, many species of *Euglena* are green and synthesize sugar when exposed to light. Some of these green species can live in darkness as colorless saprophytes if supplied with sugar and protein foods, but others have failed to grow in continuous darkness. They differ also in their ability to utilize nitrogen compounds. Some may utilize ammonia or nitrate salts, which means that they can synthesize amino acids from sugar and either ammonia or nitrate salts. Still others cannot utilize either of

these salts; consequently they cannot synthesize amino acids. Some can live only where peptones or other protein compounds are present in the external medium.

The kinds of algae. For many years algae were grouped on the basis of their color as red algae, brown algae, green algae, and blue-green algae. This classification is still adequate for a general consideration of algae, though anyone unaware of other bases of classification would be confused on being told that some algae are colorless, that the red color of arctic snow is due to the presence of a red-colored green alga, and that the Red Sea was so named because of the abundance of a red-colored blue-green alga in it.

Most students of the algae now recognize 9 or more classes (Table 17). This more critical classification is based in part on color, but also on other distinctive characters of (1) the structure of the vegetative cells and tissues, (2) the reproductive structures, (3) the successive stages in the life cycles, (4) the kinds of accumulated food, and (5) the forms of the chloroplasts or chromatophores.

TABLE 17. Classes of Algae and Their Characteristic Pigments

Classes of Algae	Common Names	Apparent Color	Chlorophyll (green)	Xanthophyll (yellow)	Carotene (orange)	Phycocyanin (blue)	Phycoerythrin (red)	Fucoxanthin (brown)	Accessory Pigments Brown, Red, etc., not Well Known
Myxophyceae	Blue-greens	Blue-green, green, yellow, brown, purple	x		x	x	x		
Chlorophyceae	Greens	Pale yellow to dark green	x	x	x				
Xanthophyceae	Yellow-greens	Yellow to yellowish green	x	x	x				
Bacillariophyceae	Diatoms	Yellow to brown	x	x	x				x
Chrysophyceae	Golden-browns	Golden-brown	x	x	x				x
Dinophyceae	Dinoflagellates	Yellow-brown	x		x				x
Euglenophyceae	Euglenas, etc.	Green, red	x		x				x
Phaeophyceae	Browns	Greenish yellow to dark brown	x	x	x			x	
Rhodophyceae	Reds	Red, purple, blue	x	x	x	x	x		

The various colors of algae are due largely to the relative abundance of certain pigments in the cells. Chlorophyll is present in all algae except the colorless ones. Carotene and xanthophyll occur in most of them. The pigment fucoxanthin ($C_{40}H_{56}O_6$) is characteristic of the brown algae,

and phycoerythrin and phycocyanin occur in the reds and blue-greens.

Economic aspects of the algae. To most people the algae of ponds and lakes, as well as those of the ocean deposited along shore after storms, are nuisances. Algae may accumulate in sufficient quantities to become an annoyance to bathers. Occasionally stock die after using water heavily populated with certain blue-green algae. Bad odors and tastes of drinking water are often attributed to the presence of decaying algae in reservoirs. Tea and other subtropical plants are severely injured by algae which grow either on the surface of the leaves, interfering with photosynthesis, or within the leaves as parasites. Small fishes often become so entangled in algal mats that they die either there or subsequently from injuries received in extricating themselves. Algae in fish hatchery ponds may so deplete the oxygen content of the water at night as to cause the death of the young fish through suffocation.

Algae are rather easily destroyed in small bodies of water by means of certain chemical compounds, particularly arsenites and copper sulfate. The latter is so effective that one part of it in a million parts of water is sufficient to kill most algae. Copper sulfate in such low concentrations is not harmful to fishes, nor is the water unfit for human consumption. Although there are on the market numerous commercial products containing copper sulfate with adequate instructions for their use, a few crystals thrown into small pools will usually suffice. For larger ponds a quantity of the chemical may be placed in a sack, tied to the rear of a boat, and allowed gradually to dissolve in the water as the boat is moved over the surface.

Among other practical measures used for eradicating algae from fish ponds are (1) the removal of the accumulating organic matter by draining the pond from the bottom instead of the surface, and (2) the maintenance of high turbidity. Young crayfish are often added to the ponds because they increase the turbidity of the water, which in turn decreases the penetration of light and algae are unable to survive. Reservoirs may be kept free of algae by stirring up the muddy bottom with large propellers on boats.

Suppose we now examine the credit side of the ledger. As has been noted before, the algae are the ultimate sources of food and energy of all strictly aquatic animals. The food chains of animals are numerous and varied (Fig. 275). Some fishes feed directly on the algae, while others obtain the energy bound up in the plants by eating animals that feed on algae. Some blue-greens, a few greens, and many species of

red and brown algae are used directly as food by human beings in many parts of the world, particularly in the Orient. Among algae, as among other plants, some species are much more important than others as sources of food, whether the consumer be man, fish, insect, or whale.

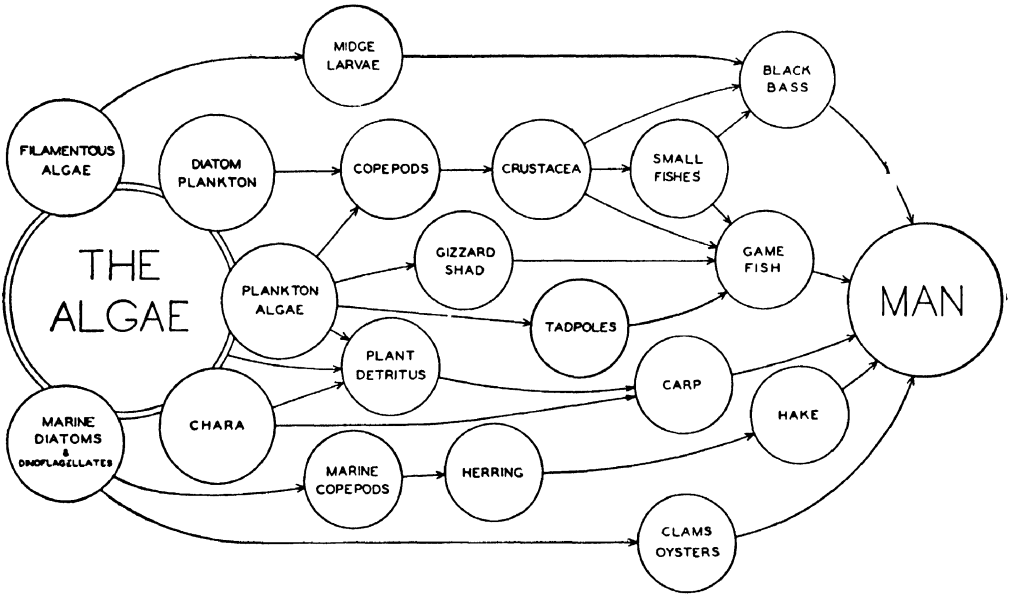

FIG. 275. Diagram of representative food chains from algae to man.

The giant kelps and other seaweeds are sources of iodine and potash. They have been used for many years by farmers along the coast as fertilizers because of their potassium content. Dried and treated in various ways, they are used as stabilizers in making ice cream, candy, shaving cream, various other creams, jellies, salads, and emulsions; and also as the source of agar-agar, so important in the culture of bacteria and fungi.

The algae of the soil are very numerous, but the extent to which they contribute to soil fertility and aeration is only partly known. Soils have definite algal floras. Those living on the surface grow and multiply rapidly whenever the soil is moist. The algae below the surface grow very slowly; and since they live in darkness they are obviously living as saprophytes, using carbohydrates from the soil solution. Algae certainly contribute organic matter to soils, and it has been proved that certain nitrogen-fixing bacteria are much more effective when they grow in association with soil algae. The fungi and algae of lichens are the

pioneer plants on certain kinds of exposed rock surfaces and are primary factors in the formation of the first layers of soil on such surfaces.

Algal periodicity. Many fresh-water and marine algae have seasonal periods of germination of spores, vegetative growth, reproduction, and dormancy similar to those of flowering plants. Many species in temperate climates attain their greatest development in winter, in spring, in summer, or in the autumn; reproductive bodies mature and the vegetative structures disappear. These algae are comparable to annual flowering plants. Their dormant period is passed as spores (Fig. 276).

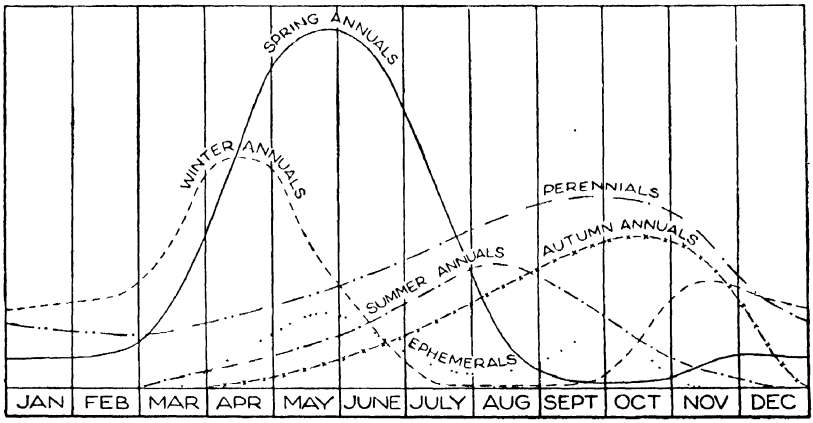

FIG. 276. Estimated relative abundance of several seasonal assemblages of green algae in central Illinois. Seasonal assemblages would be very different farther north and farther south. Ephemerals include plankton species in which a life cycle is completed in a few days.

There are also many perennial filamentous, or thick and leathery, species in which at least a part, usually the base of the vegetative plant, survives long periods of drought and cold. Each year new vegetative fronds develop. This group includes many seaweeds, certain red algae in fresh-water streams, and green algae such as *Cladophora* and *Vaucheria.*

Plankton algae and some soil algae are very short-lived. A new population of these extremely abundant and important species may develop every few days. They are the plants that form the so-called "water bloom" so common on ponds and lakes from midsummer to early autumn. Obviously, enormous numbers result from the accumulative reproduction of several generations in a few weeks.

Algae are more numerous in seasons when the water levels are high. They also reproduce most abundantly under these conditions. Their

individual periodicity determines what species will be found associated at any time of the year. Ponds that regularly dry up in late summer appear to have a greater variety of species than permanent ponds.

The situation in large lakes is somewhat unlike that in ponds because great bodies of water neither warm up quickly in the spring nor cool rapidly in the autumn. In Lake Erie, for example, the diatoms are likely to be abundant in May and June, the green algae in July and early August, the blue-greens in late August and September, and the diatoms again in October and November (Fig. 277). A few species of diatoms are more abundant in winter than at any other season.

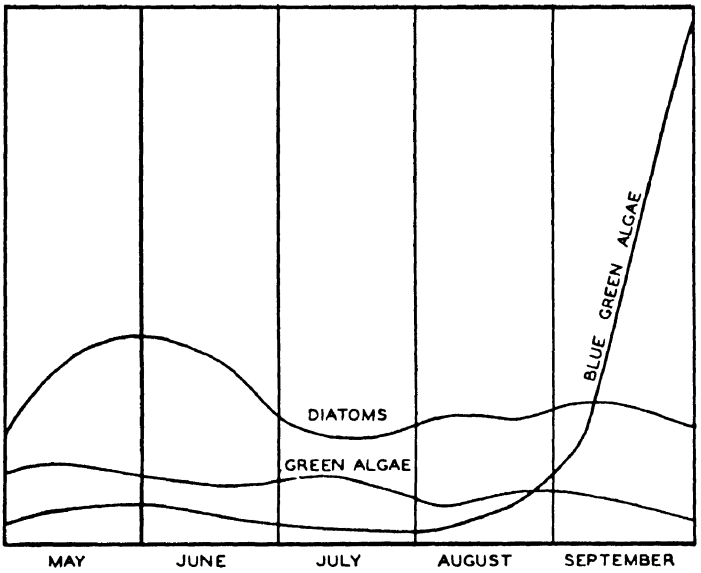

FIG. 277. Relative abundance of some plankton algae in Lake Erie.

Water blooms are just as characteristic of large lakes as of ponds. At certain seasons of the year diatoms, blue-greens, or greens may within a few days become so abundant as literally to cover acres of water to the depth of an inch or two. This colored soup-like layer may be objectionable to bathers, and it may be the source of offensive odors; but it contains an abundance of food available to the smallest aquatic animals. The life cycles of the algae composing the bloom are soon completed, and after several days the plants may disappear as suddenly as they appeared. Most plankton algae are found within a few inches of the surface of the water, although one may usually find them in collections made at depths of 10 to 50 feet.

We have discussed so far some of the general characteristics, distribution, and economic aspects of algae as a whole. They constitute such a large and diversified assemblage of plants, however, that a better understanding of their growth and reproduction depends on a study of some of the commoner ones in more detail. We shall discuss in the next few pages some representatives of each of the important classes of algae.

The Green Algae: Chlorophyceae

About 5000 species of green algae have been described and named. As a group of plants they are quite varied in structure, in appearance, and in several other ways. They are usually predominantly green in color during the vegetative phase, containing chlorophyll, xanthophyll, and carotene in about the proportion found in the seed plants. They grow chiefly in water, both fresh and marine, but occur also on and in the soil and on many other kinds of moist substrates. Biologically they influence both the abundance and the distribution of certain other plants and of certain animals. Green algae are by far the most common ones in lichens. They may be parasitized by animals and occur inside animals, such as hydras and rotifers. In size they vary from the microscopic forms to the filamentous, highly branched cladophoras, which may be several feet in length and are attached to rocks and stones of streams and lakes. A few common species are described below.

Protococcus. On the bark of trees and shrubs throughout the world there occur green-colored areas of *Protococcus,* sometimes several square feet in extent. This alga grows most frequently on the shaded parts of the tree. In drier regions it may be restricted to the lee side. Although most abundant near the ground, it may be found on the bark all the way to the tops of trees in moist open forests. No spores are formed and no sexual reproduction occurs in this alga.

Under the microscope the green areas of *Protococcus* are seen to consist of masses of rounded solitary cells or of groups of two to several cells (Fig. 278). The chloroplast occupies most of the cell, and the cell walls are comparatively thick. The plant may survive prolonged droughts and remain dormant during long periods of low temperature, in spite of the fact that there are no apparent structural modifications that might prevent desiccation of the cells. When periods of rain and higher temperatures return, the cells again become active. Propagation takes place only through the division and subsequent separation of the cells. No

reduction division occurs; and, except for mutations, all the cells of *Protococcus* have the same chromosome complement. It is a non-motile one-celled plant, though several plants may remain attached temporarily as an unorganized colony.

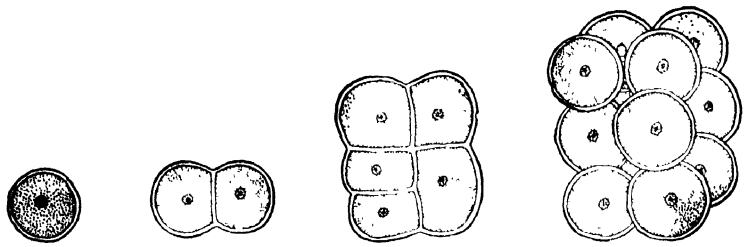

FIG. 278. Forms of cells of a *Protococcus*. Species of this genus of green algae are non-motile and mostly aerial. The individuals are usually one-celled, though they may remain united in colonies temporarily as indicated in the drawing. Species of this group are the algae most frequently found in lichens.

Chlamydomonas. In contrast to the one-celled non-motile *Protococcus* is the one-celled motile *Chlamydomonas* (Fig. 279). It is often found as a part of the plankton, sometimes occurring in large numbers in small pools or even in indoor aquaria. The cell is spherical, ovoid, or elongate, and often flattened. Two flagella project from the anterior end. Both spore formation and sexual reproduction occur.

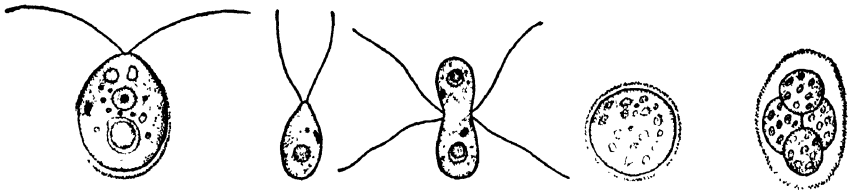

FIG. 279. Forms of vegetative and reproductive cells of a *Chlamydomonas*. Species of this genus of green algae are one-celled and motile. They reproduce vegetatively by motile spores and sexually by the union of gametes as indicated in the drawing.

Cells with flagella similar to *Chlamydomonas* may remain attached and thus form definite colonies of several to many cells. Examples of such colonial algae are *Pandorina*, *Eudorina*, and *Volvox* (Fig. 280). All of these algae are termed flagellate organisms.

Ulothrix. In the spring one may see bright green slimy filamentous growths of *Ulothrix* on the stones and rocks of the shores of streams, lakes, and ponds. Since the cylindrical cells of this alga are joined end

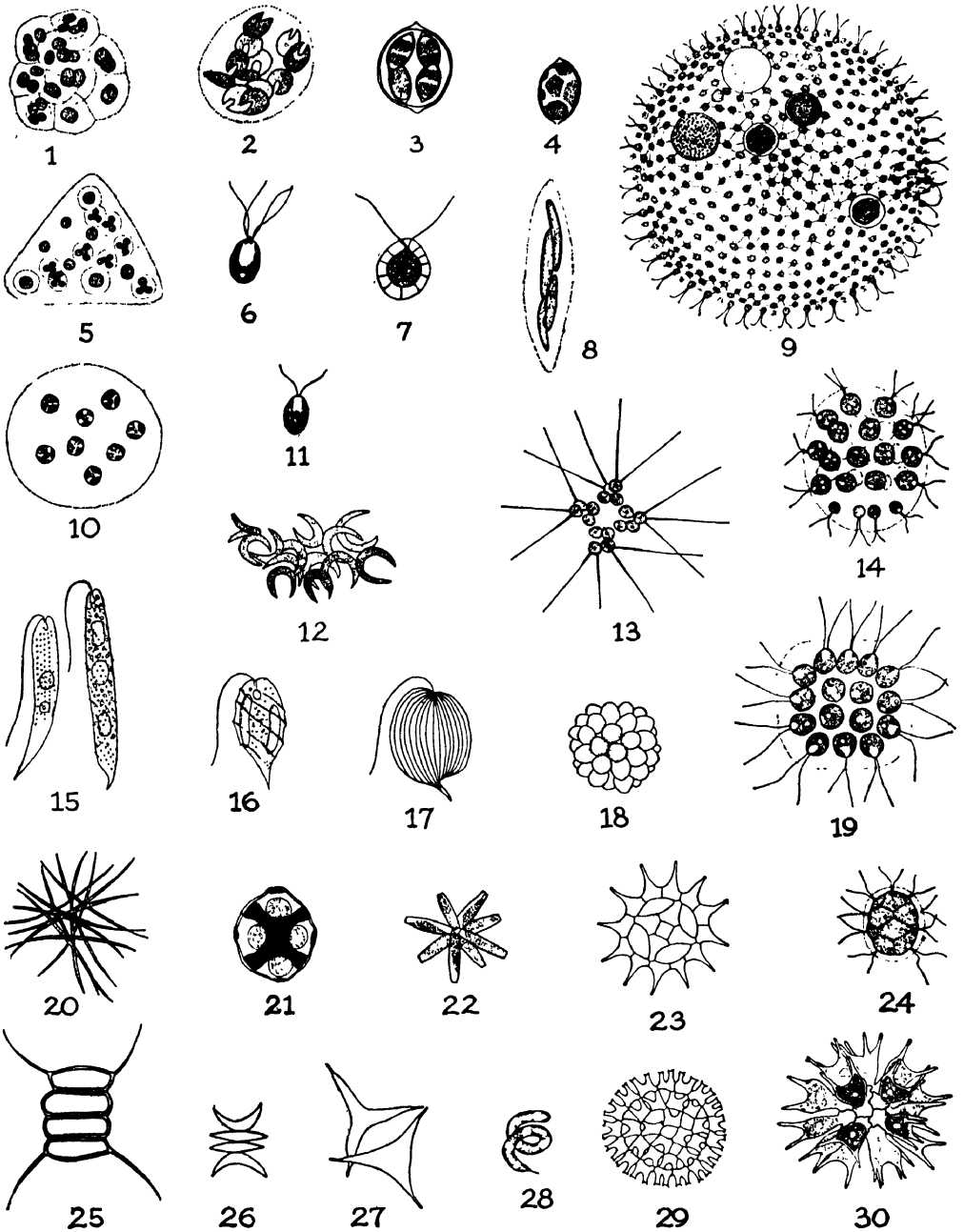

FIG. 280. Forms of some unicellular and colonial algae. Genera represented: 1 and 5 *Gloeocystis*, 2 *Kirchneriella*, 3-4 *Oocystis*, 6 *Carteria*, 7 *Sphaerella*, 8 *Quadrigula*, 9 *Volvox*, 10 *Asterococcus*, 11 *Chlamydomonas*, 12 *Selenastrum*, 13 *Micractinium*, 14 *Pleodorina*, 15 *Euglena*, 16-17 *Phacus*, 18 *Coelastrum*, 19 *Gonium*, 20 *Ankistrodesmus*, 21 *Gloeotaenium*, 22 *Actinastrum*, 23 *Pediastrum*, 24 *Pandorina*, 25-26 *Scenedesmus*, 27 *Tetraedron*, 28 *Ophiocytium*, 29 *Pediastrum*, 30 *Sorastrum*.

to end and always divide in the same plane, the plant is a single unbranched filament. Each plant is attached to rocks or other objects by a special holdfast cell (Fig. 281). The chloroplast is a green band of

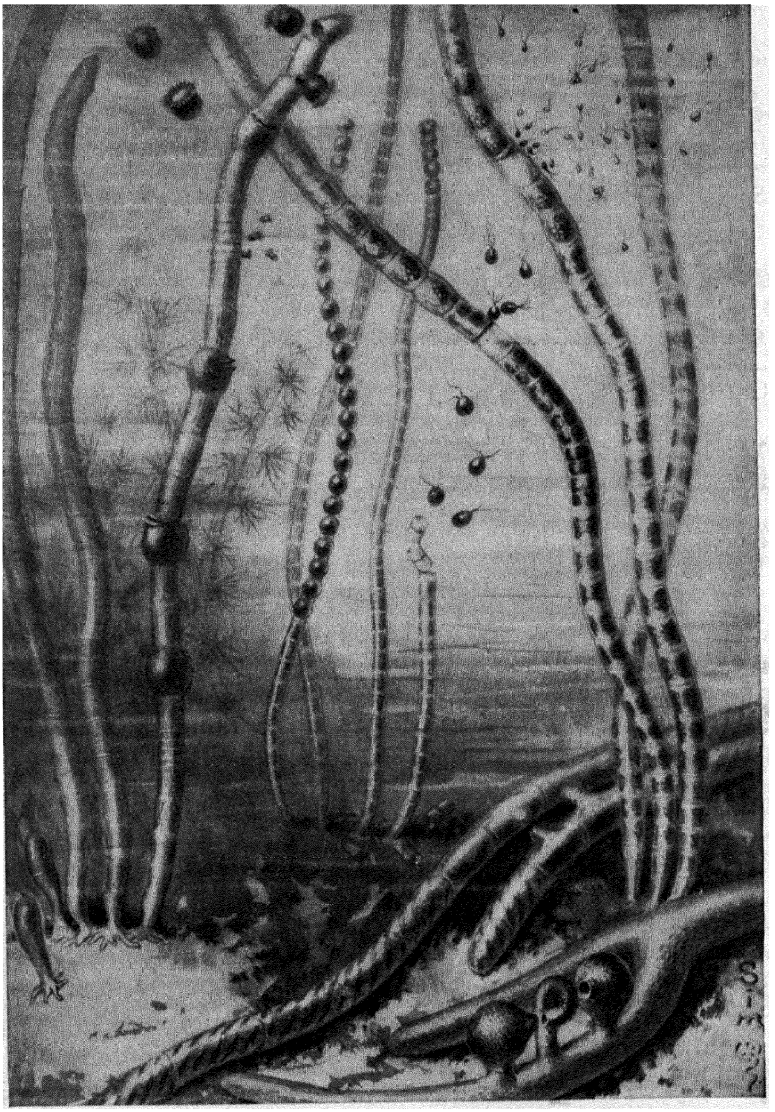

FIG. 281. Fresh-water algae. The upright filaments are, from left to right: *Oedogonium*, bearing motile spores, eggs, and sperms; *Microspora*, forming resting spores and motile spores; and *Ulothrix*, forming motile spores and gametes. The horizontal filaments are *Spirogyra* (left) and *Vaucheria* (right). Highly magnified. Courtesy of World Book Co.

cytoplasm open on one side. It appears to be pressed against the cell wall and is frequently confined to the middle section of the cylindrical cell. Its form in cross section resembles that of a horseshoe. Starches and proteins accumulate in vegetative cells, but in the spores one finds mainly oils. The life cycle of a *Ulothrix* is far more complex than that of *Protococcus.*

After vegetative development the protoplast in each of many cells may become subdivided by a succession of mitotic divisions into 2, 4, or 8 small protoplasts, each of which escapes through an opening in the wall of the parent cell and becomes a motile spore[1] with four flagella. Both big and little motile spores may be formed in different cells of the same filament. The smaller ones are formed in groups of 16 or 32. After swimming about for a short period, a motile spore may become attached to some object and germinate by elongating and then dividing transversely. Subsequent cell divisions all in the same plane result in a new filament.

In still other filaments, or occasionally in some cells of the same filament, the protoplast may become subdivided by successive mitotic divisions into 8, 16, 32, 64, 128, or rarely more cells. Each of these cells may pass through the wall of the parent cell in the same manner as the motile spore, which it resembles superficially except for its smaller size and its single pair of flagella. Such motile structures do not germinate, and new filaments do not develop from them. They are termed *gametes.* The union of one gamete with another results in a zygote, which eventually becomes thick-walled and sinks into the mud at the bottom of the pond where it remains dormant for several months. The union of the two gametes is termed *conjugation.* When the zygote germinates, its protoplast becomes subdivided into 4 to 16 parts, each of which becomes a motile spore from which a new filament grows. The two gametes that unite appear to differ chemically and are referred to as + and − gametes, and they come from different filaments. Since they are similar in appearance they are regarded as the simplest kind of sex cells.

The special method of vegetative multiplication by means of either motile or non-motile spores which develop without previous union of gametes is often termed *asexual reproduction.* The related series of processes including the formation of gametes, their subsequent union, and the development of the resulting zygote into motile spores from which new filaments develop are referred to as the *sexual reproduction*

[1] Motile spores have flagella and are frequently termed "zoospores" (animal spores) because they swim about in the water.

of the alga. Reduction division occurs during the first nuclear division in the zygote. Hence each motile spore of *Ulothrix* and each cell of the filament has the monoploid number of chromosomes. The zygote alone has the diploid number of chromosomes.

Oedogonium. In fresh water throughout the world, attached to various objects during at least a part of their lifetime are several hundred species of *Oedogonium*. All of them are filamentous and unbranched, and each cell has a hollow cylindrical meshwork chloroplast. The method of reproduction is in some respects similar to, but in others quite unlike, that of *Ulothrix*.

Motile spores develop singly in the vegetative cells (Fig. 281). Each spore has a ring of flagella at one end and escapes from the cell through a circular break in the wall. Upon coming to rest, it germinates directly, and the new plant elongates by subsequent division of certain cells scattered at intervals in the filament. The first cell is the holdfast cell.

The two kinds of gametes are quite distinct in appearance. The male gametes, or *sperms*, formed singly or in pairs from the protoplast in special short cells known as *antheridia* (sing. *antheridium*, a sperm case), are quite similar in appearance to small motile spores. The female gamete, or *egg*, develops singly within a swollen vegetative cell, the *oogonium* (pl. *oogonia*, egg cases). The egg is much larger than the sperm, never escapes from the egg case, is incapable of locomotion, and contains much food, chiefly oils.

The sperms and eggs may develop in cells of the same filament or of separate filaments. That is, some species are bisexual, or monoecious; others consist of two kinds of unisexual filaments, one of which is a male filament, the other female. They may or may not differ in size. In some species the male filaments are very small and grow as epiphytes on the female filaments near the oogonium. These *dwarf males* develop from motile spores which germinate only when they become attached to an oogonium or adjacent cells. They usually consist of a holdfast cell and one or more antheridia.

The sperm after liberation from the antheridium may swim to and enter an oogonium through a pore or slit, and fuse with the egg. This fusion appears to occur mostly late at night or early morning. The resulting *zygote*[2] is thick-walled, remains dormant for some months or

[2] The term *oospore* is often used to indicate the cell resulting from a union of two gametes that may be distinctly recognized as an egg and a sperm; *zygote* is used when the two gametes are similar in appearance. The term zygote is often used also as a general term for any cell formed by the union of gametes, regardless of their appearance.

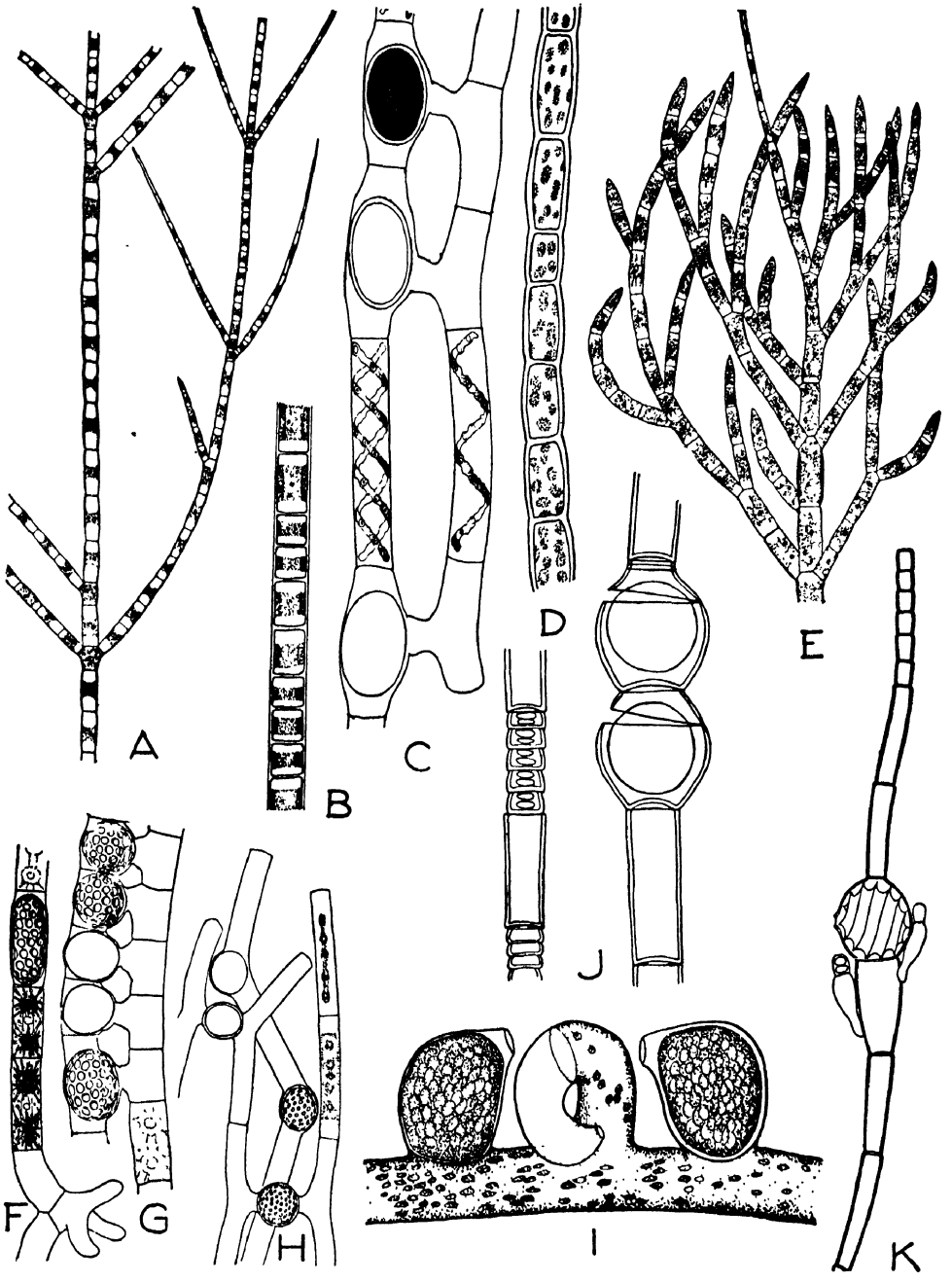

FIG. 282. Common filamentous algae. Genera represented: A, *Stigeoclonium;* B, *Ulothrix;* C, *Spirogyra;* D, *Tribonema;* E, *Chaetophora;* F and G, *Zygnema;* H, *Mougeotia;* I, *Vaucheria;* J and K, *Oedogonium.*

even years, and upon germination four motile spores usually develop, each of which has the reduced number of chromosomes. A new filament develops directly from each motile spore, and each of its cells has the reduced number of chromosomes.

Other common filamentous genera. Among the most widely distributed genera (Fig. 282) of pond algae is *Spirogyra*, with its usually

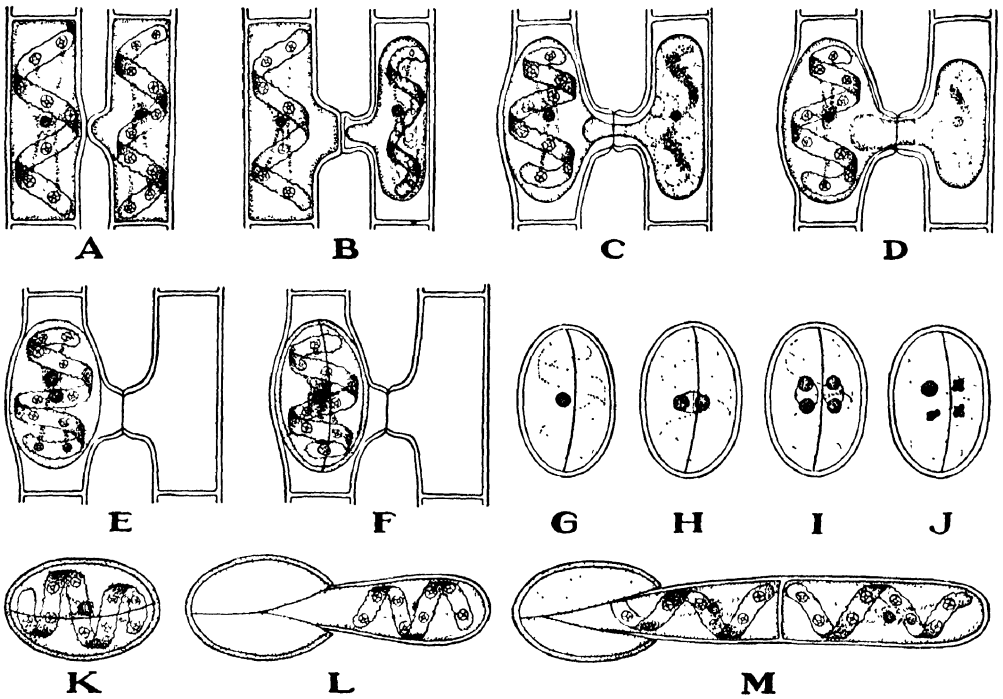

FIG. 283. Reproduction in *Spirogyra* and inheritance of the chloroplast.

spirally arranged, ribbon-like chloroplasts. *Zygnema* with stellate chloroplasts, and *Mougeotia* with a straight, ribbon-shaped chloroplast are almost as common. In the large group of algae represented by these three genera, the cells are always cylindrical and there is a complete absence of flagellate spores. Sexual reproduction is effected by the union of gametes, one (or both) of which moves ameba-like to the other through a *conjugation tube* (Fig. 283). The zygotes resulting from the union of the gametes may remain dormant for several months or years. When they germinate, new filaments develop from them. Reduction division occurs at the first division of the zygote nucleus.

The green felt-like *Vaucheria* is very common in small streams and

ditches. Cell division in it is unaccompanied by the formation of cross walls and thus the filaments are tubular and multinucleate. The motile spores of *Vaucheria* are unusual in that a number of nuclei are present in a so-called "compound zoospore," from which a new filament develops almost immediately. Most species of *Vaucheria* have an oogonium with a single egg, and an antheridium containing several sperms. These sex organs are formed at the ends of short lateral branches (Figs. 281 and 282). The oospore resulting from fertilization remains dormant for some time before a new filament develops from it. Reduction division probably occurs during the formation of gametes as it does in animals. The vegetative cells of *Vaucheria* have no starch and also differ from most green algae in the kinds of pigments present in the cells.

The algae described above and many others are usually available in their natural habitats, and the details of their life cycles may be studied from living or preserved specimens. The desmids are either unicellular or filamentous forms, a few of which are illustrated in Fig. 284.

The stoneworts. These plants are mentioned here largely because of their importance in the formation of marl deposits. The stoneworts (*Charales*) are rather widely distributed in both fresh and salt waters; a few species inhabit both. They are attached to the soil beneath the water and often form extensive meadows several feet below the water surface. The plants become incrusted with calcium carbonate in limestone regions, and as the plants die, marl accumulates. About one hundred species have been described.

The plant body consists of a cylindrical axis bearing a whorl of branches at its several "nodes." The plants are nearly always erect and may vary in height from an inch to 3 or 4 feet. The stoneworts constitute a group very distinct from all other algae.

The Blue-green Algae: Myxophyceae

The blue-greens differ from all the great groups of algae in that the nuclear substances of the cell are not organized in a well-defined structure in the cytoplasm as in other green plants. Hereditary units of matter comparable to genes must be present, however, for the species are hereditarily different. Chlorophyll and other pigments are dispersed throughout the cell and not confined to plastids. No motile spores are formed and no sexual reproduction occurs. Only about half the blue-green algae are really blue-green in color. The others vary greatly in color owing to different amounts of blue, red, green, and yellow pig-

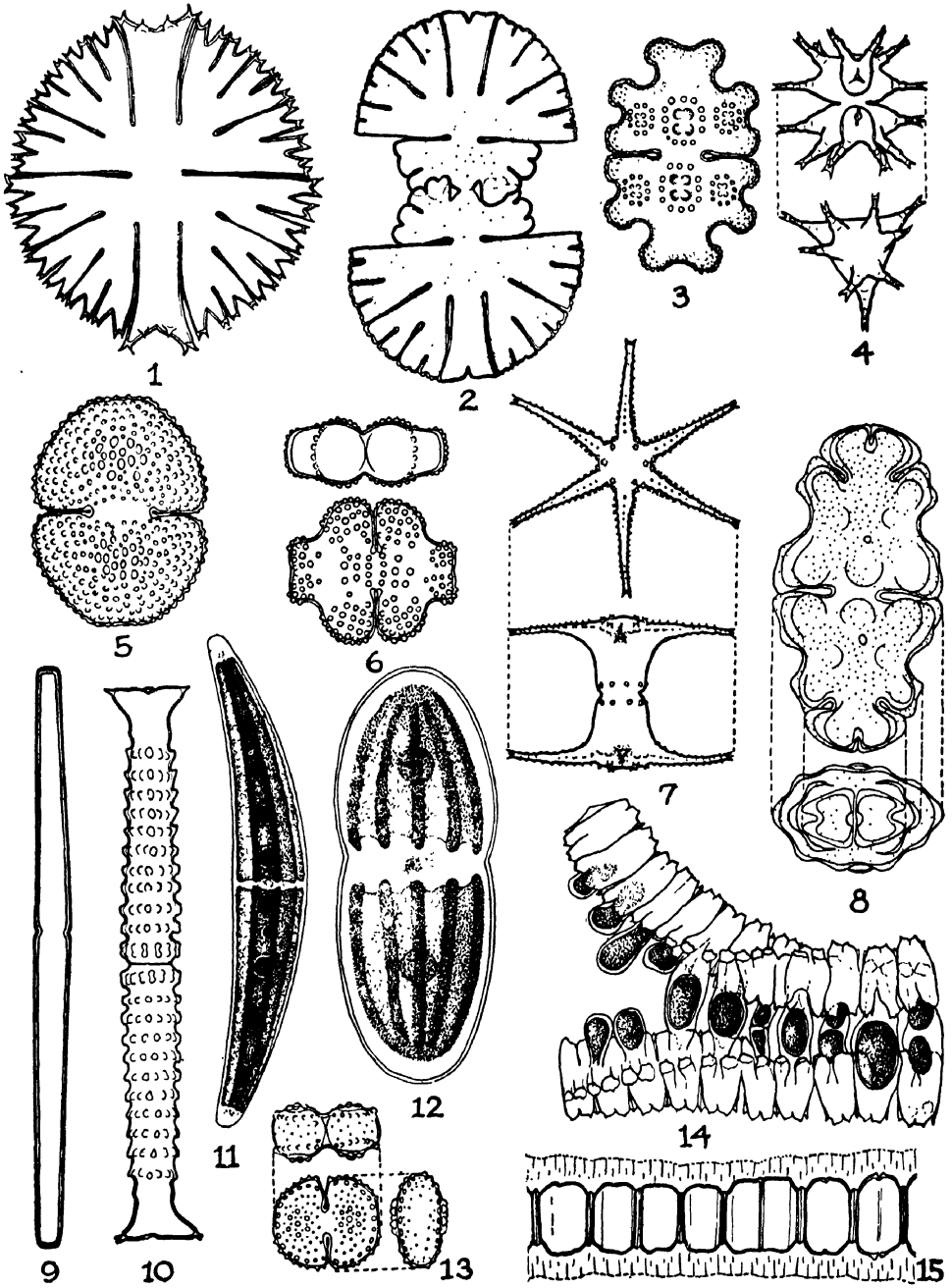

FIG. 284. Various forms of desmids, and conjugation in *Desmidium* (14). Genera represented: 1-2 *Micrasterias*, 3 and 8 *Euastrum*, 4 and 7 *Staurastrum*, 5, 6 and 13 *Cosmarium*, 9 *Pleurotaenium*, 10 *Triploceras*, 11 *Closterium*, 12 *Penium*, 14-15 *Desmidium*. Figures from Fr. Irene-Marie and H. Skuja.

ments. Common to all blue-greens is the presence of a mucilaginous outer wall which may be so thick that the filaments appear to be embedded in a mass of mucilage (Fig. 285).

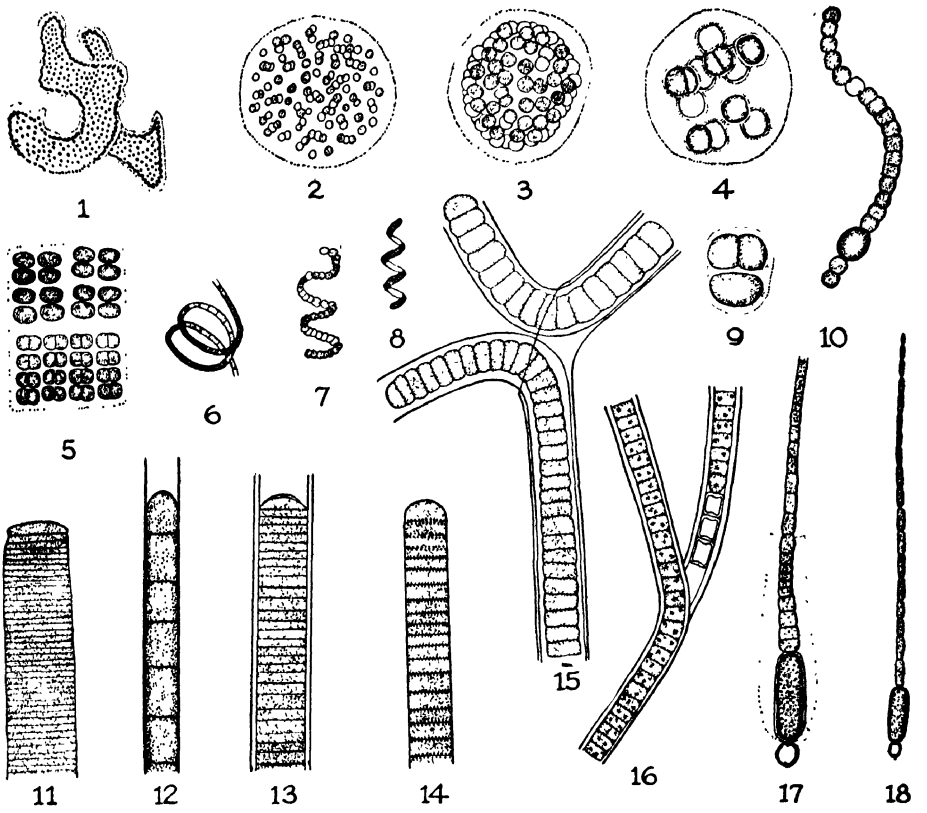

FIG. 285. Forms of blue-green algae. Genera represented: 1 *Microcystis*, 2 *Aphanocapsa*, 3 *Coelosphaerium*, 4 *Chroococcus*, 5 *Merismopedia*, 6 and 13 *Lyngbya*, 7 and 10 *Anabaena*, 8 *Spirulina*, 9 *Chroococcus*, 11 and 14 *Oscillatoria*, 12 *Phormidium*, 15 *Scytonema*, 16 *Tolypothrix*, 17 *Gloeotrichia*, 18 *Cylindrospermum*. Figures from G. M. Smith, J. E. Tilden.

Approximately 2500 species of blue-greens have been described and named. Most of them grow in fresh water, but marine and other salt-water species are not uncommon. They are able to grow in almost every conceivable habitat. They are important constituents of fresh-water plankton, and some of the water blooms of summer are due to their abundance. The Red Sea was probably so named because of the presence in large numbers of one of these plants (*Trichodesmium*), which is predominantly red in color. Blue-greens that grow in hot springs live

at temperatures between 150° and 170° F. Other species may remain frozen in ice for many months without injury. Blue-greens may become serious pests on soil in greenhouses by forming a gelatinous layer that prevents aeration of the soil beneath. They are very common in ponds in the far north.

The blue-greens constitute an important part of the algal population of soils, and their spores can withstand complete desiccation for many years. They may grow as parasites within the bodies of man and other animals; as epiphytes on other algae and on the vegetative parts, particularly leaves, of many seed plants; and as hosts of fungi in a few kinds of lichens. Species of blue-green algae regularly occur in the leaves of a water fern (*Azolla*), and on the scales of some liverworts. One blue-green species grows in the aerial roots of some cycads, and many others may be found within the gelatinous envelopes of other algae.

In general, this group of algae may be considered as the characteristic plants in bodies of water high in organic matter, but not necessarily so. When fresh-water streams are polluted by sewage, by poisonous wastes from various manufacturing processes, and by drainage from coal mines and oil wells, the blue-greens are the last to disappear. In fact, in such habitats certain bacteria are about their only living associates.

Blue-green algae are either unicellular, colonial, or multicellular. Cells of the colonial species may be loosely or definitely aggregated into globular, saccate, plate-like, or irregular colonies with a few to many cells held together by mucilage. The cells of some other species are joined end to end in definite regular or irregular filaments; the filaments may be branched or not. Division of the cells in only one plane results in a chain of cells; division in two planes, a plate-like colony; and division in three planes, a solid and often nearly cubical aggregate.

The granules of food that accumulate in the vegetative cells are not definitely known chemically. They undoubtedly are conversion products from sugar formed in photosynthesis; they are not starch. Glycogen, or possibly glycoproteins, and droplets of oil may accumulate, especially in the spores.

The plants increase in number by vegetative multiplication. Any vegetative cell in some plants, or only certain vegetative cells in other plants, may develop thick walls and become dormant. After a period of time, new plants grow from these thick-walled cells. New filaments also result from the fragmentation of old filaments into small groups of cells, followed by repeated cell division.

The Diatoms: Bacillariophyceae

The vegetative cell of a diatom has highly silicified walls (i.e., glass walls) composed of two overlapping parts (*valves*) that fit together like the halves of a petri dish. The wall is usually beautifully sculptured and ornamented (Fig. 286). The plant may be unicellular, filamentous, or joined in irregular colonies by gelatinous sheaths. Pectic compounds are present, but probably no cellulose. The chloroplasts are yellowish to brownish, and contain chlorophyll, xanthophyll, and carotene together with accessory pigments of unknown chemical composition. Some 12,000 species have been described.

Diatoms are distributed widely in both fresh and salt water. They are the important constituents of the plankton of the cooler waters of the sea, and at times are the principal algae of lakes and ponds, especially in early spring and in the autumn. Owing to the mucilage from their cells, diatoms may become attached to other plants and to all sorts of under water objects. Depending upon the amount and place of major formation of mucilage, the colonial species may form ribbon, chain, zigzag, or branching aggregates. Although not as important as either greens or blue-greens in the soil, some species of diatoms are distinctly terrestrial and capable of withstanding desiccation for many years. In regions of frequent rainfall diatoms may grow subaerially on tree trunks, on fences, and on rocky cliffs.

As noted above, diatoms may occur in prodigious numbers in both sea and inland waters at certain times of the year. They are probably the most important constituent of the ocean plankton. When the plants die, the cell walls remain unaltered after the death and decay of the rest of the cell. The empty "glass cases" may thus accumulate over a period of years in great quantities on the bottom of seas, bays, and lakes. Such deposits of fossil diatoms are known as diatomaceous earth and are found in many parts of the world. One of the largest deposits is near Lompoc, California; it covers about 12 square miles with a stratum of commercially pure diatoms some 1400 feet thick, and in addition 3000 feet of diatoms mixed with silt, sand, and gravel.

Diatomaceous earth is quarried or mined, the annual output approaching 100,000 tons. Its largest use is in the filtration of liquids, especially those of sugar refineries. The powdered earth is added to the solution, collects on the cloth screens of the filter press, and prevents the suspended matter from passing through them. Diatomaceous earth in the

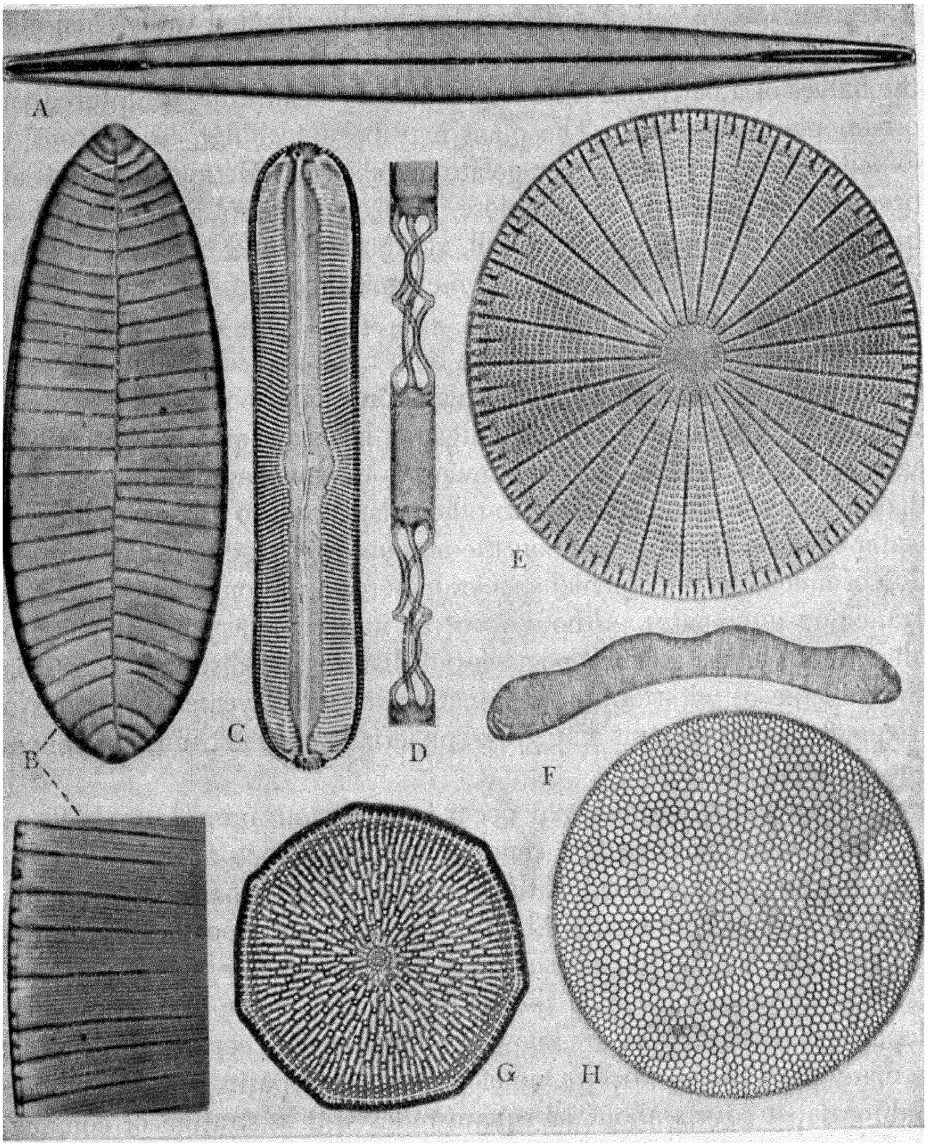

FIG. 286. Eight species of diatoms differing in structure and symmetry. Genera represented: A, *Amphipleura;* B, *Surirella;* C, *Pinnularia;* D, *Tribrachia;* E, *Arachnoidiscus;* F, *Eunotia;* G, *Stictodiscus;* H, *Coscinodiscus.* Photos from Paul Conger, Smithsonian Institution, except A from Bausch & Lomb Optical Co., and E from Spencer Lens Co.

form of bricks is used in the insulation of boilers and smelting furnaces. At high temperatures it is more effective than asbestos or magnesia. Metal polishes, abrasive soaps, and toothpaste often contain diatom shells.

