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The

ESSENTIALS OF PLANT BIOLOGY

S. FRASER

The ESSENTIALS OF PLANT BIOLOGY

By

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THE ESSENTIALS OF PLANT BIOLOGY

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PREFACE

A scholarly President of the United States once said that he was materially opposed to systematic writing, "because no man knows enough about anything to write about it systematically." He said that no man knows more about a certain subject than some parts. When starting to write systematically, he pointed out, there must be some sort of plan, a table of contents, a systematic scheme of chapters. "Some contain things he knows; some contain things he doesn't know, but has taken from somebody else; and he fixes the surface so that all will look alike, the parts not being divided," said the President.

A book about the essentials of plant biology must be written systematically, whether or no. The pattern of content and its form of presentation must be given first consideration. The plan of this book has been developed in an attempt to portray the unity of plant life—the maintenance of individual life in Part I and the preservation of racial life in Part II. The topics and materials are those in current use, the development of interest being uppermost in determining their sequence and integration. It has been my intent to make a functional approach, but to be consistent is difficult.

I had thought not to mention objectives, indispensable as they are, but I cannot forgo saying that some things have been included to emphasize certain aspects of plant science that enter into daily life; and others, to develop reflective concepts that have a bearing on human culture and progress.

I am indebted to my associates at The Pennsylvania State College for their help and cooperation in the preparation of this volume. Special thanks are due Dr. C. C. Wernham, who joined me in writing the manuscript for Chapter 12; Dr. H. W. Thurston for his aid with the proofs; Dr. J. Ben Hill for many valuable suggestions; and Miss Grace Thomas for assistance in the preparation of the index. One of my greatest obligations is to my good friend, Dr. Harold H. Clum of Hunter College, for his critical reading of the manuscript.

The illustrations include numerous photomicrographs. It has been found that they aid materially in establishing certain concepts. I have in-

cluded also many diagrams. These supplement the more conventional type of photographs and drawings. The illustrations that are not original have been obtained from various sources. I am particularly indebted to Dr. George H. Conant, Triarch Botanical Products, for making possible the inclusion of two photomicrographs in color. Mr. Philip Bonhag made many of the new drawings; Miss Louise Burpo contributed several; Dr. L. O. Overholts, Dr. D. A. Kribs, and Mr. Homer Grove assisted me with the preparation of numerous photographs. I make my grateful acknowledgment to all who have aided me.

It is impossible to name individually the many biologists whose work makes possible the presentation of such a book as this; it must be recognized that to them the real credit is due.

FRANK D. KERN

State College, Pennsylvania
August, 1947

INTRODUCTION

Through the centuries of civilization man has relied upon plants for many of life's requirements. After ages of progress in ways of living we are more rather than less dependent upon plants as the ultimate sources of many necessary products. We use them for food, fuel, shelter, clothing, and medicines. We depend also upon plants for making our homes and surroundings habitable, healthful, and attractive. Plants furnish both necessities which make our existence possible and accessories which make our lives pleasurable. To come to an appreciation of the service of plants to mankind, we must make an effort to understand how plants live, develop, and reproduce; how they are being improved; and how their products are being more widely and effectively used. Plant biology, or botany, deals with these topics.

Some persons study medicine to become physicians, others study law to become attorneys. The world needs these practitioners, but we are also aware that a general knowledge of the fundamental principles of these professions is a great asset to all of us. Likewise, professional botanists must carry on the work and development of plant science, but we cannot escape the fact that the life of no one can be complete, nor any education liberal, without a realization of the significance of plants in human affairs. Someone has truly said that man would rapidly come to such a realization if some mysterious catastrophe were suddenly to annihilate all plant life. Fortunately such a method is not necessary. Through study and observation it is possible to come to an understanding of plants, their forms, their uses, their habits, their ways of nutrition, reproduction, and adjustment to surroundings. Only with such knowledge will come an appreciation of man's efforts to utilize the wealth of plant life and a realization of the possibilities of yet undiscovered utilities. Even to be able to comprehend many references in papers, magazines, and books, we must have some knowledge of plant biology.