Living diatoms are of major importance as the food of fishes, oysters, and clams. Certain marine fishes feed almost entirely on them, or on the small animals that have consumed diatoms. The commercially important hake, for example, feeds upon herring; the herring subsist on copepods; and the copepods are dependent upon the diatoms for their food (Fig. 275).

The accumulation and decay of diatoms in water reservoirs and ponds, on the other hand, may result in compounds that are extremely obnoxious to our senses of smell and taste. Some species are able to grow in waters highly polluted with organic matter. Diatom abundance is often associated with a plentiful supply of nitrates and silicates. Paucity of diatoms is sometimes directly due to the absence of soluble silicates in the pond.

Cell division in the diatoms is an almost unique phenomenon among plants. The new cell wall in the center of the dividing cell consists of two new valves. Each of the two resulting daughter cells then has one new valve, and one older valve that belonged to the parent cell. As a result, any given diatom cell may have a valve that has been a part of many ancestral cells. Spores are formed in the diatoms both asexually and sexually; and from them, after a period of dormancy, new plants develop directly. The spores of diatoms have been indiscriminately called *auxospores* regardless of whether or not they are the result of sexual union. The prefix "auxo" refers to the increase in size of this cell. The cell formed from the auxospore is usually much larger than the cell, or cells, from which the auxospore originated. Subsequent divisions of the cells, in vegetative multiplication of some species, lead to decrease in size of cells until auxospores again form.

The diatom cell is diploid, the monoploid condition being represented only in the nuclei of the gametes, a condition not common among algae, but usual in animals.

The Yellow-green Algae: Xanthophyceae

This comparatively small group of algae is almost entirely confined to fresh water and consists of about 400 species. The yellow-greens are similar to the greens[3] in many respects, but are characterized by chloro-

[3] Since many of the green algae may often appear yellowish green during certain stages of development, it is sometimes difficult to separate species of the two groups with

plasts in which yellow pigments predominate over the green; by motile spores having two flagella of unequal length; by the presence of oils, but never starch; and by the rare occurrence of sexual reproduction.

Most of the yellow-greens occur free-floating in temporary ponds and pools, or as epiphytes upon other algae and upon the stems and leaves of submerged plants. A few species grow on small crustaceans. The aerial yellow-greens may be found on tree trunks or damp walls, or growing with liverworts and mosses. A common yellow-green alga on prairie and bottom-land soils is the balloon-shaped *Botrydium.*

The cells of the yellow-greens may be solitary, or united into colonies and filaments. The cell walls are chiefly pectic compounds (pectose or pectic acid) often impregnated with silica, with carbonates, and sometimes with small amounts of cellulose. The cells of several genera have walls made up of two overlapping halves that fit together like the two parts of a gelatine capsule used by druggists. Some of these characters of the yellow-greens resemble those of the diatoms.

Reproduction occurs through the formation and subsequent growth of motile and non-motile spores. Sexual reproduction has been observed only a few times, but seems to involve the union of motile gametes.

The Brown Algae: Phaeophyceae

The predominant color of brown algae is due to the presence of fucoxanthin, although green and yellow pigments are also present. Brown algae are almost entirely marine, and the larger ones are often referred to as seaweeds (Fig. 287). The largest ones, which are said to exceed 200 feet in length, are in the colder waters of temperate continental shores. The motile spores and gametes have two laterally placed flagella, one of which extends forward and the other backward. The cells are uninucleate and have from one to many chloroplasts. Oil, sugar, and complex polysaccharides accumulate in them. Some 1100 species are recognized.

Most species of brown algae are found on rocky shores and do not ordinarily grow at much greater depths than 50 to 75 feet, although some of the kelps are attached to rocks at depths of 200 feet. Many of the plants are completely submerged only at high tide, being exposed to

vegetative material alone. In hot concentrated HCl the chloroplasts of the yellow-greens become blue-green, whereas those of the greens remain green or become yellow-green when similarly treated. This may be taken as evidence of a difference in chemical composition of the two groups.

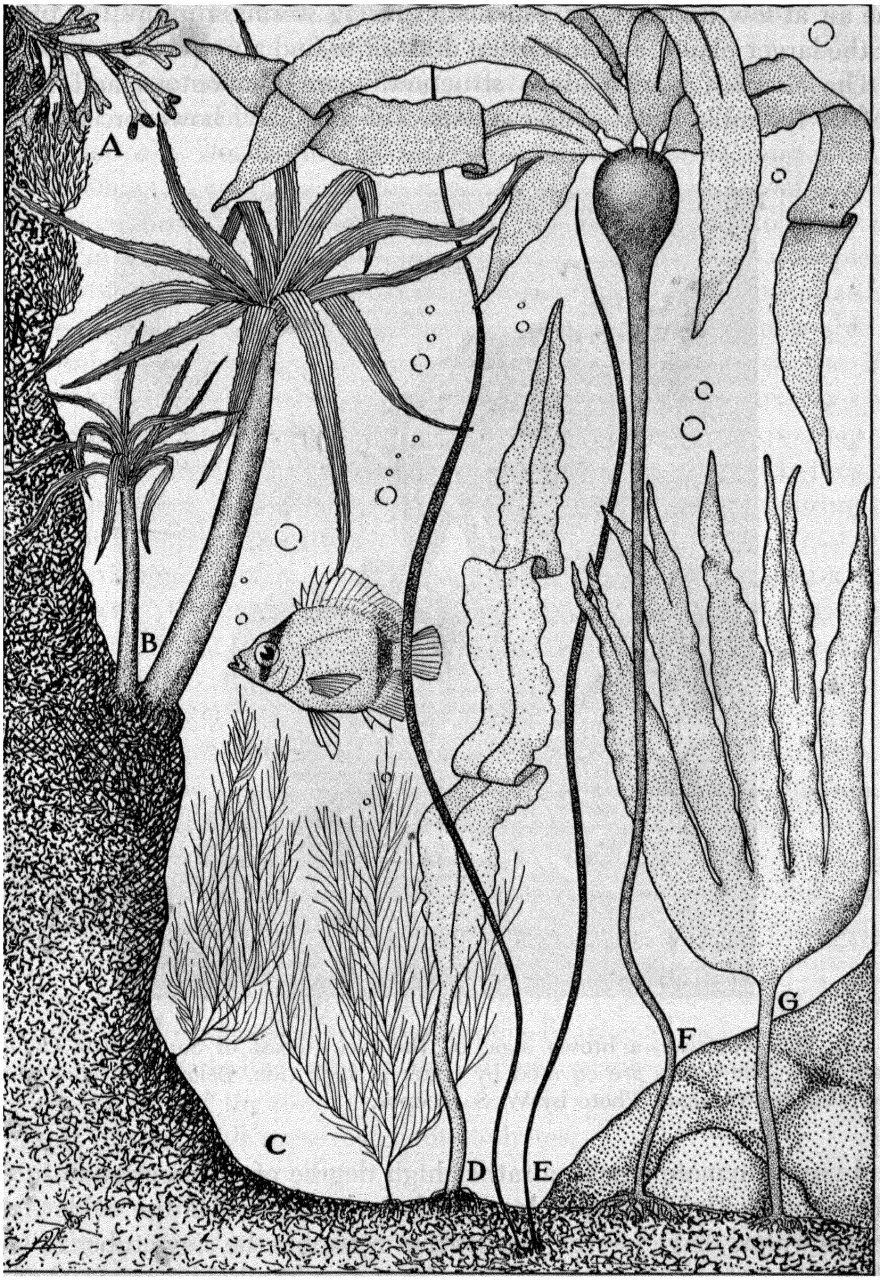

FIG. 287. Forms of brown algae (figures not drawn to scale). Genera represented: (A) *Fucus*, (B) *Postelsia*, (C) *Ectocarpus*, (D and G) *Laminaria*, (E) *Chorda*, and (F) *Nereocystis*.

the air at low tide. Waves, especially during storms, rupture the blades of the larger plants, and it is often difficult to find a perfect specimen.

The simplest brown algae structurally are filamentous and superficially resemble some of the greens. The majority, however, are large

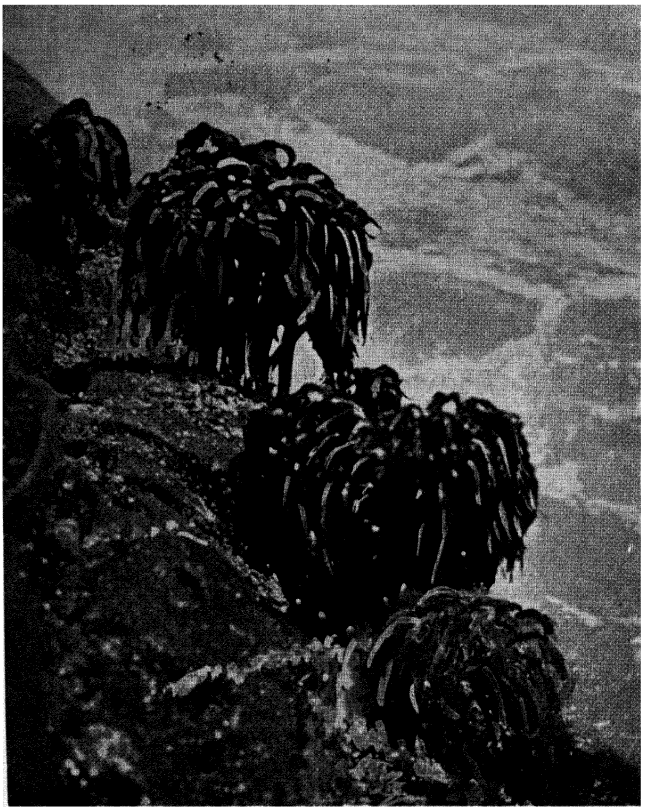

FIG. 288. *Postelsia*, a brown alga, on the rocky coast of Santa Cruz County, California. The plants are covered by water at high tide. Below, near the water, are other brown algae. Photo by W. S. Cooper.

and parenchymatous with a rather high degree of differentiation in the plant body (Fig. 288). The leathery kelps, abundant in the colder temperate waters, have internal tissues that resemble the sieve tubes of seed plants. These algae consist of branching root-like holdfasts attached to rocks or other substrates, a long submerged stalk, and one or more conspicuously large, ribbon-like, or variously shaped floating blades. Some

of the kelps are perennial, and the stalk increases in diameter by the formation of new rings of peripheral cells.

In the upper littoral zone along our coasts there grows in great abundance a branched, filamentous brown alga, known as *Ectocarpus*. It is practically world-wide in distribution. Along the Atlantic coast it is common as an epiphyte on the rockweeds (*Fucus* and *Ascophyllum*), and less common along the Pacific coast on certain kelps. Motile spores formed in some special cells may germinate and from them new plants develop. Fusion of flagellate gametes from other filaments results in a zygote. The germination of the zygote results in a plant that is able to bear only motile spores. In general, one cannot distinguish the filaments that bear the motile spores from those that bear gametes until the reproductive structures actually appear. There occurs then in *Ectocarpus* an alternation of asexual and sexual phases similar to those of seed plants, ferns, and mosses. Reduction division takes place during the formation of the motile spores.

Kelps. The body of a kelp consists of a holdfast, a stipe, and a very large blade. Kelps grow only in the colder waters of the oceans; they are absent from the warm waters of tropical and semitropical regions. Most species of kelp grow below low tide and are thus permanently in water. The life cycle of the kelps may be indicated by a study of *Laminaria*, sometimes called devil's apron, found along both coasts of this continent. On the surface of the blade occur patches of sporangia, from which motile spores escape (Fig. 289). From these spores minute gamete-bearing filaments develop. These tiny plants may be few-celled or many-celled, and each one is unisexual, producing either only male gametes or only female gametes. The union of two gametes results in a zygote, from which the large plant we know as the kelp develops. We thus have a pair of microscopic gametophytes (gamete-bearing plants) alternating with a large sporophyte (spore-bearing plant).

The large blade-like kelp is the diploid plant. Reduction division occurs in it during the formation of the motile spores, which are the forerunners of the small unisexual gametophytes.

It is interesting to recall that in nearly all green algae the conspicuous plant is the one bearing gametes. In *Laminaria*, and a few other algae as well, the gamete-bearing plant is microscopic; the spore-bearing plant is the conspicuous structure, as it is in the seed plants. Moreover, the conspicuous phase of *Laminaria* is diploid, and the microscopic gametophytes are monoploid. The conspicuous phase of green algae usually

has the reduced number of chromosomes, and spore formation (except zygotes) results only in vegetative multiplication of the gamete-bearing phase of the life cycle of the plant.

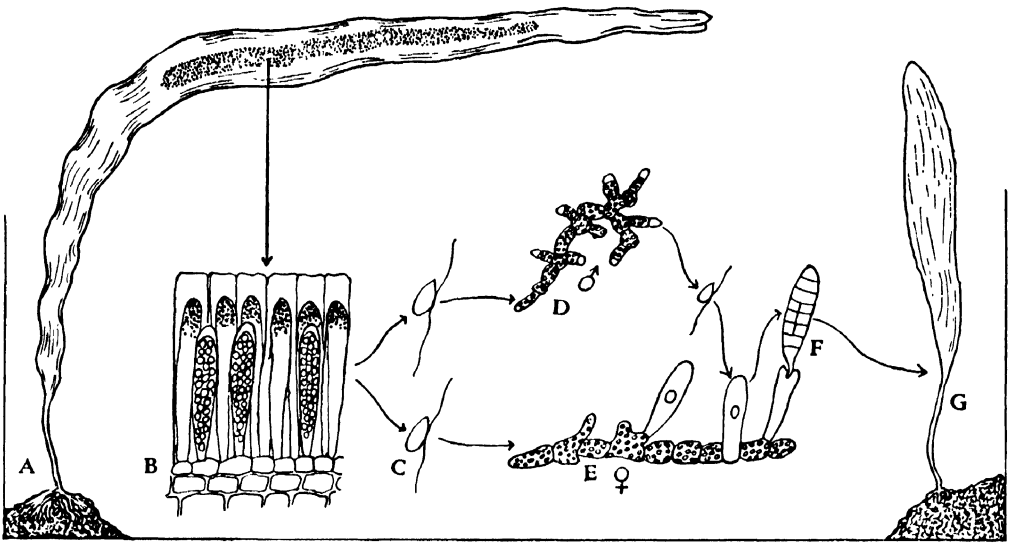

FIG. 289. Diagram illustrating the life history of a *Laminaria*. On the mature thallus (A) an enlongated patch of sporogenous tissue develops, an enlarged portion of which is represented in (B) with three sporangia from which motile spores (C) later escape. Reduction division occurs during the formation of these spores, and from one half of them male gametophytes (D) develop, and from the other half female gametophytes. Sperms are liberated from the male gametophytes and after swimming in the water unite with the egg cells in the female gametophyte. From the zygote a young sporophyte grows at first attached to the oogonium wall (F), but later it is set free and ultimately becomes attached to some other substrate (G).

Covering the rocks in the intertidal zones are the widely distributed "rockweeds" or "bladder wracks," represented on our coasts by *Fucus* (Fig. 3). They occur in tropical, temperate, and arctic seas, but the species or genera are usually characteristic in each zone. Most of the genera grow permanently attached to the rocks, although certain species of *Sargassum* are free-floating. *Fucus* is a dichotomously branched plant, attached by holdfasts and kept afloat at high tide by bladder-like structures filled with air. It has no asexual propagation except by fragmentation, and has no alternation of spore-bearing and gamete-bearing phases. The reproductive cycle is similar to that of animals. Sperms and eggs are formed by the first cell division immediately following reduction

division, and all other cells of the plant have the diploid number of chromosomes.

The reproductive organs develop only in special branches. Swollen conical structures (*receptacles*) at the tips of the branches contain rounded cavities (*conceptacles*) in which antheridia and oogonia develop. Usually 8 eggs are formed in a single oogonium, and 64 sperms in a single antheridium. Upon release from the oogonium and conceptacle, the non-flagellate egg may be fertilized by a motile sperm. A new plant grows directly from the zygote. Reduction division occurs in the mother cell (oocyte) of the 8 eggs and in the mother cell (spermatocyte) of the 64 sperms.

The Red Algae: Rhodophyceae

The red algae are by far the most beautiful of all macroscopic submerged plants (Fig. 290). They are most abundant in salt water, but are not infrequent in fresh water. Of the approximately 3500 known species, 200 grow in fresh water. They attain their greatest development in subtropical seas. Five different pigments (Table 17) are known to occur in the cells, with the red usually predominating, although various shades of blue and purple are common. The red algae have definite nuclei and chloroplasts, and the chief accumulated food is a starch-like carbohydrate. They attain greater size on the whole than either the greens, blue-greens, diatoms, or yellow-greens, but none attains the size of the brown kelps.

The red algae grow attached to rocks near shore, but considerable numbers may be found at depths of 50 to 100 feet, and a few live 200 feet or more below the surface. Some species are epiphytes upon other algae. The smallest species are little more than one-celled structures, but the majority are colonial aggregates, or filamentous and much branched, or blade-like and leathery. The larger species branch profusely, may attain lengths of several feet, and often have considerable differentiation of tissues. A single filament, for example, may have a row of axial cells ensheathed by a cortical layer several cells in thickness. The red algae superficially resemble other modern algae, but their genealogical relations are very remote.

Some of the red algae in tropical waters take part in the formation of coral reefs, and are known as coralline algae (Fig. 291). Corals are colonial animals; but always associated with them are red algae in which calcium carbonate accumulates, resulting in the massive reefs.

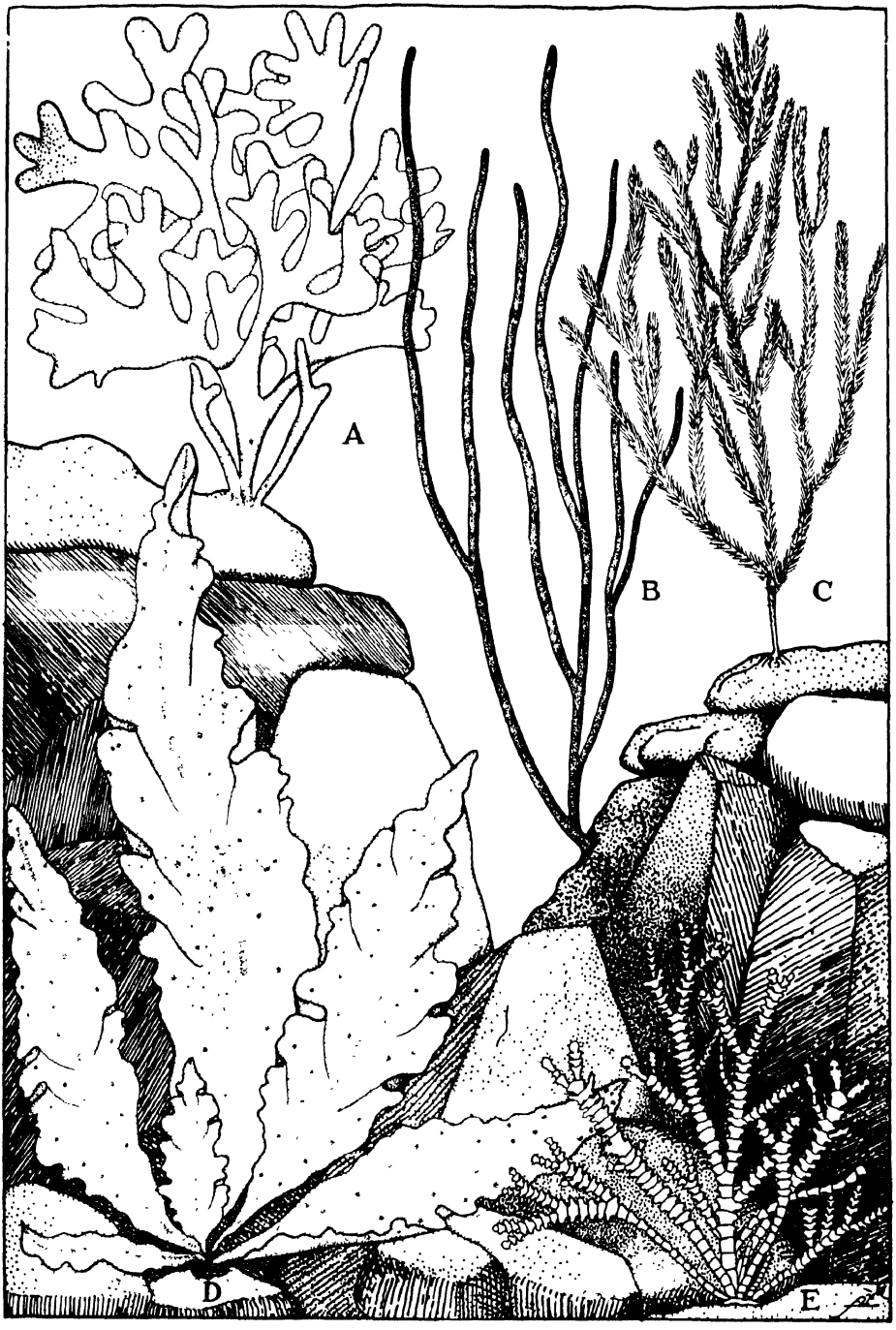

FIG. 290. Forms of red algae (figures not drawn to scale). Genera represented (A) *Chondrus*, (B) *Dasya*, (C) *Nemalion*, (D) *Grinnellia*, and (E) *Corallina*.

Fossil algal and coral reefs are found in the limestone rocks formed during the Paleozoic Era.

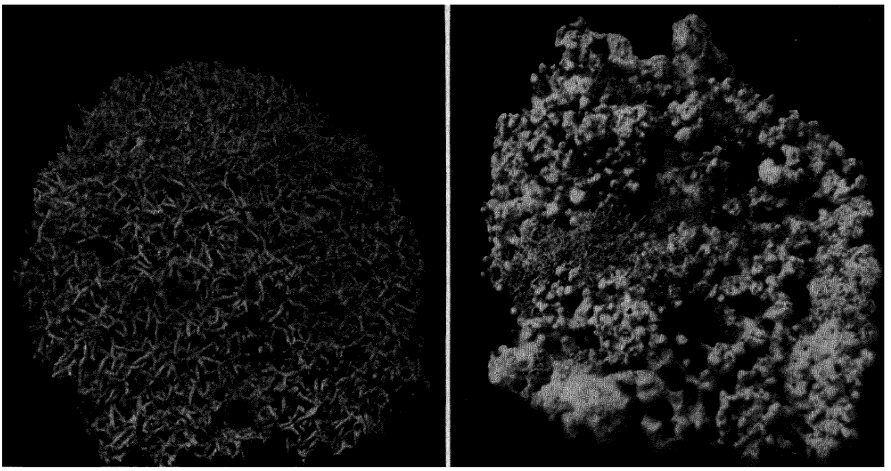

FIG. 291. Photographs of two coralline algae: A, *Goniolithon;* B, *Lithophyllum.* Courtesy of the N. Y. Botanical Garden.

Asexual reproduction among the red algae occurs through fragmentation, or the formation of non-motile spores. Strange as it may seem, no flagellate, motile cells of any kind occur in any of the plants of this group. Sexual reproduction is so unlike that known among other algae that a special terminology is necessary to describe it. The unique features of these algae are of interest mainly as examples of peculiar outcomes of evolution. A few examples are cited below.

Nemalion. When the tide is out, one may see the gelatinous strands of the marine summer annual, *Nemalion,* attached to the rocks in the midlittoral zone along coasts in temperate regions. It is a gelatinous short-branched cylindrical plant with a reddish-brown color. Compared with some other red algae its life history is simple, but it is more complex than the life histories of other algae described in this chapter. It will be described briefly.

The female sex organs are apical cells of special short branches. The apical cell (*carpogonium*), which contains the egg protoplast and resembles an oogonium, terminates in a slender outgrowth (*trichogyne*). There are also numerous small antheridia, each of which contains a non-flagellate male cell (*spermatium*) which is borne by water currents to the trichogyne. After the male cell becomes attached to the trichogyne,

Summary of Life Cycles of Algae Described

Name of Alga or of Special Groups of Algae	Sporophyte Phase, Diploid	Monoploid Reproductive Cells Produced by Sporophyte	Gametophyte Phase, Monoploid
Ulothrix	Zygote	Flagellate spores 4–16	Unbranched filaments; flagellate spores and gametes
Oedogonium	Zygote	4 flagellate spores	Unbranched filaments; flagellate spores and sperms, non-motile egg
Spirogyra	Zygote	4 nucleated zygote; 3 nuclei disintegrate	Unbranched filaments; non-flagellate gametes
Vaucheria	Zygote and probably the branched coenocytic filaments and flagellate spores	Sperms and non-motile eggs	Gametes
Diatoms	Zygote → vegetative cells and colonies; non-flagellate spores	Gametes	Non-motile gametes
Yellow-green algae	Zygote	Spores	Vegetative cells, colonies and filaments; non-flagellate and flagellate spores and gametes
Ectocarpus	Zygote → branched filaments	Flagellate spores	Flagellate spores → branched filaments and flagellate gametes
Laminaria	Zygote → large blade-like kelp	Flagellate spores	Flagellate spores → small filaments; flagellate sperms, non-motile eggs
Fucus	Zygote → large branched plant	Gametes	Flagellate sperms, non-motile eggs
Nemalion	Zygote → filaments of fruiting body (cystocarp), carposporophyte	Carpospore	Carpospores → branched filamentous plant; non-flagellate egg (carpogonium), non-flagellate sperm (spermatium)
Protococcus	Vegetative cells and temporary colonies; no spores and no gametes.		
Blue-green algae	Vegetative cells, colonies, and filaments; non-flagellate spores, but no gametes		

its nucleus divides and one of the resulting nuclei fuses with the egg. After the egg is fertilized, numerous short branches develop from it. Each of these branches is terminated by a spore (*carpospore*). Branches may also develop from cells adjacent to the fertilized egg. The whole mass

of branches and carpospores, which superficially resembles a fruiting body, is called a *cystocarp*. When a carpospore becomes free and germinates, a new *Nemalion* plant develops from it. Reduction division occurs during the formation of the carpospores.

The ordinary *Nemalion* plant, therefore, is the gametophyte phase with the monoploid number of chromosomes. The short branches of the cystocarp that developed from the fertilized egg have the diploid number of chromosomes and constitute the sporophyte (*carposporophyte*) phase in the life cycle of *Nemalion*.

Batrachospermum and Lemanea. The fresh-water *Batrachospermum* grows on the rocks in riffles and waterfalls in streams and in the wave-disturbed margins of lakes of the temperate zone. It has whorls of short branches at the nodes of a central axis, all enclosed in a heavy mucilaginous sheath. The color varies from bluish green to violet. Its life cycle is similar to that of *Nemalion*. Another common relative in rapidly flowing streams is *Lemanea*. The filaments of some species when magnified look like bamboo rods. The life cycles of these plants are more complicated than that of *Nemalion*, but they are not as complex as those of many other red algae.

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CHAPTER XLVIII

MOSSES AND LIVERWORTS

(BRYOPHYTES)

Mosses and liverworts grow throughout the world, from the high mountains of Antarctica to northernmost Greenland. Species of moss occur in nearly every habitat, from 180 feet under water in a Swiss lake to the driest deserts of Arizona. Liverworts grow in less extreme situations but in a surprising variety of them. Neither the mosses nor the liverworts live in sea water.

Bryophytes are common in the vegetation on the arctic and alpine tundra (Fig. 292). They are most abundant in moist and wet situations. Bryophytes are also abundant in the north woods and in the moist forested regions of the Pacific coast (Fig. 293). There they and the lichens not only live on the soil and on the trunks and branches of living trees, but they soon cover the fallen trees with a living green spongy mantle, beneath which the relentless processes of disintegration proceed (Fig. 294). Mosses form the primary mats of the floating and semi-solid substrates of bogs and "muskegs." Held together by the tangled fibrous roots of sedges, ferns, and shrubs, they grow above and die below, thus contributing to the gradual filling of depressions and lake basins with peat.

Clearing of the forests and cultivation of the land by man have destroyed numerous habitats of many kinds of bryophytes in agricultural regions. But these species may still be found in rock gorges, swamp woods, and other forest remnants where they have survived and are often locally abundant. On the other hand, some species are more abundant in partially cleared forests, and a few may be found in cultivated fields.

The grasses of old shaded lawns are often replaced by several species of mosses and liverworts. Examination of clover fields and pastures will reveal a surprising carpet of these little plants growing with the soil algae. When farms are abandoned, bryophytes are among the pioneer invaders of "worn-out" soils. Years later, when young woodland has occu-

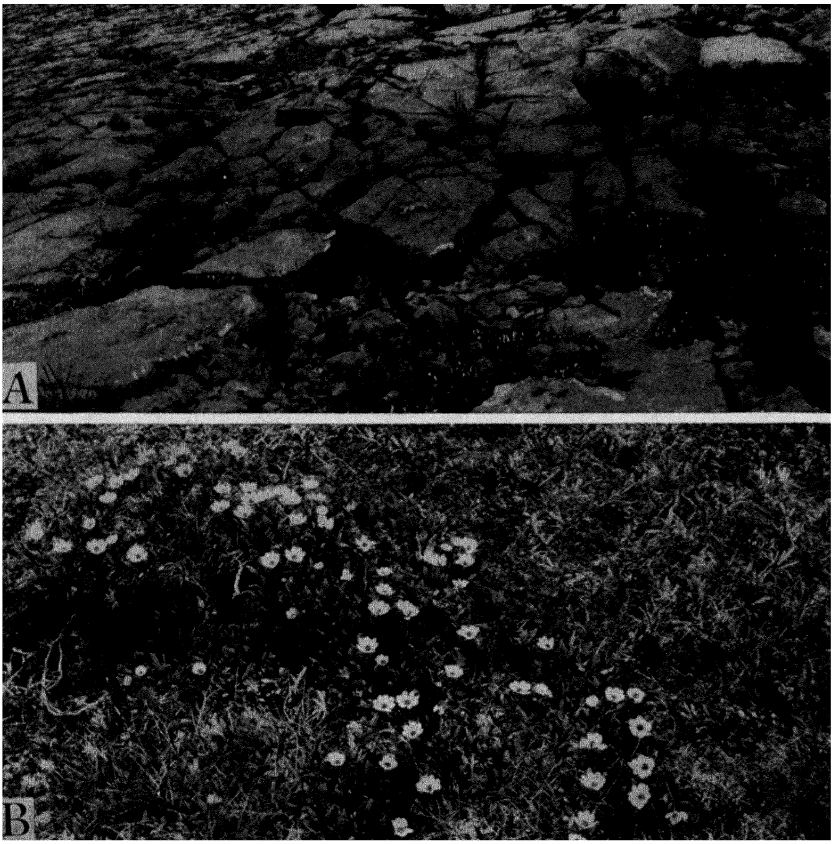

FIG. 292. Earlier and later stages in the development of alpine tundra on Mt. Robson, British Columbia. Vegetation starts in the crevices of the glaciated rock surface (A); ultimately rock and plant debris covers the entire surface; and sedges, grasses, creeping willows, heath plants, and *Dryas* (in flower) form a continuous association (B). Photos by W. S. Cooper.

pied the farm site, it is often amazing to see the extent to which the species of bryophytes that formerly lived in the forests of the region have reappeared.

In tropical and subtropical forests, where rainfall is ample, mosses and liverworts grow profusely in glades and on stream banks. Many grow as epiphytes, forming spongy cushions on tree trunks and branches in the forest canopy. Some even grow on the surfaces of leaves.

Certain aquatic species live attached to rocks in swift clear streams, and even in waterfalls. Most species of bryophytes are land plants, in contrast to the algae, most of which are aquatics.

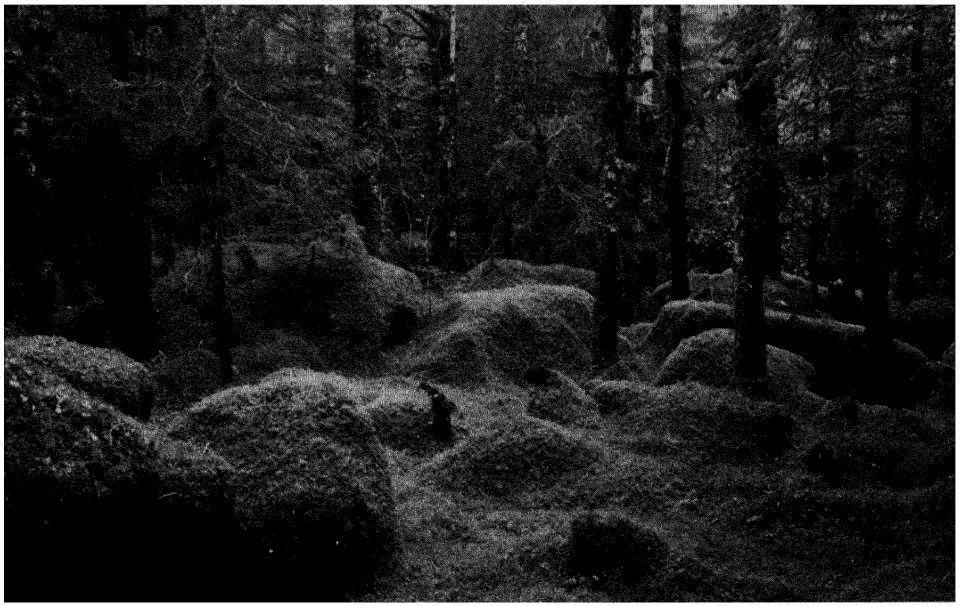

FIG. 293. Moss-covered terrain in a hemlock forest on a terminal moraine at the mouth of Glacier Bay, Alaska. The moraine was deposited 150-200 years ago and the maximum age of the trees is 110 years. Photo by W. S. Cooper.



FIG. 294. A mat of the common fern moss (*Thuidium*). Photo by E. S. Thomas, Ohio State Museum.

Locally, the occurrence of some species is limited by the acidity or alkalinity of the habitat. The pigeon-wheat moss (*Polytrichum*), the wind-blown moss (*Dicranum*), and the white-cushion moss (*Leucobryum*) grow almost wholly in acid situations. The cord moss (*Funaria*) and the silvery *Bryum* are largely limited to alkaline or neutral areas. Other mosses, such as *Climacium* and *Mnium*, grow equally well in both acid and alkaline habitats. Some species of bryophytes survive in very acid, and others in extremely alkaline, substrates.

Many mosses withstand freezing temperatures at any stage of development, and in subarctic lands live under snow and ice for the longer part of every year. Whenever the snow disappears, food-making, growth, and reproduction proceed from the stage at which they stopped the previous season. In rock crevices on the mountains of the Antarctic the Byrd Expedition found living mosses and lichens, where temperatures are seldom above freezing, and in winter often 75° F. below zero. Mosses also occur in the water of hot springs.

Their endurance of cold and drought is not dependent upon any special anatomical structures. Owing to their habit of growth as compact

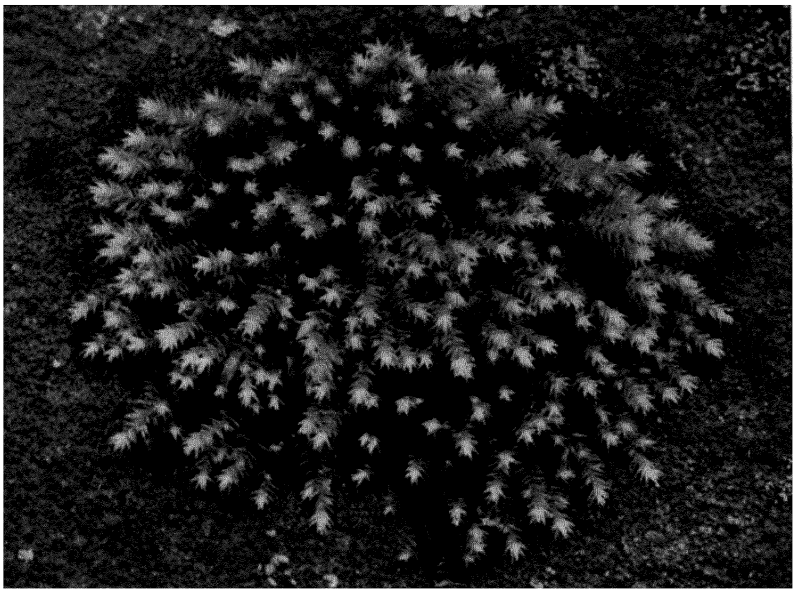

FIG. 295. A tuft of *Hedwigia* on a rock substrate where it may become dry and brittle during droughts, but will grow again when it becomes moist. Photo by E. S. Thomas, Ohio State Museum.

cushions or as sponge-like mats, water accumulates during rains and fogs by capillarity and remains available for much longer periods. When the plants become dry, their processes are largely suspended; but in nature recovery is possible even after prolonged droughts (Fig. 295). Moss plants dried for several days in the laboratory fail to recover, but the same species endure droughts of several weeks out-of-doors. Apparently they obtain enough water from the atmosphere at night to survive. The spores of certain mosses, however, have germinated after being kept for 14 years in the dry air of a herbarium.

Adequate light, a moist atmosphere, a rather constant water supply, and suitable temperatures are all essential to the abundant growth of most bryophytes. Some grow in the entrances to caves and below rock ledges, where the light is as low as 1/500 of full sunlight. Moss plants have been found living in complete darkness. Obviously these plants were living as saprophytes similar to the subterranean green algae. The species of moss that lives at a depth of 180 feet in the water of Lake Geneva, Switzerland, survives at an extremely low light intensity, and must have a very low compensation point. The so-called "luminous moss" (*Schistostega*) found under rock ledges and in dark recesses in woods is probably the material basis of the fairy tales of "goblin gold." The cobwebby threads of the green plant are easily overlooked among the rock particles. From certain angles, however, the refracted and reflected light rays from the lens-like cells of the plant are seen as a golden-green glow.

None of the bryophytes is more than a few inches tall. They are simple in structure, although many of them have organs that superficially resemble leaves, stems, and rootlets. No conducting system is present and the cell walls are not lignified. Mosses imbibe water rapidly, even from moist air. The cells of the green parts of the plants have well-developed round chloroplasts. No true parasites are known among bryophytes, but many species are probably partial saprophytes. Moss communities frequently become the substrates of lichens and die in their shade. Their remains accumulate as humus on bare rock surfaces, and become the substrate in which the roots of ferns and other plants may grow. The remains of these plants in turn contribute further to the humus, and the roots of the living plants bind the material together and anchor it still more securely. These are the pioneer stages of soil development, and of vegetation on exposed rocks.

Owing to their rapid and compact horizontal spreading, bryophytes

soon form patch-like communities in many kinds of situations. On the basis of their habitat relations, they are conveniently classified (1) as suspended, attached, and floating species in quiet water, (2) as species anchored in running water, (3) as plants on wet or dry fallen logs, soils, and rocks, (4) as epiphytes on bark and leaves, (5) as bog species, and (6) as pioneers on calcareous and non-calcareous rock surfaces.

Bryophytes are either annuals or perennials. It is difficult to estimate the age of the perennials, since they have no annual rings or bud scars.



FIG. 296. The juniper hair-cap moss (*Polytrichum*). The male branches may be recognized by their terminal rosettes of broad scales. Photo by E. S. Thomas, Ohio State Museum.

Annual stem segments are recognizable, however, in some moss plants, such as *Polytrichum* (Fig. 296), in which a characteristic rosette of permanent leaves surrounds the terminal male reproductive structures. Each year a new stem segment grows from near the center of the terminal rosette of the previous stem segment (Fig. 297). *Polytrichum* plants have been found in bogs, with 1 to 3 upper live segments and 4 to 8 dead

ones below. In most species the lower and older parts disintegrate about as fast as new growths appear terminally.

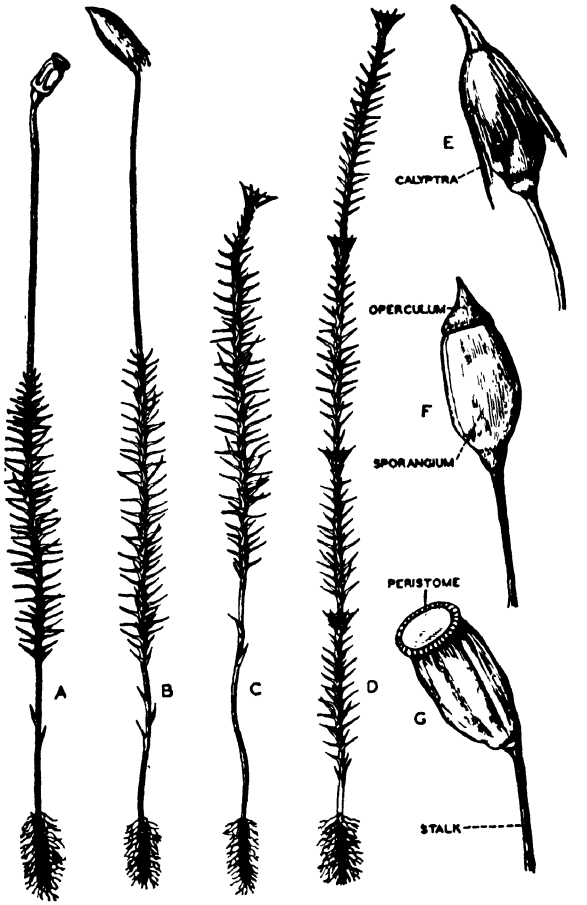

FIG. 297. *Polytrichum*. Annual stem segments and terms applied to parts of the capsule. A and B, gametophyte and sporophyte phases; C and D, male gametophytes. E, the calyptra develops from the archegonium.

The bog mosses grow in poorly aerated habitats, and as they die below they accumulate as peat deposits, several to many feet in thickness. Mosses that grow in springs heavily charged with calcium bicarbonate become incrusted below with lime and build up layers of porous hard tufa many feet thick. The tufa deposits later recrystallize and form solid masses of limestone. The moss *Gymnostomum*, important in tufa formation, is known to elongate a little over an inch in four years. In a thousand years these processes would form a layer of tufa and rock some 20 feet in thickness. Living cells occur only in the uppermost segments.

In moist, shaded habitats various small salamanders, insects, snails, worms, fungi, bacteria, and algae live with the bryophytes as a miniature microcosm. From the plants, both living and dead, the animals obtain food, cover, and a more continuous water supply. The saprophytic fungi simply grow through the mass of liverworts and mosses and become interlaced with them. Some of the fungi, however, are wholly or partially parasitic, and live on and within the bryophyte cells. Certain species of aerial and terrestrial algae as well as various soil bacteria are also sure to be found in the community. The commonest example of an alga living within liverworts is the blue-green *Nostoc* in cavities of such liverworts as *Anthoceros* and *Blasia.*

The economic and biological importance of the bryophytes is much less than that of either the algae or the fungi. They have been contributory factors in the formation of peat, muck, and brown coal through the centuries, and they contribute annually to the organic matter of the soil. They hold the soil against wind and water erosion, and decrease run-off of water by their spongy texture. They are the food of many small animals. Some species are important pioneers, sharing with the lichens the initial development of soil on bare rocks, volcanic deposits, and newly exposed land. During the World War certain bog mosses of the genus *Sphagnum* were collected, sterilized, and used as wound dressings because of their superior absorptive quality. Peat formed by *Sphagnum, Calliergon,* and other mosses is prized by gardeners as a means of increasing the organic content and porosity of soils in gardens and in lawns. A bale, or about 8 bushels, of peat moss absorbs nearly 200 gallons of water. Florists and nurserymen use these mosses as packing around the roots of shrubs and trees that are being transported and replanted.

Approximately 23,000 species of bryophytes have been described and classified. Of these, nearly 9000 are liverworts (*Hepaticae*), and 14,000 are mosses (*Musci*).

The moss plant. Some of the mosses and liverworts look much alike, but most of the common mosses are easily recognized. They usually have leafy erect or creeping stems, which develop from a much-branched filamentous or thallose green structure growing on the surface of the soil, and known as the *protonema* (Gr. *first thread*). A clone of numerous upright leafy stems may grow from each protonema. A leafless stalk may eventually develop from the apex or from the side of the leafy stem,

ending terminally in a spore-bearing capsule. At the basal end of the leafy stem, many-celled branching rhizoids, seldom more than a few millimeters long, penetrate the soil or other substrate.

Mosses multiply freely by vegetative propagation. On culture media new individuals may develop from nearly any fragment of the plant. In many species small buds occur on stems, and when they become detached new individuals develop from each of them. More specialized propagative buds, called "brood bodies," occur abundantly on leaves, stems, and even rhizoids of some species. Vegetative multiplication by fragmentation of the protonema appears almost limitless, especially if the protonema is perennial. Adventitious protonemata may develop from almost any part of the plant.

The filaments of the protonema, except for their small roundish chloroplasts, are difficult to distinguish from branching filamentous algae. They continue to branch, and soon form a thin green mat over the surface of the soil. Numerous buds, or bulbils, form on the branches of the protonema, and rhizoids and leafy branches develop from them. If the buds are numerous, the upright branches develop close together and form dense clusters or cushions. Some species have an extensive perennial felt-like protonema that completely covers the soil surface, but the upright shoots are small and scattered.

When the spores formed in the capsule of the leafless stalk fall upon soil or other moist substrates, they germinate, and from each of them a new protonema develops. These spores constitute a definite stage in the life cycle of a moss plant, which consists of two distinct phases. One phase ends with the development of spores; the other, with the development of gametes, and fertilization.

The gametophyte phase and sexual reproduction. The commonly observed moss plant composed of protonema, leafy branches, and rhizoids is the gamete-bearing phase, or gametophyte. At the apex of the green leafy stems there appear tufted heads of leaves enclosing groups of slender flask-shaped egg cases, called *archegonia* (sing. *archegonium*). An archegonium ordinarily contains one egg cell and is analogous to the oogonium of the algae, but differs from it in being a multicellular structure (Fig. 298). Antheridia also develop at the apex of leafy stems, sometimes in the same head with the archegonia, and sometimes alone on other stem tips. They may also develop singly or in pairs in the axils of leaves. They are multicellular, and many sperms develop in each of

them. Scattered among the antheridia and archegonia may be numerous sterile filaments.

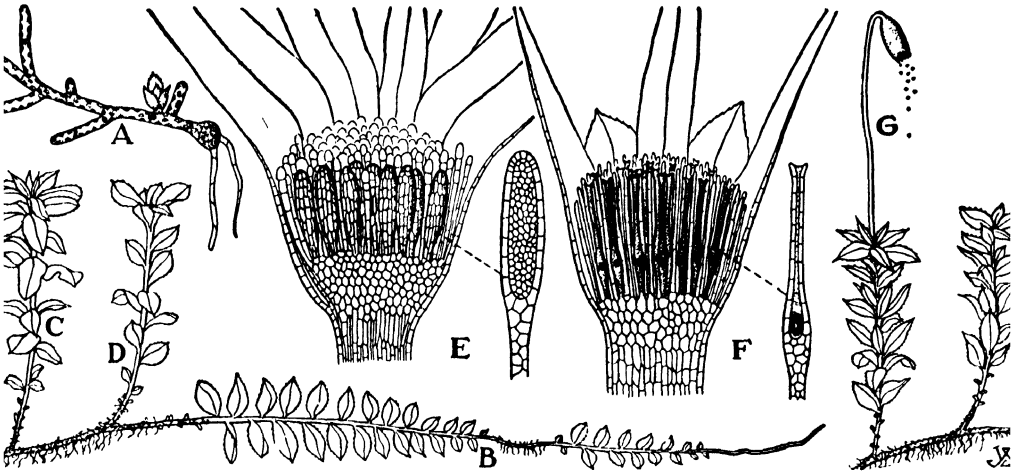

FIG. 298. Structures in the life cycle of a moss (*Mnium*): A, the protonema which develops from a spore; B, a horizontal vegetative shoot from a bud of the protonema; C, a female branch; D, a male branch; E, antheridia at the tip of a male branch; F, archegonia at the tip of a female branch; G, the leafless stalk (sporophyte) which develops from a zygote in an archegonium and bears a terminal sporangium containing numerous spores.

When the entrance of water causes a mature antheridium to swell and burst, the sperms are set free. Since they are motile they swim about in the film of water on top of the plant or mass of plants, and some of them eventually swim near the tips of archegonia. As the egg matures, the interior row of cells (neck-canal cells) of each archegonium disintegrates into a mucilaginous mass from which sugars diffuse into the surrounding water. When the sperms come in contact with the diffusing sugar they may swim toward the archegonium where the sugar is most concentrated. A few eventually pass into the neck of the archegonium, and one may finally move all the way to the egg and fuse with it. The fertilized egg, or zygote, is the beginning of the sporophyte phase of the moss plant.

The sporophyte and asexual reproduction. The zygote germinates while still within the archegonium at the apex of the leafy stem, and from it develops a slender, stalk-like, leafless structure terminating in a capsule, or sporangium. In some mosses the stalk, or seta, is very short; in others two to four inches in length. The capsule is usually simple, but in some of the common mosses it is quite complex. In most species the main body or *urn* of the sporangium is surmounted by an easily separable

lid, or *operculum*, and the whole structure, or at least a part of it, is covered by a hood or *calyptra* (Fig. 297). Extending partly across the mouth of the urn is a *peristome* composed of from 4 to 64 variously ornamented and radially disposed teeth. Large numbers of spores develop in the sporangium; and when they are released, new protonemata develop from them.

Thus the life cycle of a moss from spore to spore consists of two alternating phases: the gamete-bearing phase (the gametophyte) and the spore-bearing phase (the sporophyte). Reduction division takes place at the time of the formation of the spores within the sporangium. The spores and each of the cells of the gametophyte ordinarily have the monoploid number of chromosomes, and those of the sporophyte the diploid number.

The leafless stalk with its sporangium is the sporophyte. Since it is not a continuation of the stem of the gametophyte usually only a slight pull is necessary to separate them. The sporophyte is green when young; at most it is only a partial parasite on the green leafy gametophyte. Owing to the location of the archegonium and the germination of the zygote within it, the position of the sporophyte in some mosses is apical on the main stem, and in others on minute lateral branches.

The sporophytes of most species develop at a definite season of the year. This fact may often be helpful in distinguishing one species from another. In a few mosses, notably *Tetraphis*, the sporophyte persists for a year or more. In others the sporangia mature in autumn and remain until spring. In still other species the sporophytes mature in the spring and early summer and soon disappear. There are a few species of mosses on which sporophytes have never been found.

The gametophyte phase of the moss begins with the formation of spores in the sporangium of the sporophyte, and ends with the development of gametes, and fertilization. The sporophyte phase begins with the fertilized egg, or zygote, and ends with the formation of spores.

Among flowering plants the plant that bears the flowers is the sporophyte phase. The gametophyte phase consists of the embryo sac in the ovule, and of the pollen grain and pollen tube: a female and a male gametophyte. Among the mosses, the gametophyte (protonema and leafy branches) may be male or female, or it may be bisexual (monoecious), bearing both antheridia and archegonia with their sperms and eggs. Of all the plants in the world, the bryophytes have the largest gametophytes, and the seed plants have the largest sporophytes.

Chromosomes and the life cycle of mosses. Since reduction division occurs during the formation of spores in the sporophyte, these spores and all cells of the gametophyte have the n, or monoploid, number of chromosomes; while the cells of the sporophyte, which develops from the fertilized egg, have the $2n$, or diploid number. Moreover, all the cells of the gametophyte, including the protonema with all of its leafy branches and all of their sperms and eggs, have the same chromosome complement. Consequently if self-fertilization occurs, each of the fertilized eggs and resulting sporophytes will have two sets of like chromosomes. They will be completely homozygous. If reduction division is regular, all the spores formed in these sporophytes will have the same chromosome complement, and so will all of the subsequent gametophytes that develop from them. Similar chromosome phenomena may occur in bisexual liverworts and ferns also.

Classification of mosses. The foregoing description of a moss life cycle refers especially to the group sometimes called the "true mosses" (*Bryales*). Two other groups or orders of mosses are generally recognized: the peat or bog mosses (*Sphagnales*) and the rock or granite mosses (*Andreaeales*). These differ from the *Bryales* in various structural details of both gametophytes and sporophytes. Descriptions of these orders may be readily found in books on the mosses, some of which are listed at the end of this chapter.

The peat mosses, *Sphagnales*, differ from other mosses in several characteristics. The protonema is a flat thallus similar in appearance to a small liverwort or the prothallus of a fern. It begins as a filament, but soon becomes a flat plate one-cell thick and irregularly lobed (Fig. 299). The visible stalk (pseudopodium) upon which the capsule is borne is an outgrowth of the gametophyte and is not the lower part of the sporophyte. The sporophyte consists of a globular capsule, a very short and slender stalk, and a foot. The spore-bearing part of the capsule is dome-shaped, overarching a region of sterile tissue. The leaves are a single cell layer in thickness, have no midrib, and contain both living and dead cells. In young leaves all the cells look alike; but later, differentiation results in slender living cells, which possess chloroplasts and form a network enclosing larger, short-lived, non-green cells.

The peat mosses are of more commercial value than any others. These plants often form floating masses on the surface of lakes and ponds. Continued growth of the plants upward forces lower layers downward, and the dead and decaying parts accumulate, disintegrate but little in

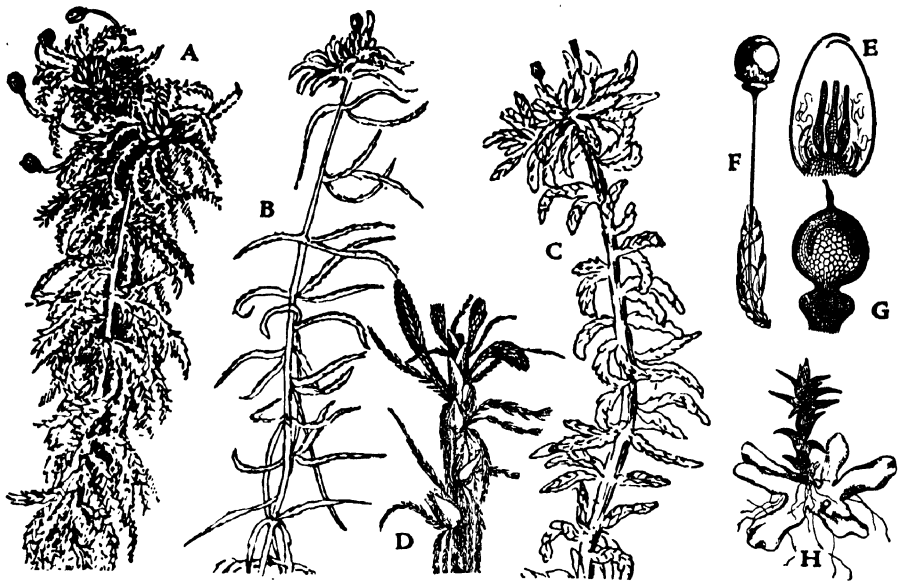

FIG. 299. Three species of *Sphagnum* (A-C), reproductive structures (D-G), and thalloid protonema with young leafy shoot (H). G represents the sporophyte stage, which consists of a sporangium and a very short stalk. The small urn-shaped bodies on A, B, and C are sporophytes.

the absence of oxygen, and become peat (Fig. 300). These mosses may also become established on the shore of a lake and gradually encroach on the water, forming a quaking bog. Creeping bogs may develop in very moist climates. The sphagnum mat grows out of the depression, invades forested land, and kills the trees by raising the water table and excluding oxygen from the tree roots. The characteristic genus of peat mosses is *Sphagnum*, more than 300 species of which have been described.

Mature peat mosses have no rhizoids, and absorption of water is direct. The upward movement of water is largely effected by capillarity through the closely adhering lateral branches and the compactness of the plant mass.

The rock mosses, *Andreaeales,* grow principally in arctic and alpine regions upon granite or slate. They are dark or almost black in appearance, have very brittle leaves densely aggregated, and are rarely more than an inch or two long. The gametophytes resemble the true mosses, while the sporophyte is supported by a pseudopodium as in the peat mosses. The capsule is unique among mosses in its longitudinal dehiscence by four valves when mature. There are approximately 120 species of rock mosses.



FIG. 300. Method of drying peat bricks cut from the black vertical wall in the foreground. Degermoor, Southern Bavaria.

The true mosses, or *Bryales*, consist of about 13,500 species classified among 80 families and 655 genera. This is the largest group of the mosses.

The liverwort plant. Two groups of liverworts are easily recognizable: the thalloid and the leafy forms. The thalloid species are easily distinguished from mosses by their irregular, leaf-like, much-branched vegetative body (Fig. 301). The *thalli* (sing. *thallus*) may be from one to several cell layers in thickness, and are sometimes dichotomously branched at short intervals. The middle line of the thallus is a groove in some species and has the appearance of a midrib, but no veins are present.

The leafy liverworts have flat shoots and the conspicuous leaves grow in two ranks. There is a third row of smaller leaves on the under side of the stem in many species. The leaves are entire, lobed, folded, or dissected.

Many of the thalloid liverworts, such as *Marchantia* (Fig. 302), have distinctly differentiated tissues. Above is an epidermis with open pores beneath which are cavities, or air chambers, containing tufts of erect green filaments. Photosynthesis occurs in these upper cell layers. Below are large, compactly arranged cells containing water; and extending from the lower epidermis are scales and one-celled rhizoids.

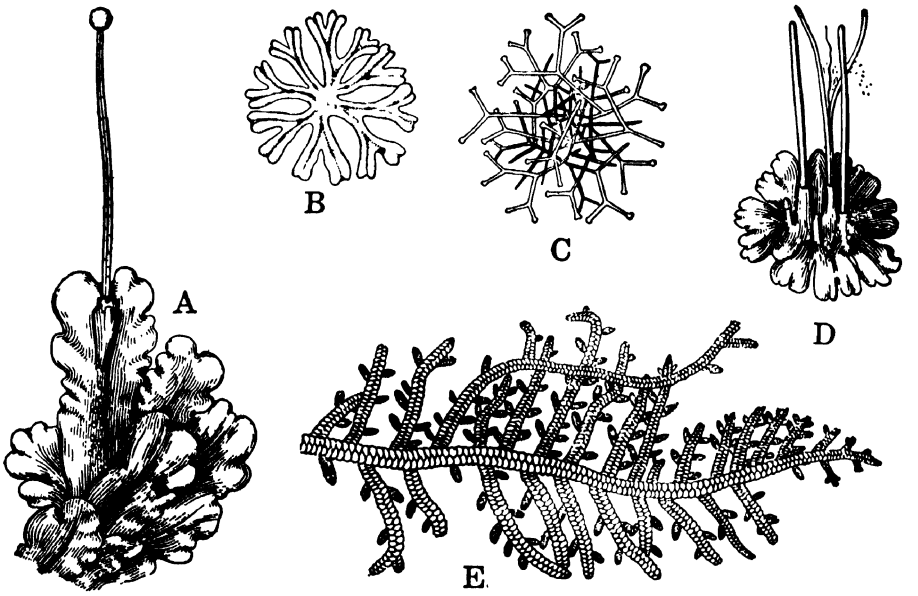

FIG. 301. Some widely distributed liverworts: A, *Pellia* thallus with antheridia (dots on surface) and a sporophyte; B and C, land and water forms of *Riccia*; D, archegonial thallus of *Anthoceros* with sporophytes; E, a portion of the thallus of *Porella*, a leafy liverwort. Courtesy of World Book Co.

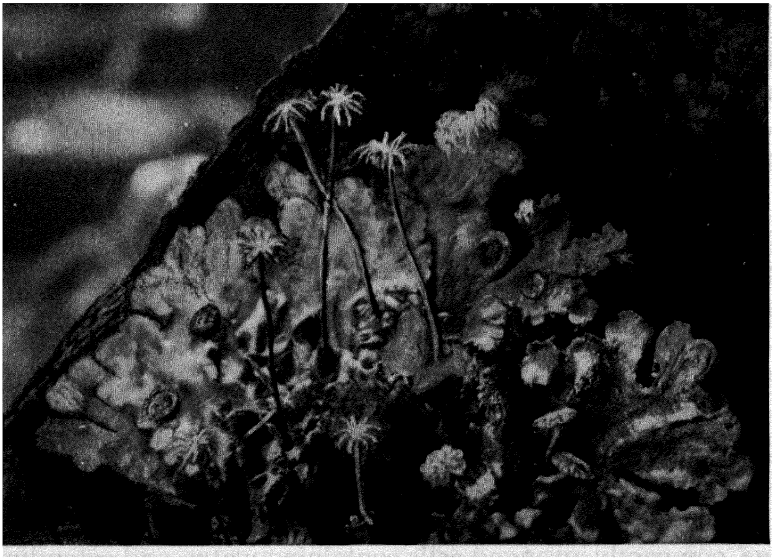

FIG. 302. *Marchantia* plants with archegonial and antheridial branches; cupules and gemmae also present. Photo by R. B. Gordon.

As an example of the foliose liverworts, *Porella* may be studied. It is common on tree trunks, on rocks, and even on walls of buildings. The novice often mistakes it for a moss. Its curved reclining stems bear three rows of flattened leaves, two on the dorsal side and one on the ventral side (Fig. 301E).

Vegetative propagation occurs in liverworts by fragmentation, by "brood bodies," and by gemmae formed in variously shaped gemmae-cups. These are small cup-shaped outgrowths from the upper epidermis of the thallus. From the bottom of the cup numerous upright fiddle-shaped green thalli develop. They germinate immediately when transported to the soil by rain or wind.

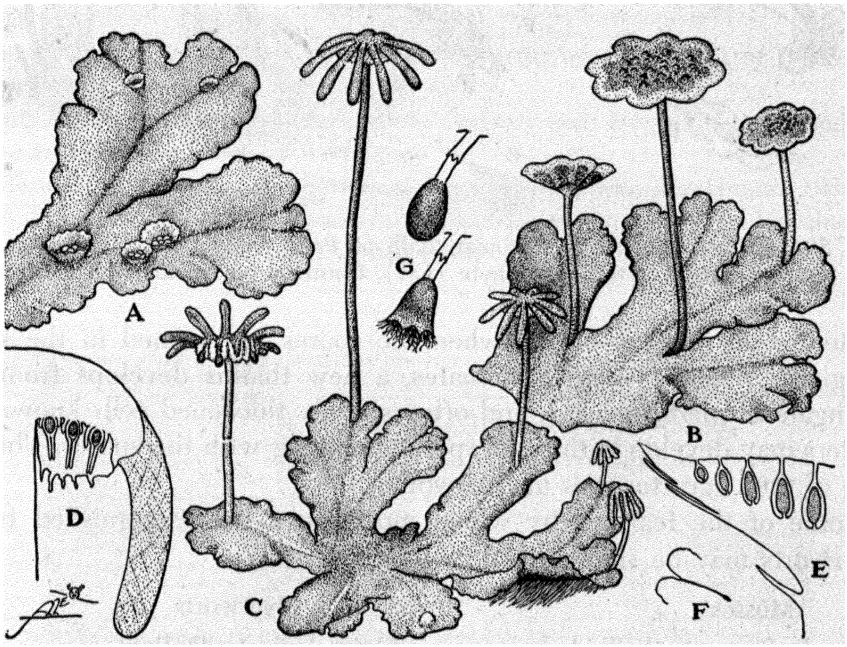

FIG. 303. Vegetative and reproductive structures of *Marchantia*: A, vegetative propagules, or gemmae, in cupules on a portion of a thallus; B, part of a male thallus with upright antheridial branches terminating in disk-like structures in which antheridia and sperms develop; C, a female thallus with upright archegonial branches terminating in radially branched structures in which archegonia and eggs develop; D, diagram of a vertical section of the apex of an archegonial branch to show location of the pendant archegonia; E, diagram of a vertical section of the apex of an antheridial branch to show location of antheridia; F, form of sperms; G, isolated sporophytes that have developed from fertilized eggs within archegonia represented in D. Elongation of the sporophyte stalk pushes the sporangium out of the archegonium, but the base of the stalk remains attached to the gametophyte as it does in mosses.

The parts of *Marchantia* and *Porella* just described are the gametophyte phases of these two liverworts. They bear archegonia and antheridia in which eggs and sperms are formed much as in the mosses. The sporophyte phase develops from the fertilized egg and is similar to the sporophytes of certain mosses (Figs. 303 and 304).

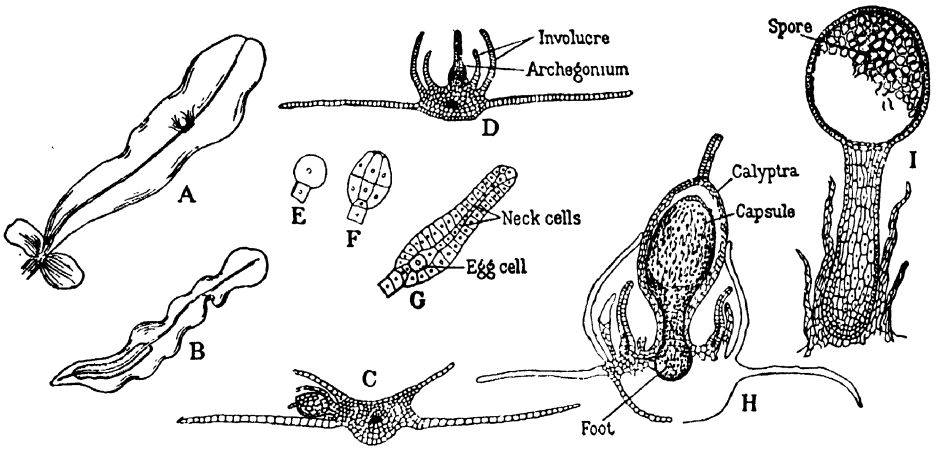

FIG. 304. Antheridial and archegonial thalli of *Pallavicinia* (A-B); stages in the development of the sporophyte (C-I). Courtesy of World Book Co.

Reduction division occurs when the spores are formed in the sporangium. When a spore germinates, a new thallus develops from it. Elongated, spindle-shaped, and often spirally thickened cells known as *elaters* may develop within the sporangia along with the spores. This is one of the characteristics of liverworts.

Some of the features by which mosses can be distinguished from liverworts may be summarized as follows:

Mosses	Liverworts
Stems leafy, never thalloid	Stems leafy or thalloid
Protonema present	No protonema
Many-celled branching rhizoids	One-celled rhizoids
Elaters absent from sporangia	Elaters present in sporangia

The hornworts. Some thalloid bryophytes, such as *Anthoceros* (Fig. 301D), have unique characteristics which distinguish them from other liverworts. They are known as *hornworts*, because of the horn-like appearance of the sporophytes. Cells of the structurally simple gametophytes usually contain a single large chloroplast, within which is an

evident pyrenoid. The cells of the capsule of the sporophyte do not all mature simultaneously, and the basal portion continues to grow after the apical portion has matured.

Some 320 species of thalloid bryophytes comprise the hornworts, which are considered by some botanists as a third group of bryophytes: the *Anthocerotae*.

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CHAPTER XLIX

FERNS, CLUB MOSSES AND EQUISETUMS (PTERIDOPHYTES)

Superficially the ferns, club mosses, equisetums, and quillworts may appear much too diverse in form to be classified within one group, known as the *Pteridophytes* (Gr. *pteris*, fern, and *phyton*, plant). The fundamental features of their life cycles, however, are quite similar, and are sufficiently unlike those of other groups of plants to warrant the consideration of them as a single group. Altogether about 10,000 species of Pteridophytes have been described and named, of which more than 9000 are ferns.

The Carboniferous forests 300 million years ago were dominated by hundreds of tree species of primitive Pteridophytes and Gymnosperms now extinct. The coal deposits of Pennsylvania were formed primarily



FIG. 305. Ferns (*Polystichum munitum*) often 4 feet in height in the moist forest region of the northwestern states. Photo by W. S. Cooper.

from the wood of these trees. These species have all become extinct, and only a few of the modern ferns are trees. Most of the modern Pteridophytes are small and comparatively inconspicuous except when they grow in masses. In the forests of today they are understory plants (Fig. 305), and are usually most abundant along stream banks, in open glades, in clearings made by man, or where the forests have been destroyed by storm and fire. In such areas some of the species reproduce so rapidly and grow in such dense masses that reforestation is greatly delayed. Some of these species also become troublesome weeds in pastures in moist climates. A few species are prized as decorative plants, and others are used in medicine.

The Ferns

Ferns grow in a great diversity of habitats. We usually associate them with shade, ample water supply, and warm temperatures. While in gen-



Fig. 306. A fern (*Asplenium*) widely distributed on rocks. Photo by C. H. Jones.

eral this is true, particularly for those of very rapid growth, ferns are not necessarily so restricted. Some species thrive in open fields and on dry hillsides, others on dry exposed rocks (Fig. 306), still others in marshes not especially shaded, and many in the forests of the tropics and semi-tropics as epiphytes (Fig. 307); a few are strictly aquatic. They are



FIG. 307. The largest known specimen of the staghorn fern, an epiphyte on trees in the tropics. Photosynthesis occurs chiefly in the upright leaves. The rounded leaves pressed against the tree cover masses of roots. Reproductive structures develop on the pendant leaves. The photograph was made on a small island near Brisbane, Australia, by C. J. Chamberlain. Courtesy of World Book Co.

*

reported from the frigid zone; but the number of species there, as well as of individuals, is small. As one goes from cool temperate regions toward the equator the number of species increases rapidly. Ferns attain their greatest size and variety in the moist tropics, where some of the species are trees. In warm temperate regions the largest and most striking ferns occur in swamps and in rich soil along streams. Most species of ferns grow in acid soils, but many of them grow on both acid and alkaline soils.

Geologically ferns are very old. Fossil remains of ferns are reported from the Devonian rocks, but their greatest abundance occurred during Carboniferous times. Some of the early ferns were trees, and some fern-like plants reproduced by seeds (Figs. 353, 355A, and 359).

Aside from their use as decorative plants, the commercial value of ferns is almost negligible. Certain species that grow in masses and invade bare soil areas contribute to soil development and the protection of soil from wind and water erosion. The young rhizomes of a few species are sometimes used as a source of food by animals and man; and the leaves have been used in the making of tea and liquors. The aquatic species are eaten by ducks, some fish, and by other water animals. The greatest common interest in ferns, however, is undoubtedly esthetic. They are cultivated for ornamental purposes, and the supply and sale of cut ferns have become an important industry.

The fern plant. Ferns are generally recognized by their leaves. They are the most conspicuous and characteristic parts of the plant and bear characteristic reproductive structures. They vary in length from an inch, or less, in the smallest species to 100 feet in species of climbing ferns. The spirally twisting petiole (rachis) of the climbing fern of the Eastern States seldom exceeds 3 feet in length. Some of the common ferns of temperate zones have a blade a yard or more in length supported by a prominent petiole often mistaken for a stem by the novice. Sessile leaves are rare among ferns.

The leaves may be simple, but they are more often compound. The leaflets of compound leaves may be further divided and dissected, resulting in a very complex frond.[1] The leaf develops from a primordium near the apex of the stem and, owing to slightly more rapid enlargements on the outer side, becomes coiled. As development proceeds, growth on the inner side catches up with the outer, and the apex uncoils (Fig. 308).

[1] Some writers use an entirely different set of terms to describe the parts of a fern plant: the leaves are called "fronds," the leaflets "pinnae," and the divisions of the leaflets "pinnules."

Leaves usually mature in one season, though in some species they grow for a period of three or more years.

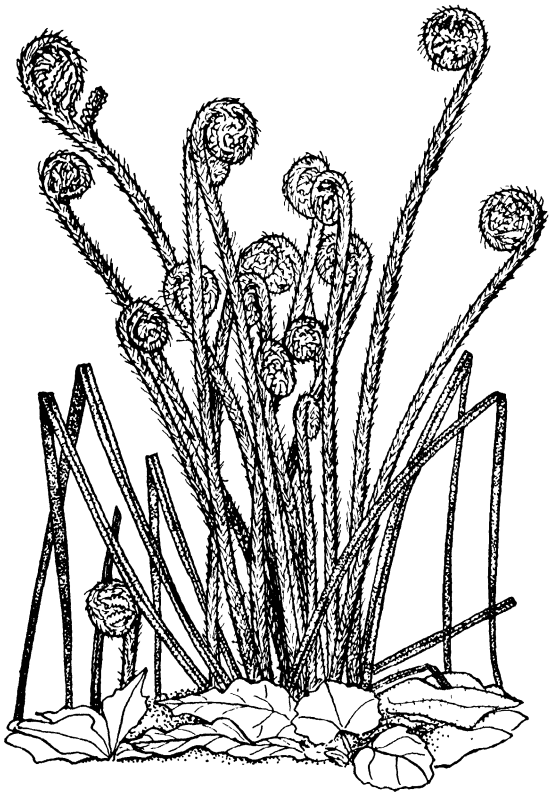

FIG. 308. Uncoiling of young leaves of cinnamon fern (*Osmunda cinnamomea*).

The characteristic venation of ferns is dichotomous, but there are all gradations from dichotomy to a very complex net arrangement that is better termed reticulate. The leaves of a few species are somewhat succulent and the venation is not easily seen. Most of our common ferns may be readily recognized, however, by their *dichotomous venation* and the uncoiling of their young leaves, known as *circinate vernation.*

The fern leaf is similar in structure to that of the seed plant. The epidermis is a definite layer with stomates usually on the under side of the leaf. Green plastids occur in the guard cells. The mesophyll is often not differentiated into palisade and spongy tissues. The leaflets of some of the filmy ferns are but a single cell layer in thickness. Structurally, the veins are quite like those of seed plants, and they are branches of the vein tissues of the stem and roots.

The stems of most ferns are horizontal branched rhizomes. They may

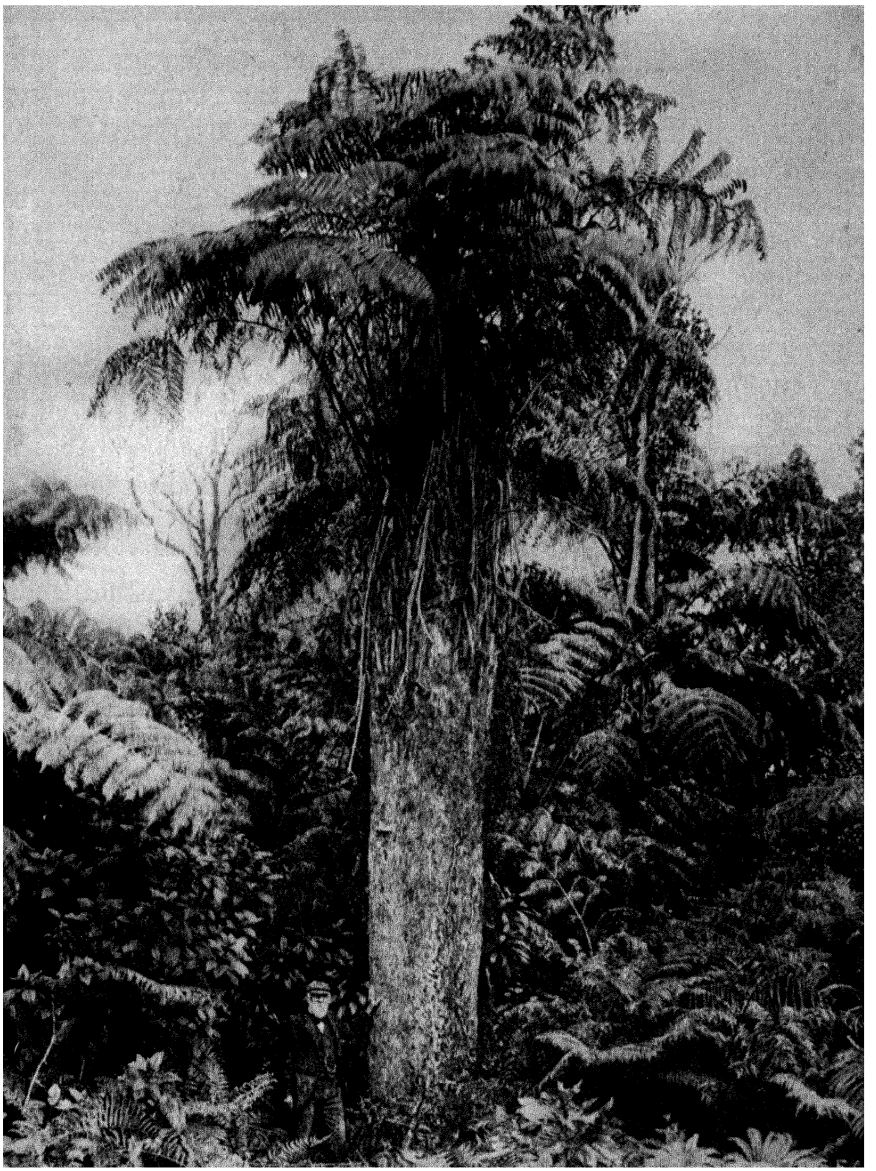

FIG. 309. The tree fern pictured here is in Hawaii and is 30 feet high and 3 feet in diameter. Photo from the U. S. Forest Service.

grow on the surface of the soil or below. The life duration of any part of a horizontal stem is relatively short, for the rhizome continues to elongate at the growing tip and die at the other end. A few of our common ferns, such as the cinnamon fern, have erect stems, sometimes extending a foot or more above the soil in swamps. The upright stems of tree ferns in the tropics may be 20 to 30 feet high (Fig. 309). Some ferns are epiphytes.

The ferns, in marked contrast to all bryophytes and thallophytes, have highly differentiated conducting systems with both phloem and xylem tissues. Special elongated cells known as tracheids are the fundamental structures of the xylem. Xylem tubes, or vessels, occur rarely. The phloem is composed of sieve tubes and phloem parenchyma. Cambium, though common in the fossil ancestors, is very rare in living ferns, having been found in only two genera. The "bundles" of xylem and phloem may be few and scattered, or sometimes numerous and arranged in a cylinder. Pith is absent in stems of some species and conspicuous in that of others. The cortex is usually prominent and may have several outer layers of thick-walled cells.

The roots of ferns in comparison to leaf surface are smaller, shorter, and less branched than the roots of seed plants. In the herbaceous ferns they originate adventitiously at the nodes and along the internodes of the rhizome. In the tree ferns the root systems are more complex, but they do not attain the size and spread of the root systems of seed plants. Their internal structure is quite similar to that of the roots of seed plants. Roots may be lacking in some aquatic species, and in the filmy ferns only rhizoids develop.

Ferns multiply vegetatively by means of their branching rhizomes, from which a succession of new leaves develops each season. New individuals may also develop vegetatively from adventitious buds (bulbils) on the surface or in the axils of the leaves of certain species. New plants of the walking fern develop from buds formed at the tips of the leaves in contact with the soil (Fig. 310). Some tropical species multiply vegetatively from the swollen leaf bases.

The sporophyte. The conspicuous fern plants described above are all sporophytes. They are much larger and far more complex than the sporophytes of the mosses and liverworts. Among the bryophytes the conspicuous phase in the life history is the gametophyte; among the ferns it is the sporophyte phase. The sporophyte of ferns has definite leaves, stems, and roots with a well-developed vascular system and other tissues comparable to those of seed plants.



FIG. 310. The walking fern (*Camptosorus rhizophyllus*). New plants develop vegetatively from buds at the apex of the leaf blades. Photo by R. T. Wareham.

Sporangia may develop on the under side of a green fern leaf (Fig. 311). They may occur in irregular lines or areas, or cover nearly the

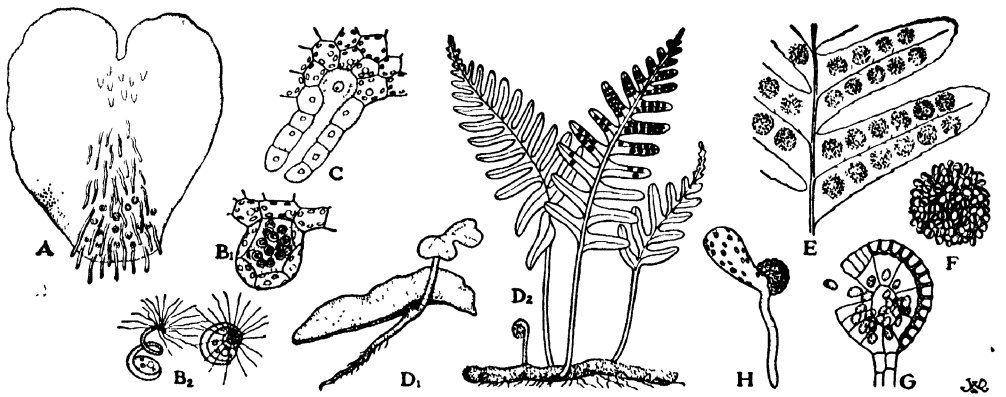

FIG. 311. The life cycle of a fern. The gametophyte (A) bears egg cells and sperms in archegonia and antheridia. When one of the sperms (B_2) from an antheridium (B_1) unites with an egg cell in an archegonium (C) a zygote is formed. From this zygote the sporophyte (D_1 and D_2) develops and bears spores in groups of sporangia (E and F) on the lower side of the leaves. By the bursting of a sporangium (G) the spores are set free. When these spores germinate (H) on moist substrates a new gametophyte, like the one represented by A, develops from each of them.

whole under surface of the leaf. The sporangia are often grouped in distinct clusters known as *sori* (sing. *sorus*). The sori may be located along the veins, at the ends of veins, or along the margin of the leaf. The shape, arrangement, and general appearance of the sori are commonly used in distinguishing different genera and species of ferns. They are usually covered by a delicate shield-like structure known as the *indusium* (Fig. 312).

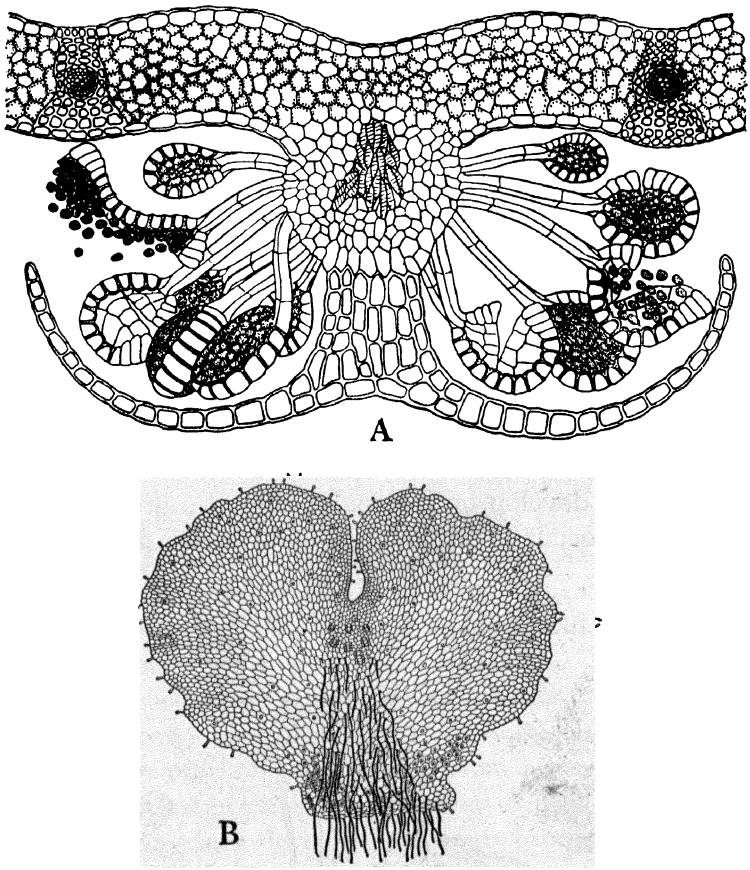

FIG. 312. Reproductive structures of a fern: A, section through part of a leaf and a sorus composed of a stalked shield, or indusium, which covers a cluster of sporangia in which numerous spores have developed; B, ventral surface of a bisexual gametophyte; the antheridia are near the bases of the rhizoids, the archegonia are just below the central sinus. B drawn by C. J. Chamberlain. *Textbook of Botany* (Coulter, Barnes, and Cowles), Amer. Bk. Co.

Species such as the cinnamon fern and sensitive fern have two kinds of leaves: the usual foliage leaf, and a smaller one on which sporangia

and spores develop. Such special spore-bearing leaves have been called *sporophylls*; and this term is applied to any spore-bearing leaf, whether of fern or of seed plant. Stamens and carpels of ordinary flowers and the scales of pine cones are often referred to as sporophylls. The cinnamon fern has cinnamon-colored sporophylls.

Fern sporangia develop at the ends of short stalks. The epidermis of the sporangium is composed of two kinds of cells: a single row of cells with walls greatly thickened inwardly (the annulus), and several larger thin-walled cells forming the remainder of the sporangium wall. Upon losing water the cells of the annulus contract, and the maturing sporangium splits open at the side. The number of spores in a sporangium ordinarily ranges from 32 to 64, but it may be higher in a few genera: 400-500 in *Osmunda,* the royal ferns; 1500-2000 in *Botrychium,* the grape ferns; and 12,500-15,000 in *Ophioglossum*, the adder's-tongue ferns. Many millions of spores may develop on one fern plant in a single season. The spores develop in tetrads following reduction division of the spore mother cells.

Familiar ferns include, besides the ones referred to above, the walking fern, *Camptosorus;* the common polypody, *Polypodium;* the maidenhair fern, *Adiantum;* the bracken fern, *Pteris;* the Christmas fern, *Polystichum;* and the sensitive fern, *Onoclea.*

The gametophyte. Under appropriate conditions the spores germinate either directly or after a short period of dormancy, and from each spore there develops a small heart-shaped thallus that superficially resembles a very simple liverwort. The first few cells form a filament that resembles an alga or a moss protonema; in a few species of fern the filamentous form is permanent. In most species, however, subsequent cell divisions result in a thallose structure. This structure, unnecessarily termed a *prothallus,* is the gametophyte of the fern. Thalli of ferns may be found growing naturally on moist rocks, on soil, and on decaying logs near the sporophytes. They grow readily from spores sown on culture media or on the surface of flower pots after the pots have been filled with sphagnum moss and inverted in a pan of water.

In two genera of ferns (the grape fern, *Botrychium* and the adder's-tongue, *Ophioglossum*) the gametophyte is quite unique. In *Botrychium* it is entirely subterranean and without chlorophyll; in *Ophioglossum* it is subterranean with green parts extending above the soil surface. In both, a fungus lives in the non-green part of the gametophyte and extends into the surrounding humus.

As the flat expanse of cells forming the fern gametophyte grows, rhizoids develop on the lower side; and soon afterward antheridia develop near them (Fig. 312). The antheridia are comparatively simple structures, with an external layer of several cells enclosing the sperm mother cells, in each of which one sperm develops. The sperms have a spirally twisted body with 40 or 50 long cilia. The archegonia develop as the gametophyte matures, and are also located on the under side near the notch or youngest part of the thallus.

Fertilization. The sperms are released by the swelling and bursting of the mature antheridium when water collects under the gametophyte. Under similar conditions the archegonium opens, and the products of the disintegration of the neck canal cells diffuse into the water. The sperms swim toward the regions of greatest concentration of these diffusing substances, and one of the sperms after entering the archegonium fuses with the egg cell, forming a zygote. When fertilization has taken place in one or two of the archegonia, the further development of the remaining archegonia of the gametophyte ceases. Consequently one sporophyte ordinarily develops from a zygote in each fern gametophyte, rarely two of them. If the young embryos of the sporophytes are removed as rapidly as they begin to develop, the fern gametophytes continue to grow vegetatively for years. Apparently a hormone-like substance formed in the young sporophyte inhibits not only the further development of other embryos, but also the further growth of the prothallus, or gametophyte.

Embryo of the sporophyte. The zygote germinates directly after fertilization. Cell division soon results in an embryo with four distinct regions: (1) the foot, or holdfast, by which the embryo is attached for a short time to the gametophyte; (2) a root tip, which rapidly elongates and penetrates the soil; (3) a leaf primordium, from which the first leaf of the sporophyte develops; and (4) a stem tip, which elongates slowly, and from which successive leaves and adventitious roots develop. The sporophyte is thus at first dependent on the gametophyte, but it soon becomes green and develops rapidly; and the thallus disintegrates. From the embryo the mature sporophyte grows.

Chromosome numbers. The cells of the sporophyte all have the diploid number of chromosomes. Reduction division occurs in the spore mother cells during the formation of spores in the sporangia on the leaves. These spores, the cells of the subsequent gametophytes, and the sperms and eggs have the monoploid number of chromosomes.

All the eggs and sperms formed in the same gametophyte have the same chromosome complement. If self-fertilization occurs, the resultant zygote and sporophyte will be completely homozygous. If reduction division is regular, all of the spores formed in this sporophyte will have the same chromosome complement; and so will all of the cells of all of the gametophytes that develop from these spores.

Mutation, hybridization, and parthenogenesis occur in ferns as in flowering plants. Changes in chromosome number in ferns, however, may also occur in another peculiar way. Gametophytes sometimes originate vegetatively from the diploid cells of the sporophyte; and sporophytes sometimes originate vegetatively from monoploid cells of the gametophyte.

Alternating phases in the life cycle of plants. In the life cycle of many algae, and of all bryophytes, pteridophytes, and seed plants, a diploid spore-bearing phase, the sporophyte, ordinarily alternates with a monoploid gamete-bearing phase, the gametophyte. In the ferns and brown algae either phase may continue to multiply vegetatively. In the bryophytes and such algae as *Oedogonium*, vegetative multiplication is limited largely to the gametophyte, while in the seed plants it usually occurs only in the sporophyte. There are no alternating phases in the blue-green algae.

The sporophyte phase of seed plants, pteridophytes, and brown algae is the conspicuous one. The gametophyte phase (pollen and embryo sac) of the seed plants and of some of the pteridophytes is very small. The gametophyte phase of the bryophytes is the conspicuous one, and the smaller sporophyte phase is wholly or partially dependent upon it as a source of food.

The gametophyte phase of the seed plants develops within the megasporangium (ovule), whereas that of non-seed plants develops on the soil or in water. The first step in the formation of seeds is the germination of the spores within the sporangia of the sporophyte. If these spores fall upon the soil, no seeds are formed. Some of the ancient ferns had seeds, and some of the modern pteridophytes occasionally have seeds or structures closely resembling seeds.

The aquatic ferns. The water ferns constitute a small group consisting of four genera that are considerably unlike the plants so far described in this chapter. *Salvinia* and *Azolla* are floating, while *Marsilia* and *Pilularia* are rooted at the bottom of small ponds or sluggish streams. *Salvinia* has a whorl of three leaves at each node, two of which are

floating, hairy, entire leaves; the third leaf looks much like a branched root. Stems and roots are more conspicuous in *Azolla*. The other two genera are larger plants with prominent leaves from rhizomes rooted in the mud below the water. Superficially the leaves of *Marsilia* resemble a four-leaved clover; those of *Pilularia* resemble leaves of grasses.

Two kinds of spores develop in the water ferns: microspores and megaspores. Male gametophytes develop from the microspores, and female gametophytes from the megaspores. Plants that bear both microspores and megaspores are said to be *heterosporous* (different spores), in contrast to *homosporous* plants in which the spores are all alike and the gametophytes that develop from them are bisexual.

The Lycopods or Club Mosses

The club mosses are relatively small in size, frequently evergreen, and flourish especially in the tropics. The common name refers to their



Fig. 313. One of the common club mosses (*Lycopodium complanatum*). The plant pictured here is the sporophyte phase. The sporangia are borne in the terminal cones. Photo by E. S. Thomas, Ohio State Museum.

moss-like leaves and club-shaped cones. The upright appearance of some species is that of a small pine tree; hence the name "ground pine." Species of the two genera, *Lycopodium* (Fig. 313) and *Selaginella*

(Fig. 314), also grow in temperate climates, and as far north as Newfoundland and Labrador. They are much more abundant in the northern conifer forests than in the deciduous forest of the Central States. The tropical species are frequently epiphytic. Many of the species have long

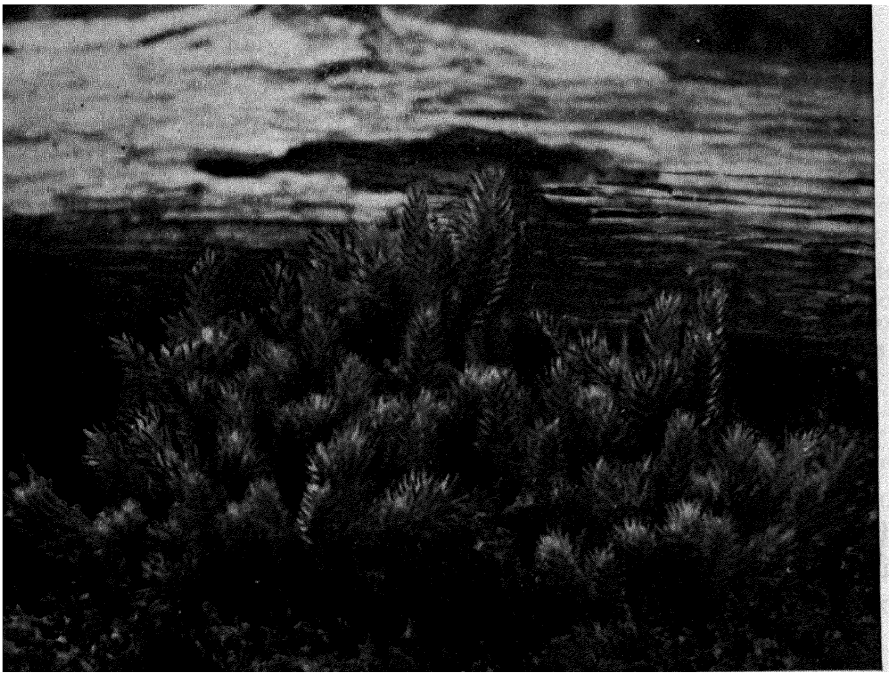

FIG. 314. A club moss (*Selaginella rupestris*) widely distributed on dry rocks. The half-decayed branch in the background is 3 inches in diameter. Photo by E. S. Thomas.

creeping stems; in others the stems are erect. The stems usually branch dichotomously. Most of the species are perennials, but a few of the smaller ones are annuals.

Some species of *Selaginella* grow in dry climates. During the rainy seasons the numerous stems are spread out in the form of a dense rosette. During dry weather the stems curve upward and inroll toward the center of the plant, with the result that the whole plant has the form of a ball and may be blown about (Fig. 315). When moisture is again available, the stems unroll and new roots grow. Such plants are the so-called "resurrection plants." The plant rolls and unrolls even when dead.

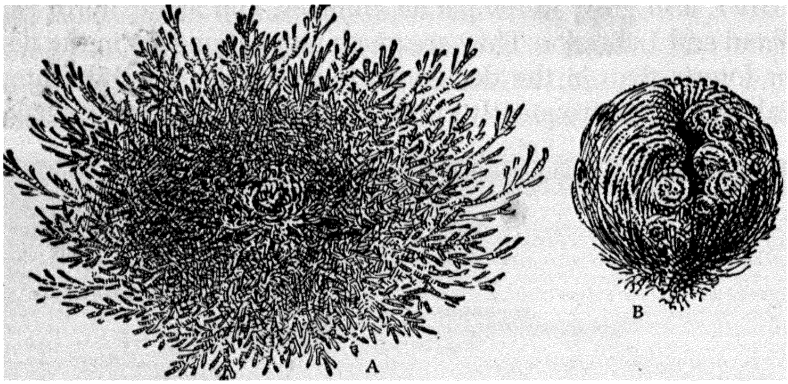

FIG. 315. Resurrection plant (*Selaginella*) of Texas and New Mexico. During the rainy season the plant spreads out and grows as a rosette. When drought comes, it dries out and curls up into a ball, as indicated at the right. Courtesy World Book Co.

Fossil records of the ancestors of the lycopods are very abundant in Carboniferous rocks. From them it is evident that during this period hundreds of species of club mosses were dichotomously branched trees up to several feet in diameter and a hundred or more feet in height. The leaves were somewhat scale-like, arranged in spirals or in whorls, and often a half-foot long. The number of species of present-day lycopods, all of which are small plants, is estimated at about 600.

The sporophyte. Both *Lycopodium* and *Selaginella* consist of a much-branched, creeping or erect stem, practically covered by small scale-like leaves attached by a broad base. The adventitious roots are filiform and develop from the under side of the stem in contact with the soil or in moist air. Both the stems and leaves have a fundamental structure similar to that of seed plants. The more primitive species have rather large sporangia in the axils of leaves; in the more specialized types the sporophylls are small, often non-green, and arranged in compact cones at the ends of upright branches (Fig. 316).

In *Lycopodium* four spores develop in each of the mother cells in the sporangium, and all the spores are alike morphologically and physiologically. Consequently *Lycopodium* is said to be homosporous. In *Selaginella* the spores are of two kinds formed in different sporangia. The small spores (microspores) develop by the hundreds in small sporangia (microsporangia), and four large spores (megaspores) develop in each large sporangium (megasporangium). *Selaginella* is thus heterosporous.

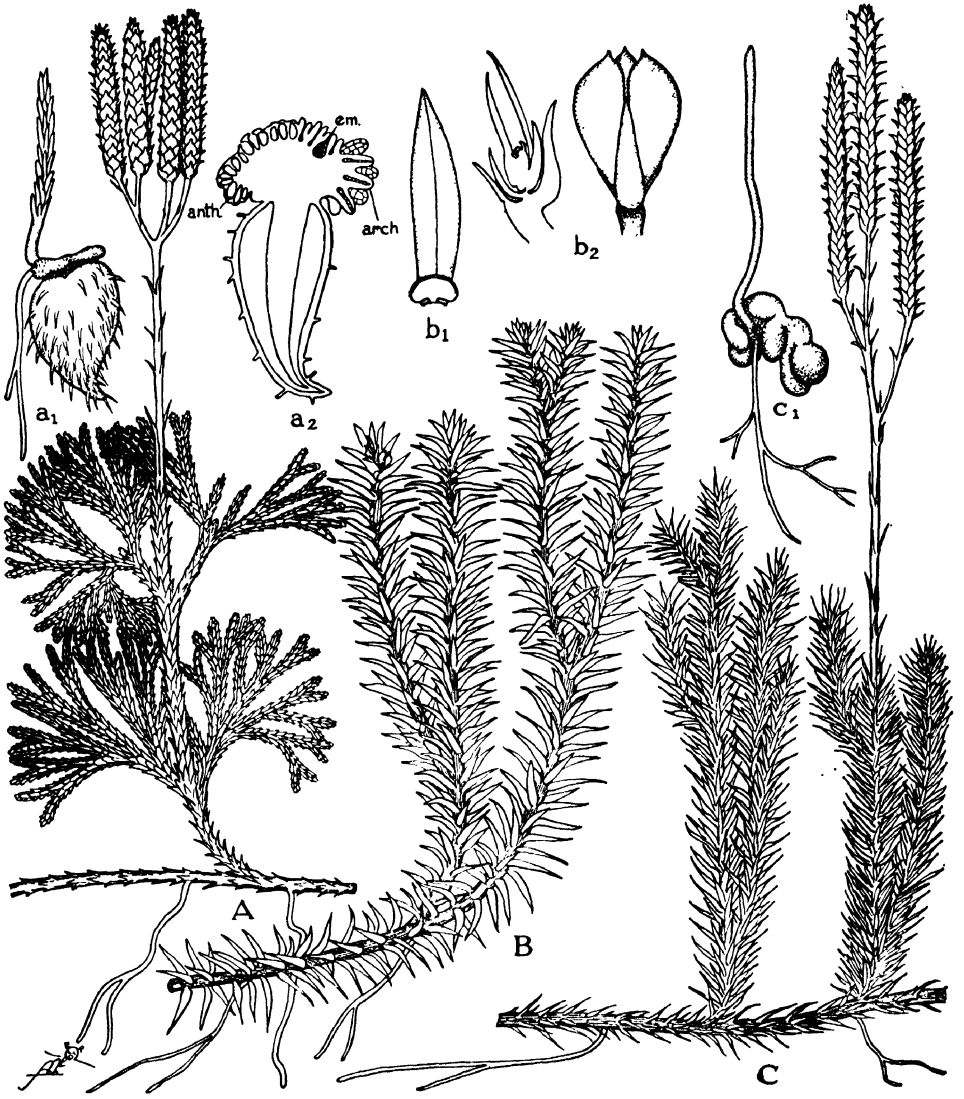

FIG. 316. Three species of *Lycopodium*: A, *L. complanatum* with gametophyte (after Bruchmann); B, *L. lucidulum* with sporangium (b_1) and vegetative propagules (b_2); C, *L. clavatum* with gametophyte (c_1).

The relative size of the two kinds of spores is perhaps insignificant, for in equisetums the spores are indistinguishable, and in some seed plants the microspores are larger than the megaspores. The significant fact is that in *Selaginella* the gametophytes resulting from the germination of the spores bear either archegonia or antheridia, but not both. A thallus bearing only one kind of gamete is *unisexual;* one bearing both kinds is ***bisexual.***

The gametophyte. From the germinating spore of *Lycopodium* cylindrical, tuberous, or fleshy thalloid gametophytes develop, either underground and without chlorophyll, or partly aboveground and green (Fig. 316). They are thus partly saprophytic or parasitic on fungi. These gametophytes are very minute, rarely more than a few millimeter in length. The antheridia and archegonia are borne at the apex of the gametophytes. The sperms are straight, uncoiled, and biciliate. Fertilization of the egg by the sperm occurs in the same manner as in ferns.

As noted above, two kinds of gametophytes develop from the spores of *Selaginella*. Male gametophytes develop within microspores, and

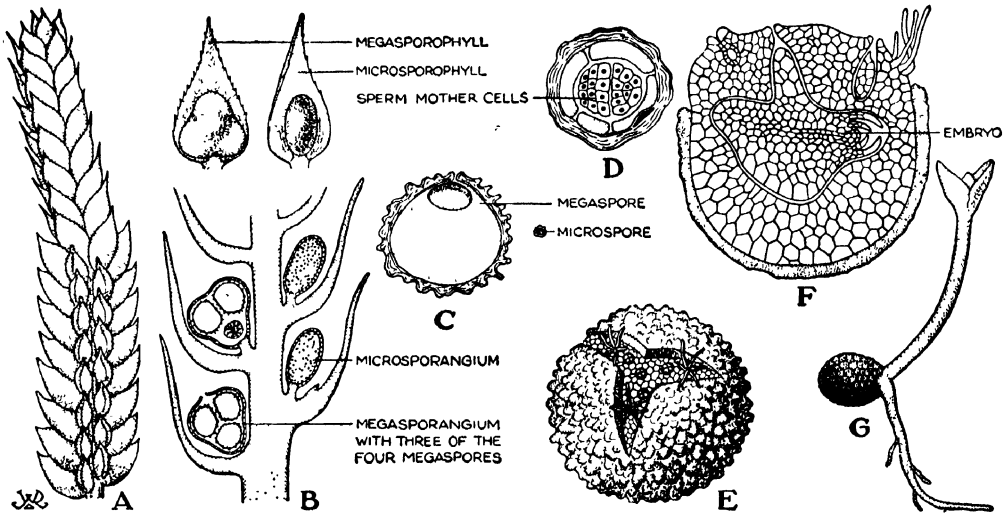

FIG. 317. *Selaginella:* A, vegetative branch with terminal cone; B, longitudinal section of a cone with megasporangia and microsporangia; C, relative sizes of megaspores and microspores; D, male gametophyte with sperm mother cells seen in section; E, female gametophyte with apical cells of 4 archegonia and 3 groups of rhizoids partly enclosed by spore wall; F, section of E with two sporophyte embryos; G, young sporophyte, the beginning of a leafy plant with branches similar to A. C and D after F. M. Lyon, E and F after H. Bruchmann.

female gametophytes develop within the megaspores. Both the male and the female gametophytes are small and are largely contained within the old spore walls (Fig. 317). The male gametophyte consists of a vegetative cell and a single antheridium. The sperms formed are few in number and are similar to those of *Lycopodium*. The female gametophyte is multicellular and at first is contained within the megaspore. Subsequent

growth bursts the spore wall, and part of the gametophyte protrudes. The archegonia develop on the apical segments that extend beyond the spore wall. Fertilization takes place as in ferns.

Germination of the zygote begins at once. The early stages of the developing embryo occur within the walls of the megaspore. Later the partly formed embryo continues growth on the soil or other substrate. These gametophytes are among the smallest found in pteridophytes, and are somewhat similar in size to those of seed plants.

Seeds. Occasionally a megaspore of *Selaginella* germinates within the megasporangium, in contrast to others that fall out of the sporangium and germinate on the soil. Consequently the female gametophyte with its archegonium and egg is inside the megaspore wall within the megasporangium. Fertilization may take place, followed by the development of an embryo sporophyte within these structures. These phenomena occur rarely in *Selaginella,* but when they do occur a seed is the result. *The seeds of pine and all other gymnosperms are formed in this same manner.* A seed is merely the result of the germination of the megaspore within the megasporangium or ovule, and the formation of the gametophyte and of a new sporophyte within the megasporangium. If the spores fall out of the sporangium and germinate on the soil as they ordinarily do in mosses and ferns, no seeds are formed.