THE PLANT BODY

For the past hundred years there has been an increasing tendency to liken a plant to a mechanism "having specialized parts which perform the vari-

ous functions upon which the maintenance of its life depends." It must be understood that a reference to a plant as a machine is made in a figurative and not in a literal sense. A machine does not build, repair, or reproduce itself. A plant does all these things and thus is fundamentally different.

We shall do well to begin our studies by obtaining a general plan of the structure of the body of ordinary seed plants (Fig. Introd.–1). Roots, stems,

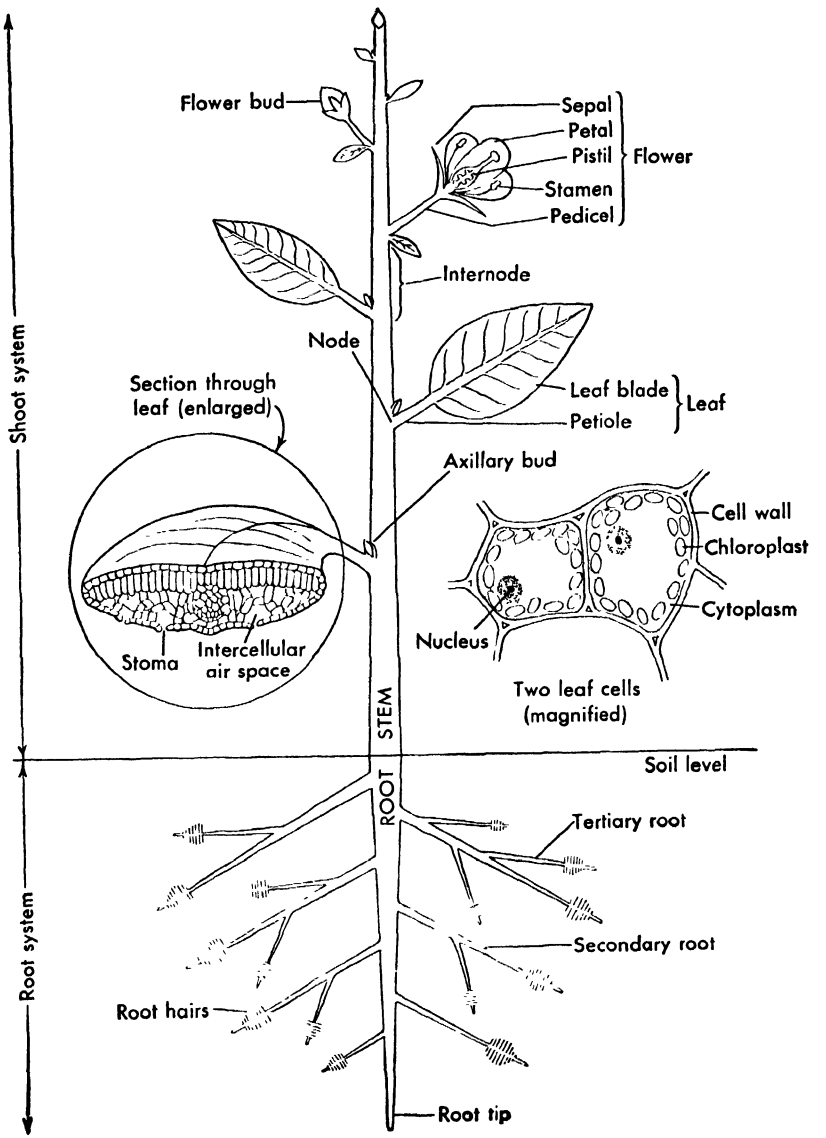


Fig. Introd.–1. Organization of a seed plant (Diagrammatic).

leaves, flowers, fruits, and seeds are familiar objects. From past experiences most people have formed general ideas of these several parts of plants. In order to understand the inner working of a living plant it is necessary to expand somewhat these general ideas of the grosser features and relations of the different parts and also to learn something of the minute structure as well.

Plants show a great variation in the form, arrangement, and development of their parts and yet the general plan is rather uniform. There are two principal working parts, root system and shoot system. We refer to these systems as the working parts because they carry on the life processes of the individual; botanically they are known as the vegetative organs. These life processes include the absorption of materials, their distribution and use, and the provision of energy for growth and development. Flowers are concerned with the perpetuation of the race through the formation and dispersal of seeds from which new plants arise; they are reproductive organs. Not all plants produce flowers. Ferns are without flowers and their reproduction does not take place through seeds, but by other special reproductive structures known as spores. The algae and fungi are other flowerless plants reproducing by spores. Their working bodies are also different in not having roots, stems, or leaves.

For the present, however, let us consider the body of a seed plant. The usual root system grows beneath the surface of the ground, serves to anchor the plant firmly in the soil and to withdraw from it water and dissolved substances, which form part of the raw materials used in growth. Roots conduct the absorbed water and dissolved substances upward into the shoot system and receive other substances from the shoots. Under the term shoot system a stem and its leaves are collectively included. The shoot system normally extends above the ground as a continuation of the root system and often grows extensively both upwards and outwards. The stems bear and support the leaves, flowers, and fruits, and conduct materials from roots to leaves and from leaves to roots. The majority of leaves are flat green structures. The green leaves are essentially the food-making organs of the plant. The veins, which are usually evident in leaves, serve as a supporting framework and also as conductors of materials both to and from the leaf.

Having in mind the general plan of the grosser construction of the body of a plant, we should endeavor to obtain next some concepts of the more minute structural features. These ideas and concepts may seem vague at first, but they will be useful for reading, discussion, and observation, and they gradually will become expanded and more adequate.

If parts of the body of a plant are examined with the aid of a microscope they are found to have a honeycomb appearance. The individual structural units are called *cells.* The cells vary in size in the different organs of the plant body, but a general idea of their minuteness is gained from the fact that there are about 50,000,000 of them in an ordinary apple leaf. Many plant cells are more or less box-like structures. The early workers with the microscope saw the framework, or walls, of the cells and were much impressed by them. Later it became evident that life was inherent in a substance within the cells which came to be called *protoplasm,* and that the walls are a product of its activity. The protoplasm is almost universally divided into two portions, an outer colorless jelly-like mass (*cytoplasm*) enclosing a denser globule (*nucleus*). The *cytoplasm* commonly surrounds cavities (*vacuoles*) which are filled with watery solutions (*cell sap*), one or more protoplasmic bodies (*plastids*), and also non-protoplasmic particles (*food granules*) which give it a grayish granular appearance.

Cells are arranged in groups called tissues. A plant tissue may be composed of living cells, or of dead cells, or of both living and dead cells. The cells vary greatly in shape and structure in the different tissues. In the conducting tissues they are elongated and narrow; in supporting tissues they have thick strong walls; in growth tissues at the tips of roots or stems they have thin walls and abundant protoplasmic contents. There are many kinds of tissues and there is a correlation of structural features with the different functions.

The bodies of all plants, and animals too, grow and develop through the formation of new cells by division of preexisting cells. The living body is composed of organized protoplasm and its products. It is important to think of cells as component structural units of the body but it is also important to realize that they have functional relations to the activities of the individual organism of which they are parts. There is an interdependent relation between the cell units and the organism as a living being—the parts affect the whole and the whole affects the parts.

THE STUDY OF PLANTS

The field of biological study is extensive; the science of *biology* includes all knowledge of plants or of animals or of both. The facts and principles of biology are commonly separated into those pertaining to plants, called *botany,* and those pertaining to animals, *zoology.*

Because there are so many different kinds of plants and their life rela-

tions are so varied and complex, there have been developed within the science of botany a number of specialized divisions, such as *taxonomy,* dealing with names, description, and systematic classification; *physiology,* the study of the processes and reactions which go on in the living body; *morphology,* concerned with the form and structure of parts, and their relationships to one another; *pathology,* which is a consideration of diseases; *ecology,* which explains the relations between plants and their environment; *genetics,* the study of heredity; and *cytology,* which deals with the structural and functional organization of protoplasm. A broad study of plant life involves some consideration of all these interacting phases of biology and requires also a general background of physical and chemical knowledge.