The quillworts. This group of unique plants is quite unlike any other pteridophytes. Approximately 60 species of quillworts have been described and named, and all of them belong to the genus *Isoetes.* They have the general appearance of a small tufted rush and grow on muddy flats or in the water. They are perennial, and native to north temperate regions. The plant has a bulb-like axis consisting of an upper leaf-bearing part and a lower part from which lateral roots grow. The leaves are narrow and grass-like, with a bulbous clasping base, rarely more than a few inches long. *Isoetes* and the grape fern, *Botrychium,* are the only modern pteridophytes in which the stem uniformly has a cambium. Each leaf of *Isoetes* is a potential sporophyll. The plants are heterosporous, and as many as 300 megaspores or 300,000 microspores may be formed within a single sporangium. The sperms are multiciliate, but the other reproductive structures are similar to those of *Selaginella.*

The Equisetums

The equisetums constitute another small group of about 25 living species that superficially bear little resemblance to the ferns. Their life

cycles, however, are very similar. Like the ferns and lycopods, they are the modern descendants of an ancient phylum of plants. During the Carboniferous period equisetum-like plants with trunks 90 feet in height and 3 feet in diameter formed extensive forests. Fossil equisetum-relatives have been found also in rocks of the Devonian age. The modern species are usually less than 3 feet high, although there are two tropical species that may grow to a height of 10 or 15 feet, and a South American species that is said to attain a height of 40 feet when partly supported by trees.

Equisetums occur today in the tropics and semi-tropics, and in the temperate and arctic zones. None has as yet been reported from Australia or New Zealand, from the islands of the Indian Ocean, or from Antarctica. The plants grow best in mildly acid habitats; in the north they are likely to be found in peat bogs. Elsewhere they are found generally in sandy areas, particularly along streams and rivers, or where there is an underground source of water. One species, *Equisetum kansanum,* is found in prairie patches and the more moist situations of the plains.

The horsetails—or scouring rushes, as they are often popularly called —have columnar, upright, jointed stems, externally fluted and internally characterized by long, tubular air cavities. The central axis of the young stem is pith, but this soon disappears, and the older stem is hollow. Laterally fused colorless scales occur in whorls at the nodes (Fig. 318). Photosynthesis takes place in the chlorenchyma of the stem. Some of the ancient fossil species had true foliage leaves. Stomates occur regularly in the furrows of the stems, and their arrangement is used in the classification of the various species.

The name horsetail is probably suggested by the brush-like character of the numerous slender whorled branches occurring on the upright stems of a few species. The name scouring rush refers to the accumulation of silica in the walls of the stem tissues. In pioneer days these were gathered and used for scouring metal utensils. The roots are small and adventitious, and arise along the perennial rhizomes, mostly at the nodes.

The sporophyte. The plant described above is the sporophyte phase of *Equisetum.* It is perennial, although the erect aerial branches may be annual. The peculiar shield-shaped sporophylls are arranged in whorls within a terminal cone and each bears five to ten sporangia.

Within the sporangia are numerous spores which are peculiar in having four long appendages that coil around the spore when moist and



FIG. 318. Three widely distributed species of *Equisetum*: A, *silvaticum;* B, *hiemale;* and C, *arvense;* D and E, underground tubers; F, spores with appendages; G, prothallus with four young sporophytes.

uncoil when dry. The spores contain chlorophyll, are short-lived, and cannot withstand desiccation. Consequently, they survive longest and germinate best on shaded moist banks.

The gametophyte. The gametophytes of equisetums are irregularly lobed, thalloid structures growing on moist substrates near streams or in bogs. The spores from the sporangia are essentially alike in appearance, and the gametophytes of most species, if not all, are potentially bisexual. But the expression of sex in bisexual gametophytes is influenced by environmental factors, and may be controlled by experimental conditions. Some species such as *E. arvense,* which may be bisexual under certain conditions, are usually unisexual. Archegonia usually develop on the larger gametophytes, and antheridia on the smaller ones. Fertilization takes place when a motile sperm fuses with an egg. The resulting zygote germinates at once, and an embryo sporophyte is formed.

Summary. The ferns, club mosses, quillworts, and equisetums are classified in one group, the pteridophytes. The sporophyte of these plants, in sharp contrast to liverworts and mosses, has a vascular system and is much more conspicuous than the gametophyte. The vegetative phase of the sporophyte generally consists of definite leaves, stems, and roots; but modern pteridophytes rarely bear seeds. The gametophyte is generally thalloid; it may be wholly green and grow on the soil or in other moist situations; it may be subterranean, devoid of chlorophyll, and hence saprophytic; or it may be partly green and partly non-green. The terrestrial ferns and the lycopods bear one kind of spore only (homospory); aquatic ferns and *Selaginella* bear microspores and megaspores (heterospory). The spores usually germinate on the ground or in the water, resulting in the formation of a gametophyte separated from the sporophyte. The megaspore of *Selaginella,* however, sometimes germinates in the megasporangium. This is a step in a series of events that leads to the formation of a seed. Geologically the pteridophytes are very ancient.

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CHAPTER L

THE SEED PLANTS

(SPERMATOPHYTES)

In most places throughout the world the seed plants constitute the conspicuous part of the land flora. They may be magnificent trees over 300 feet high with trunk diameters of 25 to 50 feet. They may be vines that climb to the tops of the tallest trees, or that extend horizontally for distances approaching a quarter of a mile. The majority

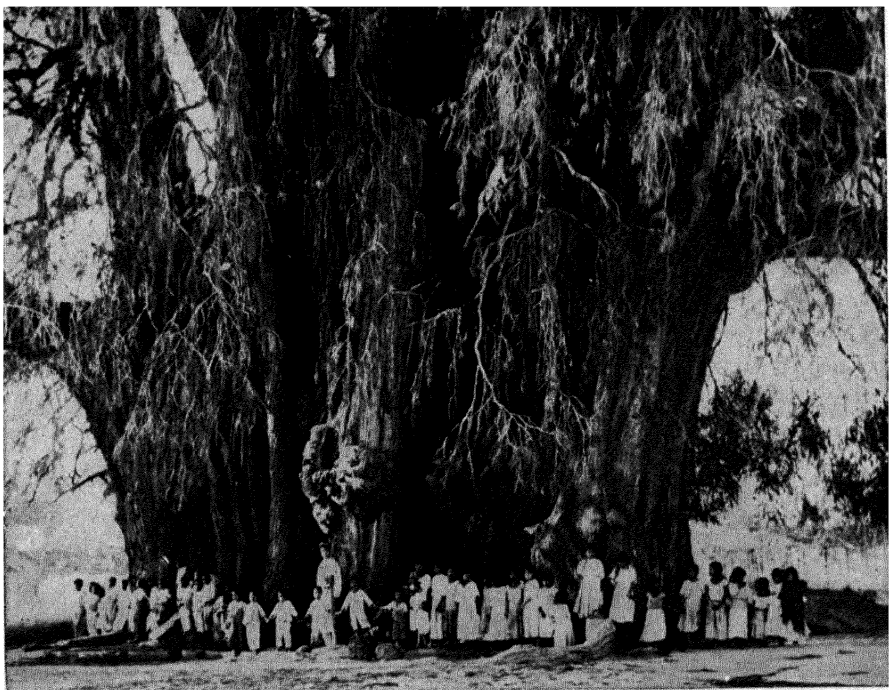

FIG. 319. The longest diameter of this largest cypress (*Taxodium mucronatum*) is more than 50 feet. This tree is in a churchyard in the village of Santa Maria del Tule, Oaxaca, Mexico. Photo by Don Glassman. Courtesy of New York Botanical Garden.

of the seed plants are herbs, commonly less than a few feet in height and rarely over 25 feet. The smallest seed plant known is a floating duckweed (*Wolffia*) scarcely more than 1/20th of an inch in diameter.

Many seed plants complete their life cycles in a single season, others in 2 to 30 seasons; the remainder flower annually over a long period of

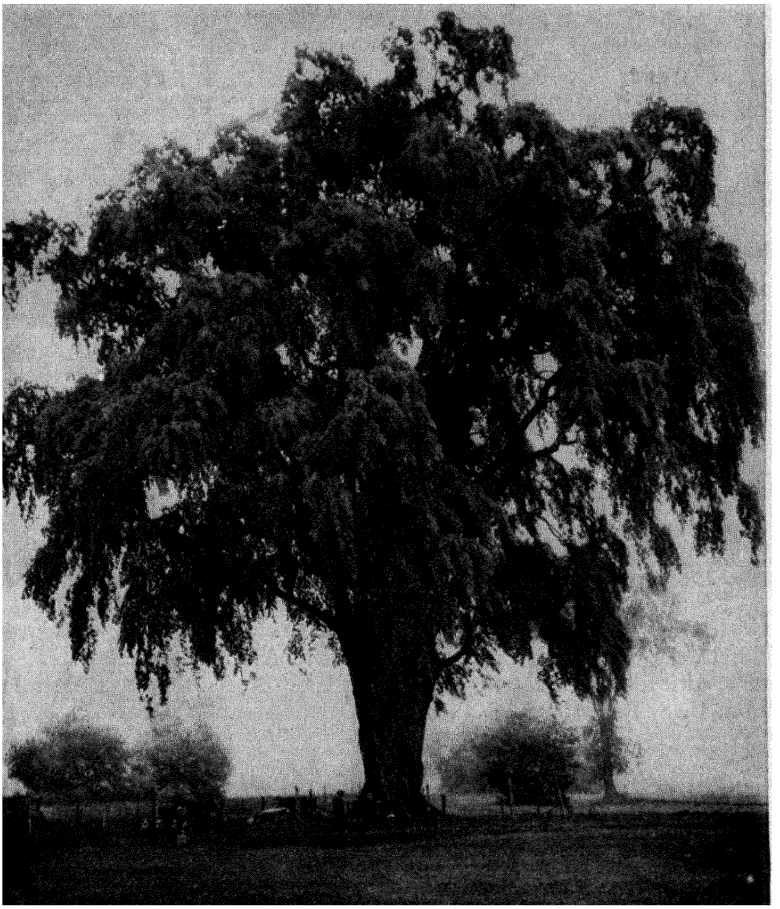

FIG. 320. A large American elm at Lancaster, Massachusetts.

years. The oldest living things on earth are trees. The Big Cypress Tree of Tule (Fig. 319) and the giant sequoias of California have lived for 3000 to 4000 years. Elms (Fig. 320) and maples rarely live longer than 300 years, oaks 500 years, and Douglas fir and western arbor vitae 700 to 800 years.

Seed plants are by no means restricted to land habitats; but if aquatic they are generally confined to shallow waters of swamps and marshes and along shores of lakes and rivers. They never grow in the open waters of oceans or deep parts of lakes. Many flowering plants cannot survive in deserts, but a few species grow in the most arid regions on the continent. They are absent from polar areas and alpine heights that are covered by ice and snow most of the year (Fig. 321).

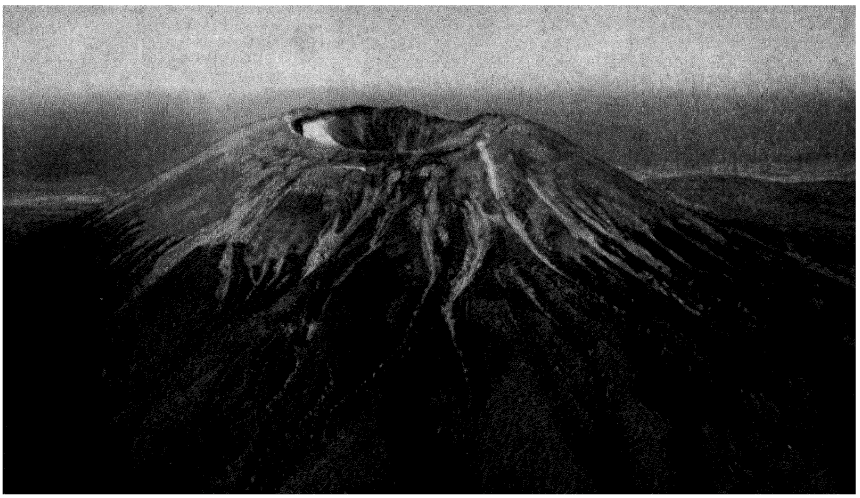

FIG. 321. Timberline on Mt. Edgecumbe, near Sitka, Alaska. Note valleys and avalanche tracks. Below timberline is the hemlock-Sitka spruce forest; above is the tundra. Altitude of mountain, 3,465 ft. Alaskan Aerial Survey Expedition, 1929. Photo from U. S. Forest Service.

The spermatophytes may be distinguished from all other plants by the formation of pollen tubes and seeds. They are either gymnosperms or angiosperms. The seed of the gymnosperm is usually not enclosed by any tissue corresponding to the carpel, and is said to be exposed or naked. The seed of the angiosperm on the other hand is surrounded by carpels.[1]

The gymnosperms are represented by the palm-like cycads (Fig. 322), the *Ginkgo* (Fig. 323) with its dichotomously veined leaf, the shrubby *Ephedra*, the shrubby or vine-like *Gnetum*, and the more common

[1] The so-called berries of cedars, yews, and arbor vitae which are gymnosperms superficially resemble fruits. Certain buttercups which are angiosperms have seeds incompletely enclosed by carpels.



FIG. 322. Cycads (*Cycas revoluta*) in a temple garden in Chimizu, Japan. From Wieland's *American Fossil Cycads*, photo by Chicago Natural History Museum.

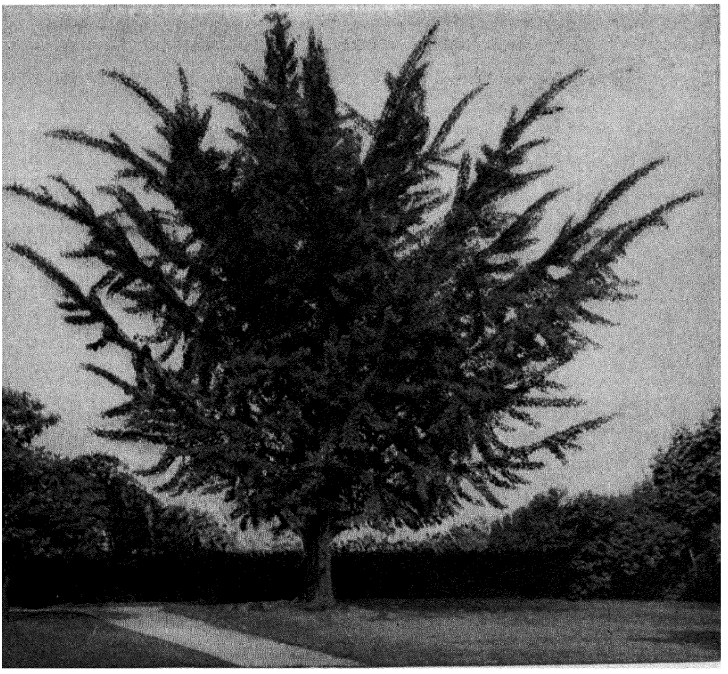

FIG. 323. Ginkgo tree, now native only in China. In former geological periods there were several species of ginkgo widely distributed in North America.

conifers, such as the pine, spruce, hemlock, cedar, sequoia, and auracaria. No herbaceous gymnosperms are known. The angiosperms may be herbs, shrubs, or trees, and are classified as monocots and dicots. The gymnosperms will be described first.

The Gymnosperms: Conifers

The gymnosperms are woody perennials, and nearly all of them are evergreen. Of the approximately 650 species, about 450 are conifers, among which are the oldest and largest of living plants. They are widely distributed from the tropics to the tundra border and the tree line on mountains. In contrast to the pteridophytes they bear seeds, have deep and well-developed root systems, much-branched stems, and extensive leaf surfaces. The buds of conifers are scale-covered; they may be dormant or grow similarly to those of angiosperms. The pine may be used to exemplify the life cycle of the group.

The pine sporophyte. The pines are generally recognized by their excurrent branching, needle-like leaves usually in clusters of two to five

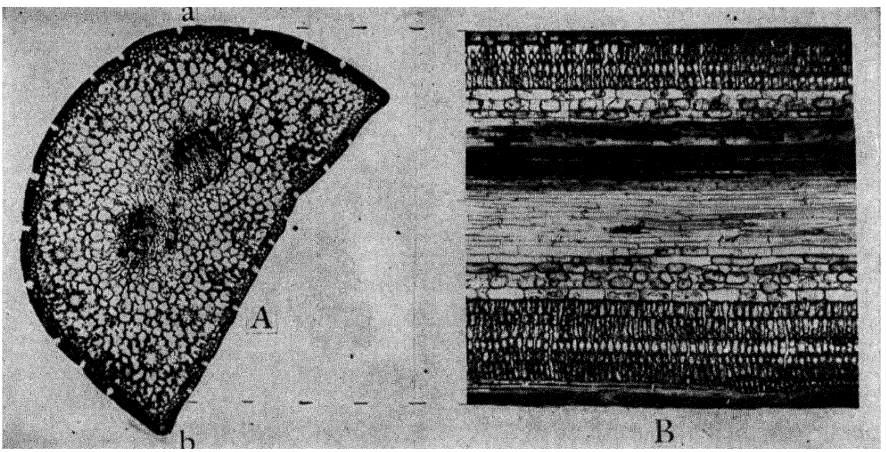

Fig. 324. Cross and longitudinal sections of an Austrian pine needle. An endodermal sheath one cell thick surrounds the centrally located veins. The chlorenchyma, in which several resin ducts occur, is composed of peculiarly lobed cells. The stomates are in pits, which are bordered by sclerenchyma, located just beneath the epidermis. Section B was cut in the plane a-b of section A.

on dwarf branches, and their evergreen habit. Leaves may remain on the tree from 3 to 15 years, but their photosynthetic value decreases rapidly with age. The linear leaves have a thick cuticle, sunken stomates,

and two or three rows of sclerenchymatous cells beneath the epidermis (Fig. 324).

The stem of the pine is quite similar to a woody dicot (Chapter XXVII) except for the absence of xylem vessels. The pine tree with its leaves, branched stem, and root is the sporophyte.

The sporophylls of the pine are spirally arranged in *cones* or *strobili* (sing. *strobilus*). The cones are of two kinds: *staminate* and *ovulate*, both occurring on the same plant (Fig. 325).

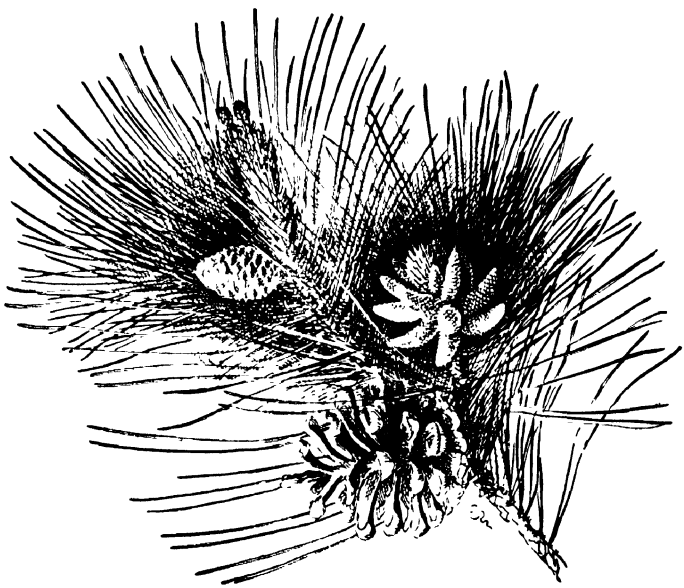

FIG. 325. Diagram of a branch of Austrian pine in June. At the tip of the youngest stem segment are two small ovulate cones. At the tip of the next stem segment is a one-year-old cone, and below it is a two-year-old ovulate cone. On the branch to the right is a cluster of staminate cones.

The staminate cone. The staminate cones are comparatively small and develop in clusters near the base of the new stem soon after the beginning of the growing season. They live for a few weeks only, and wither and fall from the tree after the pollen is shed. The cone consists of an axis on which membranous cone scales, or "microsporophylls," are arranged spirally. Each microsporophyll contains on the under side of its scale-like portion two microsporangia (pollen sacs). Within the microsporangia are the microspores which later become pollen grains.

Microspore mother cells are formed in the scarcely differentiated

cones in the terminal buds, sometimes as early as the autumn preceding the spring in which the cones mature. Early in the spring the tetrad of microspores is formed from the mother cell, and the number of chromosomes becomes monoploid. At first the microspore is a cell with a single nucleus. It germinates about a month before the pollen is shed, and ordinary cell division results in a generative cell and a tube cell.[2] The outer spore wall of the pollen grain has by this time enlarged and become separated from the inner wall, forming two balloon-like sacs. The cells within the pollen constitute the male gametophyte of the pine.

Pollination. At this stage the pollen sacs dehisce and the released pollen grains are blown about by the wind. Pollen grains are formed in prodigious numbers, and their yellow color gives the soil and objects nearby the appearance of having been sprinkled with powdered sulfur. A few of these pollen grains fall upon the ovulate cones in which the cone scales are at this time somewhat separated, and some of them come in contact with the megasporangia.

The ovulate cone. The larger, or ovulate, cones develop singly or, more often, two or three close together near the upper end of the new stem segment. Each cone consists of an axis upon which the cone scales, or "megasporophylls," are spirally arranged. The sporophylls of the young cone are small green scales that enlarge and become woody at maturity. The ovulate cones remain on the trees for nearly two years and on the trees of some species indefinitely.

Each megasporophyll has on the upper side of its scale-like portion two megasporangia or ovules. The ovule consists of an oval body of tissue (nucellus) enclosed by a single integument containing an opening (micropyle) near the base of the sporophyll.

In each ovule of the very young ovulate cone a megaspore mother cell becomes differentiated, and upon two successive divisions there result four megaspores arranged in a row. Reduction division occurs when the spore mother cell divides. Each megaspore has the monoploid number of chromosomes. The megaspore most distant from the micropyle enlarges as the other three disintegrate, and later the female gametophyte develops from it within the ovule.

Gametophytes and fertilization. Pollination occurs in May or June

[2] The nucleus of the microspore first divides into two *vegetative nuclei*, one of which is the forerunner of the antheridial cell in the mature pollen. When the pollen germinates the antheridial cell divides, and in one of the two daughter cells two sperms are formed.

about the time the megaspore is developing within the nucellus. Soon after pollination, the scales of the ovulate cone close and the whole cone becomes inverted. Sometimes the outer surface of the cone is practically sealed by exuded resin.

There is little development of the male gametophyte during the rest of the year, except the formation of a very short pollen tube from each pollen grain. The tube does not grow through the nucellus until the following spring, although the distance is extremely short. In the meantime the generative cell has divided into two cells, one of which divides and forms the two sperms.

During the first year the megaspore germinates inside the ovule and from it there develops a body of tissue often called "endosperm."[3] This body of tissue is in reality the female gametophyte. At the end of the gametophyte nearest the micropyle two or three archegonia develop

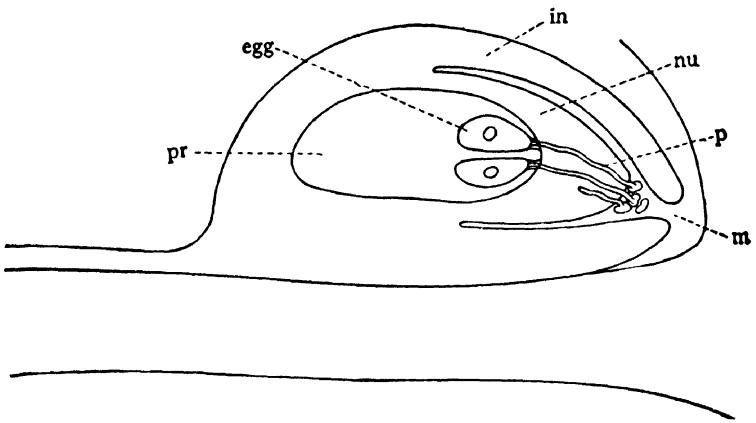

FIG. 326. Diagram of a vertical section of a pine ovule and the scale to which it is attached and of the male and female gametophytes at the time of fertilization: *pr* represents the prothallus with two archegonia; *in* represents the integument, *nu* the nucellus, *m* the micropyle, and *p* pollen tubes, two of which have reached the neck cells of the archegonia. Redrawn from Strasburger.

(Fig. 326). When mature, each archegonium consists of eight small neck cells, a ventral-canal cell, and an egg. When the pollen tube grows between the neck cells to the egg, it swells and bursts and the two sperms are discharged. One sperm disintegrates and the other fuses with the egg.

The fertilized egg or zygote with its diploid chromosome complement is the beginning of a new sporophyte. Its development is de-

[3] Not to be confused with the real endosperm of flowering plants. The cells of the pine "endosperm" are monoploid; those of the corn endosperm are triploid.

pendent upon the food that comes through the female gametophyte and the nucellus. Pine embryos multiply vegetatively during their early stages of development from the zygote; a young pine ovule may contain four or more embryos (Fig. 327), but usually only one of them is

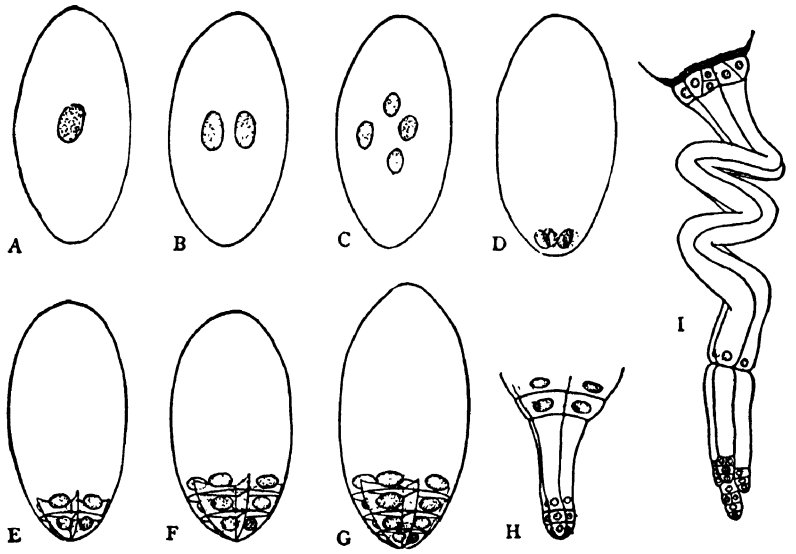

FIG. 327. The formation of the embryo of a pine from the fertilized egg (A) to the development of four rudimentary embryos. Only one of the embryos may survive in the mature seed. After Buchholz. Courtesy of the World Book Co.

fully developed in the mature seed. It is usually about a year from fertilization to the fully formed embryo.

The seed. Two years have thus elapsed since pollination. In the meantime the ovule coat has grown and become the seed coat, the nucellus has been reduced to a membranous layer, and the female gametophyte ("endosperm") has continued to grow (Fig. 328). The embryo consists

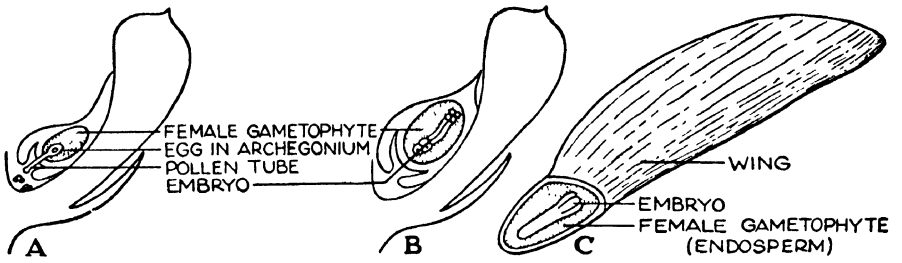

FIG. 328. Diagrammatic representation of the forerunners of the various parts of a pine seed.

of the plumule, many cotyledons, and the hypocotyl, at the end of which is the root primodium. The seed thus consists of the embryo, female gametophyte, perisperm (nucellus), and integument.

In late autumn or early winter, the tissues of the ovulate cone become dry, the sporophylls curl outward, and the seeds are liberated. The seed has a thin membranous wing derived from the upper part of the scale on which it develops.

Summary. The principal steps in the life cycle of the pine are: (1) the formation of microspores and pollen in microsporangia of the staminate cone; (2) the development of two sperms in the pollen grain; (3) dehiscence of the microsporangia and liberation of the pollen grains; (4) the formation of megaspores in megasporangia (ovules) of the ovulate cone; (5) development of the female gametophyte from the megaspore within the ovule; (6) formation of archegonia, each containing an egg cell; (7) pollination and growth of the pollen tube into the archegonium; (8) union of a sperm with the egg, resulting in a zygote; (9) development of embryo from the zygote, further growth of the "endosperm," and formation of seed coats from ovule coats.

The pine tree is a sporophyte. The male gametophyte is a simple structure composed of the cells within the pollen grain. The female gametophyte is a small mass of tissue within the nucellus of the ovule. The gametophytes of the pine, in sharp contrast to those of liverworts, mosses, and some ferns, are never green and are parasitic upon the sporophyte. Ciliate sperms occur in cycads and ginkgo, but not in the other gymnosperms (Fig. 329).

Classification of gymnosperms. The living gymnosperms include four orders:

Cycadales (cycads): *Zamia, Dioön, Macrozamia*
Ginkgoales: *Ginkgo* (maidenhair tree)
Gnetales: *Tumboa, Gnetum, Ephedra*
Coniferales: *Pinus, Larix, Taxus, Picea, Thuja, Sequoia, Juniperus, Podocarpus, Auracaria,* etc.

The Angiosperms: Flowering Plants

About 200,000 flowering plants are known, of which about three-fourths are dicots and one-fourth monocots. They have great diversity of vegetative and reproductive structures. They may be found in all land and shallow water habitats, except the permanent snow and ice fields

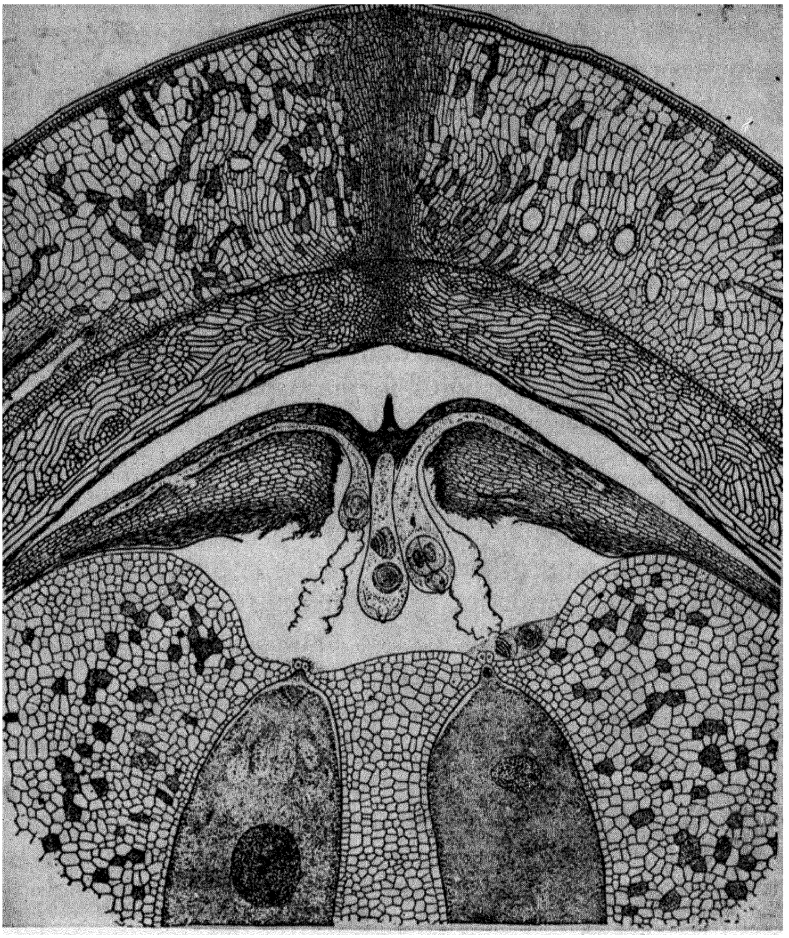

FIG. 329. Longitudinal section of a part of an ovule of a cycad (*Dioön*) at time of fertilization. The reproductive structures represented are the pollen tubes in the nucellus; the spirally ciliated sperms; and two archegonia, one (right) with egg, the other (left) after union of sperm and egg nucleus. Surrounding the archegonia is the female prothallus. Drawing by C. J. Chamberlain.

and the driest deserts. The vegetation of prairies, plains, deserts, most tropical forests, and the deciduous forests is dominated by angiosperms. Furthermore, the undergrowth of most conifer forests contains flowering plants. Our most valuable crop and forage plants and our most annoying weeds are angiosperms.

The seeds of angiosperms are enclosed in ovularies. Variously colored bracts and floral leaves appear in whorls around the spore-bearing

stamens and carpels. The floral organs are of many forms, colors, and arrangements (Chapter XXXII).

The life cycle. The earlier chapters of this book include discussions of the physiological processes, the structures, reproduction, and heredity of flowering plants. The life cycle of angiosperms may now be briefly compared with that of other great groups of green plants. As would be expected, the details of the life cycle are not the same in all plants.

The sporophyte. The familiar plant of angiosperms, such as tulip, wheat, or maple, is the sporophyte. Leaves, stems, roots, and flowers are conspicuous in most species. A perianth, usually composed of calyx and corolla, surrounds the microsporophylls (stamens) and the megasporophylls (carpels).

The microspores form in the anther and become pollen grains upon nuclear division. The dehiscence of the pollen sacs liberates the pollen, and pollination may be effected in various ways. Just prior to being shed, or sometimes shortly after, the pollen grain contains a *tube nucleus* and *two sperms* formed from a generative nucleus. The pollen with the pollen tube is the male gametophyte.

The megaspores form in the megasporangia (ovules), which are enclosed in ovularies. Each ovule ordinarily has one megaspore which upon nuclear division becomes the embryo sac. Subsequent nuclear divisions result in an embryo sac with eight nuclei, one of which becomes the egg; two unite and form a fusion nucleus, and the remainder usually disintegrate. The embryo sac is the female gametophyte, but no structures comparable to archegonia occur.

Fertilization. After pollination and germination of the pollen grain on the stigma, the pollen tube penetrates the tissues of the style and enters the ovule, often through the micropyle. When the pollen tube enters the embryo sac and bursts, the two sperms are released and two fusions occur: one sperm unites with the egg, resulting in a fertilized egg or zygote; the other unites with the fusion nucleus, forming the triple-fusion nucleus.

The embryo. The zygote germinates, and from it an embryo or young sporophyte develops. In some seeds an endosperm develops around the embryo from the triple-fusion nucleus. The growth and hardening of the ovule coats (integuments) complete the formation of the seed. The embryo consists of a hypocotyl, a plumule, and cotyledons.

Chromosome constitution. Reduction division in most angiosperms occurs during the formation of megaspores and microspores. Each of

these structures as well as the egg and sperm contains the monoploid number of chromosomes. The zygote and every subsequent cell of the sporophyte have the diploid number of chromosomes. The endosperm has developed from a nucleus that resulted from the union of three nuclei, and hence each cell of the endosperm has the triploid number of chromosomes. The endosperm is neither gametophyte nor sporophyte: it is termed the xeniophyte.

Comparative summary of life cycles of the great groups of green plants. Several life cycles in each of the great groups of green plants have been considered. Many of the main features of the structure, growth, and reproduction of algae, mosses, liverworts, ferns, and their near relatives, and of seed plants are familiar. If now the fundamental similarities and differences among the life cycles of the great groups of green plants can be visualized, we shall have made a start toward understanding this diverse assemblage of plants as a whole, rather than as individuals or groups. In addition, such an analysis should form a broader basis for an appreciation of the evolution of plants.

The following statements are true for a majority of the plants belonging to the groups indicated. Exceptions may be made, however, to all of them, because simple generalizations can scarcely be formulated for groups containing thousands of species having the greatest diversity of form and habitat. Finding and listing exceptions to these generalizations may prove to be as interesting and profitable as accepting them as universally true.

1. There are two reproductive phases in the life cycles of most green plants: a gametophyte, in which gametes develop; and a sporophyte, in which spores develop.

2. In a complete life cycle (or generation) of the plant the gametophyte regularly alternates with the sporophyte. Zygotes germinate and sporophytes develop; spores formed in the sporophytes germinate and gametophytes develop.

3. The gametophyte phase begins with the spore and ends with the formation of gametes.

4. The sporophyte phase begins with the zygote and ends with the formation of spores.

5. Reduction division occurs during the formation of spores in the sporophyte.

6. The cells of the gametophyte are characterized by the monoploid

number of chromosomes in each nucleus, whereas each cell of the sporophyte has the diploid number of chromosomes.

7. Monoploid and diploid numbers of chromosomes are not causes of the two phases in the life cycle, but are merely associated with them. Doubling or other multiplication of the number of chromosomes neither changes the phase nor necessarily prevents the alternation of phases.

8. The conspicuous phase of many algae, the liverworts, and the mosses is the gametophyte; the conspicuous phase of brown algae, the ferns, and seed plants is the sporophyte.

9. The sporophytes of the liverworts and of the mosses are partial parasites on the gametophytes.

10. Both the gametophytes and sporophytes of ferns develop as separate green plants.

11. The gametophytes of seed plants are parasitic on the sporophytes.

12. Some ferns, some club mosses, and all seed plants have two kinds of spores: microspores and megaspores.

13. Two distinct gametophytes develop from these spores. From the germination of microspores there result gametophytes in which sperms only are formed; and from the germination of megaspores there result gametophytes in which egg cells only are formed. The size of the spore, however, is not a cause of the difference in development of the two gametophytes.

14. In the equisetums the spores are physiologically unlike but similar in appearance. From half of them antheridial gametophytes develop, and from the other half archegonial gametophytes result in certain habitats.

15. In ferns, club mosses, and equisetums the two kinds of spores germinate on the soil after falling from the parent sporophyte.

16. A megaspore of *Selaginella* occasionally germinates in the megasporangium, resulting in an enclosed gametophyte with archegonia and egg cells. The germination of the fertilized egg may result in the development of an embryo within this sporangium, and the final result is a *seed*. If the megaspore falls to the ground and germinates there, no seed results.

17. In seed plants the germination of the megaspore occurs within the ovule (megasporangium), and this is a first step in a series of processes that results in the formation of a seed.

18. Seeds of flowering plants consist of seed coats, endosperm, and embryo; or only of seed coats and embryo.

19. The embryo is a young stage in the development of any individual. Embryos may develop from fertilized eggs or from vegetative cells. The endosperm is a tissue that develops from a triple-fusion nucleus. Seed coats develop from the coats of the ovule.

20. The so-called "endosperm" of the gymnosperms is gametophytic tissue and is not analogous to the endosperm of angiosperms except in location. Its cells have the monoploid number of chromosomes.

21. In the angiosperms, each cell of the embryo has the diploid number of chromosomes, and each cell of the endosperm has the triploid number of chromosomes.

22. The endosperm of flowering plants is neither gametophyte nor sporophyte, but is an accessory phase termed the xeniophyte.

CLASSIFICATION OF PLANTS

We have now discussed all of the major groups of plants and have noted some common representatives of each. Botanists have long divided the plant kingdom into four "great groups": Thallophytes (bacteria, algae, and fungi); Bryophytes (liverworts and mosses); Pteridophytes (ferns, club mosses, and equisetums); and Spermatophytes (gymnosperms and angiosperms). Current usage in more advanced discussions of the classification is the recognition of a far greater number of major groups apparently of independent origin. The following classification is somewhat better than the one above and will suffice for our purpose.

I. Non-vascular plants (without organized conducting tissue).
- Bacteria (Schizomycophyta).
- Slime molds (Myxomycophyta).
- Fungi (Eumycophyta).
- Algae. (See page 608.)
- Liverworts and mosses (Bryophyta).

II. Vascular plants (with highly organized conducting tissues).
- Psilophytes (Psilopsida)—extinct.
- Lycopods (Lycopsida)—mostly extinct.
- Equisetums (Sphenopsida)—mostly extinct.
- Ferns (Pteropsida)—many extinct.
- Seed ferns (Pteridospermae)—extinct
- Cycad-like plants (Cycadophyta)—mostly extinct } (Gymnospermae)
- Conifers, ginkgoes and allies—many extinct
- Flowering plants
  - Monocotyledons } (Angiospermae)
  - Dicotyledons }

CHAPTER LI

FLOWERING-PLANT FAMILIES AND EVOLUTION OF CULTIGENS

The most numerous species of plants that make up the vegetation of the earth, whether in tropical, temperate, or arctic regions, are flowering plants (angiosperms). They have been classified in more than 300 fami-

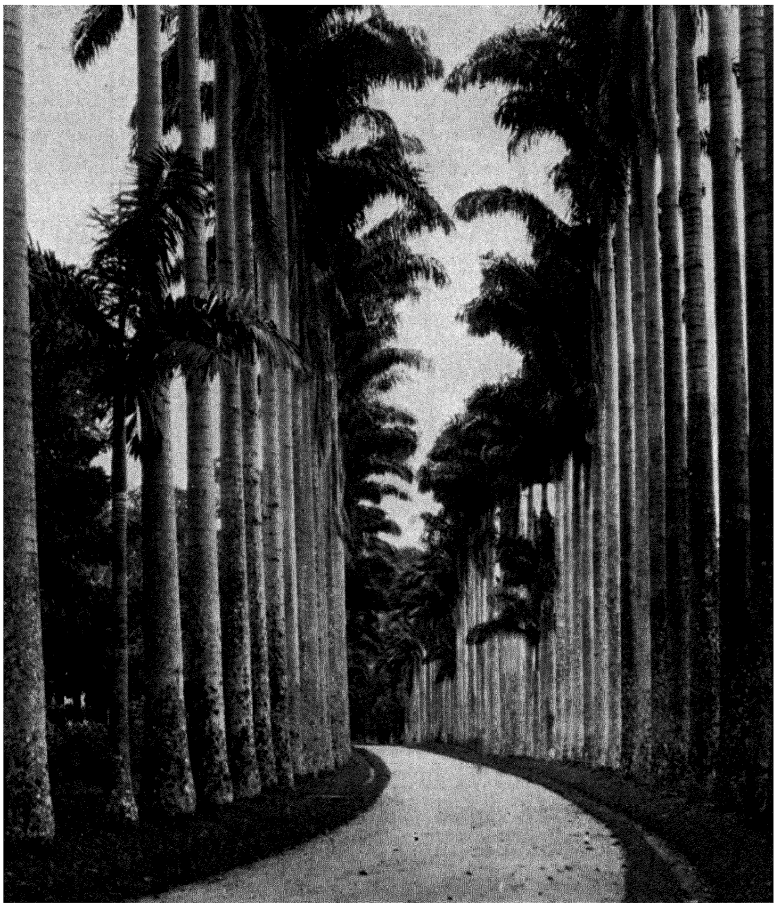

FIG. 330. Royal palms border a pathway in the Botanic Garden at Paradeniya, Ceylon.

lies. It is obvious that in a single chapter only a small number can be mentioned even briefly. The few families mentioned here have been chosen because of their economic and aesthetic human interest and their significance in the history of civilization.

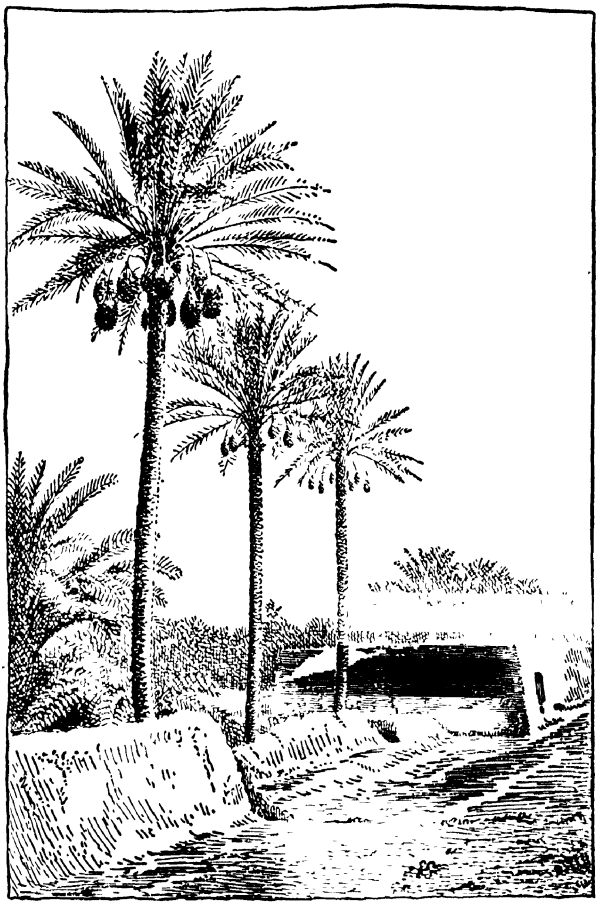

FIG. 331. Date palms, the oldest known tree species in cultivation, and unknown in the wild. Courtesy of World Book Co.

The palm family. These are usually conspicuous plants of the tropics and subtropics commonly recognized by their tall columnar unbranched trunks capped by a crown of large pinnately or palmately branched leaves (Figs. 330 and 86). A few grow as tall as 200 feet, but the height of most species is less than a hundred feet. The palms also include important tropical climbers, the rattans. In our own southern states there are species of palmettos that have horizontal stems and form thickets. Fossil palm leaves are evidence that at an earlier period in the earth's

history (Cretaceous) palms grew as far north as Alaska and Greenland. Today more than 1200 species have been described, 17 of which grow naturally in the southern United States; but numerous imported species are in cultivation in the same region.

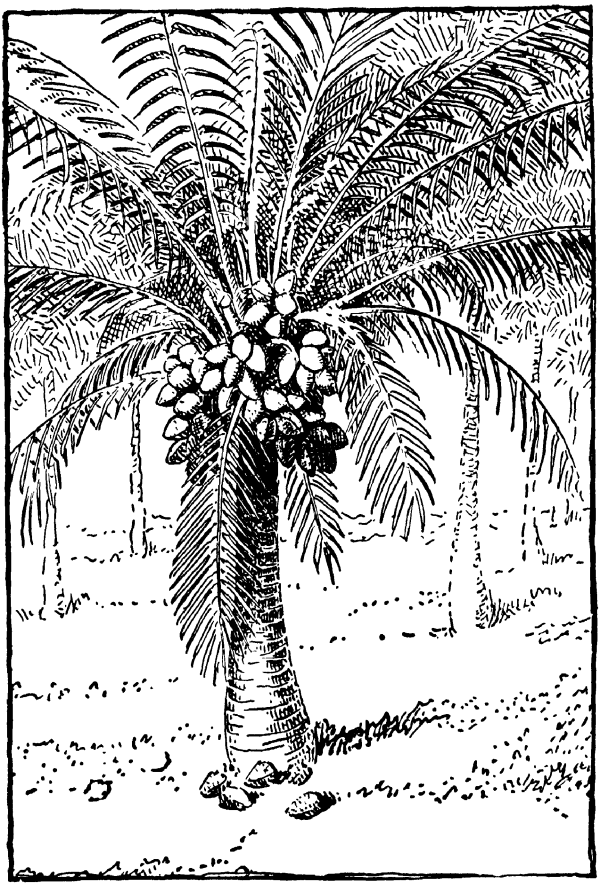

FIG. 332. Coconut palms, known only as a cultivated species in coastal areas of the moist tropics. Courtesy of World Book Co.

In the vast arid expanse of northern Africa the date palm has been cultivated since prehistoric times in oases and other irrigated areas (Fig. 331). In some localities this palm has been the chief source of food used by man and his domesticated animals. It has been pictured as the "tree of life" and had an important place in ancient religious rituals and symbols. Its stems and leaves have been made into timber, thatch, mats, and numerous household utensils. With advancing civilization selection of better varieties has been practiced, and raiding warfare has been carried

on for centuries by tribes seeking possession of superior varieties. The date palms of our own southwestern desert gardens were imported from the Sahara.

In the rainy tropics throughout the world, especially near the coasts of the innumerable islands of the Pacific, the coconut palm has played a similar role as the "tree of life" for unnumbered generations of natives (Fig. 332). There seems to be good evidence that this palm attained its round-the-world distribution through transport by human carriers, and like the date palm in the desert it has often been a complete source of food, shelter, and household conveniences.

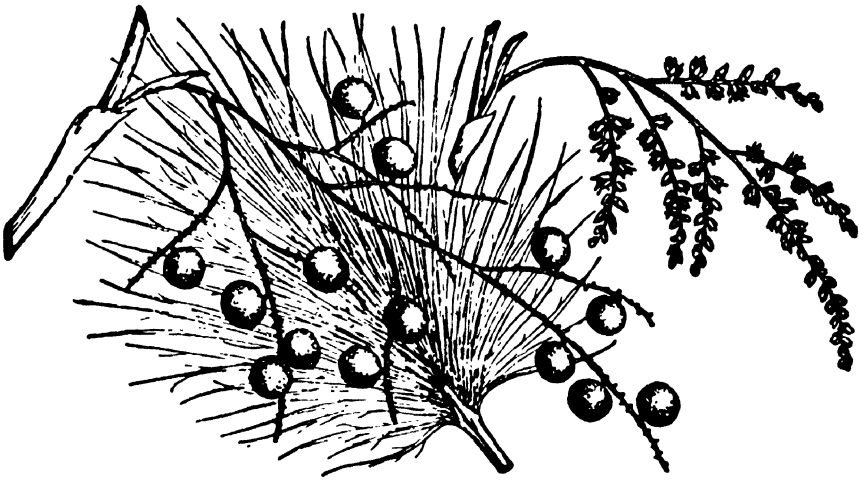

FIG. 333. Leaf, flower cluster, and fruits of the cabbage palmetto, a native palm of the southeastern coast. The succulent terminal bud is edible. After Sargent, *Manual of Trees of North America,* courtesy of Houghton Mifflin Company.

Many other palms have been extensively cultivated. From sugar palms a flow of sweet sap is obtained by first crushing the young flower clusters and then collecting the sap from cut-off peduncles. Oil nut palms are common in many parts of the tropics, and the oils obtained from them supplement the oils derived from the coconut. How important the various palm oils are to us is evident from the fact that the United States imports about a billion pounds a year. From sago palms natives gather starch by cutting the trees and reducing the interior stem tissues to chips from which the starch is washed free with running water into settling vessels. After drying, the starch is used in cooking and baking. Sago palms may grow to be two feet in diameter and a hundred feet tall.



FIG. 334. Two important grasses of the western plains: blue grama (left) and buffalo grass (right) in bloom. Photos from U. S. Soil Conservation Service and F. H. Norris.

Of the many palms cultivated for aesthetic reasons the majestic royal palms of Florida and the West Indies have been planted along parkways and famous avenues in tropical cities around the world (Fig. 330).

The grass family. This family in its broadest sense embraces more than 5000 species, and includes our cultivated cereals, sorghums, sugar canes, and bamboos. Wild grasses dominate the prairies, plains, steppes, llanos, and dry savannas in all latitudes and at all altitudes where plants grow. Grass species are most abundant in the tropics, but individual plants are most abundant in temperate regions.

The origin of cultivated grasses is definitely linked with the beginnings of agriculture and civilization. Stable human community life cannot persist without a permanent local supply of the highly nutritious seeds of cereals that can be gathered annually and readily stored for use during the remaining months of the year.

The cereal grasses that developed along with agriculture are all annuals and rarely survive from year to year without human harvesting, storage, and planting. Certain perennial grasses survive pasturing, and these became the foods of man's domesticated grazing animals, the flesh

of which supplemented the cereals as condensed sources of vitamins, proteins, and fats. Wheat, rice, barley, and rye are of Eurasian origin. Sorghums originated in Africa; and the most productive of all the grains, corn, originated in South and Central America, where the Indians in the course of time selected and preserved many varieties.



FIG. 335. Field of mature sugar cane in Hawaii, where this amount of growth of cane occurs in from 18 to 24 months. Photo from Hawaiian Sugar Planters' Association.

The early food gatherers merely continued and extended the practices of their primate ancestors. They became skilled in selecting food from certain species and in avoiding other species. Moreover they became aware that combinations of cereals, fruits, leafy vegetables, and fleshy roots enhanced their well-being and their satisfaction. With this background of experience the early cultivators could select those species and varieties that were most easily planted, harvested, and stored. The selection of annual varieties of these plants is another problem, but in view of modern experiments it is not too difficult, given time, watchfulness, and intelligent planning.

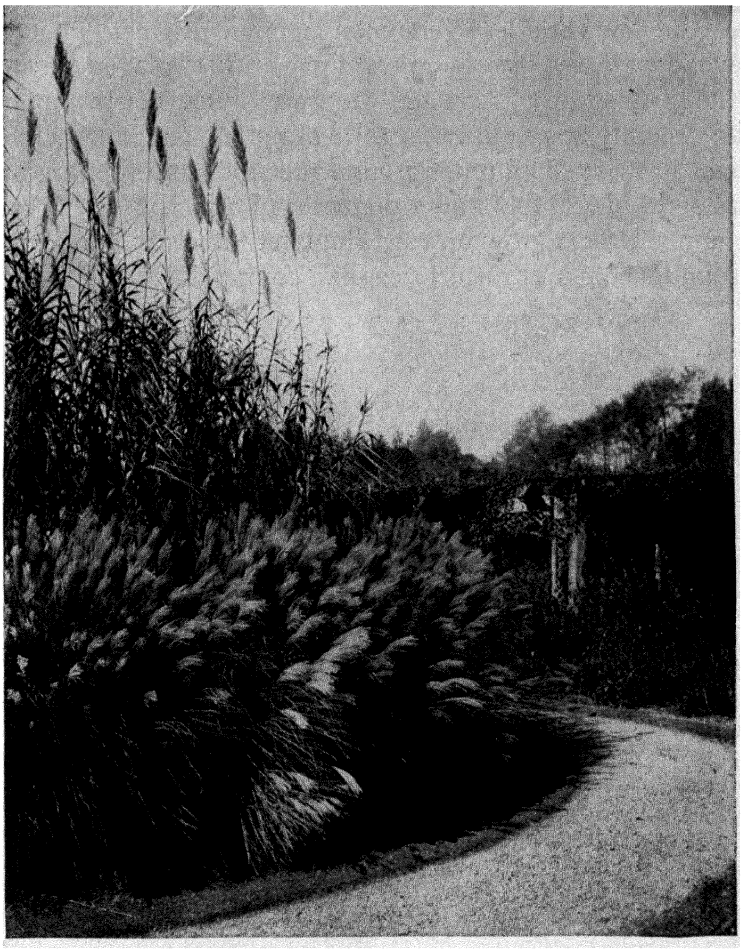

FIG. 336. Ornamental grasses: on the border, eulalia (*Miscanthus sinensis*); the taller grass pictured in the background is the giant reed (*Arundo donax*).

Cultivated species and varieties such as those of cereals have been called "cultigens," an excellent term for them since they have survived under cultivation only because our ancestors selected and cared for them through untold generations. This selection may be carried on as long as evolution of hereditary units and the consequent development of new variants continue. It is a feature of cultigens that they display great variability. When their seeds are obtained by persons having different preferences, further selections lead to the preservation of plants that

differ greatly from their ancestry in form, size, taste, and composition. These are the new varieties so common among cultigens.

The woody grasses, the bamboos (page 272), played an important role in the civilization of Asia and the East Indies, not so much as food plants as a readily adaptable structural material. The hollow jointed upright stems grow from an underground rootstock and the largest species attain a height of 120 feet and a diameter of a foot. Many species form dense clumps. Others grow upward singly at intervals along widespread underground stems and form forest-like communities (Fig. 337). Most

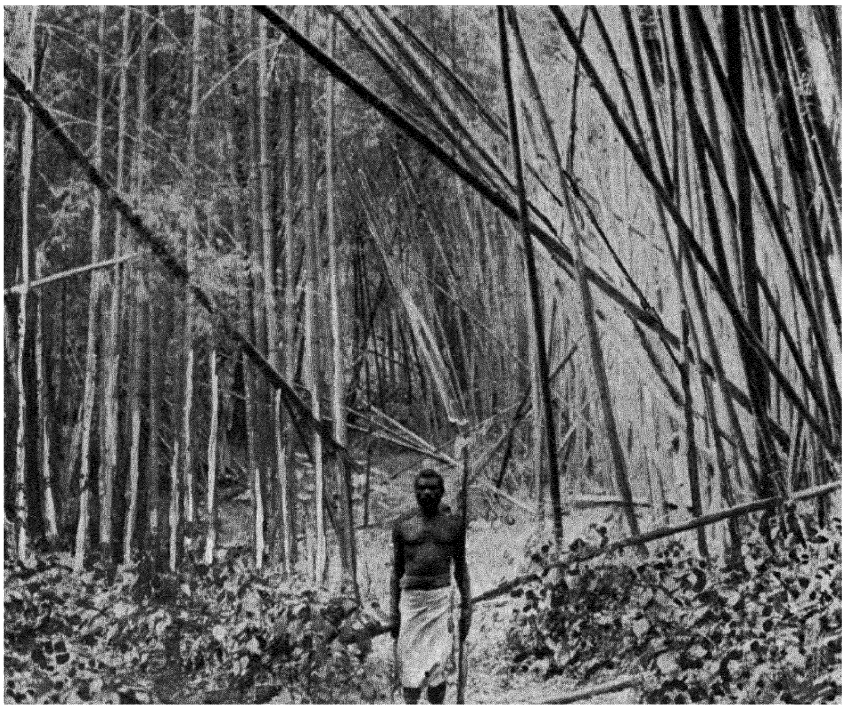

FIG. 337. Bamboo forest on the slopes of Mt. Ruwenzeri, East Central Africa. Photo from the Belgian Congo Survey.

bamboos flower and fruit only after a period of time which may be as much as thirty years. Fruiting usually is simultaneous wherever the particular species lives and is followed by the death of the canes. Two species of *Arundinaria* formed the canebrakes of the southern states, now largely exterminated because in fruiting years cattle and hogs went

into the swampy "brakes" and fed on the bountiful seeds and young shoots that started to develop.

In oriental countries temples, houses, fences, screens, furniture, agricultural implements, water pipes, musical instruments, ship masts, and hundreds of household utensils and art objects are fabricated from bamboo stems. The macerated inner fibers have been extensively used in making paper.



FIG. 338. One of the cultivated varieties of banana.

The banana family. Although a small family (80 species) centered in the East Indies, its species have become widely dispersed by man in the tropics because of their rapid growth and nutritious fruits. Bananas are large-leaved herbs 10 to 30 feet tall (Fig. 338). The plants consist of a thick rhizome, from which a cluster of erect leaves grows. The sheathing petioles form a trunk-like body topped by the spreading leaf blades. Meanwhile a stem grows upward inside the cylinder of petioles and on emerging above the sheaths turns downward and continues to elongate. Successive flower clusters appear at the nodes, soon followed by the fruits. The banana fruits sold in temperate regions contain starch that changes to sugar as they ripen.

Other species have fruits that remain starchy. These are cooked be-

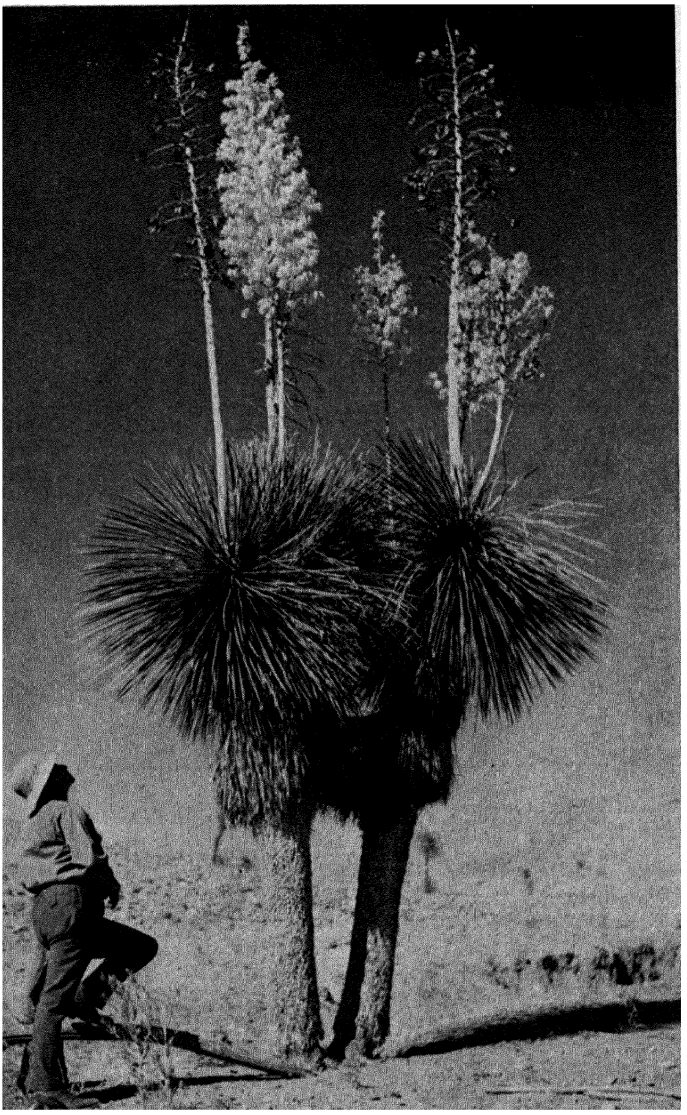

FIG. 339. An arborescent yucca. Photo from U. S. Forest Service.

fore eating and are of greater economic importance in the tropics. These species are called "plantains" and their fruits may be larger than the bananas of commerce. As food sources in the moist tropics bananas and plantains are surpassed only by the coconut palms.

One of the tallest plantains has leaves with very long tough veins. When freed from the other leaf tissues the veins become the "Manila hemp" of commerce. These fibers are most prized for the manufacture of heavy ropes used on shipboard because of their great strength, elasticity, and durability in salt water.

The lily family. This family comprises about 2800 species of largely perennial herbs with underground bulbs, corms, or fleshy rootstocks. Many species have conspicuous flowers with six similarly colored parts of the perianth: white, yellow, red, or purple. Often the colors are mixed in striking patterns. Well-known species include lilies, asparagus, onions, garlic, tulips, hyacinths, trilliums, autumn crocuses, day lilies, and climbing smilaxes.

In arid American regions there are woody yuccas (Figs. 100 and 339) often cultivated as ornamentals, or for their fibers. In the Old World other woody species include *Dracaena* (dragon tree) and *Sansevieria* (Indian hemp), both cultivated in greenhouses in temperate climates.

Closely related to the lilies is the amaryllis family with a thousand species, among which are agave, narcissus, daffodil, and spider lily. Most species occur in the tropics. In the dry regions of Mexico and Central America there are 275 species of *Agave* (page 88). The best-known agave is the so-called "century plant" with its rosette of large, rigid, succulent leaves and a flower stalk that may grow to a height of 30 feet and bear a large cluster of yellow flowers. This plant has become naturalized throughout the dry tropical world. Flowers and seeds develop only after a food-accumulating period of 20 to 30 years and then the entire above-ground shoot dies.

The bromelia family. The pineapple, with its sugary multiple fruit (page 367), and a few other bromelias grow on soil, but the bulk of these strictly American plants are epiphytes perched on the branches of trees (page 300). Many have brilliantly colored flower clusters and urn-shaped leaf rosettes which also may be variously colored. The "Spanish moss" is a conspicuous bromeliad in the southern states. It has no roots and is merely draped over the branches of trees (page 508).

The orchid family. This family embodies the extremes of differentiation and specialization of roots, stems, leaves, and flowers among mono-

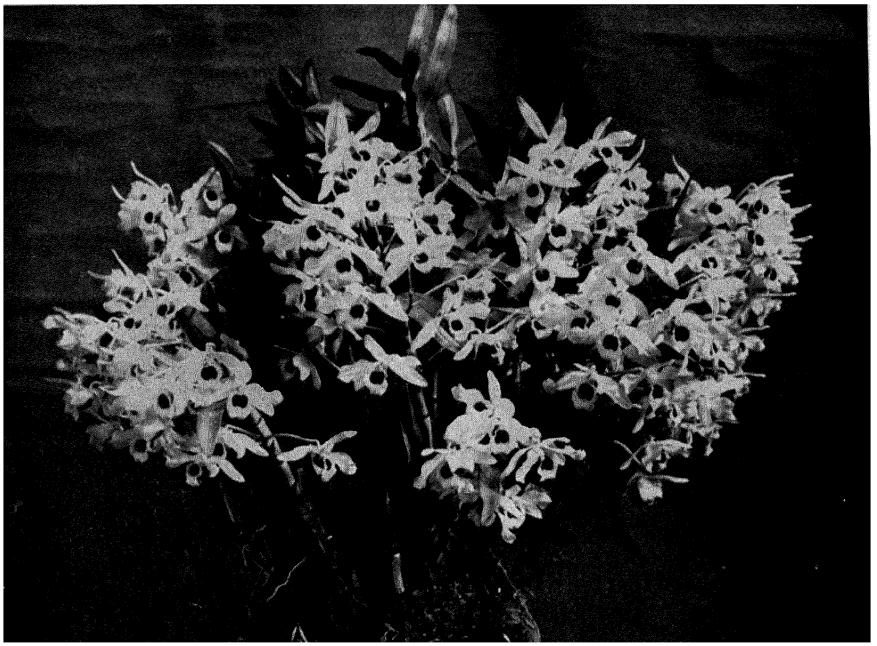

FIG. 340. A tropical epiphytic orchid (*Dendrobium*) in cultivation.

cot plants. The relatively few temperate zone orchids are terrestrial, and a few of them are rootless parasites on fungi. Most orchids are epiphytes living in the tropics and subtropics (page 507). The nutrition of all orchids is in part dependent on fungi growing in the roots, or rootstocks, and substratum (page 510). All the species are noted for their very minute seeds (page 388).

Altogether there are over 700 genera and 17,000 species, equal to 40 per cent of all monocot species. Even though the habitat of a flowering epiphyte is the most unfavorable of all habitats with respect to water and inorganic salts, these orchid species outnumber the grass-like species three to one. Various genera and species are localized on certain continents, mountain ranges, and islands. Even by the most primitive and isolated human tribes flowering orchids are collected and cherished as household ornaments because of their bizarre shapes, brilliant colors, and vivid color patterns.

The composite family. In striking contrast to the orchid family is the family of the composites which represents the culmination of evolution in the dicots. It is the family that includes the sunflowers, dandelions,

goldenrods, and thistles. Its name is based on the fact that the so-called "flowers" are composed of several or many flowers closely arranged in a "head" (page 361). There are 15,000 species, which is about 10 per cent of the dicots.

The composites are world-wide in their distribution and they may be found in nearly every plant habitat. They are mostly herbs, though there are some shrubs such as the sagebrush of the semi-deserts of the northern hemisphere and the tall baccharis shrubs of the warmer parts of the Americas. Many composites are troublesome weeds.

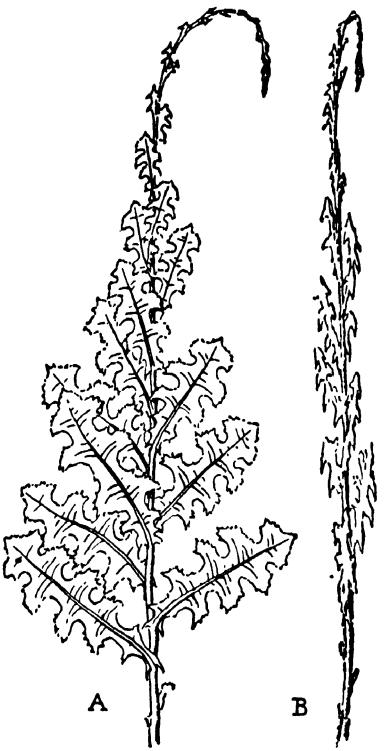

FIG. 341. Prickly lettuce when growing in full sunlight is a "compass plant": A, as seen from the west; B, as seen from the south. It is believed to be the progenitor of the cultivated varieties of lettuce.

One of our commonest weeds of Eurasian origin is prickly lettuce (Fig. 341). This species is interesting not only as a "compass plant" but as the ancestor of the cultivated varieties of lettuce—the universal choice of leaves for the salad bowl. The three types of lettuce—leafy, cos, and head lettuce—are good examples of cultigens. Moreover in this instance one can easily observe how greatly cultigens may vary from their wild ancestors. The leafy type was served to the Persian kings of the 5th century B.C. Cos lettuce, which has rather narrow upright leaves, appears to have developed on one of the Dodecanese Islands of that name. The head lettuce originated much later in northern Europe, probably about the 16th century. Of the three types it is interesting to note that only cos lettuce can withstand high temperatures and for this reason was preferred by the Romans—whence the French name "romaine." In China a fourth type originated. It has succulent upright stems and small leaves.

Other vegetable composites are salsify, endive, globe artichoke, and Jerusalem artichoke. Sunflower seed is an important bird food crop. Ornamental composites are very numerous and include asters and chrysanthemums, mostly from the Orient; and cosmos, zinnias, mari-

golds, and gaillardias from Mexico, which are not so very different from their wild ancestors.

The legume family. These plants are characterized by the form of the

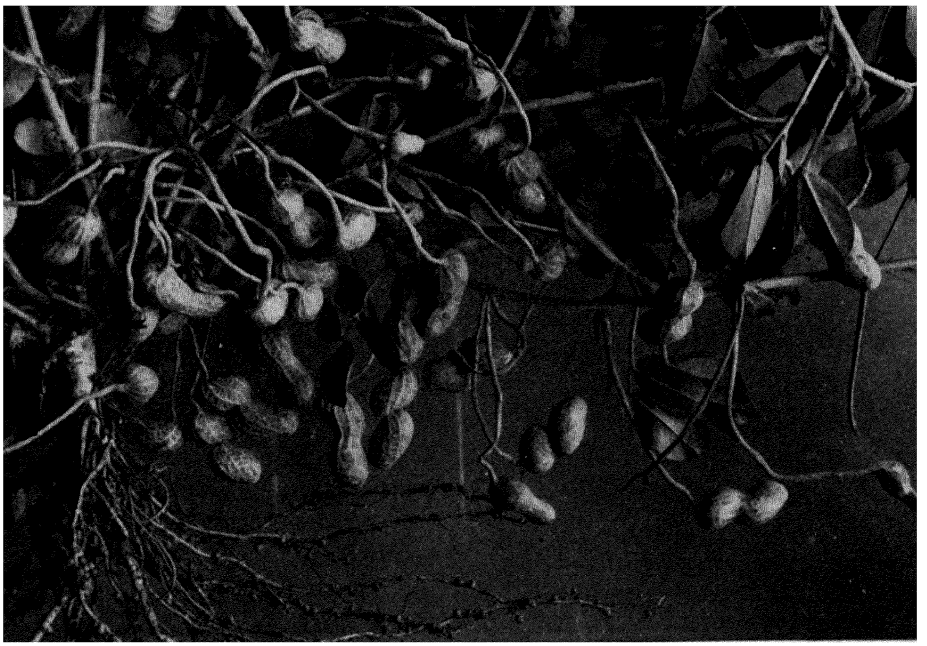

FIG. 342. The subterranean fruits of a peanut plant. A few days after pollination occurs in a peanut flower the stalk-like base of the pistil begins to elongate, grows downward, and pushes the ovulary into the soil where the fruit and seeds develop.

seed pods, typified by those of peas (page 355), beans, and redbud trees. There are more than 12,000 species, and some species grow in many habitats from the tropics to the arctic regions. One of their most important properties is their high content of proteins and other nitrogen compounds, particularly in the seeds. The abundance of these compounds in legumes results in part from the fixation of nitrogen by bacteria that live in nodules in the roots of legumes (page 534).

As in the history of cereals, the origin of the cultivated varieties of beans, lentils, peas, and soybeans took place so long ago that they cannot be traced to their wild perennial ancestors. The more important economic legumes are all cultigens.

Kidney, lima, and tepary beans are of American origin and were



FIG. 343. White clover in bloom.

widely cultivated in the western hemisphere in pre-Columbian days. From western Asia and adjacent Africa came lentils, broadbeans, and chickpea beans, as well as the garden pea. India and Malaya were the original homes of moth bean and cowpea. Early man in China and the Netherlands Indies domesticated several other beans, and above all the soybean. In recent years in America soybeans have become the basis of an astoundingly varied number of uses: pasture, silage, soil improvement, livestock feed, paints, enamels, plastics, soaps, rubber substitutes, and human foods such as flour, vegetable milk, butter substitutes, candies, soy sauce, seasoning powders, and many others. It is little wonder that the annual production of soybeans in the United States jumped from 13 million bushels in 1930 to 225 million bushels in 1950.

Another legume, the peanut (Fig. 342), originated in Brazil and was carried into the Andes valleys, and in historic times to all tropical and warm temperate regions. Peanuts are an important source of both protein and oil in America, Africa, and southern Asia. The forage legumes are numerous and include the clovers (Fig. 343), alfalfas, lespedezas,

and vetches—not to mention the many wild species everywhere.

Among the leguminous trees and shrubs are those with flowers similar to the flowers of the locust tree. There is another group with more or

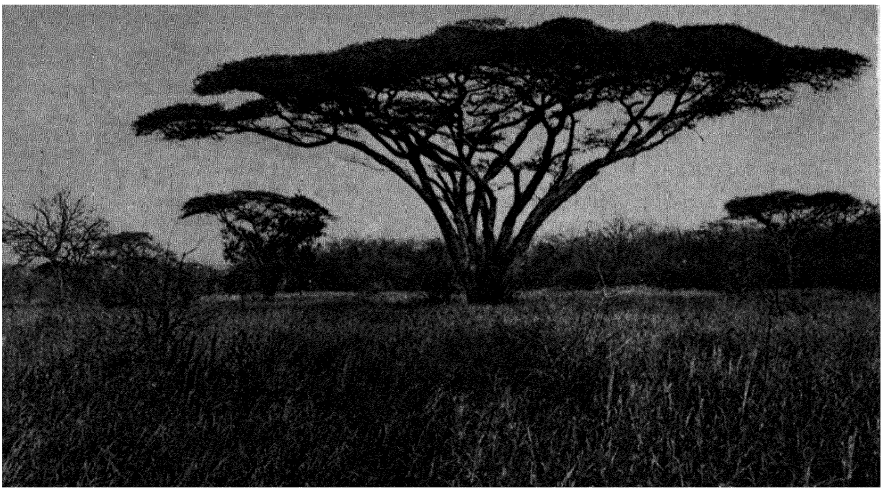

FIG. 344. An acacia savanna in Kenya Colony, Africa. In the background is an area of "thornbush." Photo by Walter Busse.

less regular very small flowers clustered in spikes or heads, often brilliantly colored: the acacias and mimosas, so very common in the seasonally dry tropics or subtropics. They are horizontally branched trees scattered over the grasslands of the great game preserves of Central Africa. Their greatest abundance and diversification, however, are found in Australia. The acacias make up most of the woodland and the desert scrub in the vast dry interior of that continent.

The cucurbit family. Of the 800 species in this family there are many cultigens that first delighted the aborigines of America, Africa, and western Asia (Persia). Here belong the pumpkins, squashes, cucumbers, muskmelons, watermelons, and gourds. In the 16th century when sailing ships began their vast trading adventures they introduced seeds of these plants to the natives of all the continents. This has resulted in much difficulty in locating the original homes of these succulent and flavorful fruits. Cucumbers apparently originated in India, since closely related species are native there. They were dispersed to China and Asia Minor along the early caravan trade routes. Muskmelons were selected and diversified in Persia and then introduced to the Mediterranean countries.

Columbus carried them to the West Indies in 1494. The many forms of the netted-skinned muskmelons, the honeydew, the yellow banana, the casaba, and the Persian melon were all derived from the same wild source.

Watermelons originated in Africa. David Livingstone found them there growing wild and covering many acres. He recorded (1848) that some were sweet and some were bitter and that the natives "plugged" them before picking them.

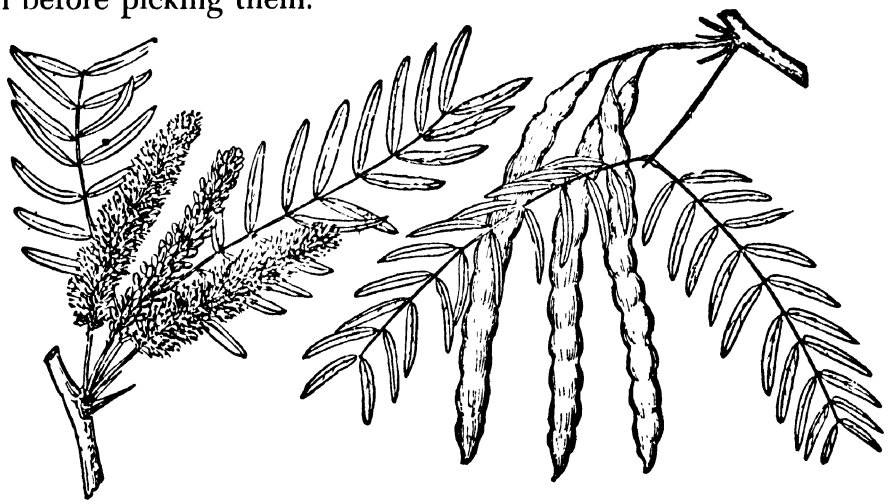

FIG. 345. Flowers, fruits, and leaves of mesquite (*Prosopis*), a characteristic tree of semi-desert areas of the southwestern states. After Sargent, *Manual of Trees in North America,* courtesy of Houghton Mifflin Company.

The many kinds of cultivated squashes and pumpkins were derived from three wild species, one from the southern Andean valleys, the others from Central America. When the Europeans settled in America, they found the Indians of Florida and even New England cultivating them. At that time bush varieties of summer squash had already been stabilized as a crop, as were many varieties of both squashes and pumpkins that bore fruits of different forms, sizes, and colors.

The gourds with the thin hard rinds and bitter pulp seem to have been carried to South America from Africa in pre-Columbian days and utilized, when dried, as household vessels by the aborigines of both continents. They are now cultivated in America chiefly for ornament.

The mustard family. This family of 200 genera and 3000 species is most abundant in the northern hemisphere, especially the cold temperate regions. The flowers are quite characteristic with four petals, and four long and two short stamens. Many species have a rather pungent

taste and odor due to essential oils containing sulfur. Since these oils are concentrated in the seeds, flour made from the seeds is used as the basic flavor of many meat and salad dressings. Black mustard is one of a score of species of the genus *Brassica* that was brought into cultivation in Eurasia in prehistoric times. Modern varieties that resulted from mutation, hybridization, and selection include many cultigens. Among them

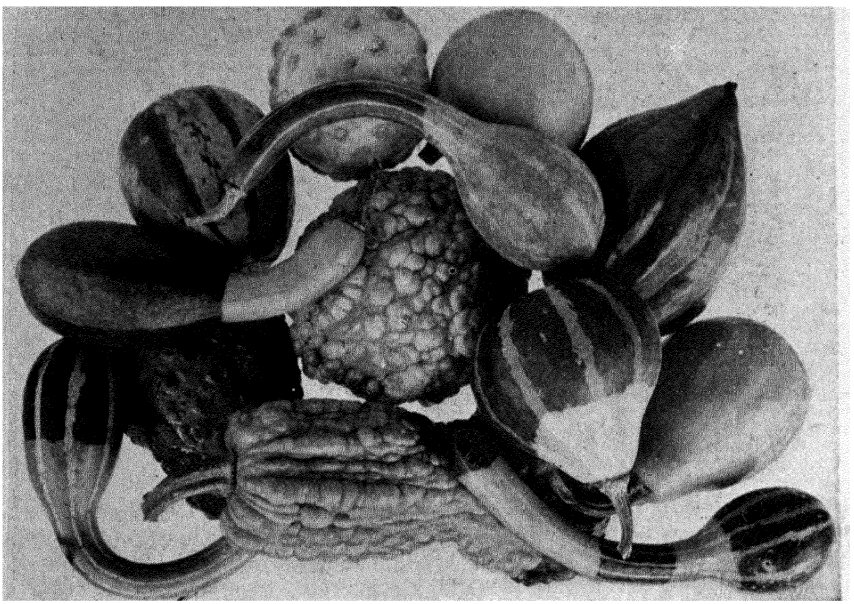

FIG. 346. A few of the many forms of gourds and squashes.

are Indian mustard, cabbage, cauliflower, broccoli, Brussels sprouts, kale, collards, kohlrabi, turnips, rutabagas, radishes, and Chinese cabbage. If you examine a seedsman's catalogue you will find that each of these vegetables has many forms, but no American catalogue contains the scores of Asiatic forms. The history of the cultigens derived from the wild cabbage is well known; several of them are illustrated with drawings in Fig. 196 (page 426).

The rose family. This cosmopolitan group of 100 genera and 2000 species is most abundant in the north temperate zone, and includes perennial herbs, shrubs, and trees. The flowers are very similar throughout the family, but the fruits are of three distinct types: akenes (roses), pomes (apples), and drupes (plums). Of all flowers the rose has first place in literature, and perhaps in art also. Most cultivated roses are

derivatives of Eurasian wild species. They have become cultigens, with genes from many sources. Certain tree species of the rose family have become the sources of the most important orchard fruits of temperate regions. These cultigens are the numerous varieties of apples, pears, peaches, plums, apricots, and nectarines mostly of Eurasian origin. Our

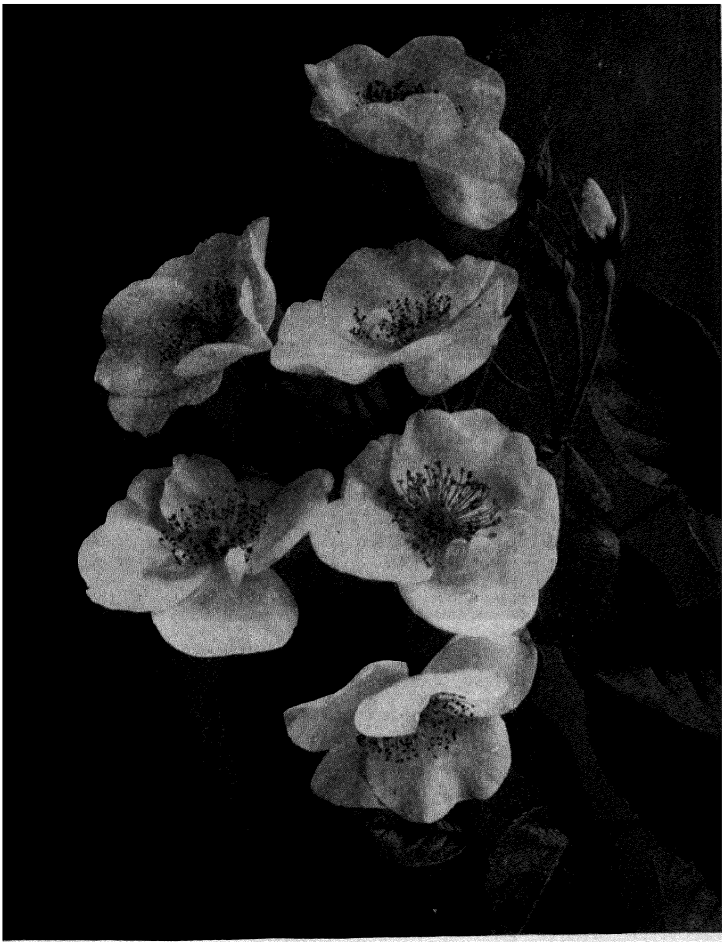

FIG. 347. Floral structures of a rose (*Rosa moschata*).

cultivated shrub fruits—blackberries, raspberries, and dewberries—are mostly of recent American origin. The modern large-fruited strawberry is the result of crossing our wild Virginia strawberry with a species long cultivated by the Indians of northern Chile.

The cactus family. The hundred genera and 1500 species classified here are desert and semi-desert succulents, very different in structure and appearance from the plants of moist climates.

The cactus family seems to have originated in Central America and Mexico. From there it spread to the semi-arid parts of the West Indies and North and South America. The prickly pear (Fig. 348), barrel cactus



FIG. 348. Opuntia with flowers and fruits. Opuntia is a genus of the cactus family with oval, flat segments and small temporary leaves.

(Fig. 400), crab cactus, sahuara (Fig. 12), and organ cactus (Fig. 349) are examples. The stems of prickly pears consist of round, or ovoid flat segments, with prominent nodes spirally arranged and marked by spines and spicules.

The largest species of cacti (Cereus type) have thick columnar fluted stems with few or many branches 20 to 50 feet in height. Structurally the stem consists of a hard cylindrical wood "skeleton" enclosing a central pith and surrounded by a thick layer of parenchyma tissue. The hard outer rind is composed of parallel ridges capable of expanding and contracting as the water content of the stem increases or decreases. The permanent root systems are usually shallow and widespreading with an outer cork layer. Whenever the rains wet the soil fine temporary rootlets

grow out through the cork layer and most of the water that enters the plant comes through these rootlets. When the soil dries these temporary rootlets die. A large organ cactus may accumulate as much as 25 to 30 tons of water.

In recent years many species have been brought into cultivation as glasshouse and household ornamentals. When they survive for several years in these conditions of low light intensity, their appearance is very different from those growing in the desert.

The potato family. This family of about 2000 species is world-wide in its distribution, but is most diversified in the tropics and subtropics. On the one hand it includes several important food plants and on the other many plants that synthesize alkaloids and are more or less poisonous. Several of these alkaloids have long been used in medicinal preparations, for example atropine, belladonna, hyocyamine, and scopolamine.

The most important cultivated vegetable in the world is the potato, which originated in the cool high valleys of the Andes. It was carried from Peru to Europe by the Spanish conquerers in the 16th century. It was planted as a curiosity in various gardens in northern Europe but did not come into general cultivation until the middle of the 18th century. It was introduced into New England from Ireland about the same time, and was given the epithet "Irish potato" to distinguish it from the "battata" (sweet potato) widely cultivated by the Indians in the eastern states.

Closely related to the white potato is the tomato plant, with its luscious succulent fruits, which was brought into cultivation in the same general regions as the potato, and also introduced into Europe about the same time. At first planted as an ornamental, it gradually came into use for culinary purposes. It was cultivated for its edible fruits in the southeastern states before 1800. It has now become available in American markets throughout the year, either through glasshouse culture, or by shipment from the southernmost states.

Another cultigen of the potato family is the eggplant, noted for its many form and color varieties in different parts of the world. Originally from India, it spread by way of the caravan routes to China and the Mediterranean countries, and then to everywhere it would grow.

Garden peppers are another savory group of vegetables carried to Europe by Columbus and the Spanish voyagers who followed him. Everywhere they touched the coasts of the Americas they found the

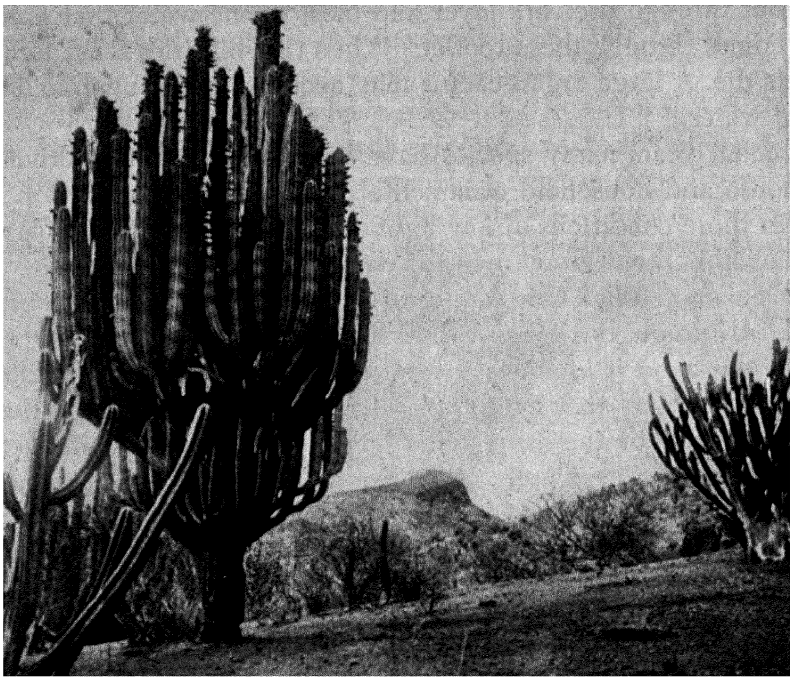

FIG. 349. One of the massive species of *Cereus* which grows in the Sonora Desert, Mexico. Photo by C. J. Chamberlain.

Indians cultivating and mixing pungent red peppers with their various cooked meat and meal dishes. Peppers certainly add zest to unrefrigerated meat.

In Spain not only were the "hot" peppers cultivated but also a round sweet pepper called "pimienta"; in America it became the "pimento" used in relishes and cheese preparations. The Hungarians selected a long, rather thick sweet pepper which they called "paprika" and which they used extensively in their own cookery. These peppers were also dried and ground under state supervision and exported to all parts of the world.

In the United States the sheep-nosed type became the important form of garden peppers used when either green or red in salads and various meat-vegetable combinations.

Man's favorite alkaloid is today dispensed throughout the world in various preparations made from the leaves of the tobacco plant. So ancient was the custom of smoking tobacco among the Indians, at the time of the discovery of America, that they had learned not only to culti-

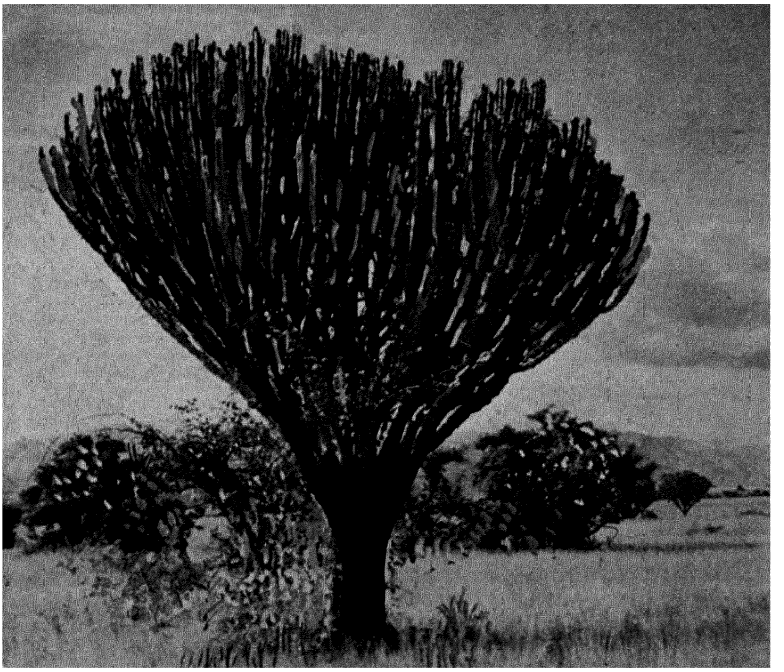

FIG. 350. On the semi-deserts and deserts of Africa tree-like, shrubby, and small succulent species of the euphorbia family superficially resemble the quite unrelated species of the cactus family of the American deserts. Photo from the Belgian Congo Survey.

vate, harvest, and cure the leaves, but to prepare them as cigars and cigarettes, and to break them up for pipe smoking.

Along with corn, beans, and squashes, tobacco was regarded as a gift from the gods. Accordingly it had a symbolic part in their social customs, their religious rituals, and tribal ceremonies.

Introduced into Europe in the early 16th century, tobacco soon became popular in spite of social taboos, religious antagonism, and excessive taxation. King James of England in 1604 called it "a custom loathsome to the eye, hateful to the nose, harmful to the brain." William Barclay of Scotland (1614) described tobacco as having "much heavenly vertue in store," and America as the country that has been "honoured and blessed with this happie and holie herbe." As early as 1619 a guild of tobacco-pipe makers was incorporated in London.

From the small beginning at Jamestown (1610) the cultivation of tobacco in Virginia and Maryland so increased that by 1639 one and a



FIG. 351. Potato plants in bloom. The flowers usually abscise and no fruits develop. When formed, the fruits resemble small green tomatoes.



FIG. 352. Texas cotton field. Cultivated cotton is a group of cultigens independently domesticated in South America, Mexico, Africa, and India. One-half of the world's cotton crop grows in the United States. This country exports annually about 2.5 billion pounds of cotton. Photo from Elizabeth Wagner.

half million pounds were exported to England. In 1949 the export of tobacco from the United States was a half-billion pounds, and the import from foreign sources 88 million pounds. The total American production was more than 2 billion pounds. Tobacco cultivation is now world-wide, but quality tobacco can be obtained only from plants growing on carefully selected soil and in climatic areas.

This account of certain flowering-plant families, their distribution, their diversity, and the utility of some species is merely a brief introduction to a botanical field of the greatest importance to mankind everywhere. No civilization can improve the health and economic welfare of its people without giving intelligent attention to the possibilities of the continued discovery, cultivation, and selection of old and new cultigens.

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There are interesting notes on many plant families in the recent edition of the *Encyclopædia Britannica.*

CHAPTER LII

PLANTS OF THE PAST

Your own observations and discussions in the laboratory or elsewhere, supplemented by information in the preceding chapters, have acquainted you with numerous hereditary differences in many kinds of plants now living. Among these differences are the specific characteristics you distinguished when you were classifying trees, and when you were comparing processes in different organisms, structures in different flowers, fruits, and seeds, or the processes and structures in various representatives of the major groups of living plants.

✔You also have some understanding of the manner in which these hereditary differences come about by evolution (mutations) of the hereditary units of matter in cells, and by subsequent segregations and recombinations of these units resulting from hybridization and crossing over. You know that these units condition the development of each individual. Furthermore, you have become conscious of organic evolution as a natural process that one may study and try to understand.

In continuing this study it is well to remember that the structures one organism organically inherits from another must be very small since thousands of them are contained in a single cell such as a fertilized egg, that it is these small hereditary units that evolve, and that the nonheritable fluctuations among plants caused by differences in environment do not result in evolution. Evidently any attempt to tell what heritable changes in plant structures are for is really to personify or deify minute hereditary units of matter. No less remarkable than evolution is the relative constancy in hereditary units that condition such basic processes as those underlying the development of specific form in each generation or the formation of protoplasm in each cell that has developed since plants appeared upon the earth.

All these concepts are essential parts of the background one needs to appreciate plants of the past, for these plants were the visible consequences of evolution over a very long period of time. Conversely, some knowledge of these former plants, and of former animals too,

is essential to one's over-all concept of evolution and of one's own position in a world community of living organisms—concepts that are cultural as well as practical. There are many other phenomena we would

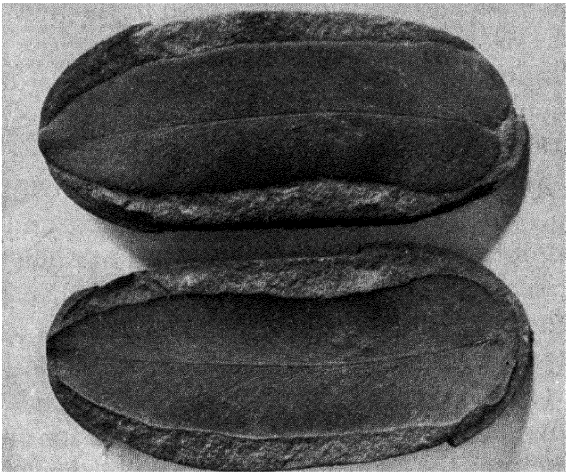

FIG. 353. Positive and negative imprints of a seed-fern leaflet (*Neuropteris*). Courtesy of Chicago Natural History Museum.

be unable to understand without some knowledge of the plants that grew upon the earth during the various geological periods. Among these phenomena are the relations of ancient vegetations to our present economy, to the present geographic distribution of plants, and to the bases of devising and evaluating natural systems of classifying plants.

Fortunately, some of the plants that lived a thousand, a million, and even a billion years ago have left a record—though a meager one—in the sedimentary deposits in ponds, lakes, and shallow seas. Some of the later deposits are still unconsolidated, and we can study the plants or parts of plants in peat, marl, and silt deposits.

The plants that grew millions of years ago shed their spores and seeds, their leaves and branches just as modern plants do. Forests were overwhelmed by catastrophes and were buried in unaerated mud and water and in shore and delta deposits just as they are today. Fine "ashes" from violent volcanic eruptions have at various times quickly buried living vegetation. Owing to the poisonous gases and vapors emitted during such eruptions, all living organisms nearby were killed and the plants were often buried in sterile debris. Some of the plants and animals

that lived in or fell into bog lakes, where decay is comparatively slow, have been preserved in peat and coal for centuries. Some of the peat deposits of Alaska and Siberia have remained frozen since glacial times, and in these natural refrigerators organisms as large as mammoths and rhinoceroses have been preserved in the flesh to the present time.

Both the remains and the various traces of organisms are called fossils. Some fossils are merely imprints (Fig. 353), similar to those formed when leaves fall upon freshly laid cement and a detailed outline of their form and venation is preserved as the cement solidifies. Sometimes the material of the plant was carbonized by oxidation-reduction processes which removed most of the oxygen and hydrogen and left beautiful outlines of parts of the plant in carbon (Fig. 354). Molds, casts, and less commonly petrified parts of plants were formed. When an organism is buried in silt which solidifies, the organism may slowly disintegrate and a mold of its form is left. If the mold is filled with mineral matter, the result is a cast (Fig. 355). If the substances of the cells are preserved until replaced by mineral matter in sufficient detail for one to recognize the cellular structure, the plant is said to be petrified (Figs. 356 and 357).

Fossils may be found in consolidated rocks, sand dunes, cave deposits, peat beds, coal, river deltas, ooze at the bottom of lakes and oceans, glacial drift, and in soil formed by the weathering of rocks. Studies of the rocks and fossils within them have enabled paleontologists to re-

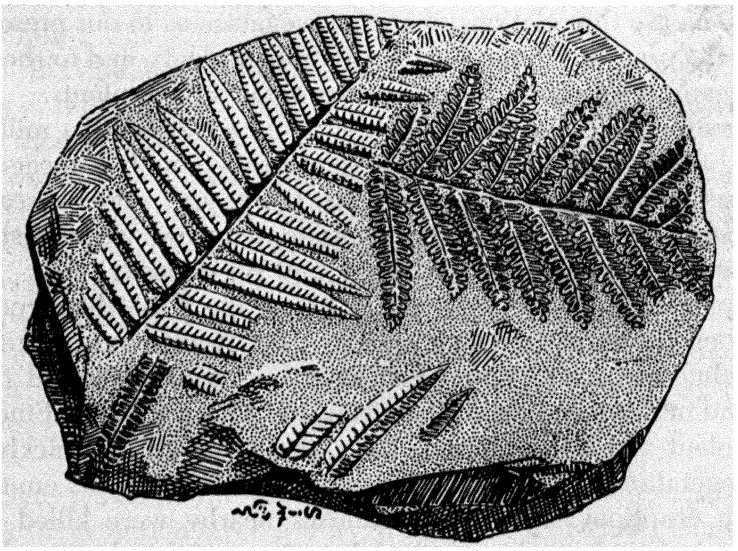

FIG. 354. Carbonized fossils of fern-like leaves in a rock of the carboniferous period.

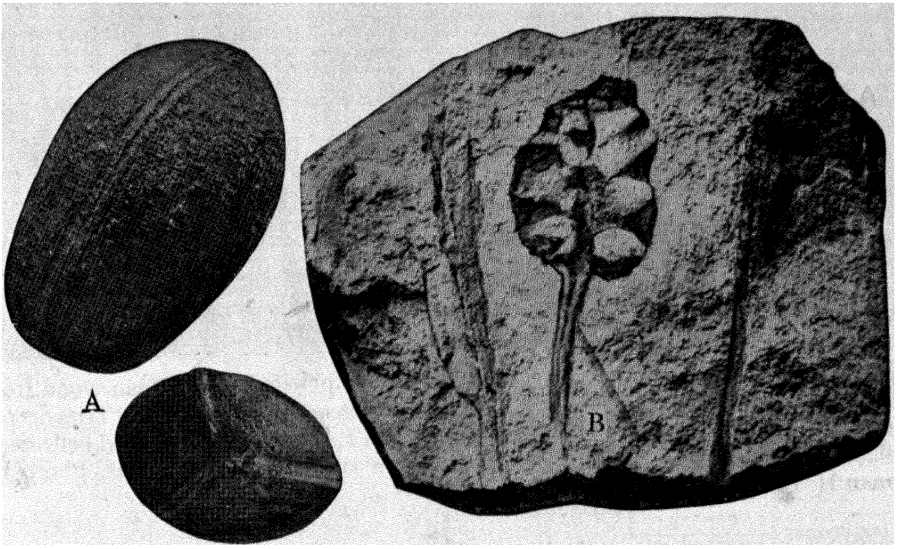

FIG. 355. A, side and end views of cast of seed-fern seed from the Upper Carboniferous; B, cast of redwood (Metasequoia) cone of the Upper Cretaceous age of Alaska. After W. Berry and C. C. Martin.



FIG. 356. Petrified trunks of araucarian trees that were living in this locality during the Triassic period, Fossil Forest Park, Arizona. Photo from U. S. National Museum.

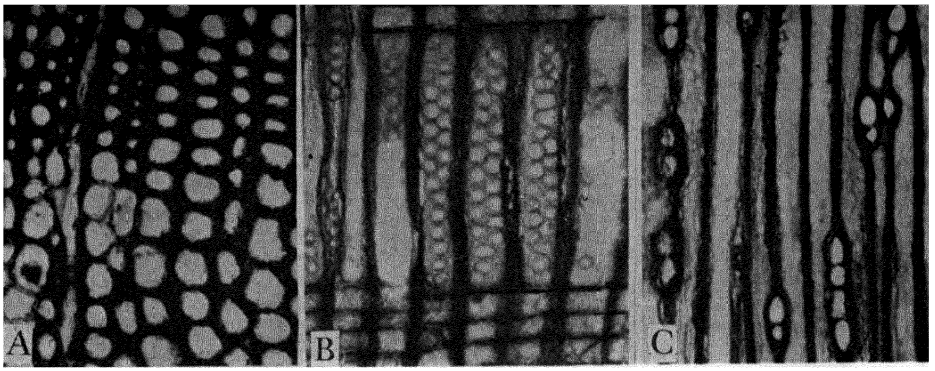

FIG. 357. Cross, radial, and tangential sections of petrified Cordaitean wood from trees that lived in the region of Arizona about 200 million years ago (Triassic period). During petrification cellulose and other wall substances in the wood cells were replaced in great detail by the silica present in subterranean solutions. Photo by Lyman H. Dougherty.

construct many phenomena and organisms of the different geological periods (Fig. 358).

Various means are used to estimate the relative and approximate ages of fossils. For long-range estimates, measurements of the extent to which uranium in the rocks has disintegrated to lead and helium appears to be far more reliable than any of the methods previously devised. The rate of this chemical process is not affected by the ordinary changes in temperature and pressure near the surface of the earth. Similarly, for estimates of 10,000 years or less the relative amounts of radiocarbon in bones of animals or in parts of plants has been an additional check on other methods formerly used.

The plants of a billion years ago were structurally less complex than many plants of today, and apparently were neither very large nor woody. They were aquatic plants, and some of them were deposited in situations where oxidation and disintegration were delayed for at least sufficient time for casts and imprints to be formed. Unfortunately, after the sediments had become rocks, the rocks were subjected to enormous pressure, high temperatures, and the forces of crystallization, and were so altered that very little is known about the fossils that undoubtedly occurred in them when they were first formed.

In such metamorphosed rocks we can infer the existence of plants from certain structural features of the rocks or from certain mineral deposits within them. For example, in the region west of Lake Superior

GEOLOGIC ERAS	PERIODS		LIFE	MOUNTAIN MAKING EPISODES	FIRST FOSSIL RECORDS	YEARS AGO
CENOZOIC	QUATERNARY	RECENT	AGE OF MAN			15,000
		PLEISTOCENE			(GLACIATION)	1,500,000
	TERTIARY	PLIOCENE	AGE OF FLOWERING SEED PLANTS AND MAMMALS	CASCADES AND 2nd SIERRA NEVADAS 2nd UPLIFT OF APPALACHIANS HIMALAYAS ROCKIES	GREAT INCREASE OF HERBACEOUS PLANTS & FLOWERING PLANTS	30,000,000
		MIOCENE				
		OLIGOCENE				
		EOCENE				65,000,000
MESOZOIC	CRETACEOUS		AGE OF GYMNOSPERMS AND REPTILES	1st SIERRA NEVADAS	WILLOW, BEECH MAGNOLIA	
	JURASSIC				DIATOMS CONIFERS	
	TRIASSIC			1st APPALACHIANS	CYCADS	
PALEOZOIC	CARBONIFEROUS	PERMIAN			(GLACIATION)	240,000,000
		PENNSYLVANIAN	AGE OF FERNS SEED FERNS CLUB MOSSES AMPHIBIANS FISHES	ACADIAN	MOSSES AND LIVERWORTS FOSSIL FORESTS GYMNOSPERMS FERNS FUNGI SEA WEEDS	
		MISSISSIPPIAN				
	DEVONIAN					
	SILURIAN					
	ORDOVICIAN		AGE OF THALLOPHYTES AND INVERTEBRATES	GRAND CANYON UPLIFT LATER LAURENTIAN EARLIER LAURENTIAN		700,000,000
	CAMBRIAN					
PROTEROZOIC					(GLACIATION) ALGAE AND BACTERIA	1,000,000,000
ARCHEOZOIC						

FIG. 358. Diagrammatic summary of the divisions of geologic time, important mountain building episodes, and oldest known occurrence of certain plant groups. The time scale is based on the disintegration of uranium to lead and helium. Note the time interval between the first and second Appalachians. During that interval the first Appalachians were eroded to a peneplain.

are great deposits of iron in pre-Cambrian rocks. In view of what we know about the deposition of comparable deposits in recent times we may rightfully infer that iron bacteria were living in the water where these deposits accumulated. Nearby are deposits of graphite, a compact form of carbon, which is the end product when crushing pressures, heat, and recrystallization have acted upon coal which in turn is a derivative of peat and other plant debris. Small amounts of carbon in metamorphic rocks might possibly have a different origin, but large deposits are derived only from vast accumulations of plant remains. Elsewhere deposits of sulfur compounds are evidence that sulfur bacteria formerly lived there.