We cannot proceed very far with the study of plants without using names for them, or without referring to them as groups. It will be well, therefore, to learn some of the basic facts about plant names and classification early in our studies.

Many plants have common names. They are much used and serve a useful purpose, but they have their limitations. They lack definiteness and cannot be used satisfactorily in different languages. Botanists use Latin names which can be internationally applied. In applying common names to plants we recognize the fact that they fall into groups according to the degrees of their likenesses. We speak of the oaks, the maples, the roses, and the buttercups. The trees that we call oaks are not all alike; hence we refer to some of the different kinds as white oaks, red oaks, or black oaks. Botanically the name of the oak group, or *genus* as it is called, is *Quercus;* the different kinds, or *species,* must have two names, e.g., white oak, *Quercus alba,* red oak, *Quercus rubra,* and black oak, *Quercus nigra.* Similar individuals constitute a species; groups of species which resemble one another more or less closely form a genus. When one Latin name is used alone it is always the genus name. In detailed schemes of classification many larger groups are successively established.

To some of these large groups we have already referred; a further description, even though brief, will be helpful, with other references which will come later. The *fungi* are non-green plants including such groups as the yeasts, molds, mushrooms, and toadstools. The *algae* are seedless plants, comprising especially pond scums and seaweeds. The *liverworts* and *mosses* are small, seedless plants, occurring typically as a ground cover in the woods. They may have a leafy shoot but do not have roots. The *ferns* are larger, seedless plants, best developed as undergrowth in the forest shade. They

have shoots and roots. The *seed plants* constitute the largest and most widely known group. In the majority of them seeds are produced through the development of flowers and fruits. (See Figs. Introd.–2 and 3.)

In brief outline we have sketched the body of a green, leafy, seed plant and we have said a word about other kinds of plants. These general con-