If one surveys the probabilities of fossil formation under present conditions, rough estimates may be made of how many of the plants of today are falling into situations where they, or their imprints, will be preserved. He may then more fully realize how few are the land plants that are leaving a record which might be found in the earth a thousand years from now, and thus understand more clearly why the fossil plant record is so fragmentary and so scattered.

In the United States, however, there were long periods of time when shallow seas and lakes were far more extensive than at present. For example, during the Cretaceous period a broad waterway extended from what is now Texas to Alaska and connected the Gulf of Mexico with the Arctic Ocean. By late Cretaceous time the northern part of this area was elevated and the sea gradually receded southward, leaving a series of shallow fresh-water lakes and swamps. These became the sites of rich fossiliferous strata and soft coal deposits. At the present time in Canada and the bordering states there are hundreds of thousands of lakes and swamps in depressions of glacial origin in which peat is accumulating.

Extensive forested swamps existed over the eastern two-thirds of the states during Carboniferous time (Fig. 359), and in them trees and other plant remains accumulated. The major coal fields from Texas to the eastern Appalachian Mountains are the compressed and altered plant debris from these swamp forests. The coal is bituminous where the land was buried by later deposits and finally uplifted. In eastern Pennsylvania not only were these strata buried and uplifted, but the rocks were crushed and folded, and the bituminous coal there was changed to anthracite by compression and heat.

There were also long periods when the continent was far drier than it is today and the desert areas were much larger, for example during

the Permian period. When the Rockies were uplifted during the early Tertiary, the deciduous and broad-leaved evergreen forests that existed in the interior of North America were gradually killed by the increasing drought and were replaced by grasslands—the precursors of our present plains and prairies. The eastern deciduous forest in North America today



FIG. 359. Restoration of Carboniferous forest trees, ancestral ferns, club mosses, and equisetum. Courtesy of Chicago Natural History Museum.

and also such forests in Japan, China, and Europe are remnants of an earlier circumpolar mixed deciduous forest.

Many changes in the area and shape of the land surface of North America have occurred. During the Pliocene and prior to the Glacial period (Pleistocene) the North American continent was elevated more than 1000 feet above the present level. At that time more of the continent was land above sea level than at present. During the early Paleozoic there were periods of widespread submergence and emergence of the continent. The Paleozoic was the period during which the thick and extensive beds of limestone, sandstone, and shale of the eastern states were deposited in seas west of a high land mass that existed east of the present Appalachian Mountains. This ancient part of the continent has long since been eroded and in large part submerged.

Obviously, all these phenomena—elevation of the continent, uplift

of mountains, periods of volcanic activity, and long intervals of erosion and deposition—greatly altered the land surface. The accompanying fluctuations in climate were favorable to the growth and survival of certain kinds of plants but led to the death of others. These same phenomena occurred on other continents, and they are occurring at present perhaps as rapidly on the average as they did in the past. The processes by which plants change and the manner in which environment may affect their survival and rate of change were discussed in Chapters XXXIX and XL.

At times North America was broadly connected with Asia through the Alaskan peninsula. Likewise, land connected North and South America during certain millions of years, and during certain other millions of years the ocean covered parts of Central America. Land connections over long periods of time make possible the migration of species from one continent to another. The severing of these connections leads to the isolation of the plants of one continent from those of another. Isolation by restricting hybridization makes possible the independent evolution of species, genera, and families, and the consequent differences in modern continental floras.

These facts are necessary for one to understand why both plants and animals of Australia and New Zealand are so very different from those of the other continents from which they have been isolated since Cretaceous time when evolution in flowering plants and mammals was in its early stages. Eucalyptus trees there became dominant in moist temperate regions, and acacias in the drier areas.

Facts gleaned from the fossil record prove beyond a doubt the long period that plants have lived on the earth. Studies of fossils have definitely proved that the vegetation of the present is derived from that of the past. The dominance of flowering plants in the present flora is only slightly greater than in the flora of the Pliocene, but very much greater than in that of the upper Cretaceous. In the lower Cretaceous there were apparently only a few flowering plants in a flora dominated by ferns, cycads, and conifers. Evidently all through the geological periods new kinds of plants have developed as a result of evolution and older kinds have become extinct.

Pre-Cambrian and Paleozoic floras. The fossil record is ample proof that the simplest and least specialized plants were the first on the earth. Studies of Archeozoic and Proterozoic rocks have up to this time yielded no evidence of organisms more structurally complex than the bacteria

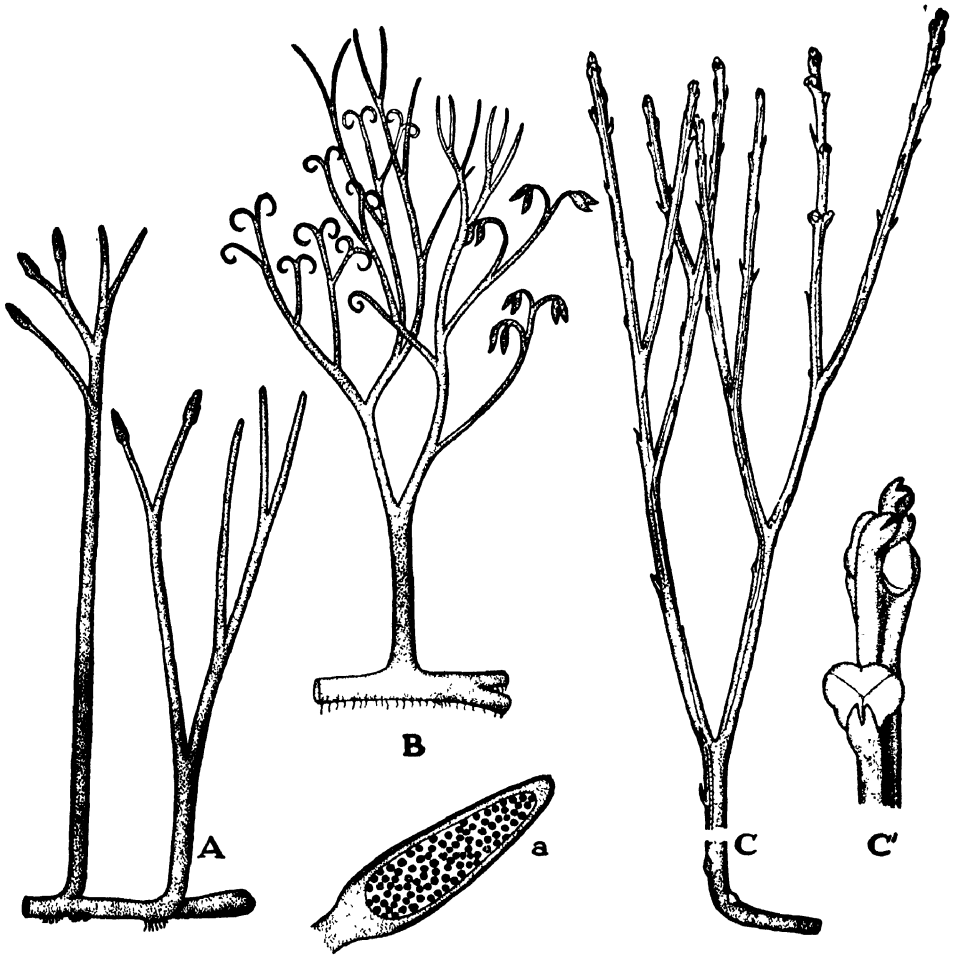

FIG. 360. Two small Devonian land plants (A-B) belonging to the *Psilophytes*. A-a, *Rhynia* and an enlarged section of one of its sporangia; B, *Psilophyton*. C-C', *Psilotum*, a modern tropical epiphyte reminiscent of the early land plants. Restoration by Kidston and Lang (A), and by Dawson (B).

and blue-green algae. But early in the Cambrian there is evidence that the blue-green, the green, the red, and the brown algae—all lime-depositing species—were present, and it is probable that they were present also in pre-Cambrian waters. So meager are the facts about the algae of the Cambrian and Ordovician that any detailed description must be postponed until better-preserved fossils are discovered.

Silurian rocks contain fossils of ancestral vascular land plants. Their dichotomous vegetative body bore apical sporangia containing spores in groups of four (tetrads). In vascular plants of today the formation of spores in tetrads is associated with reduction division and sexual re-

production. These ancestral plants (Fig. 360) have been distinguished as Psilophytes (leafless plants).

The middle Devonian Psilophytes included plants with upright dichotomously branched stems having stomates, scale-like appendages, and terminal sporangia. Moreover, the growing stem tips uncoiled like those of fern leaves. The stems of some species had spirally arranged scales, others were naked. The stems consisted of distinct tissues: epidermis, cortex, phloem, and xylem. The upright stems formed dense colonies which developed from horizontal rhizomes bearing rhizoids but no roots. These are a few of the characteristics of early vascular land plants known from various scattered localities in Australia, North America, and Europe.

Primitive lycopods (club mosses) were also present in the middle Devonian, and the tree species became the dominant plants of Carboniferous time. Lepidodendrons and Sigillarias are the best known of these plants (Figs. 359 and 362A). They had lance-shaped leaves, and sporophylls arranged in terminal cones on branches, and their stems had cambiums by which secondary thickening occurred. The leaf scars and their imprints are among the commonest and most beautiful coal shale fossils.

The ancestral plants of present-day equisetums, the Calamites, were present also. Apparently they were common in the Devonian and abundant in the Carboniferous. Some of them were trees with jointed stems up to 100 feet tall. Their branches occurred in whorls. Leaves were simple and the sporophylls were arranged in cones. Some had large underground rhizomes.

Ancestral ferns appeared in the Devonian period. Not all the representatives were large, but again the woody species seem to have been most abundant. The leaves bear a close resemblance to those of modern ferns, but several differences in stem structure and in reproductive organs are evident. Some of these ferns were heterosporous, and others were homosporous.

For many years all the fossil leaf imprints and carbonized leaves that resembled fern leaves were thought to be ferns, but evidence is continually appearing that many of the fern-like leaves belonged to plants that bore seeds, the Pteriodsperms (seed ferns). These were the earliest seed plants. The seeds, however, were primitive (Fig. 355A). The female gametophyte grew inside the ovule (megasporangium) as it does in modern gymnosperms (Fig. 328). The sperms were motile as in

ginkgoes and cycads (Fig. 329). Their leaves resemble those of ferns and the microsporangia resemble those of the Psilophytes, but because

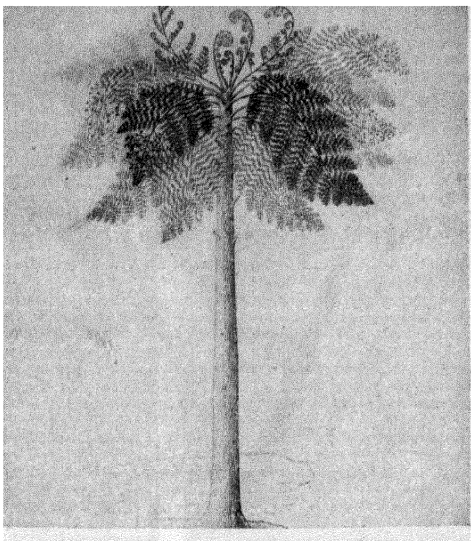

FIG. 361. *Aneurophyton*, a Devonian fern-like tree with structural features that combine certain characteristics of the *Psilophytes*, the primitive *Pteridophytes*, and the *Pteridosperms*. Restoration by W. Goldring. Courtesy New York State Museum, Albany.

of their naked seeds they are classed among the primitive gymnosperms, between the ferns and the cycads. Another group of gymnosperms associated with the seed ferns was named Cordaites. These plants had long slender leaves and sporangia borne on short lateral branches (Fig. 362B).

The luxuriant vegetation of the Carboniferous must have grown in swamps in a warm temperate and very moist climate where the annual range of temperature was very narrow. Large trees and other woody plants were predominant, and constituted the bulk of the parent material of the coal strata. More rarely the coal strata contain great masses of spores and even thick layers of algal remains.

Permian "red beds" in America were deposited under arid conditions, and in low latitudes around the world there were high areas with glacial climates. Drought and low temperatures led to the extinction of the Carboniferous swamp-forest floras. Both climatic changes were associated with the great crustal uplifts that closed the Paleozoic Era.

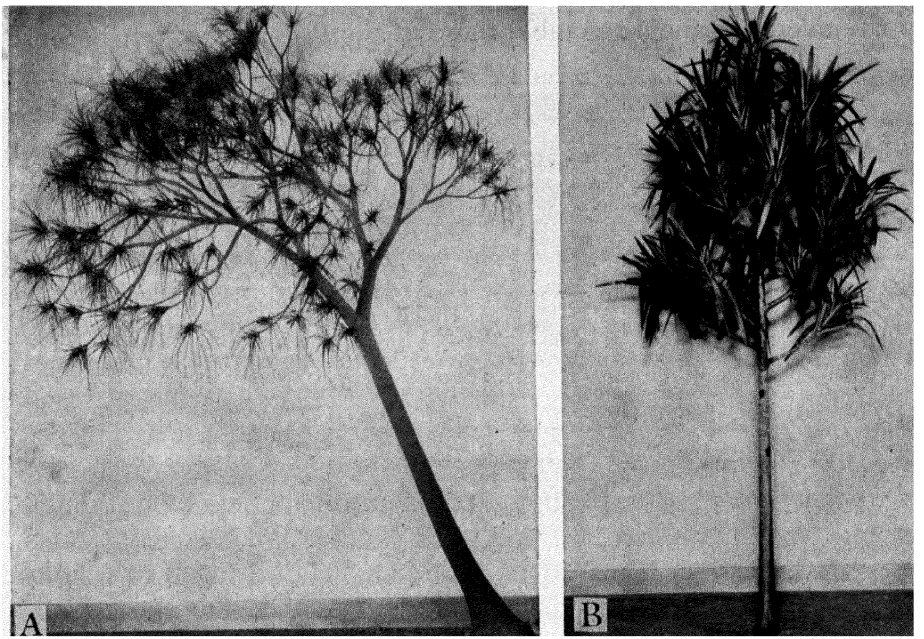

FIG. 362. Restorations of Carboniferous trees: A, *Lepidodendron*, a forerunner of the club mosses; B, *Cordaites*, a primitive gymnosperm. Courtesy of Chicago Natural History Museum.

No fossil flowering plants (angiosperms) have been definitely identified in Paleozoic rocks. The evolution of sepals, petals, pistils, fruits, fusion nuclei, triple-fusion nuclei, and endosperms is comparatively recent. Some of the features found in flowering plants, however, had been evolving since pre-Cambrian times. The reader may find it interesting to give thought to the relative ages of some of these features. How old, for example, are the processes of seed formation, pollen formation, cambial growth, development of leaves, organization of cells in a multicellular individual, gamete formation, mitosis, spore formation, chlorophyll synthesis, vegetative multiplication, and respiration? Have these inherent processes remained unaltered since their first appearance?

Mesozoic floras. The world-wide physical revolution that ended the Paleozoic Era resulted in the most profound changes in the plant and animal populations of the earth during geological history. During the Triassic and Jurassic periods ten of the most characteristic orders of trees and smaller plants of the Paleozoic became extinct. The Pterido-

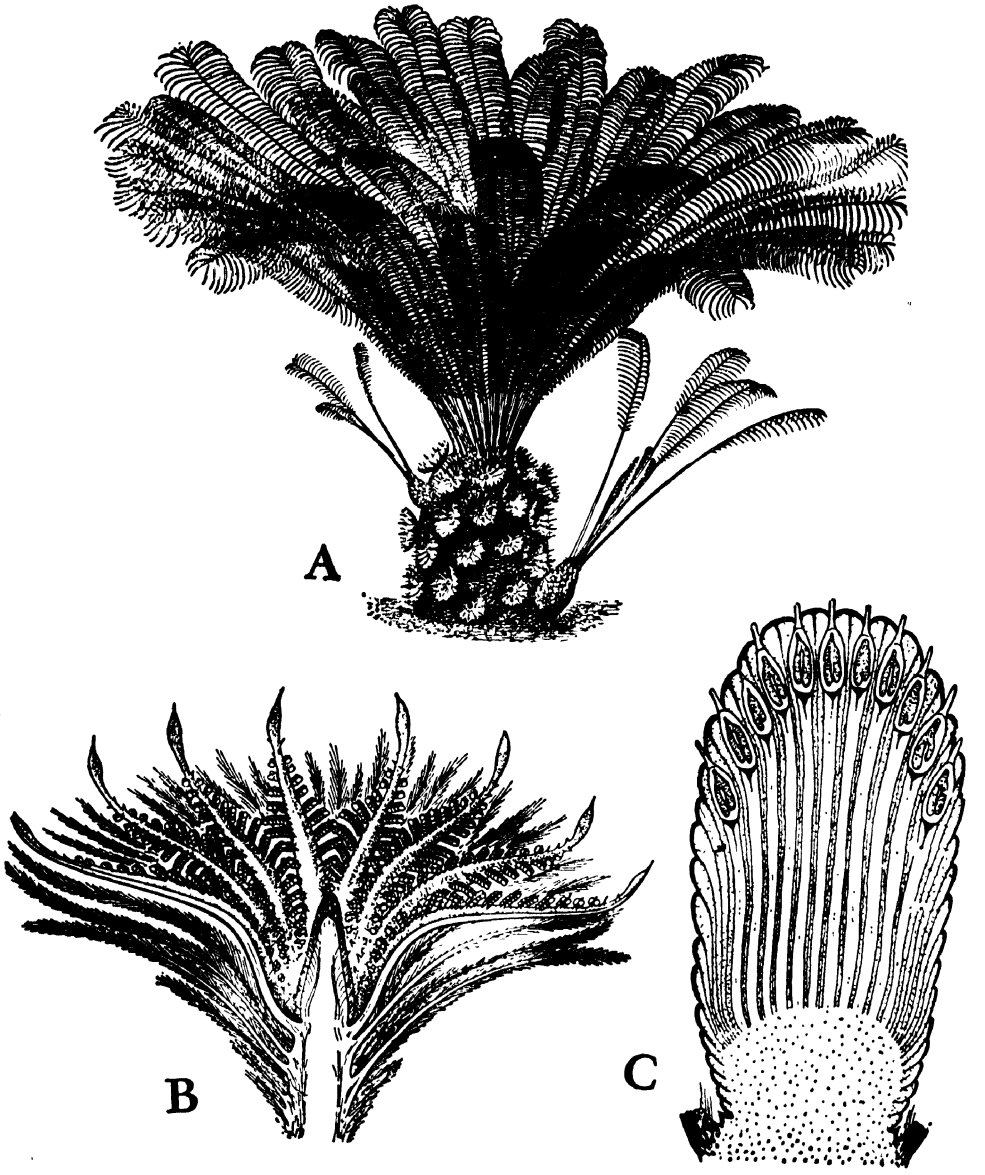

FIG. 363. *Cycadeoidea ingens.* Restoration of a Lower Cretaceous cycad-like plant bearing many flower-like cones. Each cone, or "flower," contained a central ovulate cone surrounded by stamen-bearing bracts and sterile bracts. These "flowers" grew as short lateral branches in the axils of scales on the thick erect stem which also bore a crown of simple compound leaves. A, general form of the plant. B, vertical section of a flower. C, vertical section of a mature ovulate cone. From drawings by G. R. Wieland.

In contrast, cycads have terminal cones of sporophylls, ovulate or staminate, on different individual plants. See Fig. 322.

sperms continued to exist. The early Mesozoic floras were dominated by ferns, cycads, equisetums, ginkgoes, primitive conifers, and cycad-like plants (Cycadeoidea). The Cycadeoidea, unlike the cycads, had short lateral branches bearing whorled ovulate and staminate sporophylls that formed lateral flower-like cones (Fig. 363). The conifers included araucarians, redwoods, and primitive pines. The most striking feature of the flora was the abundance and diversity of cycads and cycad-like plants; hence the first two periods of the Mesozoic are often called the "Age of Cycadophytes." The zoologists call it the "Age of Reptiles"

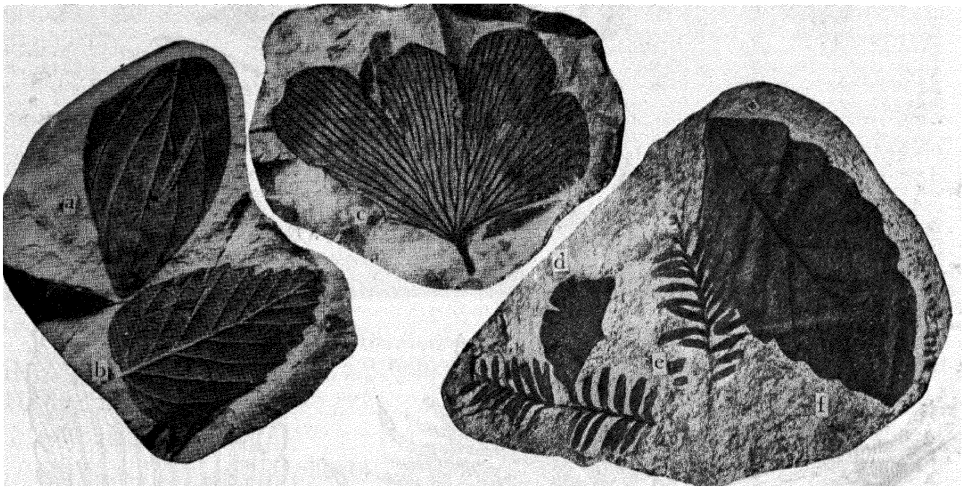

FIG. 364. Leaf prints in rocks of Upper Cretaceous age in Alaska. Represented here are (a) dogwood, (b) alder, (c-d) two species of Ginkgo, (e) redwood, and (f) oak. From *Professional Paper No. 159*. United States Geological Survey.

because that group reached its greatest diversity then and the saurians dominated the animals of the sea, the land, and the air.

The land plants of the early Cretaceous period in America were dominated by conifers, ferns, and cycads. During this period the land surface became lowered and much of it was submerged for long intervals. The sedimentary rocks formed at this time contain a large number of fossils belonging to angiosperm genera similar to those of present-day vegetation (Fig. 364). Apparently angiosperms had been developing on the earth for many thousands of years previous to this time. Ferns and cycads declined rapidly, but the conifers remained abundant. Among these conifers were species of pine and redwood and species of genera now extinct.

The amazing part of the upper Cretaceous fossil record is the great diversification of the angiosperms and their migration to most parts of the northern hemisphere. Representatives of some families migrated even into and through the tropics to the temperate regions of the southern hemisphere. In the fossil floras studied there is abundant evidence of the presence of scores of genera and hundreds of species of woody dicots and lesser numbers of herbs. Of familiar genera were species of sassafras, magnolia, sweet gum, oak, elm, willow, poplar, ash, sycamore, and eucalyptus. Monocot species have been found in smaller numbers but include palms, grasses, sedges, cattails, and water lilies. Another remarkable feature of this widespread flora was its uniformity in generic composition in such widely separated areas as Greenland and Texas. This does not imply that the plants represented by the fossils were living simulanteously in these two distant areas. The Cretaceous period was long—perhaps 60 million years. This is equivalent to all the time that has elapsed since the Cretaceous period.

Cenozoic floras. Tertiary floras became more and more differentiated as the climate of the polar regions grew colder and mountain-making and volcanic activities in the western mountains broke up the uniform temperate regions into areas with different rainfall patterns, various amounts of precipitation, increased or decreased humidity, and zonation of environments on mountain slopes. Apparently the greatest evolutionary process of Cenozoic time has been the development and dispersal of herbaceous plants.

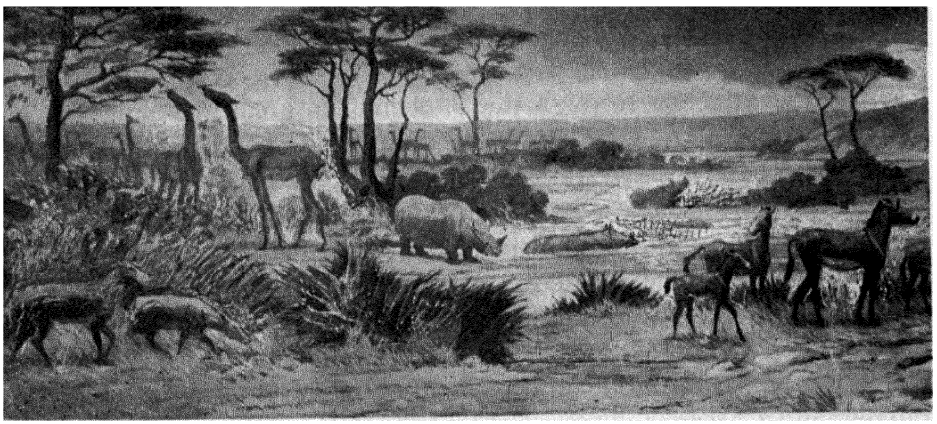

FIG. 365. Species of antelope, camel, rhinoceros, and horse in western Nebraska during the Pliocene. Restoration by C. R. Knight. American Museum of Natural History, New York.

By the beginning of the Tertiary there had been a migration of angiosperms to Australia, New Zealand, South Africa, and South America, and also a rapid development and differentiation of modern genera and species. Plants and plant communities very similar to those of modern temperate climates occurred in polar regions in both America and Eurasia. Warm temperate plants were characteristic of the middle latitudes, and subtropical plants were abundant in the southern half of the United States. Throughout the Tertiary there was a progressive cooling



FIG. 366. Animals of the Mississippi Valley at the close of the Glacial epoch. Restoration by C. R. Knight. Copyright by American Museum of Natural History, New York.

and these three zones of plants gradually shifted southward and the arctic floras became segregated in the north. Redwoods that grew earlier in circumpolar regions are now represented by a meager remnant in Oregon and California. Some of the subtropical plants have survived only in Mexico and Central America, the Florida peninsula, and the islands of the Caribbean Sea.

From the Miocene through the Pliocene the greatest changes in the vegetation of the United States resulted in the restriction of the deciduous forests of the eastern states, the segregation of the eastern and western conifer forests, the northward expansion of grasslands and semideserts from the southwestern states to the Canadian boundary. These migrations led to the extinction of some species, and the survival of other species in certain habitats or restricted areas. All these changes in distribution and relative survival of plants resulted from changes in climatic factors that followed the elevation of the Rockies, Sierras, coast ranges, and Cascades. Toward the close of the Pliocene the northern part of the continent was a thousand feet higher than at present and islands off both coasts were part of the mainland.

During the Pliocene and early Pleistocene land connections between Asia and Alaska and between Central and South America were routes by which plants and animals migrated into and out of North America. The most striking evidence of these migrations is the fossil record of the abundance of large mammals, some of which originated here, others being known to have lived previously in Eurasia or in South America. There is evidence that analogous migrations of plants occurred, but the facts are more difficult to portray.

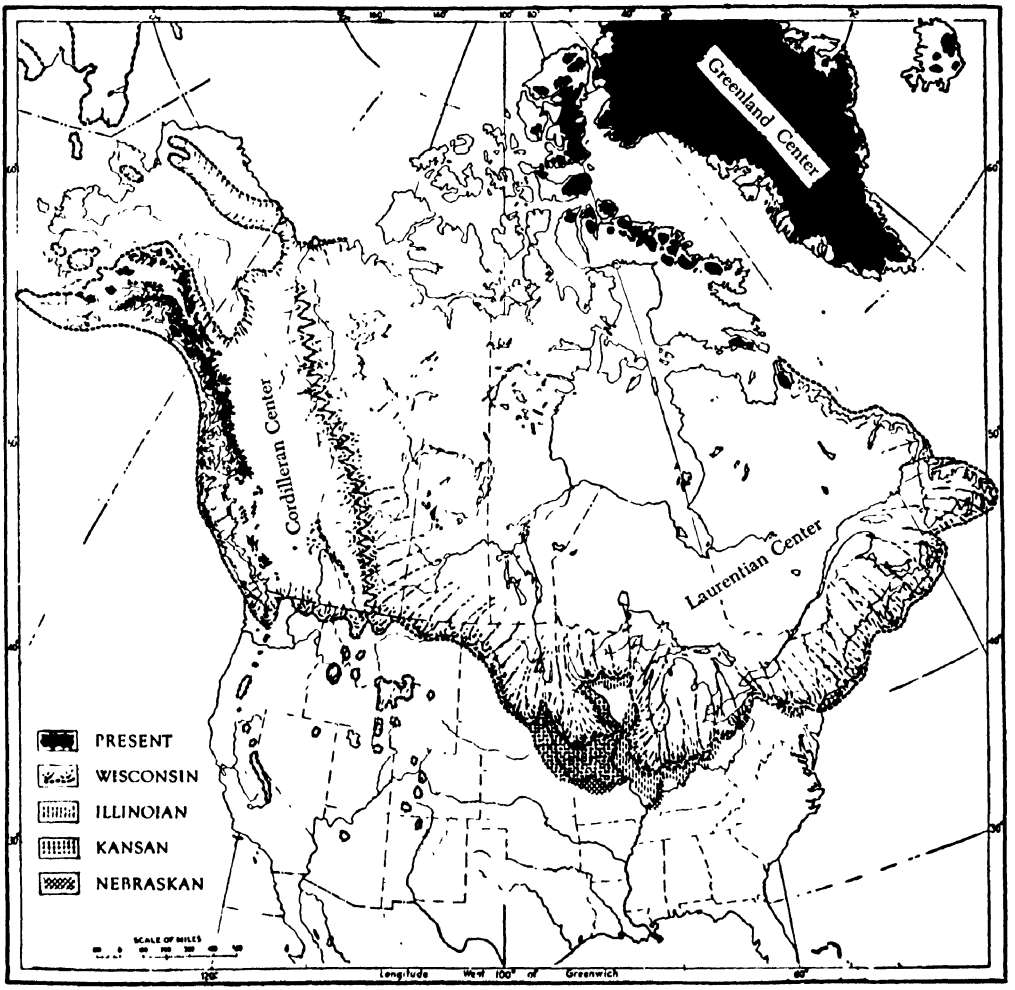

FIG. 367. Extent of North American present and past ice sheets. During each of the glacial epochs the centers of ice accumulation were in the Cordilleran, Laurentian, and Greenland regions. The present ice sheets cover an area of 700,000 square miles. The altitude of the ice surface on Greenland is 10,000 feet above sea level. After Geol. Soc. Amer., *Special Paper 60,* 1945.

During the Pleistocene there were four epochs of ice accumulation and development of continental glaciers. In each epoch the high mountains (Cordillera) in western Canada, the Laurentians in the east, and Greenland seem to have been the centers in which the ice accumulated and from which it spread in all directions. Ice from these sources eventually met on the high plains of Alberta, and the Laurentian ice flowed southward to the Ohio and Missouri Rivers (Fig. 367). Between the glacial epochs there were long warm intervals when the climate was not very different from that of the present, except that warm climates extended much farther northward.

The first ice invasion into the states probably occurred about a million years ago. The last invasion, known as the Wisconsin ice sheet, attained its maximum about 25,000 years ago and disappeared from central Canada only a few thousand years ago.

The causes of great continental glaciers are not fully known, but two of the contributing factors seem to be well established. First, all present and past epochs of glaciation have been centered in high mountain ranges where the temperatures are lower than at lesser elevations, and the annual precipitation of snow exceeds the rate of melting. Second, when continental glaciers occurred in North America they likewise occurred in Eurasia, and in the cold temperate mountains of the southern continents. In other words, when the average temperature is lowered the 5°-10° F. necessary to bring on glaciation the whole earth is affected. Apparently the only factor that can bring about this general lowering of temperature is a decrease in the amount of radiant energy from the sun.

The lowering of the temperature took place a long time before the ice sheets accumulated to a depth of two or three miles and the ice invaded the northern states. Meanwhile the northern cold temperate plants as well as the warm temperate ones increased in abundance southward. The plants left behind died or were destroyed by the ice sheet. This process went on until the ice flowed into regions where the average annual melting and the average forward movement at the ice front were equal. Later when the temperature rose, the melting and wastage of the glacier were greater than the ice accumulation, and the glacial front receded. Northward migration of plants onto the land laid bare by the ice followed.

How far from the ice front the vegetation was greatly disturbed at the maximum is unknown, but the best estimates are that the effects on

vegetation were about a hundred miles from the ice—except in mountains extending southward. Some pre-glacial southern species survived in the warmer coves and rock gorges near the glacial boundary.

There is evidence that precipitation south of the ice sheets was greatly increased. On the western high plains and plateaus forests replaced grasslands and sagebrush steppe. On the high plateau we know that there were many large and deep lakes that existed for many centuries and that today are either dry or nearly so.

Major migrations of plants southward and then northward preceded and followed each of the four epochs of glaciation during the Pleistocene period. The time intervals between these repeated migrations are measured in hundreds of thousands of years. In spite of these long migrations there is little evidence that many pre-glacial species of plants were exterminated. In this respect the Pleistocene record of plants is unlike that of the mammals. Although the mammals survived the climatic variations of the four glacial and interglacial epochs, many of them became extinct during the melting back of the Wisconsin ice front. Species of mammoth, mastodon, camel, horse, ground sloth, giant bison, giant beaver, musk ox, tiger, and many others disappeared with the last ice sheet, but their fossil bones attest their previous abundance and widespread distribution.

The land surface left by the melting ice was highly irregular and poorly drained, and in many localities buried masses of ice which subsequently melted left thousands of small lake basins. As vegetation moved into these areas many of the lakes were occupied by boreal plants and became bogs—plant communities consisting of mosses, aquatic herbs, and low shrubs that built floating mats along the shores of lakes and finally over the entire surface. The plant debris gradually filled the basin with successive layers of peat containing pollen of the period. Recent studies of the kinds of pollen entrapped in the peat have contributed to our knowledge of the successive kinds of trees and shrubs that lived in the vicinity. The pollen of some species of plants disintegrates sooner than that of others in peat deposits, and plants with wind-blown pollen are more apt to be represented than those with insect carried pollen. These are two sources of error in the interpretation of pollen records from peat (Figs. 368 and 369).

Summary. On the basis of the fossil record, it appears that plants have been living on the earth for a billion years or more. The first plants were very small and simple in structure. Their physiology probably was com-

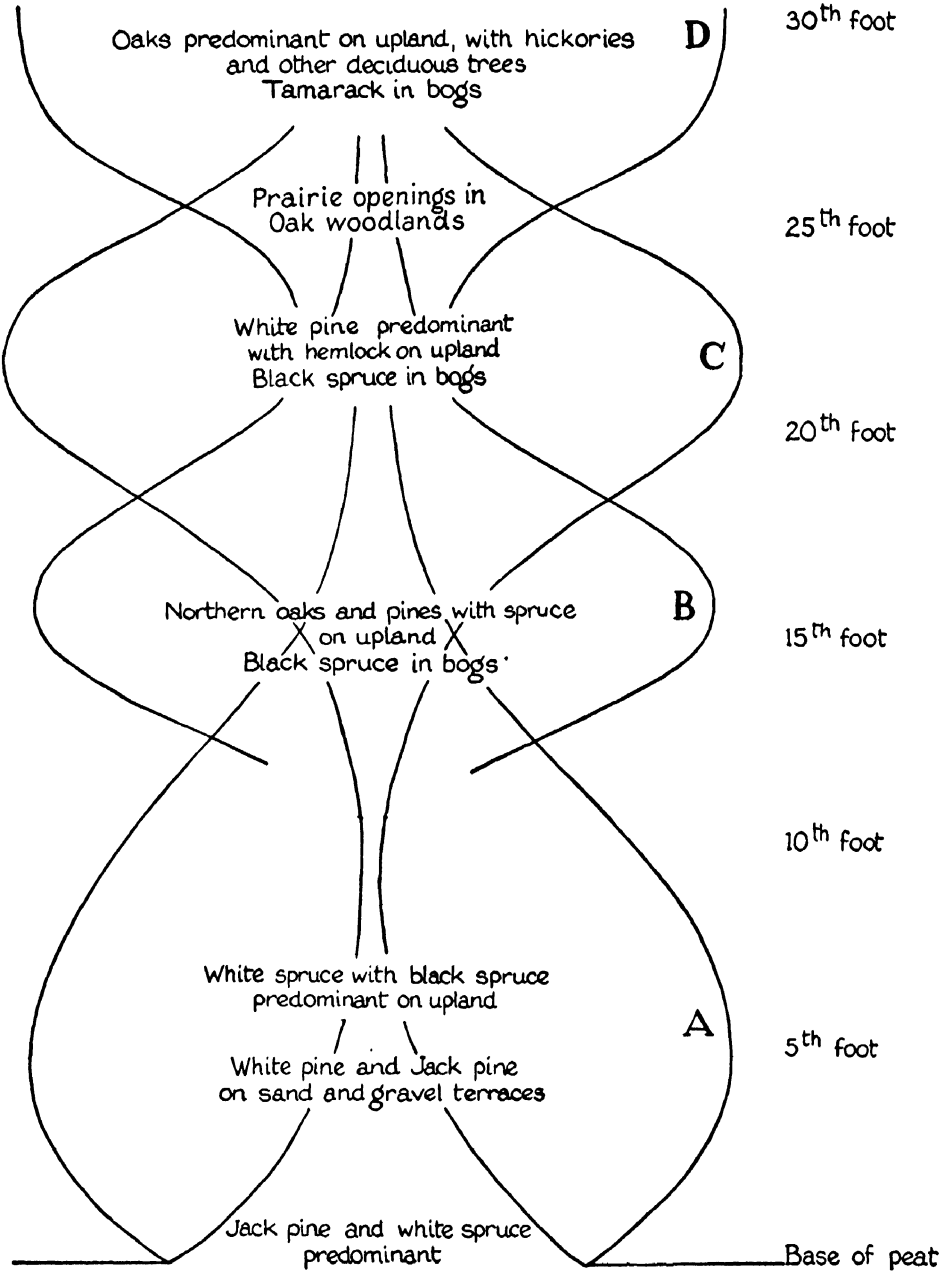

FIG. 368. A diagrammatic representation of the relative abundance of tree pollens in successive layers of peat in a bog in central Ohio together with the forest types inferred to be living near or in the bog at the time the layer of peat was deposited. The diagram should be read from the bottom upward. Data from L. R. Wilson and P. B. Sears.

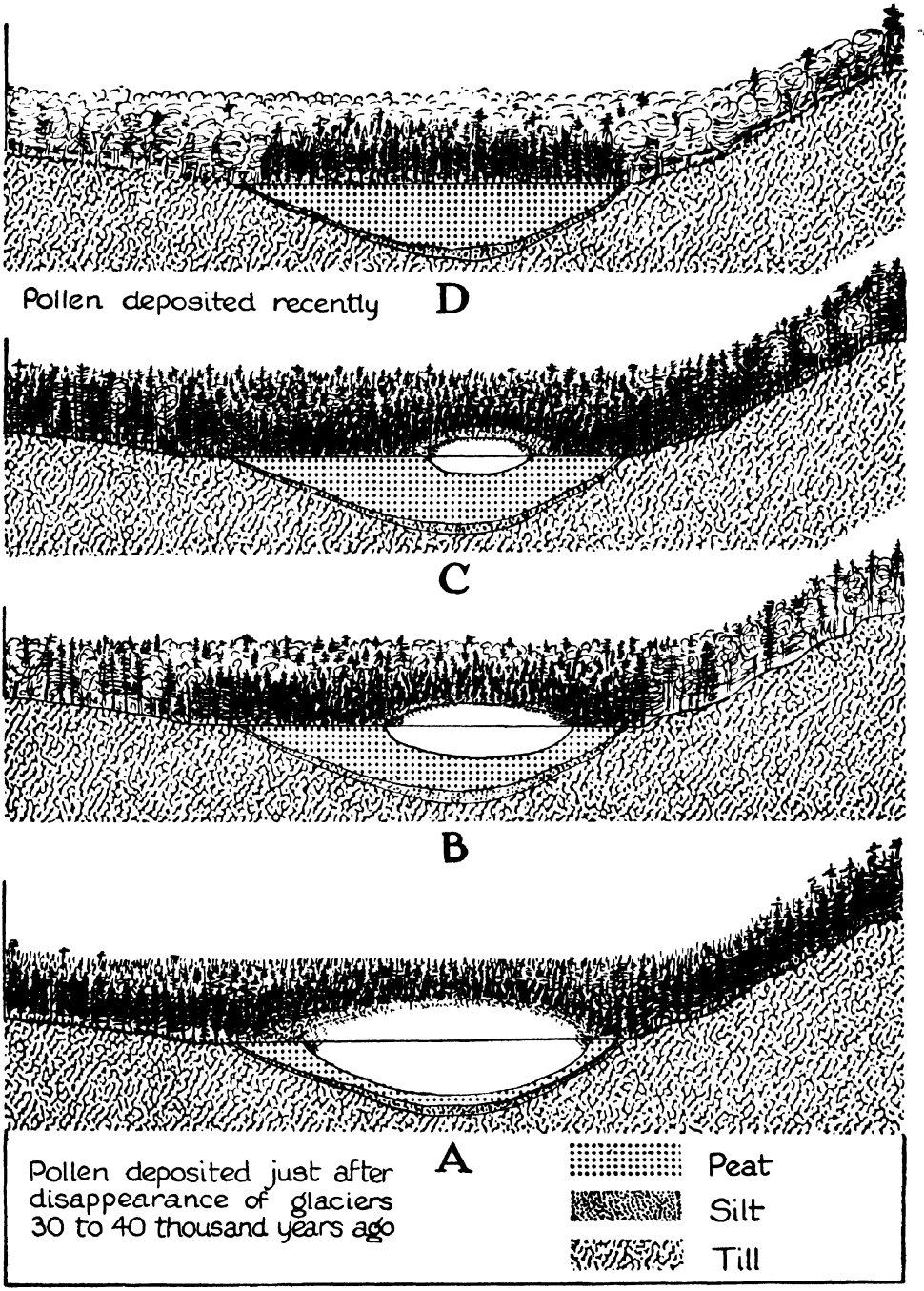

FIG. 369. Four stages of the filling of a bog basin and the appearance of the adjoining landscapes in central Ohio since the disappearance of the continental ice sheet. The composition and succession of the forests are inferred from observations made of present northern forests as well as the relative abundance of fossil pollens in the peat bog referred to in Fig. 368.

plex, for no living systems are known to have a simple physiology. Through the process of evolution of hereditary units of matter in living cells (Chapters XXXIX and XL), new kinds of plants have, at all times since their origin on the earth, continued to develop from preexisting ones.

Diverse groups appeared, became abundant and widespread over the earth, waned, and either became extinct or are represented in our present flora only by isolated species. Early evolution in land plants seems to have resulted in the development and dominance of woody plants, often of tree size. Herbs are apparently more recent, for they constitute a far larger proportion of the fossil flora of the Cenozoic than of all previous eras.

Evolution in plants previous to the close of the Paleozoic resulted in the formation of most of the fundamental features of plants today, except those found only in the flowering plants (angiosperms). Early evolution in angiosperms during the Mesozoic seems to have been both rapid and widespread in the temperate lands of the northern hemisphere. From there angiosperms spread across the equator to the southern continents.

The vegetation of the present is composed of remnants of past vegetations, together with new combinations of old and new species. The distribution of modern species and plant communities is dependent partly upon the present physical and biological environments, and partly upon the historical background, such as elevation and submergence of the land, formation and erosion of mountains, land connections with other continents, changes in climate and local diversification of the climatic factors, prolonged intense drought, and glaciation. Some appreciation of all these biological and physical factors is essential to an understanding of the vegetation of a continent, such as that of North America.

Plant and animal fossils have been used by geologists to identify rock strata, the sequence of their development, and the conditions under which they were formed. Engineers have found them of prime importance in the identification of underground strata when drilling for certain products such as metalliferous deposits and water supplies as well as for the coal, petroleum, and natural gas derived from plants. The various compounds and chemically bound energy in these organic products of plants of the past are very important factors in our present economy, but the geologically slow replacement of these products stands in sharp contrast to the amount of energy chemically bound annually in

compounds in our present plants. Among other deposits resulting from activities of former plants are iron ore, certain sulfur deposits, diatomaceous earth, and various constituents in soils.

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CHAPTER LIII

THE VEGETATION OF NORTH AMERICA

Recent improvements in facilities for land and air travel have afforded millions of people the opportunity of visiting most parts of the North American continent. The outposts of civilization in Canada, Mexico, and Central America have rather suddenly become fairly accessible to anyone interested in going there. This has awakened a new interest not only in unfamiliar human populations, their customs, industries, and foods, but also in the native vegetation, which has always been the chief source of biological supplies of isolated peoples and pioneer settlements.

Such trips may now be even more enjoyable and enlightening, for enough has been learned about the biological and economic relations of plants and their heredity and physiology that observations may be made with increased understanding. Never again will plants be just something green along the route, put there merely to be enjoyed, ignored, or destroyed at will, for we know that they are the basis both of our existence and of much of our individual and national wealth. The development of the plants, on the other hand, is dependent upon their physical environment, a part of which we may alter, either to the advantage of both the plants and ourselves or to the detriment of both.

This chapter on the vegetation of North America is a brief sketch of the vegetation of a continent (Fig. 370). Only a few of the many biological and economic relations of this vegetation are mentioned; but many others, together with interpretations of the phenomena described, can be inferred from the facts presented in preceding chapters.

The differences in climate from place to place on the various continents are so numerous that areas of similar climates and equivalent types of vegetation occur on each of them. Most of the species, many of the genera, and a few of the families, however, are different.

Climatic contrasts of the continent. From north to south the greatest contrasts result from differences in light and temperature conditions. North America extends southward from a region of nearly continuous ice and snow, where three-fourths of the year is winter and one-fourth



FIG. 370. Map of the climatic plant formations of North America. In the east the forest boundaries are those of about a century ago.

spring, where light intensity is never high, and the daily light period is 24 hours long during the short growing season. The southern extremity of the continent lies within the tropics, where, on the basis of temperature, there is but one season, summer, which may be wet or dry or periodically wet and dry, where light intensity is high, and the daily light period is 12 hours long throughout the year.

A west-to-east belt across the continent from Oregon to Massachusetts is the region of prevailing westerly winds and is marked by great differences in total precipitation, in snowfall and rainfall, in the prevalence of drizzling rains or sudden downpours, and in seasonal distribution of precipitation. These variations affect the atmospheric humidity and the available soil water. Starting at the west coast, with a hundred inches of rain principally during the colder months of the year, and persistent fogs, the high coastal mountains lead to a reduction in rainfall on their eastern slopes, so that grassland and semi-desert conditions prevail on the high plateau. Precipitation again increases in the Rockies, but they in turn cast a rain shadow eastward on the high plains where 10 to 15 inches of precipitation is general. The annual precipitation in the eastern half of the United States varies from 30 to 60 inches and comes from the moisture in the air masses moving in from the Gulf of Mexico. Central America extends into the trade winds, or prevailing easterlies, and rains are abundant east of the mountain crests and meager on the western slopes.

As a result of the many possible combinations of light intensity, length of day, temperature extremes, length of growing season, rainfall, snowfall, frequency and length of drought periods, fogs, and hot dry winds, the continent as a whole has many climatic regions, large and small, extending in various directions; and the nature of the vegetation reflects the diversity of conditions. Indeed, students of climates have long recognized that the larger patterns of vegetation are among the best indicators of climatic patterns and boundaries. High mountain slopes and crests may approximate conditions of high latitudes; northern protected river valleys and warm seacoasts may simulate conditions of the south.

Prehistoric factors. In addition to the amount and intensity of present-day factors, the distribution of many plants has been limited by prehistoric or geologic factors. Among these factors, slightly lower temperature and glaciation, with their attendant effects on precipitation, drainage, and soils, have left their imprint on the vegetation of many parts of the continent. Climatic shifts involving prolonged periods of drought or of

increased rainfall in postglacial time have caused many of the irregularities of plant distribution. On the margins of the continent the position of the seashore has varied, in part because of the uplift or sinking of the land and in part because of changes in the height of sea level itself.

Climatic Plant Formations

Tundra (Figs. 371, 373). This name has come into general use throughout the world for the low, sometimes scanty vegetation which



Fig. 371. Tundra in southwestern Mackenzie in June when anemone, mountain avens, and lupine flowers are conspicuous in the fescue grass ground cover. Photo by Hugo M. Raup.

encircles the polar ice caps and in America covers the "barren grounds." At its southern border is what the Indians called "the land of little sticks" and the boreal forest. Here and there the barren grounds are broken by rivers flowing into the Arctic Ocean through deep valleys where the snow melts somewhat earlier and the growing season is longer. Some valley slopes are also less exposed to dry winter winds, and on them the northernmost outliers of the forest occur.

The land in general is poorly drained and wet from the melting snows and gradual thawing of the ice within the surface soil. The drier parts are covered with grasses, sedges, and rushes interspersed with lichens,



FIG. 372. Sixty years ago this mature spruce forest grew above the ice at the lower margin of Malaspina glacier, Alaska. In later years the ice melted, the trees tumbled, and the forest was destroyed. Photo by I. C. Russell, U. S. Geol. Survey.



FIG. 373. Remnants of a western hemlock-Sitka spruce forest buried under 200 feet of gravel about 1000 years ago. They have been uncovered recently by flood water from a rapidly melting glacier farther up the valley. These tree trunks and the plants of the forest floor are in a perfect state of preservation. Photo and data from W. S. Cooper, Fourth Expedition to Glacier Bay, Alaska, 1935.

mosses, and a variety of small herbs with relatively large brilliant flowers (Plates 1 and 3). There are also areas of such evergreen heaths as bearberry, crowberry, and leatherleaf, together with creeping willows and low birches. Alder, birch, and willow thickets occupy the warmer slopes and stream banks. The myriad pools become covered with sphagnum and other bog mosses. Flat areas covered with peat and mosses and with scattered shrubs or dwarf trees are called "muskegs."

Even during the growing season, below a depth of a few inches, or a few feet, the subsoil is frozen to depths as great as three hundred feet—fossil ice, it might be called, since some of it was formed at the close of the period of glaciation. In our latitude plants are affected by the depth to which soils freeze in winter, while in the tundra they are affected by the depth to which soils thaw in the warmer season. In general, the tundra is a region of fogs, drizzling rains in summer, and snows accompanied by violent winds during the winter. Alternate freezing and thawing between seasons stirs up the soil and moves it down slope.

Plants of the tundra survive freezing night temperatures during the growing season and grow at low average temperatures. Moreover, the plants may freeze at any stage of development, including the flowering period, survive under the snow, and continue growth the following season (Figs. 374 and 375). The vegetation of the tundra, then, is composed



FIG. 374. Adder's-tongue (*Erythronium montanum*) that grew through a 3-inch layer of snow and bloomed. Photo taken by W. H. Camp at Mt. Ranier, Washington.

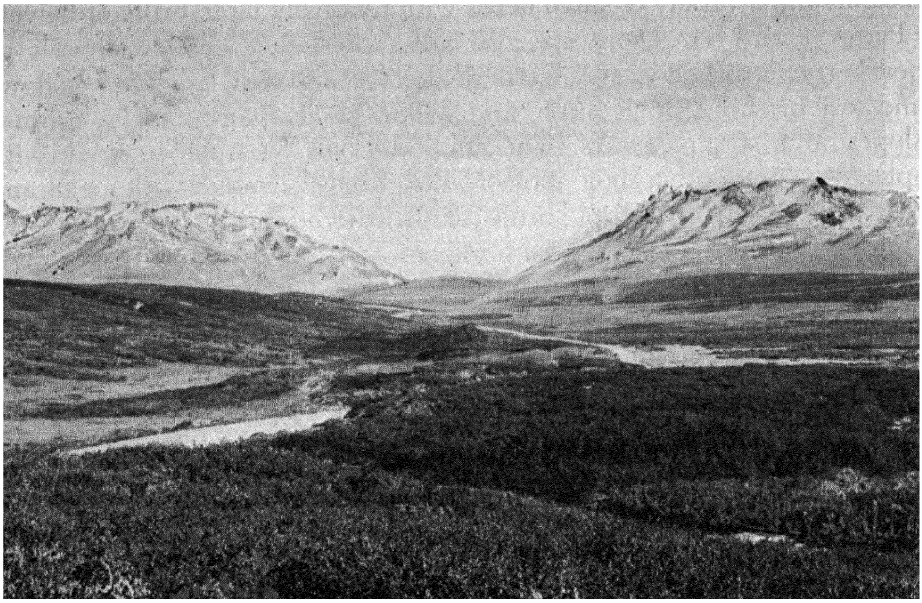

FIG. 375. Dwarf birch-willow-tundra, in Dalton Pass, southwestern Mackenzie. Shrubs are less than 3 feet tall. Photo by Hugh M. Raup.

of plants that pass most of the year in low-temperature dormancy, and grow during only two to three months.

The survival of plants in different situations in the tundra is determined far more by the direct effects of environment than by the interference of other plants. Consequently, apparent successions are more in the nature of fluctuations in the proportion of different species than of the progressive development of more highly organized communities.

The southernmost isolated communities of tundra vegetation occur in bogs, on sand plains, on cliff edges, and on the summits of high mountains above the timber line. The conditions in alpine tundra are somewhat different from those in the polar tundra, especially the light intensity, the length of day, and the quality of light. The length of the growing season, however, and the soil conditions may be much the same. The absence of trees is not due to the intense cold. The Siberian fir forest grows in the coldest locality in the northern hemisphere.

Boreal forest (Figs. 376-377). This is the most extensive forest on the continent and extends south of the tundra from western Alaska to Newfoundland. The most characteristic tree is the white spruce, which

occurs throughout the forest. Black spruce and tamarack (a deciduous conifer) also occupy large areas, especially the poorly drained ones, as well as wet bogs, and "muskeg." Both species sometimes occur on the upland, and the black spruce is frequent on rock outcrops, cliffs, and mountain tops. Other trees of importance are balsam fir, which is a common associate of the white spruce east of the Rockies; jack pine, on



FIG. 376. Black spruce forest on a bog near Big Falls, Minnesota. Photo from U. S. Forest Service.

sand plains and on sand and gravel terraces; balsam poplar, on flood plains; and trembling aspen and canoe birch, now occupying extensive burned-over areas. The most characteristic shrubs are thickets of alder and birch, low junipers, with blueberries, huckleberries, and other heaths, and sweet gale on acid soils. This formation is also characterized by an abundance of mosses, liverworts, and lichens.

The northern boundary is an intricate pattern of interlacing sites. Those with deeper soils and a longer growing season are occupied by forest peninsulas and isolated groves; the tundra occupies the shallow soils and short-season areas. The southern boundary in the west merges

with the northern boundary of the western evergreen forest. Across the plains it is bordered by grasslands and aspen-grass savannas. Eastward it intermingles with the hemlock-hardwood forest of the Great Lakes region and the northern Appalachian Mountains.

The climate of the region is exceedingly rigorous, but the winter temperature rarely falls to −40° F., and the snowfall is deeper than in



FIG. 377. A spruce-fir forest in the White Mountain National Forest of New Hampshire. Photo from U. S. Forest Service.

the tundra. In the plains region the soil may freeze to a depth of 10 feet; where the snowfall is greater the depth of freezing is much less. The growing season is a month or two longer than in the tundra. There is a distinct spring and summer period, but the autumn is short and winter follows closely. Frosts may occur during any month of the year.

The boreal forest has occupied much of its present area only a comparatively short time, for this is the region which was covered ten to twenty thousand years ago by continental glaciers, similar to the great

glacier that now covers Greenland. The trees of the forest survived about the edges of the several successive ice masses; and as the masses melted, the forest spread into its present transcontinental region.

The tundra plants survived the glacial periods on the northern islands, on transitory areas not occupied by ice, and near the coast, just as they today live on the fringes of land encircling the Greenland ice. The poor drainage, shallow soils, and frequent ponds and lakes are also the results of glacial erosion and deposition. Irregularities result from the unequal deposition of rock material in the ice at the final melting, and from the melting of buried, detached ice masses after the retreat of the main masses of the glaciers.

Tundra and boreal forest are examples of climatic plant formations. Each is a large area of nearly homogeneous vegetation limited in its occurrence by a group of characteristic climatic conditions. The tundra is covered by a mixed population of perennial herbs and low shrubs, which vary in proportion from one locality to another; but organized communities are indistinct. The boreal forest, on the other hand, has well-defined communities of specific tree, shrub, and herbaceous layers, with mosses and lichens in all layers. There is also more diversity of communities on sand, on clay, and on rock exposures; on alkaline and acid soils; and on well-drained soils in contrast to wet, poorly aerated soils.

On burned-over lands there is abundant evidence of recent succession from bare soil to annual and perennial weeds, to aspen thickets, or to alder thickets on wetter soils, followed by jack pine or balsam poplar, and finally to white spruce and balsam fir. Bogs and muskeg, first covered by sphagnum and other mosses, are invaded by black spruce and tamarack and in less acid situations by arbor vitae; and in the most mature communities white spruce eventually becomes dominant. The youngest flood plains have sedge, rush, and grass communities, soon followed by willow and alder thickets. These in turn may be succeeded by balsam poplar communities, and followed by mixtures of balsam poplar and white spruce; eventually white spruce becomes dominant.

White spruce may thus predominate in the final stage in the development of vegetation which started with a variety of different communities on such diverse habitats as flood plains, sand plains, bogs, and muskeg. For this reason white spruce is regarded as a climax tree; and since a comparable sequence occurs in similar habitats from Alaska to Labrador,

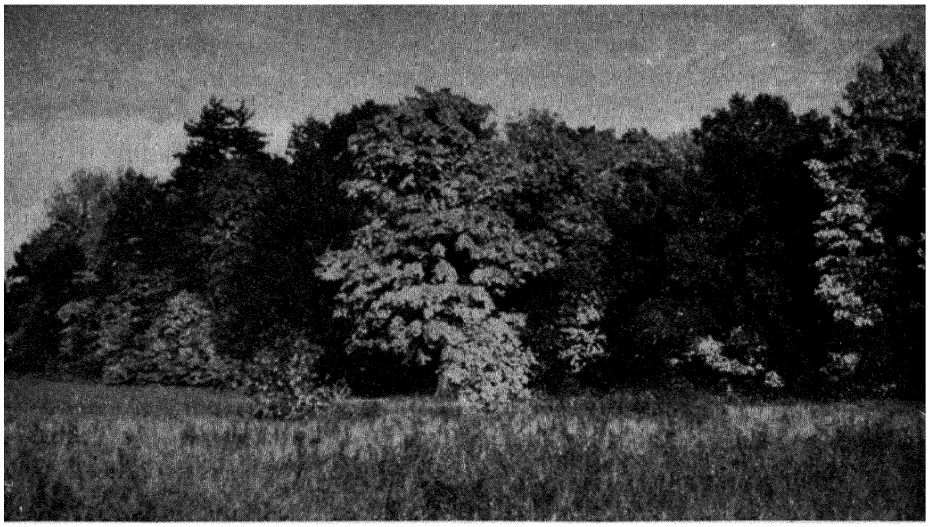

FIG. 378. Exterior view of a forest of hemlock, white pine, beech, birch, and maple on the plateau of northwestern Pennsylvania.



FIG. 379. Interior view of a hemlock-beech-birch-maple forest in northern Pennsylvania.

the white spruce forest is regarded as the climax community or association of the boreal forest formation.

Hemlock-hardwood forest (Figs. 378-380). From Winnipeg through the Great Lakes region to Nova Scotia, and at gradually increasing elevations southward in the Appalachians, is a far more complex formation

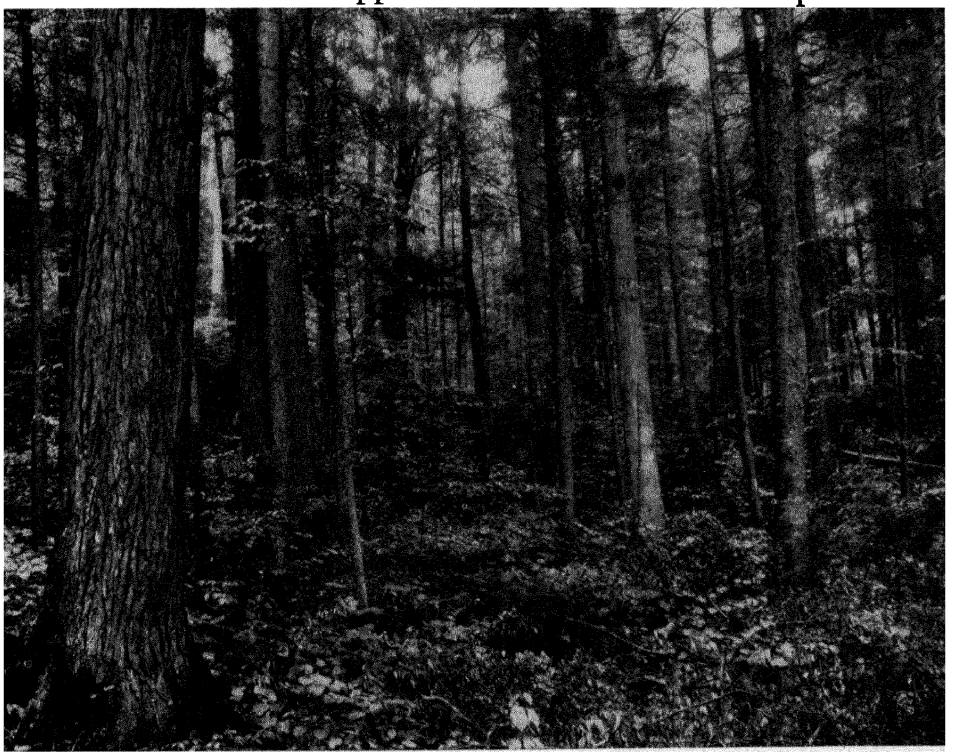

FIG. 380. Interior view of a mixed red spruce-hemlock-hardwood forest in the Monongahela National Forest of West Virginia. Photo from U. S. Forest Service.

composed of many more species of plants and consequently of a greater number of distinct communities.

This plant formation was originally characterized by the abundance of hemlock, eastern white pine, red pine, yellow birch, red spruce, sugar maple, red maple, beech, and black cherry. The hemlock-hardwood formation extends between the boreal forest formation and the deciduous forest formation on the south. Since general climatic regions are never separated by sharp lines because topography modifies climatic factors locally, many small areas containing boreal communities have persisted

from early postglacial times, when the boreal forest dominated this whole region. Likewise, there are areas of valley slopes and lake shores where deciduous forest plants and communities have moved in and become established. The hemlock-hardwood forest on its southern borders has been most frequently replaced by deciduous forest communities on the better soils and climatically warmer areas.

The climatic conditions within this region are less rigorous than in the boreal forest. The growing season is usually four to five and a half months. Increased rainfall and deeper snows limit or prevent the freezing of the soil in forested areas. Frosts seldom occur between June and August, although night temperatures may frequently approach 40° F. Winter temperatures of 20°-25° below zero are not uncommon, and at rare intervals temperatures 40°-50° below zero are recorded.

The period of dormancy thus is somewhat longer than the period of growth, and the extreme winter temperatures limit the establishment of many species common southward. For example, in some valleys of the western Adirondacks during the winter of 1935-36 beech trees more than 200 years old were killed by extreme low temperatures, and of course many of the younger trees died also. This is an example of the fact that elimination of species from climatic formations may be effective even if the extreme of a limiting factor occurs but once in many years. The beech and maple trees near their northern limits are scrub-like trees with numerous dead branches.

Agriculturally the area occupied by the hemlock-hardwood forest is a region of hay crops, interspersed locally with potato and root crops and certain northern varieties of apples. Vegetables, grapes, and other fruits are cultivated near the larger lakes where in autumn killing frosts are delayed by the heat liberated from the water.

Plant associations. As one studies the local diversity of plants and plant communities within a climatic plant formation, he finds certain communities with a similar appearance repeated again and again, much the same group of species, and a similar internal organization. They may occupy large or small areas, depending on physiography and soils. These communities within a formation are called *plant associations.* They are the smaller units of the vegetation of a great climatic region which includes many topographic situations with different exposures to light, wind, temperature, and precipitation. They are also limited by soils of different depth, chemical composition, water content, aeration, and texture.

Plant associations have a rather definite organization. This may be illustrated by a forest such as the white pine association or the hemlock hardwood association. Both are named for their *dominant* species, but both have *accessory* and *subdominant* species of trees, and in the under growth characteristic shrubs, herbs, and smaller plants. The dominant trees that form the *canopy*, or *top layer*, of the association are exposed to more sunlight, more wind, and a drier atmosphere than are the successive lower *layers* of small trees, shrubs, herbs, and ground cover beneath. Atmospheric moisture and carbon dioxide concentrations are highest near the soil. After long periods of occupancy the accumulated duff and underlying soils become strikingly different. These different layers of plants in a forest and the relations of the plants in each layer to those above and below constitute the ecological structure and organization of an association.

Succession. Land forms are continually undergoing change. Uplands are eroded by water and wind, and lowlands and flood plains are built up by deposition of the products of erosion. Lakes and ponds are filled up gradually; hill and mountain slopes are modified by slumping. All these physiographic processes result in an orderly series of changes in the environments of the various plant associations of these different sites, and consequently most associations are undergoing changes in composition.

When new land areas are exposed as when lakes are drained, cut-over forest areas are subjected to intense fires, or sand dunes and other windblown deposits cover an older landscape, a comparatively rapid succession of plant associations follows one another until a final stabilized association forms a *climax*. These stages, beginning with weeds and passing through pioneer shrub and tree stages to the climax forests, have been described for many parts of the country. Similar studies have been made in the grasslands.

Succession may be readily studied wherever there is abandoned farm land; the age of the community can often be definitely ascertained from historic records. On many of these sites the primary cause of succession is the changing of the soil and atmospheric factors by the plants themselves: shading, increasing or decreasing the water supply, adding humus, increasing the stability and porosity of the soil. Pioneer plants may make the habitat suitable to other species, which in turn may alter it in ways that result in the death of the pioneers. Still other species may follow these in time and have a similar effect on them. This influence of

plants upon each other indirectly through their effects upon the environment results in progressive changes in the communities that occupy an area. It is sometimes referred to as "competition" among species and communities.

The processes of vegetation change, however, are best studied in your own locality and in the field. Here it is possible only to call attention to their occurrence. Many of the recent projects in forest planting, soil erosion control, irrigation, and building of dams are excellent sites for such studies.

Vegetation, then, consists of larger and smaller groups of plants each having a characteristic structure and appearance. The occurrence of the larger groups (formations), such as the boreal forest, eastern deciduous forest, and prairie, is rather definitely related to climate. The distribution of the smaller communities (associations) within a climatic formation is correlated with local modifications of climate and diversity of soil conditions. Because of gradual changes in climate, physiographic modification of land forms, changes in available water, and the modification of the environment by the plants themselves, rather definite successions of plant associations occur within each of the formations.

Succession includes changes in composition, in organization, and in the dominant and accessory species. If continued for long periods of time, it leads ultimately to plant associations in which the component species are in equilibrium with the local climate, with the soil, and with each other. These are called *climax associations* and may cover larger or smaller parts of a climatic formation. Man has frequently altered these natural changes in vegetation.

Deciduous forest (Figs. 381-384). The most widely distributed forest communities of the eastern United States belong to the deciduous forest formation. The most characteristic trees of these various communities are a score of oaks, several species of hickory, elm, ash, maple, linden, poplar, and birch; also the beech, tulip, sycamore, and, until recently, the chestnut. In the primeval forest many of these trees attained heights of 125 to 175 feet and trunk diameters of 5 to 14 feet. Many of the largest trees of which we have records occurred in the lower Ohio River bottoms and in the moist coves and valleys of the Appalachian Mountains and plateaus. Probably the most important single species was the white oak, which excelled in both abundance and dominance in a great variety of habitats, partly because of its height, longevity, and freedom from disease. The region of the deciduous forest was glaciated in the northern

and northwestern part, and there the topography is comparatively smooth or rolling. Most of the area, however, consists of stream-dissected high and low plateaus and mountains, with a great diversity of underlying rocks and residual soils adjoined by low plains.

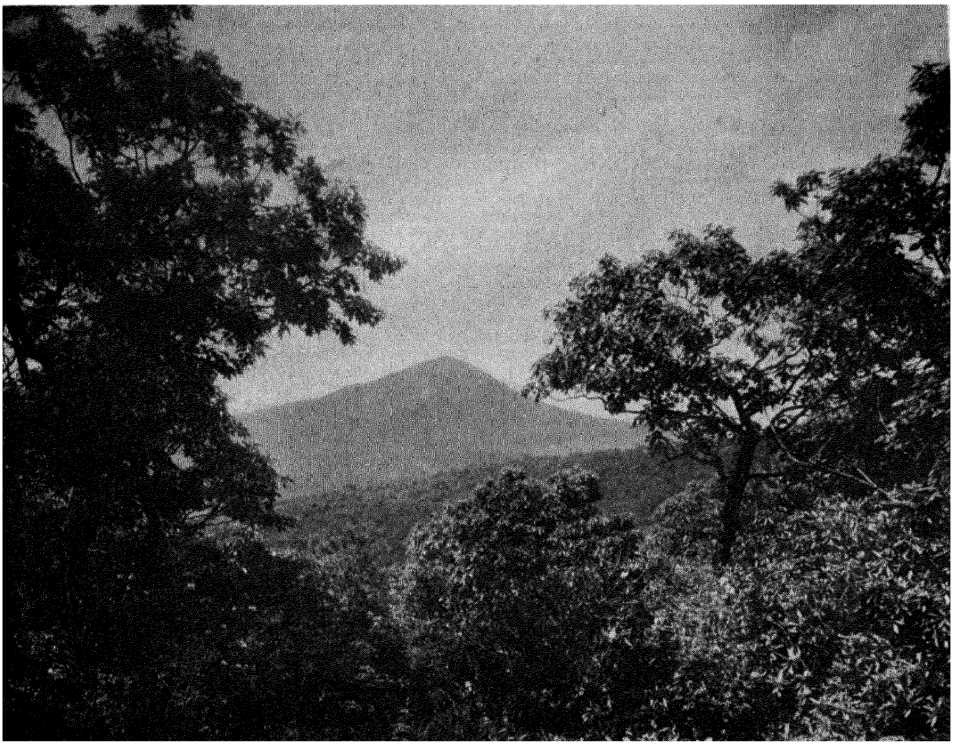

FIG. 381. Deciduous forest communities near Mt. Pisgah, North Carolina. In foreground, oak-chestnut-rhododendron community. Photo from U. S. Forest Service.

The most extensive communities of the deciduous forest on the uplands and slopes are the mixed hardwood, mixed oak, oak-hickory, white oak, oak-maple-linden, beech-maple, and southward the beech-magnolia. Interspersed among these upland types are the lowland forests of willow-cottonwood-sycamore, elm-ash-maple, and swamp oak-hickory. On ridge tops, cliff edges, gravel hills, and sand plains there are pioneer communities of scrub, pitch, and short-leaf pines, either singly or in combination. Usually associated with them are scrub oaks as undergrowth, and various tree oaks that eventually replace them on the better sites.

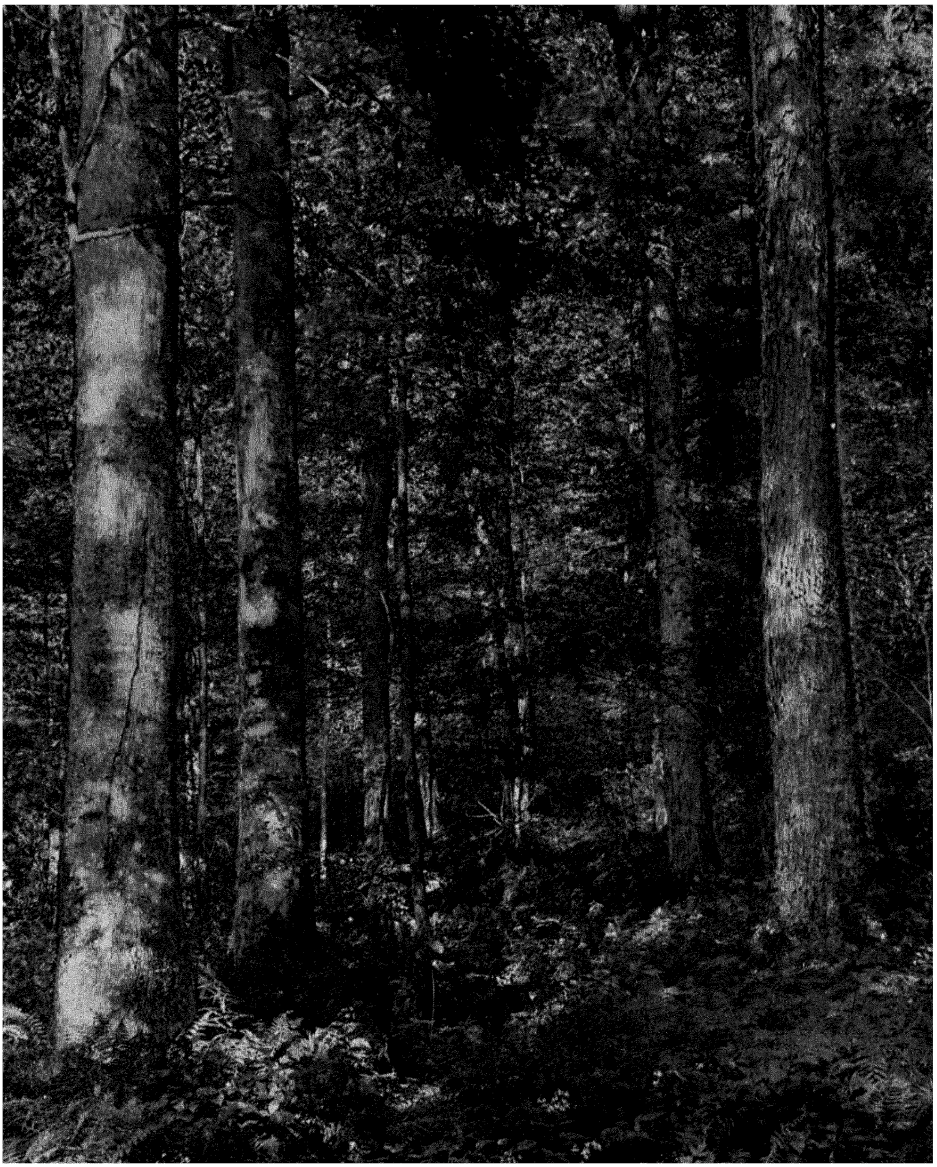

FIG. 382. A beech-sugar maple forest in West Virginia. Photo from U. S. Forest Service.

Because these areas are subject to frequent droughts they are more subject to fires than other forest sites, and the resinous leaves that accumulate beneath the pines add to the fire hazard. Recurring fires that destroy the ground cover and young trees restore the pioneer character of the habitat; hence succession to oak and other broad-leaved deciduous trees may be delayed or prevented. Pine communities if undisturbed by



FIG. 383. An oak-hickory forest in Ohio.

fire are relatively short-lived and are succeeded by oak and other communities.

Toward the west the deciduous forest is limited by the decreased precipitation—35 inches annually in Texas to 25 inches in Minnesota—and by the frequency and longer duration of droughts. The dry condition of the atmosphere during the summer is often accentuated by periods of hot winds from the southwest. The upland forest border is characterized by open groves of small trees with a ground cover of grasses, or by scattered clumps of dwarfed oaks. Where the soils have more water in them than that derived from direct rainfall, as in river valleys, the deciduous forest extends farther into the grasslands.

Northward the deciduous forest species are limited by extremely low

winter temperatures, by the shortness of the growing season which prevents the maturing of the vegetative branches and seeds, and by the presence of species of the hemlock-hardwood and white spruce forests.

Southward some species of the northern deciduous forest are restricted by the absence of a period of low-temperature dormancy, necessary both for the renewal of growth of the buds and cambiums of the perennial plants and for the after-ripening of seeds. Leached sandy soils and the absence of humus due to recurrent fires on the coastal plain



FIG. 384. Eastern white pine. An original stand at Cook Forest, Pennsylvania.

and mountain tops make conditions more favorable to the southern pines and to other coastal plain species. Far south on the coastal plain, surrounded by pine forests, are outlying communities of the deciduous forest called "hammocks." The soils where they occur are better than those of the general region, and the sites have been protected from fires. These communities consist of either mixed oak and hickory or beech-magnolia, with an undergrowth containing many typical deciduous forest shrubs and herbs.

In many parts of the deciduous forest region are local communities which are relicts of communities that lived under various former climates. Scattered bogs dating back to early postglacial time are still covered with mosses and flowering plants characteristic of the boreal and

hemlock-hardwood formation. These plants became established when the climate was cooler and the uplands adjoining the bogs were clothed with spruce, fir, pine, hemlock, and northern deciduous trees.

In protected coves and rock gorges there are localities with interesting mixtures of trees, shrubs, and herbs, some of which antedate the last glaciation, while others are relicts of postglacial time, when the hemlock-hardwood forest extended much farther westward into Kentucky and Indiana.

A third type of relict community was represented in the prairie openings that the pioneers found in the deciduous forests from western Pennsylvania and New York to Illinois and western Tennessee. These were remnants of a period drier and warmer than the present, during which prairies extended much farther eastward than at the time of settlement.

On the Atlantic coastal plain are both relicts of southern plants that extended far northward in preglacial times and remnants of northern vegetation that extended farther south when moraines were being built on Long Island by the continental glaciers.

Southeastern evergreen forest (Figs. 385-387). The most conspicuous feature of the Atlantic and Gulf coastal plains is the prevalence of pine barrens. There is no abrupt change eastward from the Piedmont region, or southward from the Cumberland and Ozark plateaus toward the Gulf. One merely passes from regions predominantly oak, with pines on overdrained and infertile sites and on abandoned farms, to regions where pines were the dominant forest trees and oaks either formed the undergrowth or occupied the scattered areas of good soil and sites protected from fires.

Long-leaf, loblolly, slash, and short-leaf pines are the most important species. Long-leaf was the best source of lumber, as well as of resin and turpentine. Loblolly predominated northward and is the weed tree of old fields and cut-over lands of the inner coastal plain, just as slash pine is the weed tree near the coast and on the northern half of the Florida peninsula. The short-leaf pine occurs not only on the inner coastal plain but also far inland, from Pennsylvania to Missouri, either scattered among the oaks or in pine forests on shallow, poor soil.

On the overdrained, sandy, and leached soils are the dry pine barrens, with open stands of pine either alone or with an understory of various oaks. Where trees are scattered and oaks infrequent because of repeated fires, there is often a ground cover of grasses. Near the south coast are the moist and wet pine barrens, in which slash and long-leaf occurred

either separately or associated in various proportions. These resemble the dry pine barrens except that oaks are less frequent or represented only by shrubby species. Other shrubs, including several species of holly, various heaths, and a large number of herbs with bright-colored flowers



FIG. 385. Short-leaved pine (*Pinus echinata*) in New Jersey. Photo from U. S. Forest Service.

are also present. A characteristic plant here is the creeping saw palmetto.

Coastal salt marshes of tall cord grass, adjoined inland by saw grass, salt grass, or tall reed grass, occupy large areas of the Mississippi delta. Still farther inland they merge with the canebrakes and the live-oak-cane savannas. Westward they grade into the coastal prairies.



FIG. 386. A young stand of longleaf yellow pine, Talladega National Forest, Alabama. Photo from U. S. Forest Service.



FIG. 387. Bald cypress in a submerged area in Arkansas. Photo by G. W. Blaydes.

Canebrakes were very extensive in pioneer days, not only near the coast but also far up the slow-flowing rivers and streams. The cane, *Arundinaria,* is the only native American bamboo (Fig. 388). At or just below the soil surface it has extensive branching rootstocks, from which upright leafy poles grow to heights of 10 to 20 feet. These hard, rigid stems, which develop from the numerous nodes of the rootstocks, form almost impenetrable tangles in low ground. Canebrakes are often invaded by evergreen "live oaks" on slightly higher land. Live oaks, with their wide-spreading branches hung with the rootless flowering plant



FIG. 388. A canebrake on the edge of a cypress pond near Baton Rouge, Louisiana.

"Spanish moss," form an unforgettable feature of the coastal region. Canebrakes also occurred on the bluffs of the Mississippi embayment as far north as Illinois as undergrowth in the beech-magnolia and oak forests. These brakes now have been largely destroyed by burning and by grazing in early spring when the young shoots appear above ground.

A second unique feature of the muddy rivers that cross the coastal plain is the cypress swamps. This deciduous conifer grows in wet, low grounds subject to flooding, and under these conditions upright conical "knees" develop from bends in the shallow roots. When the tree is planted on the upland such outgrowths do not occur. Associated frequently with cypress is the tupelo, or black gum, in which the base of the trunk is enlarged when growing in similar situations subject to prolonged flooding.

The southeastern pine forest has been the source of much lumber and many resin products. More recently processes have been discovered by which the wood of the hard pines may be used in the manufacture of paper and wall board. This region is the "cotton belt," the principal source not only of cotton fiber but also of many secondary cellulose products, as well as cottonseed oil and its by-products. Other important crops are sugar cane, certain varieties of tobacco, soybeans, sweet potatoes, peanuts, rice, early vegetables and fruits, and pecans.

Many of both the wild and the cultivated species are limited northward by the occurrence of extreme winter temperatures, by the length of the growing season, and by the prevailing temperatures during the period of growth. Many of these plants when planted farther north fail to grow well or to mature their fruits and seeds. Some trees continue to live northward as shrubs, the shoots of which freeze to the ground almost every winter. Other wild species have been cultivated successfully more than a hundred miles north of their natural boundary.

Grasslands (Figs. 389-394). Between the eastern forests and the Rocky Mountains from Alberta to the Gulf of Mexico is a vast area of rolling or flat land originally dominated by grasses, among which numerous species of legumes, composites, and other herbs were conspicuous at the time of their flowering. The rivers and streams are more or less entrenched in the plains which rise from an elevation of less than 500 feet near the Mississippi to four or five thousand feet near the mountain front. In presettlement days this was the grazing land of several million buffaloes and antelopes; of rabbits, jack rabbits, prairie dogs, pocket gophers, ground squirrels, and smaller rodents; as well as of several hundred species of grasshoppers and other plant-consuming insects.

The eastern prairie border extended as a wedge into the deciduous forest in the region now called the "corn belt." Here the average annual precipitation is about 35 to 40 inches; northwestward it drops to about 20 inches, and southwestward to 30 inches in Texas. In general, the precipitation in the grasslands is more irregular than in the forested regions eastward and northward. Westward the precipitation gradually declines to 10 to 12 inches near the mountains. Rains are most frequent in the spring months and are usually in the form of showers. Drizzling rains are rare. Droughts are characteristic of late summer, and the average winter snowfall is light. Blizzards and deep snows, however, do occur northward during occasional winters.

Late summer droughts are often intensified by the hot winds from

the southwest. During such periods temperatures near 100° F. may prevail day and night for a week or for several weeks, and upland vegetation is soon desiccated. The underground parts of many grasses are far larger than the tops, and they are less injured than are trees. But when



FIG. 389. Tall bluestem (*Andropogon furcatus*), a dominant grass in areas intermediate in moisture (the present corn belt) on the natural prairies of central North America. In the eastern part of the prairie it grew in dense stands as pictured above; the pioneer settlers had great difficulty in plowing the sod formed by the meshwork of roots and rhizomes of this grass. It grows as a bunch grass in the dryer western part of the prairie region. Photo by C. H. Jones.

severe droughts occur during several successive years there is a high mortality even among the native grasses.

The central grasslands may be conveniently subdivided into three types characterized by tall grass, mixed grass, and short grass. The boundaries between these grasslands were neither permanent nor regular, but in general they ranged north and south paralleling the mountain front.

The tall grass prairie, with grasses 5 to 10 feet in height, occupied both

wet and drier areas of the corn belt and extended northward to Manitoba and southward to Texas. The deep, dark soils that developed under the grasses are among the most fertile in the world; and the vast population of big bluestem, Indian grass, little bluestem and slough grass have long since been destroyed and replaced by crop plants. The Gulf coastal



FIG. 390. Little bluestem (*Andropogon scoparius*), a dominant grass of the dry prairie areas. Like the tall bluestem, it grows in dense stands and also as a bunch grass. Photo by H. L. Shantz.

prairies have become rice fields. Farther inland cotton is cultivated and to the northward sorghums and winter wheat. Corn is the prevailing crop in the middle region, while spring wheat, barley, flax, and hay grasses are the important crops northward. Alfalfa and other legumes are widely planted and thrive without irrigation.

The mixed prairie is composed of grasses up to 4 feet in height including needle grass, dropseed, little bluestem, June grass, wheat grass, side oat grama and several shorter ones. Most of these grow as "bunch" grasses, but some are sod formers in moist situations. Among the grasses

a great variety of flowering herbs, notably legumes and composites, add color to the landscape when in bloom. Just as the tall grass prairie was invaded by deciduous tree communities along the streams, the mixed prairie was invaded along river bottoms and terraces by finger-like extensions of the tall grasses. Trees are more restricted to stream margins, seepage areas, and ravines.



FIG. 391. A dense sod prairie of needle grass (*Stipa spartea*) and slender wheat grass (*Agropyron tenerum*) in the central northern grasslands. Photo by H. L. Shantz.

In the mixed prairie the several divisions of crop plants mentioned under the tall grass prairie reach their western limits. Beginning in the south and going northward one passes by fields of cotton, kaffir corn and milo, hard winter wheats, corn and alfalfa, and finally hard spring wheat and hay in Canada.

The western high plains are characterized by short grasses, especially grama and buffalo grass, with local areas of taller species common to the mixed prairies. This is a region of restricted rainfall and only the upper two or three feet of soil contains water. Here water evaporates both at the upper soil surface and at the under surface of the moist horizon.

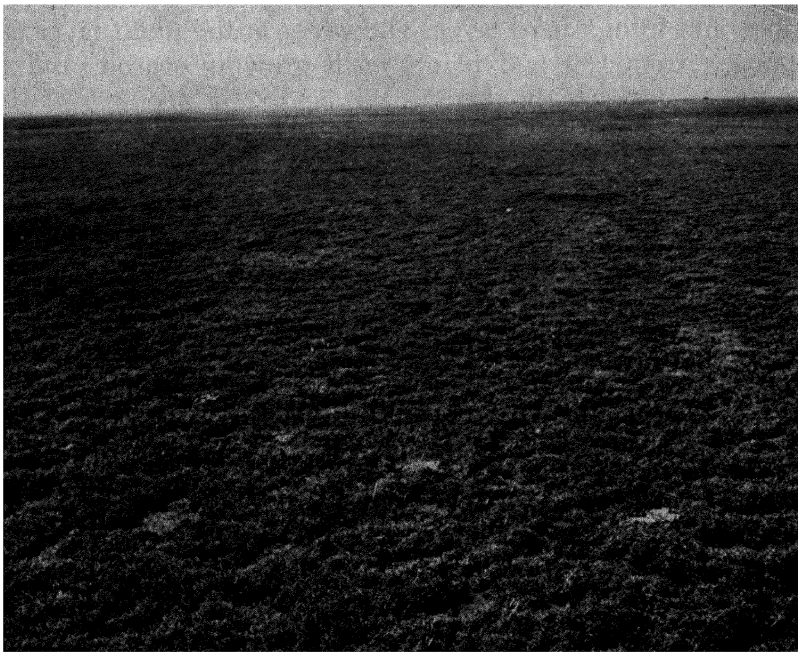

FIG. 392. Plains grassland near Akron, Colorado, dominated by grama and buffalo grasses. See also Fig. 332. Photo by H. L. Shantz.



FIG. 393. An excellent stand of blue grama grass in New Mexico. Photo from U. S. Soil Conservation Service.

At this lower surface calcium carbonate and other less soluble salts accumulate and form a hard layer. The water in the moist layer is lost by evaporation from soil and plants each growing season, and there is rarely a surplus from one year to the next. The deeper soil is permanently dry. During a period of wet years taller grasses appear on the short grass sod, and during dry years the short grasses form an interrupted cover. The buffalo grass is most abundant from Colorado southward, but the grama grass continues far to the north. Toward the mountains sagebrush (*Artemisia*) intermingles with the grasses and in Wyoming and Montana it dominates in scattered areas.

This is grazing land and farming is perilous. During a succession of wet years, however, profitable crops of hard wheat have been harvested; but in succeeding dry years there have been crop failures, accompanied by wind erosion, dust storms, and crop failures.

The desert grasslands extend still farther west and south from Texas to Arizona and far into Mexico. These grasslands are much like the short grass of the high plains, but the plants are farther apart and areas occupied by grasses alone become smaller and more scattered. More often the grasses form the ground cover under scattered desert shrubs such as mesquite, creosote bush, yuccas, cacti, and scrub oaks. The rainy period occurs in summer and evaporation is excessive. The growth period therefore is short and does not extend much beyond the rainy season. Curly mesquite grass, black and crowfoot grama grasses, tobosa grass, and "winter-fat" (Fig. 394) are characteristic, together with other species common to the high plateaus.

Desert shrubland (Figs. 395-396). The evergreen creosote bush characterizes the southern part, and sagebrush the northern part, of the vast arid plateaus from Idaho to central Mexico and from eastern California to western Colorado. Here precipitation is always insufficient for long periods of growth, and the perennials that form the conspicuous vegetation are either those that can dry out without injury between rainy periods, or those that accumulate water in thickened stems or roots. In southern Arizona and California there are two rainy periods, one in winter which is followed by a profusion of flowering winter annuals, the other in summer which is also accompanied by an abundance of summer annuals. Of course in the desert there are seepage areas and rather constant underground water in many valleys, where water covers the river bottoms only after torrential rains. In such areas trees may grow, and some of the characteristic shrubs may become tree-like in size.

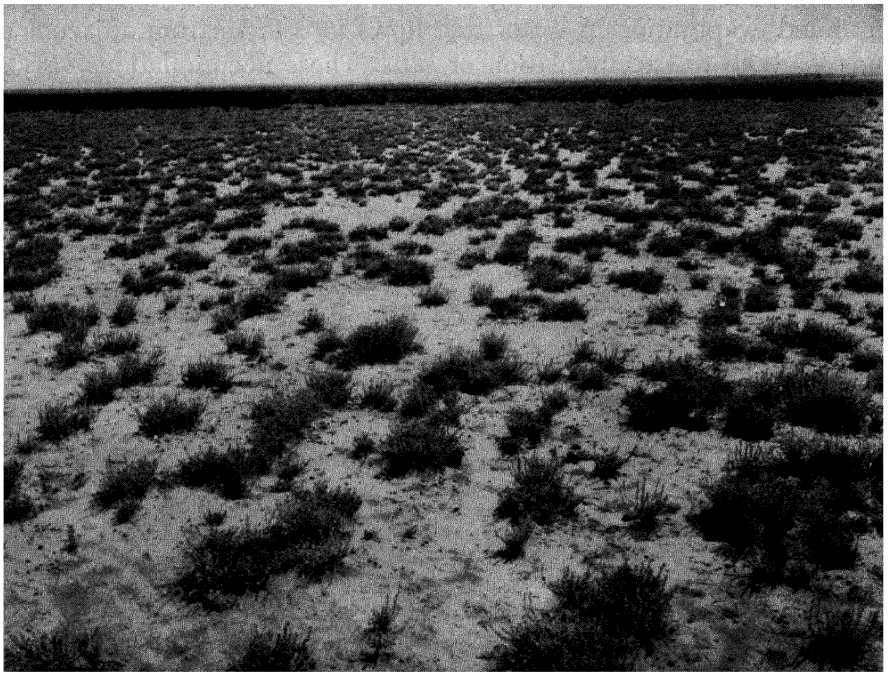

FIG. 394. Winter fat (*Eurotia lanata*), one of the most valuable forage plants of the Great Basin region, where it covers hundreds of square miles, especially in Nevada and Utah. This shallow-rooted plant grows on mildly alkali soils, dryer than those occupied by sagebrush. Photo by H. L. Shantz.

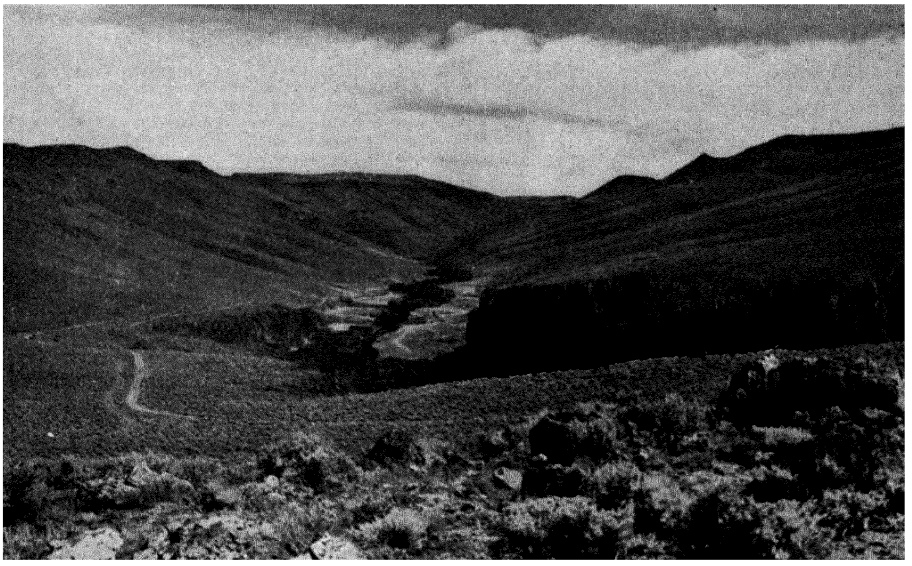

FIG. 395. Sagebrush vegetation on Trout Creek, Oregon. Photo by W. H. Camp.

In all semi-arid and arid regions there are undrained basins where continued evaporation of water that flows into them from adjacent uplands leads to the accumulation of salts. These accumulations vary all the way from common salt, basic carbonates, sulfates, to borax. These salts are variously toxic, and when concentrated exclude all plants, but when dilute may not interfere with the growth of a limited number of plants such as greasewood, several species of salt bush, salt grass and the succulents: seepweed, pickleweed, and samphire.

Desert (Figs. 397-400). The driest areas of North America are in Lower California, adjacent parts of California, and parts of the Sonora

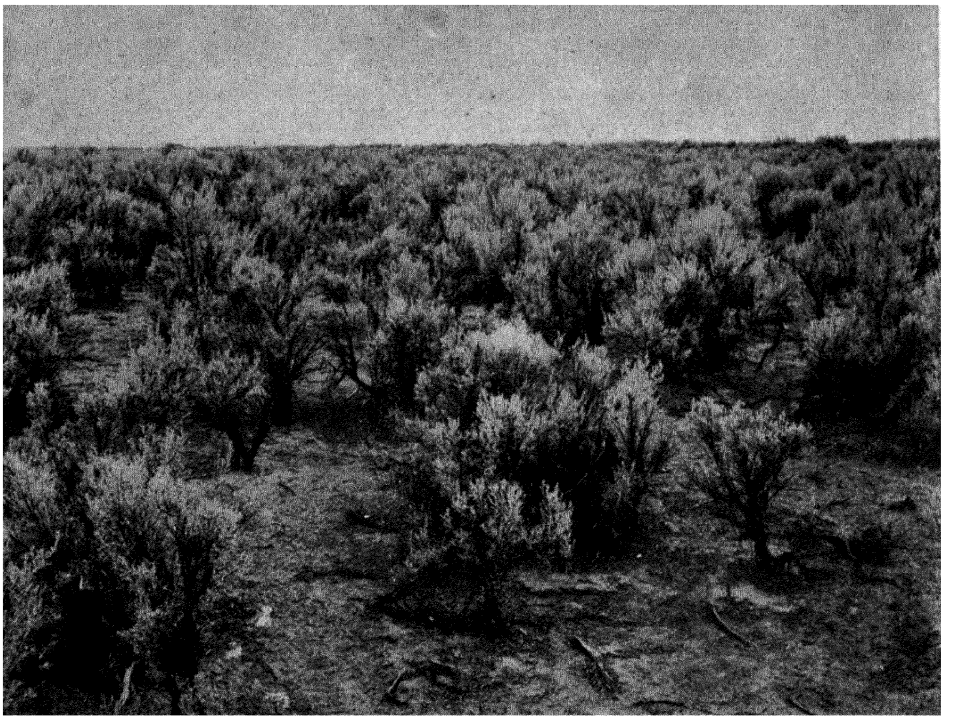

FIG. 396. A sagebrush desert near Nephi, Utah. The plants pictured here are about 4 feet high and range in age from 30 to 50 years. The associated species are mostly annuals which grow only during the rainy periods. Sagebrush is the characteristic natural vegetation on the better soils of the Great Basin region. Photo by H. L. Shantz.

and Chihuahua deserts. The region as a whole has about 10 inches of rainfall, but local areas have as low as 3 inches and in some years no

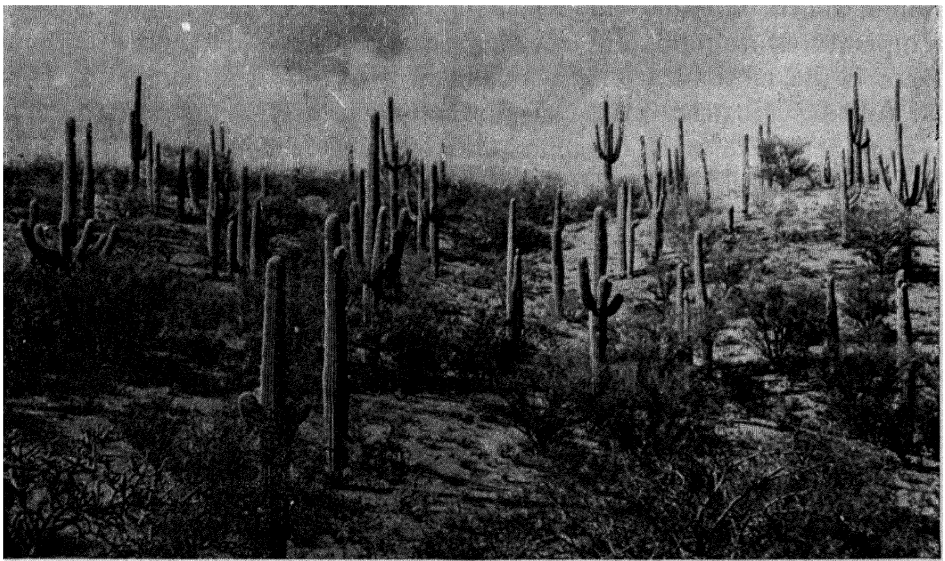

FIG. 397. Giant cactus and desert shrubs near Tucson, Arizona. Photo by A. E. Waller.



FIG. 398. Desert vegetation on sand along the shore of the Gulf of California, Libertad, Sonora. The cactus in the foreground is *Opuntia bigelovii*; in the background, *Pachycereus pringlei*. Note the osprey soaring in the background. Photo by W. S. Cooper.

rain at all. At the same time it has the highest evaporation rate. Winter temperatures are mild, and freezing temperatures are of short duration. Here is the most bizarre assemblage of plants on the continent. The largest and greatest variety of the columnar cacti are found in this region. Some are much-branched and up to 40 feet in height. They all have shallow wide-spreading root systems. All have exceedingly low transpiration rates, because of impervious outer layers of cortical tissue.

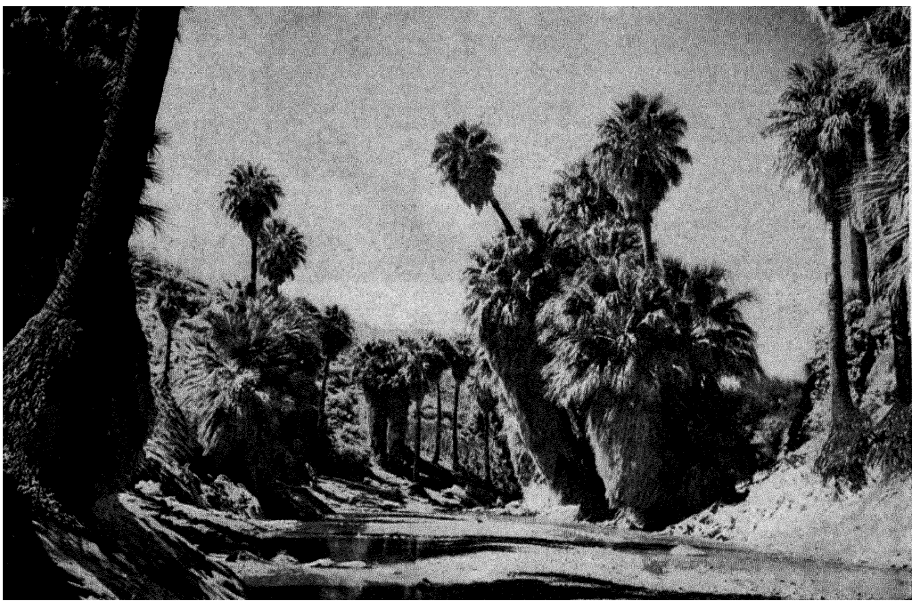

FIG. 399. The native "desert" palm of southern California (*Washingtonia*) in Palm Canyon, where underground water is always available. Photo by U. S. Forest Service.

Some have closed stomates during the daytime. A year's supply of water has accumulated in many of these plants, and this may amount to as much as 25 to 30 tons in a single plant.

In Arizona there are two rainy periods, winter and summer. The rains are typical downpours of short duration. During the winter rains the desert "blossoms" with various flowering plants, some of which are common farther north. During the summer rains another assemblage of annuals and perennials with more tropical affinities becomes conspicuous. Between the rainy periods the perennial scattered woody plants and succulents give character to the landscape. Mesquite, creosote bush,

acacias, yuccas, and the various species of flat-jointed and cylindrical cacti are most conspicuous. These plants either have a low rate of transpiration, accumulate water during rainy periods, or are uninjured by prolonged droughts. The yuccas are deep-rooted, the cacti shallow. The annuals live as long as the soil water lasts.

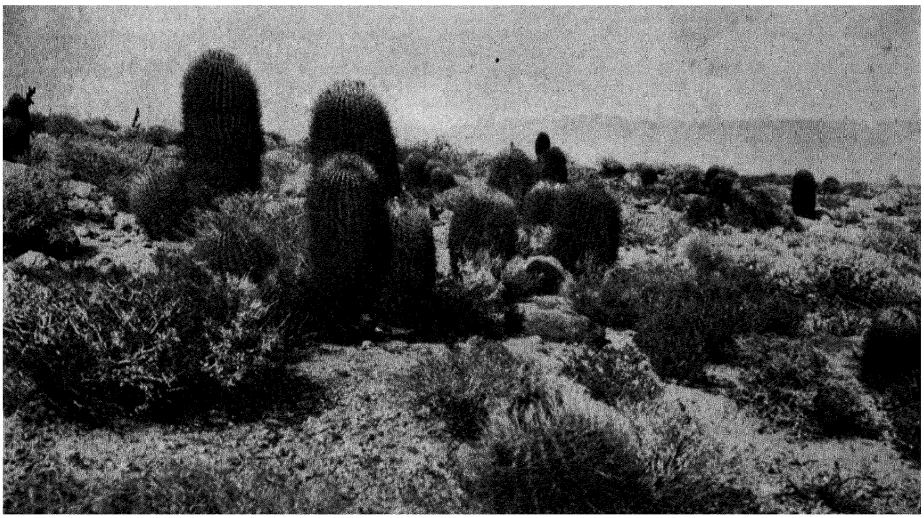

FIG. 400. Colorado Desert, in southern California. The "barrel cactus" is *Ferrocactus cylindraceus*. Photo by W. S. Cooper.

Forests of the western mountains. From southern Alaska to southern Mexico is a series of high mountain ranges, and between the Sierras and Rockies a series of high plateaus. The plateaus also have small north and south ridges on them, many of which are of sufficient height to intercept rainfall in excess of that of the arid plateau. The vegetation of all these mountains is dominated by coniferous forests as far south as central Mexico. To be sure, there are fringes of deciduous and evergreen oaks, poplars, willows, and, locally, other broad-leaved trees. Oaks are proportionately more numerous and widespread on the mountains of southern California and Mexico. In Central America they are gradually replaced by tropical scrub and jungle. Considering the great extent of the forests from the tundra to the tropics, and the frequency of local differences in altitude of 3000 to 15,000 feet, the diversity of climatic and soil conditions may be inferred.

To describe the vegetation adequately would require consideration of

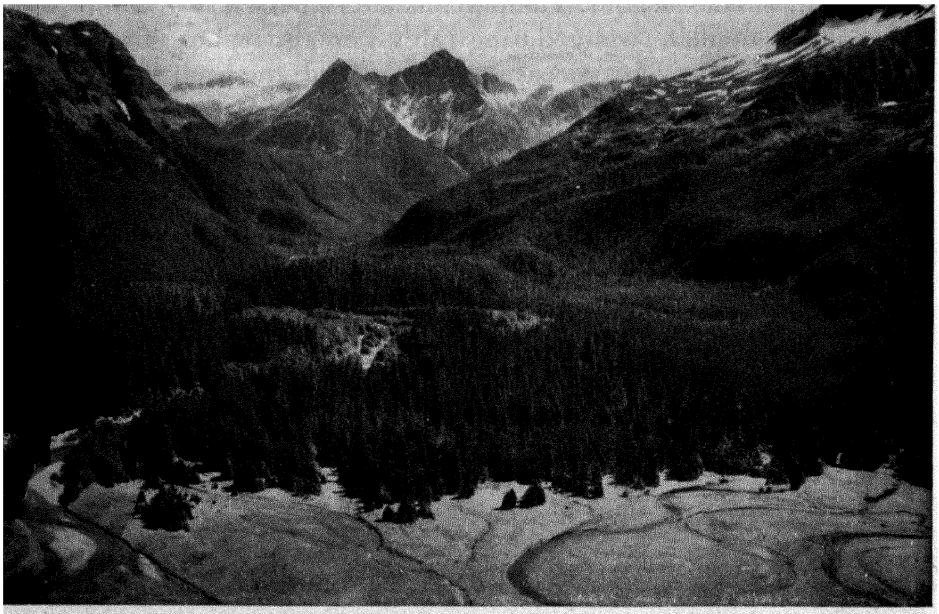

FIG. 401. Sitka spruce and western hemlock forest near the Alaskan coast. Alaskan Aerial Survey Expedition, 1929. Photo from U. S. Forest Service.