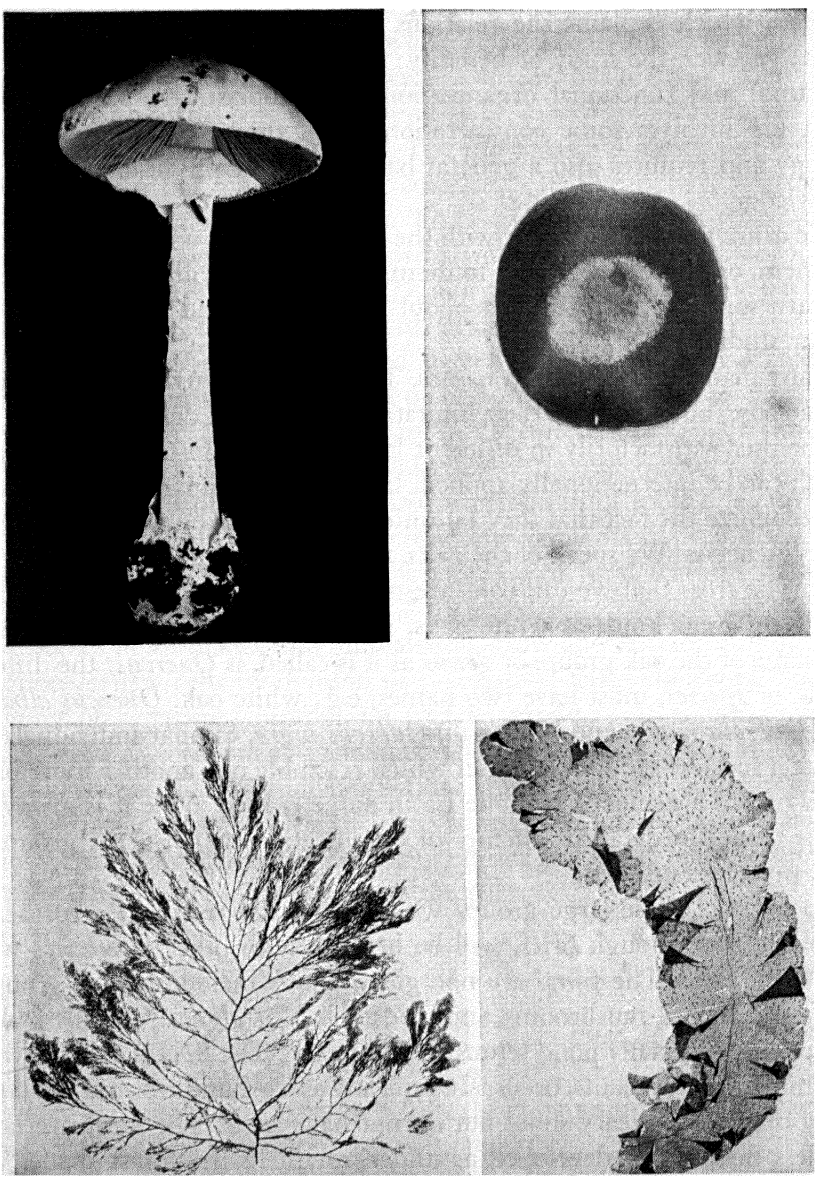


FIG. Introd.–2. Fungi (above) and red algae (below).

siderations of form; of organs, tissues, cells, and protoplasm; and of classification, are a prelude to the main biological considerations which follow. The highest aim must be a unified view of functions and forms. Plants are our inheritance from nature, and the importance of studying them has

FIG. Introd.–3. A fern; a flowering plant; a liverwort; a moss.

long been recognized. Everyone can come to an appreciation of what man has done toward conquering and utilizing the plant world. Those who wish to go further will find that the conquest is incomplete; there are still many interesting and unsolved problems, many rich opportunities for original research work.

PART I

THE MANIFESTATION OF LIFE

(*Individual Maintenance*)

CHAPTER 1

THE FOOD SUPPLY OF PLANTS

(*Nutrition*)

It is a well-appreciated fact that animals must have food to sustain life. It is equally true of plants but not equally well appreciated. Animals move about and many times their movements are associated directly with a search for food. Plants remain rooted to a spot. Animals, at least many of them, feed in such a way that we are well aware of their intake of food. We do not see plants take anything into their bodies.

But plants grow and this may be taken as indirect evidence of their nourishment. Since plants do not move, we would seem to be justified in concluding that their food comes to them. This is not quite true, but it is true that raw materials come to them from the air and the soil, and the plants construct their food from these raw materials inside their own bodies. In these general statements we are referring to green plants and not to parasites or other non-green plants, such as mushrooms, toadstools, and puffballs.

It should be understood that the term *food* may be defined and used in a broader sense than we have determined to use it. We have just said that the inorganic substances which enter the plant from the soil are not food. Practical agriculturists, however, usually speak of fertilizers as plant foods. Many scientific agriculturists also adopt this usage. They say that soils lack certain plant foods and that these need to be added in order that the plants may grow well. What they add are inorganic salts or unavailable organic materials which are converted in the soil into available inorganic compounds. Such a conception of food is not without support among biologists. It can be held, also, that the term food must be broad enough to include mineral constituents because they are found in the living substance of the body called protoplasm. However, in this discussion these things are not to be considered as foods. For our purposes the term food includes only organic substances (we call them carbohydrates, fats, and proteins). The term nutrition is used to include all the processes by which food is secured or transformed.

The first step in the natural production of foods is known as photosynthesis. The term means "putting together in the light" and is an appropriate one because the process takes place only in the light. Under the influence of the green coloring matter, chlorophyll, the living plant combines the elements carbon, hydrogen, and oxygen, of the compounds carbon dioxide and water, to form carbohydrates. In this process the free energy of light is stored. These carbohydrate foods, better known as sugar and starch, may be used as such, or they may be used as the basis for the synthesis of fats and proteins. For protein synthesis there are used also several minerals such as nitrates, sulphates, and phosphates which plants absorb from the soil.