FIG. 402. Close-up of Sitka spruce and western hemlock on coastal island near the site pictured in Fig. 401. Alaskan Aerial Survey Expedition, 1929. Photo from U. S. Forest Service.

each of numerous subdivisions. Here we can sketch briefly only a few characteristic forests.

Pacific coastal forest (Figs. 401-409). The most magnificent forest in temperate regions occupied the western slopes of the coastal moun-



FIG. 403. Interior view of mature forest of western hemlock (*Tsuga heterophylla*) on a mountain in Washington. Note density of stand.

tains between Vancouver and San Francisco. Rainfall up to 125 inches occurs along the Oregon coast, with a gradual decrease northward to Alaska and southward to San Francisco. Moreover, this is a belt of fogs and low clouds. Rainfall is least during summer. These conditions rarely extend more than 30 miles inland except in northern Oregon and Washington where there is a break in the coast ranges.

Beginning in Alaska the Sitka spruce is most abundant in the shore

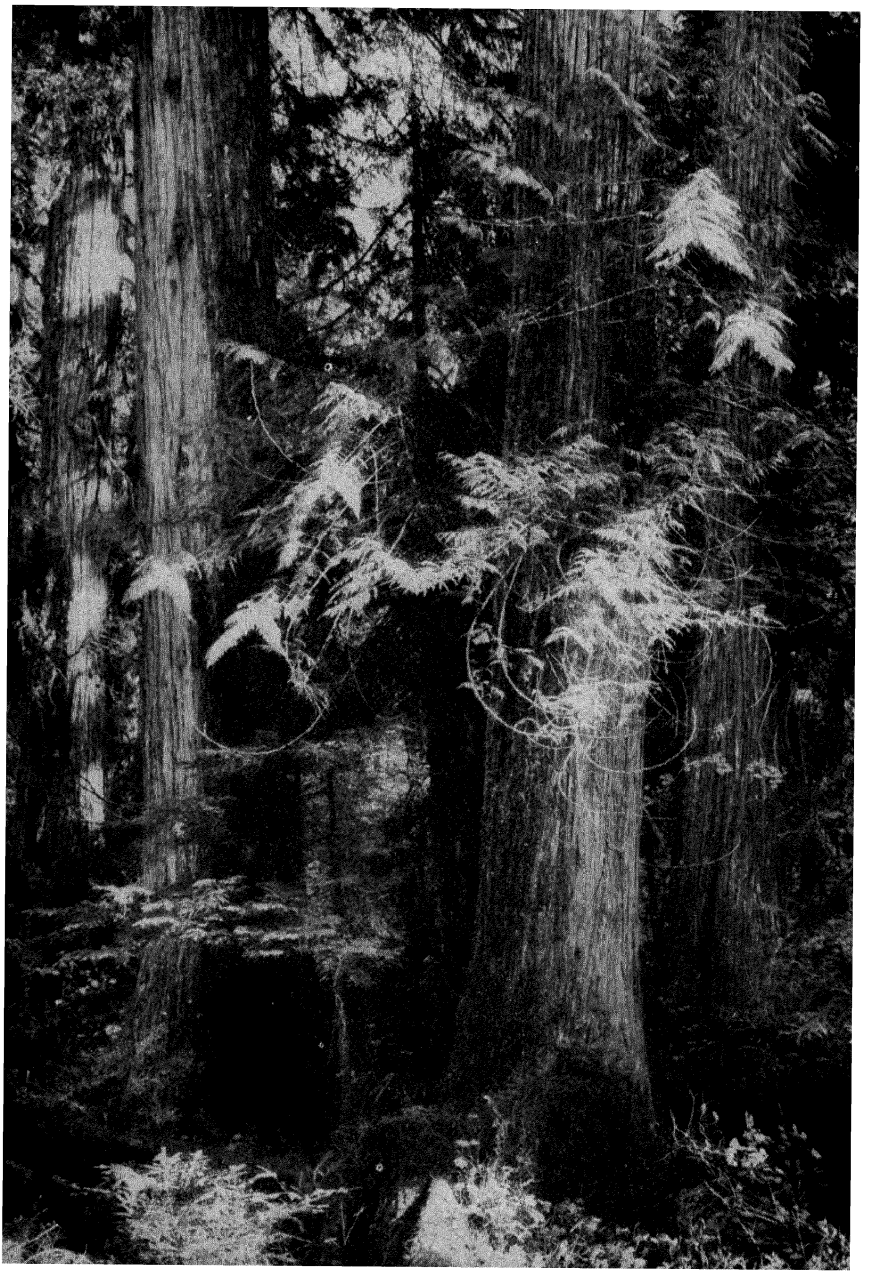

FIG. 404. Western arbor vitae (*Thuja plicata*) in the Columbia National Forest, Washington. The larger trees pictured here are from 4 to 6 feet in diameter. Photo from U. S. Forest Service.

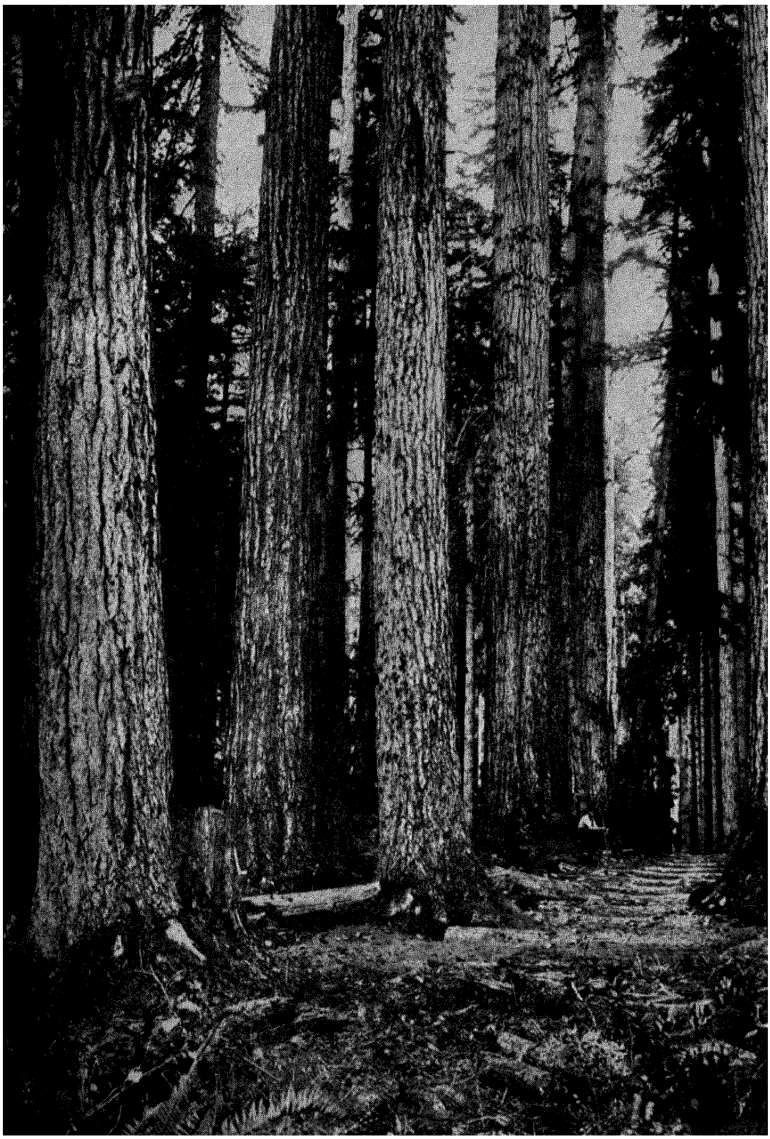

FIG. 405. A mature stand of Douglas fir (*Pseudotsuga taxifolia*) in Washington. Photo from U. S. Forest Service. In the coastal region this species attains its largest average size, with trunk diameters of 10 to 12 feet. See also Fig. 192.

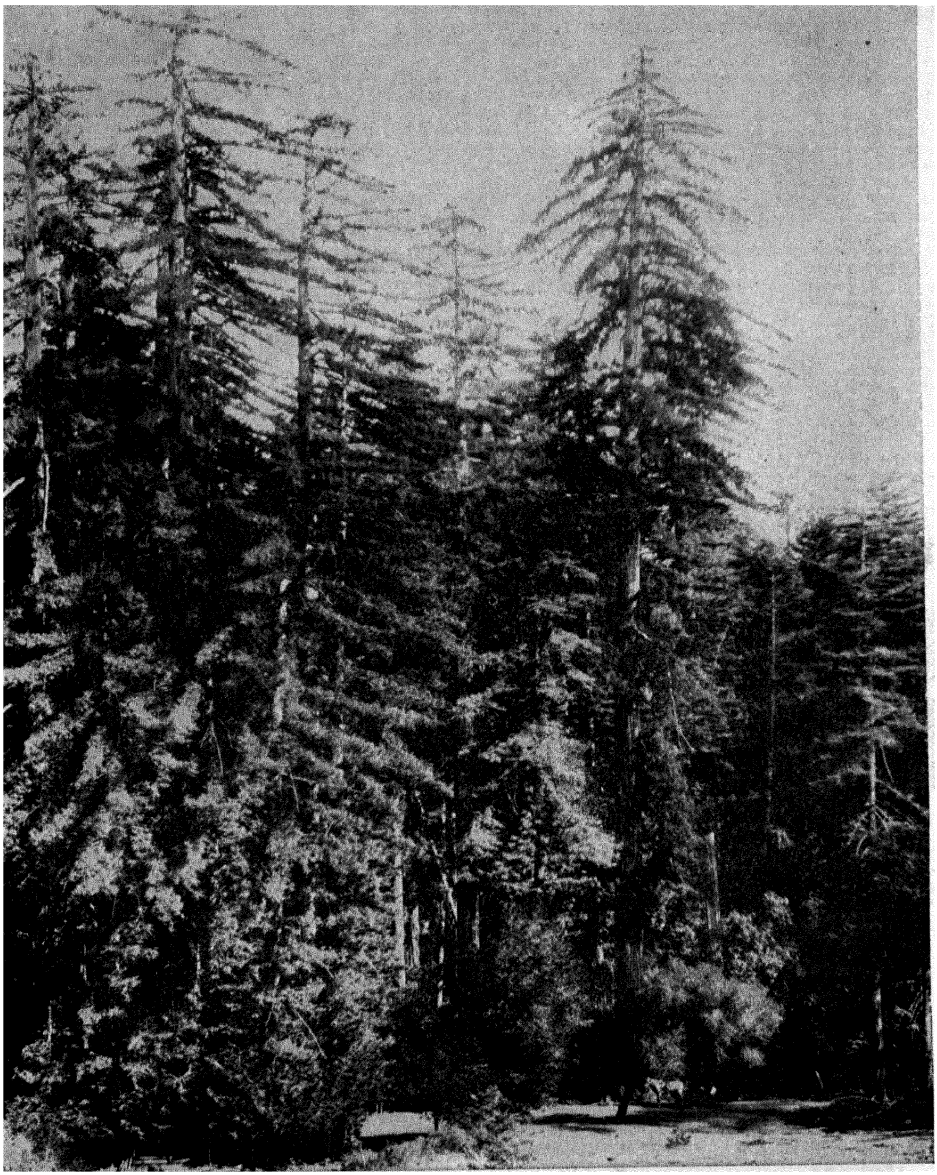

FIG. 406. Margin of a redwood (*Sequoia sempervirens*) forest in California. Three large trees near the horse in the picture are 7 feet in diameter and 260 feet high. Photo from U. S. Forest Service.

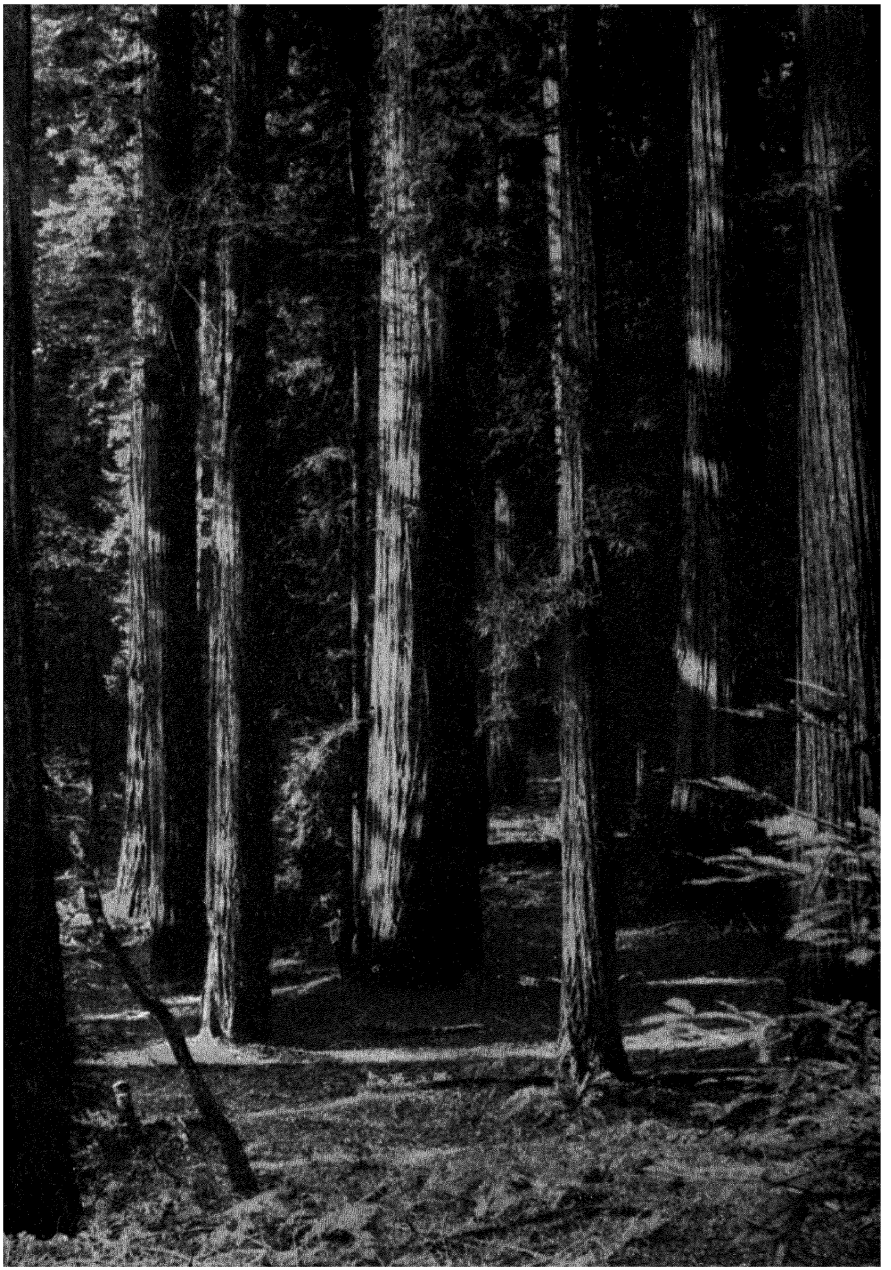

FIG. 407. Interior view of redwood forest on Bull Creek Flat, Humboldt Co., California. The largest tree in the picture is about 15 feet in diameter.

forest southward for nearly 2000 miles. Because of this distribution it is often called tidewater spruce. At higher elevations and in the more mature forest western hemlock is dominant in the Puget Sound region; both these trees attain heights of over 200 feet. The spruce has trunks up to 15 feet in diameter, but the hemlock is more slender and the maximum diameter is about 8 feet. In Washington and Oregon, Douglas fir is by far the most abundant species. Its greatest recorded height is near 400 feet. It grows rapidly and overtops other species, is long-

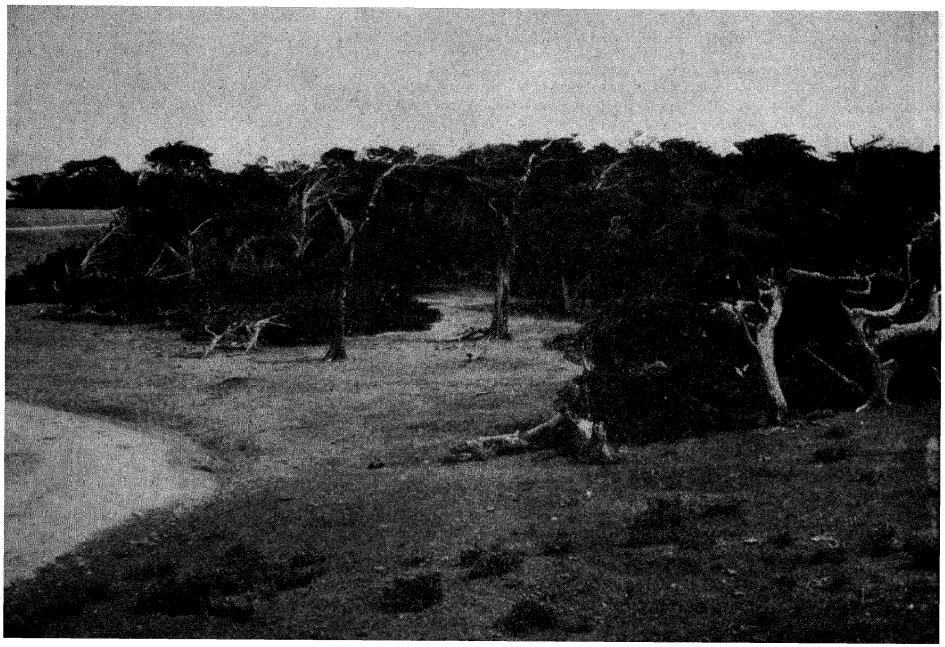

FIG. 408. The Monterey cypress is the characteristic tree on the coast of Monterey Bay, California. Many of the trees are distorted by wind and salt spray. Photo by U. S. Forest Service. See also Fig. 93A.

lived and but little injured by fire. Other important species in these forests are the western arbor vitae, a cedar, and several firs—all large trees.

From southwestern Oregon the redwood becomes the dominant tree of the moist, fog-laden slopes. It grows to a height of 340 feet, and the trunk is usually 10 to 15 feet, rarely 20 feet in diameter. The coastal forest not only contains these giant trees, but is noted for the luxuriance

of the undergrowth which includes tall ferns, and shrubs among which are the devil's club, salmonberry, rhododendron, and dogwood. One of the most remarkable features of this forest is the short distance between trees. It is quite evident that the root systems are small compared with the tops. Such enormous top development is possible only where transpiration is low because of fog, and soil water always available.

Still farther south the coastal ranges are clothed with evergreen oaks and chaparral, a community of hard and leathery-leaved evergreen shrubs and trees.

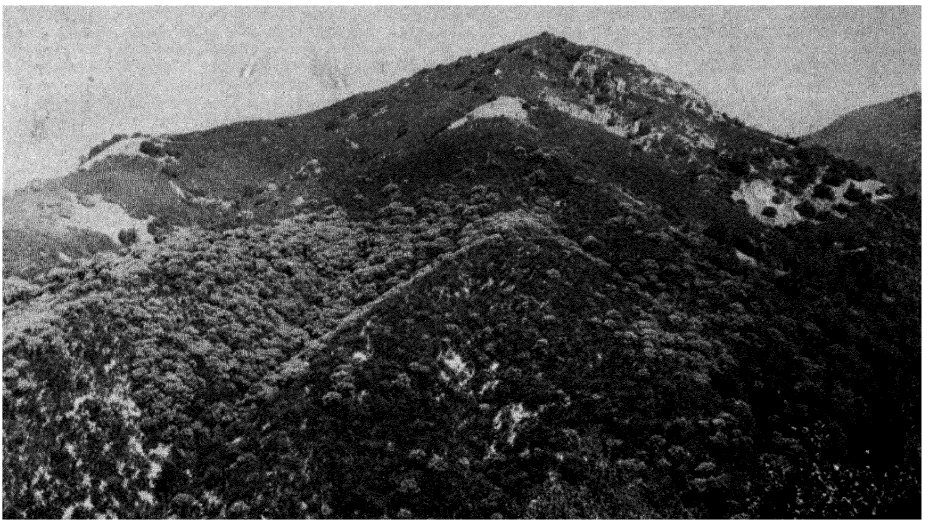

FIG. 409. Chaparral, Santa Lucia Mountains, California. Manzanita (*Arctostaphylos glauca*), grayish-colored trees in shallow valley on left; coast live oak (*Quercus agrifolia*), dark-colored trees in deep valley (lower right); chamiso (*Adenostoma fasciculata*), the apparently smooth vegetation cover on the crests and the more exposed slopes. Photo by W. S. Cooper.

Other western mountain forests (Figs. 410–416). In the region of Washington, Idaho, and Montana are extensive areas dominated by western white pine, which is accompanied by the western larch, western hemlock, white fir, and red cedar. These latter species form an eastward extension of the coastal forest and here reach their eastern limit as understory trees among the western white pines in the Rockies.

Of all the Cordilleran forest trees, the western yellow pine and

Douglas fir cover by far the largest areas. The western yellow pine occurs in open stands alone, or associated with other conifers, from the eastern slopes of the Cascades, the Sierras, the Columbia basin, the lower elevations of British Columbia southward in the Rockies to the Arizona Plateau and the mountains of Texas. It occupies rather dry sites in regions with 20 to 30 inches of rainfall adjoining grasslands, chaparral, oak scrub, or the dry piñon-juniper woodlands.

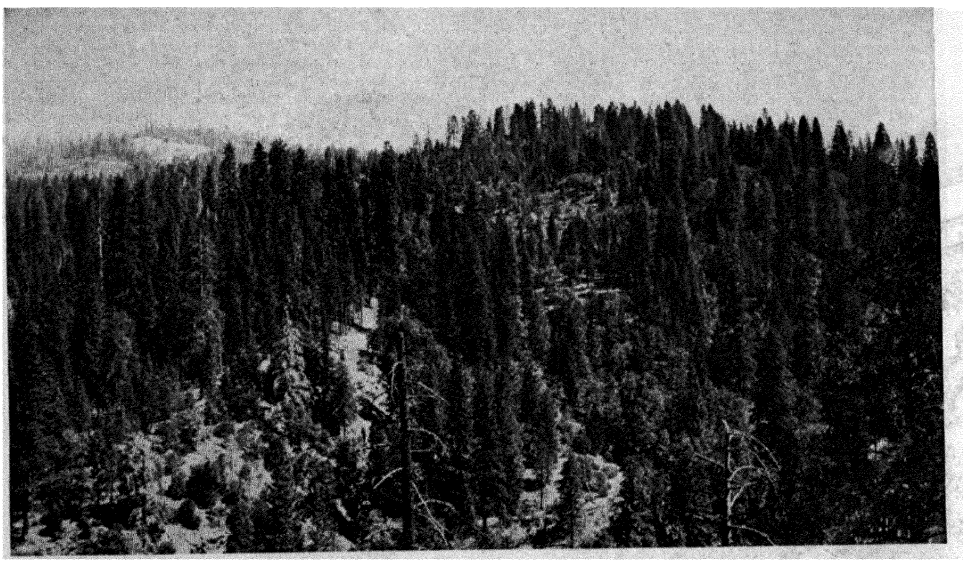

FIG. 410. Mature western yellow pine (*Pinus ponderosa*), Eldorado National Forest, California. Photo by U. S. Forest Service.

At its northern limit the yellow pine occurs at elevations up to 3000 ft., and in Arizona and New Mexico, 6000 to 8000 ft. In the Sierras on cool and moist slopes it is associated with Douglas fir, sugar pine, and incense cedar. The mixed forest of pine and fir occurs in the Sierras up to 5500 feet and at from 6000 to 9000 feet in the central Rockies. Forests predominantly of Douglas fir occur at somewhat higher elevations. In the northern Rockies the western larch, the western white pine, and the lodgepole pine may occur with Douglas fir in varying proportions. The lodgepole pine is a pioneer tree that invades burned-over lands at all levels from the dry yellow pine belt at low elevations through the belts

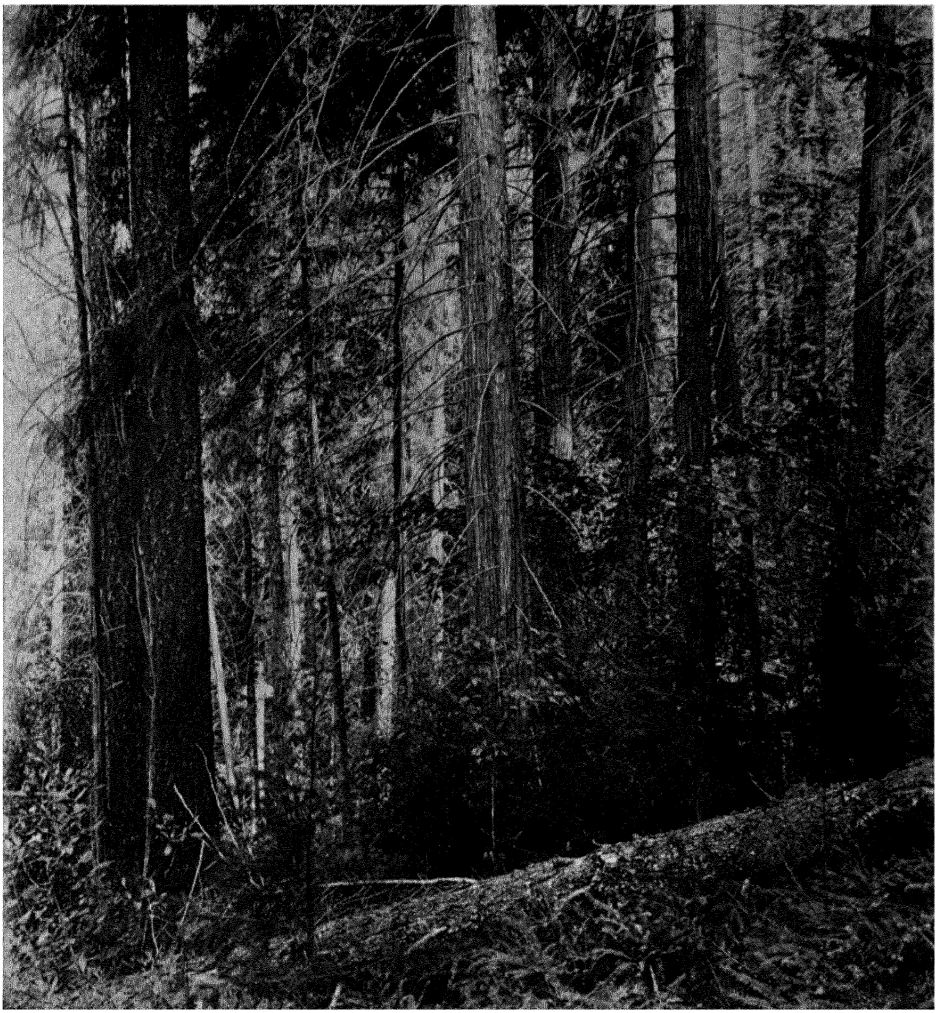

FIG. 411. Forest of western arbor vitae and Douglas fir on a mountain slope in Idaho. A common forest type from the Pacific coastal region to the mountains of northern Montana. The arbor vitae has cinnamon-red bark and trunk diameters up to 10 feet. Photo from U. S. Forest Service.

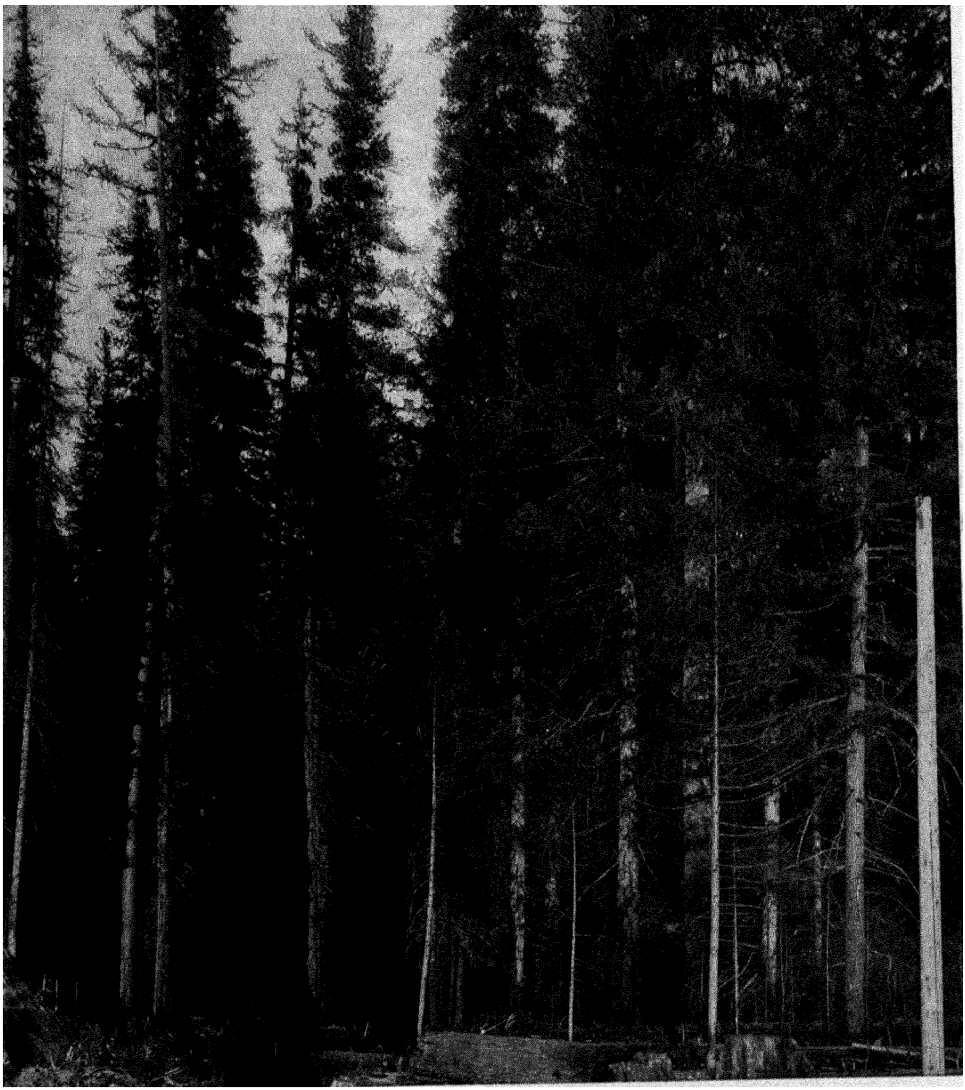

FIG. 412. A mature stand of western white pine, larch, arbor vitae, and hemlock in the Kaniksu National Forest, Idaho. Photo from U. S. Forest Service.

of Douglas fir and Englemann spruce. This spruce forms the highest belt of widespread forests in the Cordillera. The lodgepole pine grows best in cool moist regions where the Douglas fir belt and Englemann spruce overlap.

Englemann spruce dominates on cool, moist slopes where there is abundant snow and a long dormant period. In British Columbia these

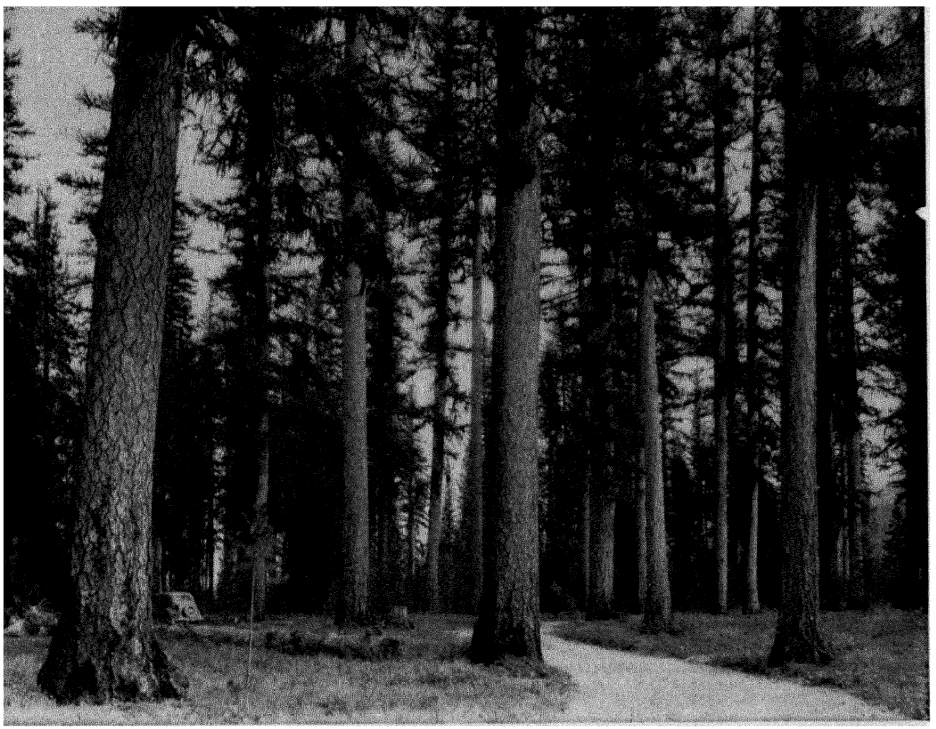

FIG. 413. A mature stand of western larch (*Larix occidentalis*) in the Lolo National Forest, Montana. Tree diameters up to 10 feet. Photo from U. S. Forest Service.

slopes are only a few thousand feet above sea level while in Arizona they lie between ten and twelve thousand feet. Associated with the Englemann spruce in various parts of its range are several species of fir, the alpine larch, mountain hemlock, white-bark and bristle-cone pines. Above this belt lie the Alpine meadows, or high mountain tundra, dominated by sedges, grasses, heaths, and low-growing willows, birches, and alders.

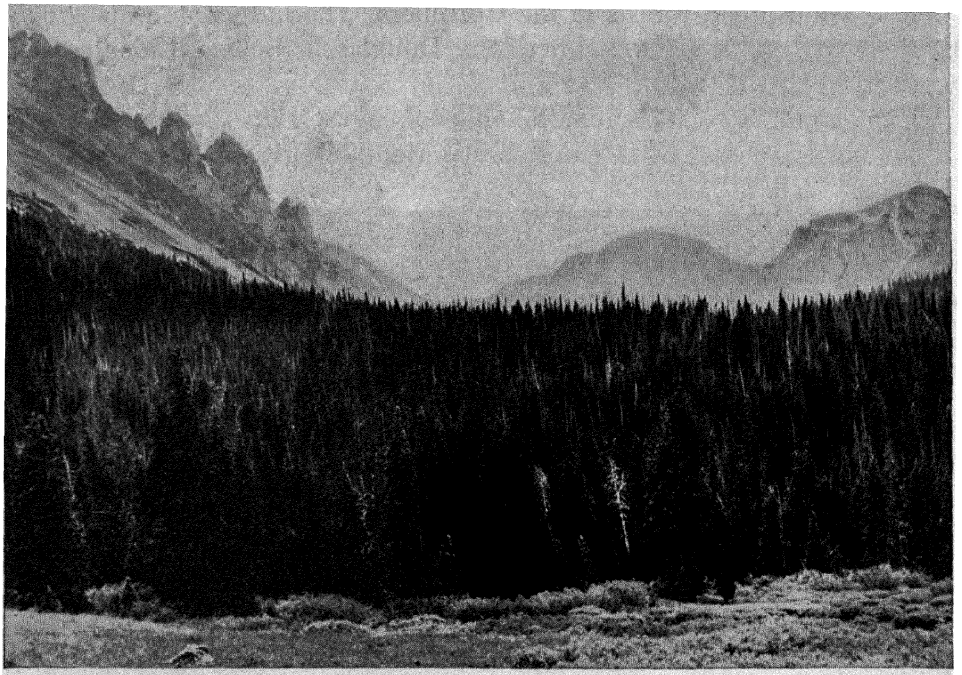

FIG. 414. Englemann spruce (*Picea engelmannii*) in a valley of the Sawtooth Ranges, Arapaho National Forest, Colorado. Photo from U. S. Forest Service.

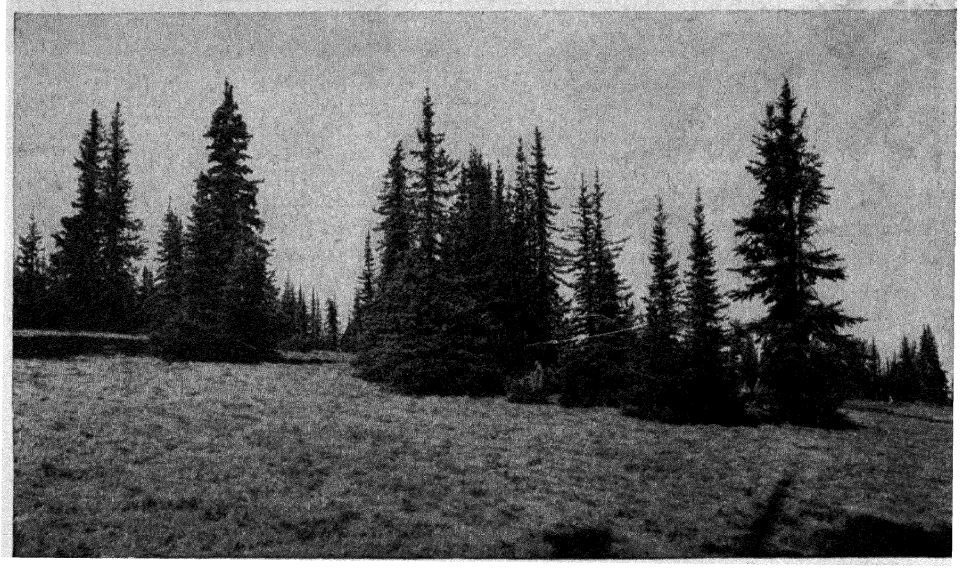

FIG. 415. Subalpine clumps of alpine fir and Englemann spruce scattered in alpine meadow, Chelan National Forest, Washington. Photo by U. S. Forest Service.

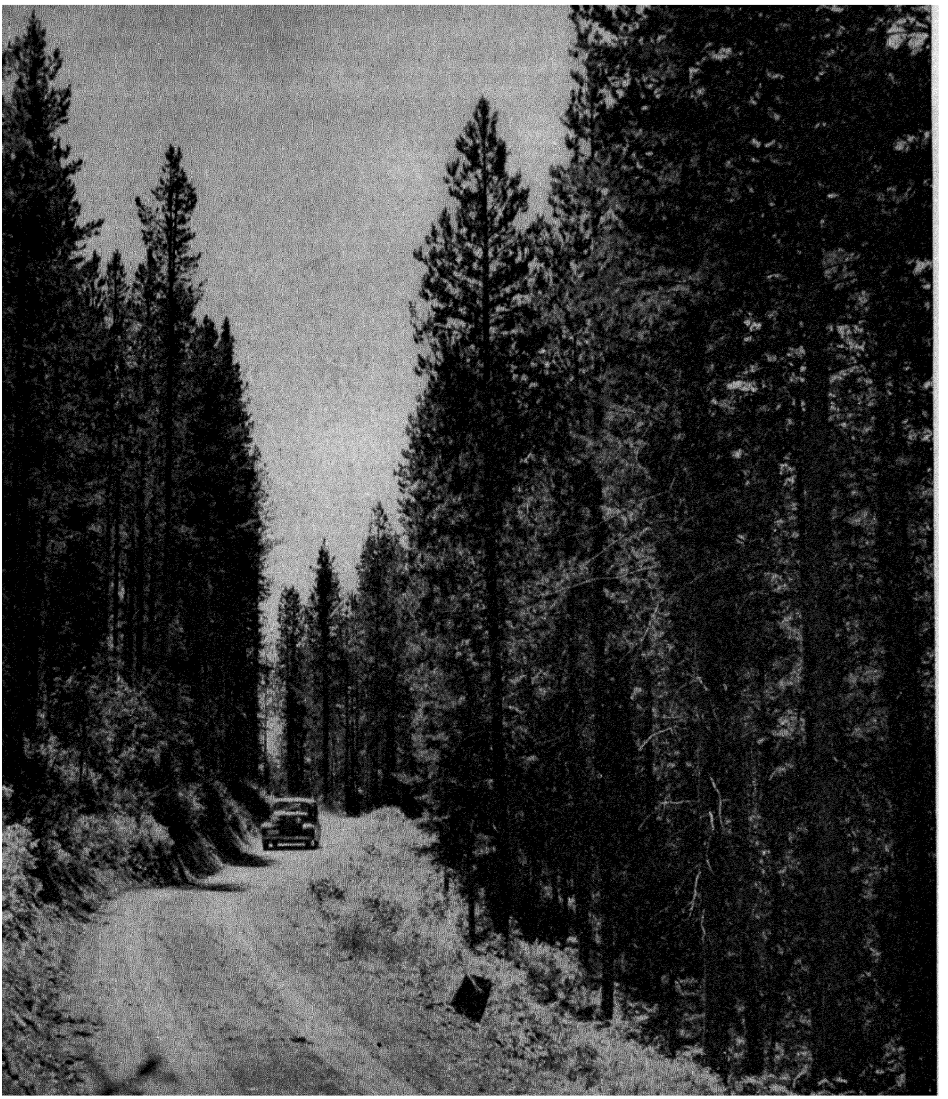

FIG. 416. Lodgepole pine (*Pinus contorta*). Cache National Forest, Utah. Photo from U. S. Forest Service.

Piñon-juniper woodlands (Fig. 417). Usually below the western yellow pine belt where the rainfall is somewhat less or the evaporation greater, there are extensive open woodlands particularly in the Great Basin region between the Sierras and the Rockies and on the Arizona

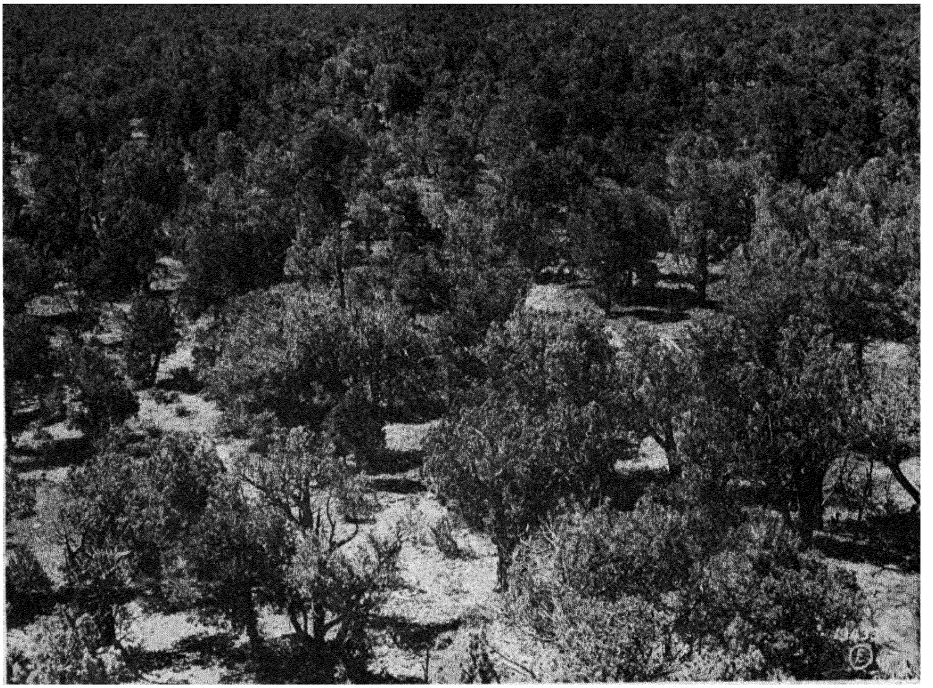

FIG. 417. Juniper and piñon pine form the characteristic woodland on the plateaus and lower slopes of mountains in the Southwestern States. Photo by U. S. Forest Service.

plateau. Two small species of pine and several species of juniper occur in various combinations over vast areas. Collectively they may be called the piñon-juniper woodland. South of the Arizona plateau it is mixed with and finally replaced by scrub oak woodlands (encinal). Below it are the still drier grasslands and semi-desert scrub.

The higher levels of the Mexican plateau are also covered by pine forests, which contain at least 6 species in addition to the western yellow pine. Douglas fir is again present on mountains above 9000 feet, with lodgepole pine, trembling aspen, and a Mexican fir. At levels below the pine forests are areas of the piñon-juniper, or the scrub oak encinal, together with shrubs and low trees of the dry tropics.

Tropical forests (Figs. 418-420). The tropical forests of southern Mexico and Central America are made up of a large number of broad-leaved evergreens, including palms, tree ferns, figs, rubber trees, various kinds of mahogany, silk-cotton trees, Spanish cedar, logwood, and hundreds of other species. The rainy tropical forest when undisturbed attains heights of 200 feet, and there may be several tree layers beneath the

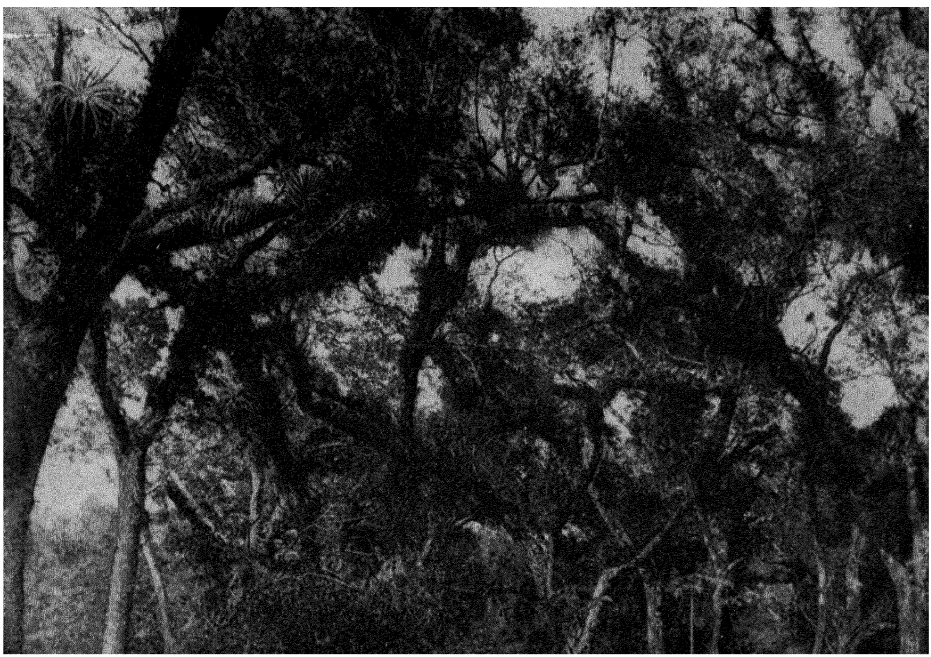

FIG. 418. Natural live oak forest near Miami, Florida. Branches are covered with epiphytes. Photo from U. S. Forest Service.

highest canopy, but the forest is open below. Stands of this kind still occur on certain of the Caribbean islands, and in Guiana and Venezuela. Mostly the present-day rainy tropical forests are jungles: tangled growths of trees, vines, shrubs, and tall herbs difficult to penetrate, and containing so many species that the forests can scarcely be described. The rainfall is as much as 200 inches a year and the dry season is very short. Temperatures are always high.

Jungles result from repeated cutting, burning, and clearing of the land. The lateritic soils of the rain forest are not rich in mineral salts and are soon leached and eroded under native methods of cultivation. Furthermore, weeds from seeds and from underground roots and

rhizomes are difficult to suppress. Consequently the area is soon abandoned and the native moves to a new area. This kind of "migratory agriculture" has been going on for several thousand years, and few are the areas in which secondary forests have actually reached a completely stable condition. One has only to travel through our southeastern states to see comparable effects of migratory agriculture in this country.



FIG. 419. Tropical jungle on a mountain slope in western Cuba. The palm-like trees are cycads (*Microcycas*). Photo by O. W. Caldwell.

Tropical muddy coasts are characterized by mangrove swamps. These small trees have extensive root systems which interfere with wave action and increase the deposition of sand and mud by the shore currents. Certain species also have embryos that germinate and grow more than a foot in length before they drop from the tree into the mud below. Mangrove swamps consequently cause the extension of land seaward. It is said that this process has added 2500 square miles to the west side of the Florida peninsula. Succession of plant associations occurs; and the mangroves may be followed by grasslands as in Florida, or by scrub or rain forest as along the Central American coasts.

The western slopes of Central America have decreased rainfall be-



FIG. 420. A tropical jungle in Hawaii: tree ferns, the climbing rattan palm, and a banana plant in the foreground. Photo by U. S. Forest Service.

cause of the mountains, and the vegetation varies from deciduous dry forest to tree savannas, scrub, and desert.

The products of the tropical forest region include bananas, cotton, sugar cane, cacao, coffee, and many kinds of fruits. The banana plantations are at lower elevations, the coffee at elevations of two or three thousand feet.

One must not forget that on the mountains of tropical regions there is a temperate belt and even cold temperate summits where frosts occur regularly, and, on a few of the highest peaks, permanent snow. Unlike the continental temperate regions the climate is more uniform, the daylight period constant; the most variable factor is the length of the rainy and dry seasons.

The wettest forests in the rainy tropics are those on mountain slopes in the cloud belt. The trees are usually of low stature, and variously gnarled and twisted. They are shrouded with epiphytic orchids, bromelias, filmy ferns, mosses, lichens, fungi, and algae which accumulate and continuously destroy the plants beneath. Constant moisture, moderate light, abundant mineral salts in the plant debris, and nearly constant temperatures form an environment so nearly "ideal" that hundreds of plant species compose an ever-changing living mass of vegetation.

Two centuries of destruction. Except along the sea coasts, most of the United States was a wilderness less than two hundred years ago, and

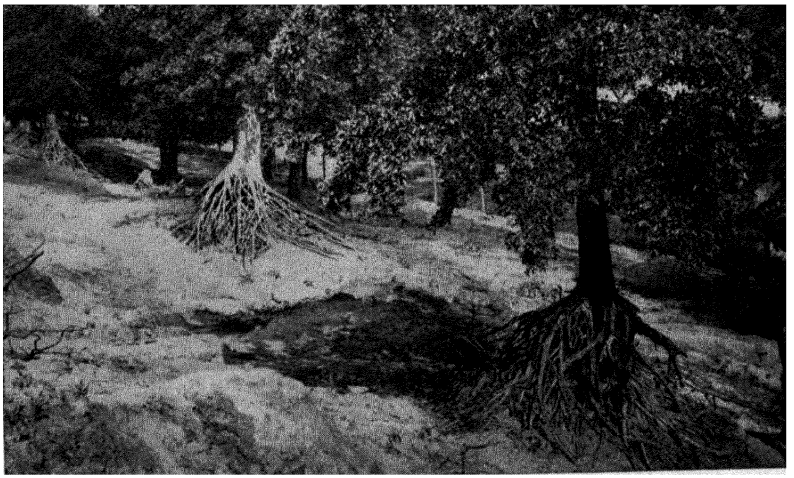

FIG. 421. Effects of sheet erosion in a forest in Oklahoma started by overgrazing of the grasslands higher up the slope by sheep. Photo from U. S. Soil Conservation Service.

only a little more than a century has passed since the lands away from the larger rivers and lakes were occupied and brought under agricultural and industrial control. During this short period most of the original vegetation has been destroyed. The accumulated fertility of the upper soil horizons has been exploited by wasteful methods of cultivation and destructive grazing, often accompanied by excessive drainage, erosion, and the floating of the top soil to the river bottoms and the ocean.

Conservation (Figs. 421-424, 25-26, and 180-181). Only recently has there been official recognition of and real concern about our decadent



FIG. 422. Ungrazed and overgrazed grama grassland in New Mexico. Photo from U. S. Soil Conservation Service.



FIG. 423. Photo taken during a sand storm in northwestern Texas. Periodic droughts are a regular feature of the high plains, and if prolonged for several successive years the vegetation is destroyed and the soil in part is blown elsewhere.



FIG. 424. Dust storm in southeastern Colorado. Wind velocity 30 miles per hour; duration of storm about three hours. This top soil is being blown elsewhere. It is possible that another storm may bring in new soil from farther west. This movement of soil by wind has been an important geological process in the building of plains soils. Photo by Soil Conservation Service.

woodlands and the depletion of our agricultural, game, and recreational resources. This belated awakening has resulted in the initiation of widespread research in land classification and utilization. Sincere attempts are now being made to apply the results of scientific research to the complex problems of reforestation, range improvement, soil conservation, game management, stream control, and recreational facilities.

Detailed knowledge of the original vegetation of America as it was when the explorers and first settlers saw it is a valuable index to climatic conditions in relation to the growth of different kinds of forests, crop plants, and grass. Natural vegetation is a reliable index of the possibilities of plant growth, because it portrays the results of the operation of both climatic and soil factors on plants over a long period of time. The original soils no longer exist; and many years of natural processes and intelligent procedure on the part of man will be necessary to restore the qualities that made possible the best growth of trees and cultivated plants. We can decrease the rate of present wastage and follow procedures that will speed up the redevelopment of top soil where we are now farming the lowest soil horizon, or its "parent material."

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