PHOTOSYNTHESIS

Photosynthesis is a factor of such importance in life, not only for plants but also for animals and man, that an attempt to learn more about the process and the conditions under which it is carried on is incumbent on the student of biology. The great majority of living organisms, both plants and animals, depend upon the process and products of photosynthesis to sustain life. There are some plants, such as the fungi, which cannot carry on photosynthesis and hence are also dependent directly or indirectly upon the plants which are independent through photosynthesis. Some kinds of bacteria manufacture their own food by another process; these organisms are not dependent upon the photosynthetic process for their food supply. With these exceptions, the process of photosynthesis furnishes the food for the entire living world. Of equal significance is the fact that photosynthesis is the means by which the supply of atmospheric oxygen, upon which all life depends, is replenished (see Fig. 2–10).

Photosynthesis is of broader benefit to man than in the supplying of food. Photosynthesis is an energy-storing process of great importance. The radiant energy of sunlight is transformed by the green plants to potential energy in sugar. For every gram of sugar made, 3.75 calories of light energy are transformed to chemically bound energy. Most of the energy that man uses in the form of heat, electricity, and mechanical power can be traced to plants. The potential energy of fuel, whether wood, coal, or oil, is sunlight stored in photosynthesis.

Relation Between Chlorophyll and Photosynthesis

Reference has been made to the fact that green plants are the ones in which the process of photosynthesis is carried on. If the entire plant body

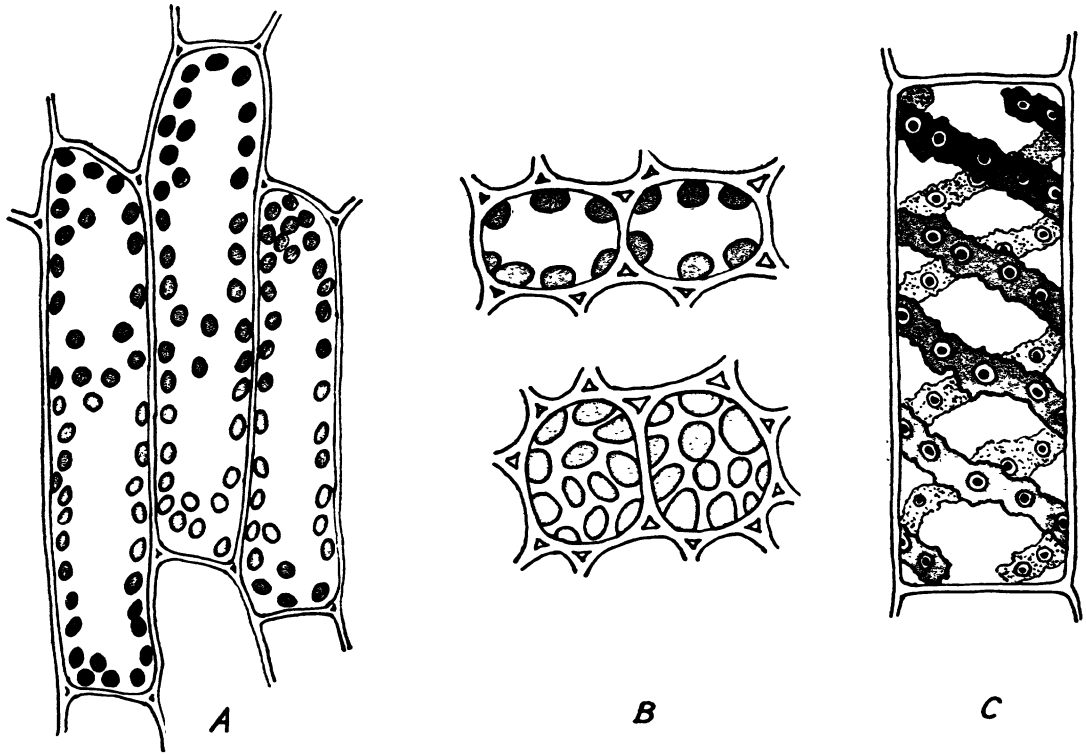


FIG. 1-1. Structure and distribution of chloroplasts. *A*, in cells of ditchmoss (*Elodea*); *B*, in cells of a moss (*Atrichum*)—above in strong light, below in light of diminished intensity (after Schimper); *C*, spiral band-like chloroplasts in a pond scum (*Spirogyra*).

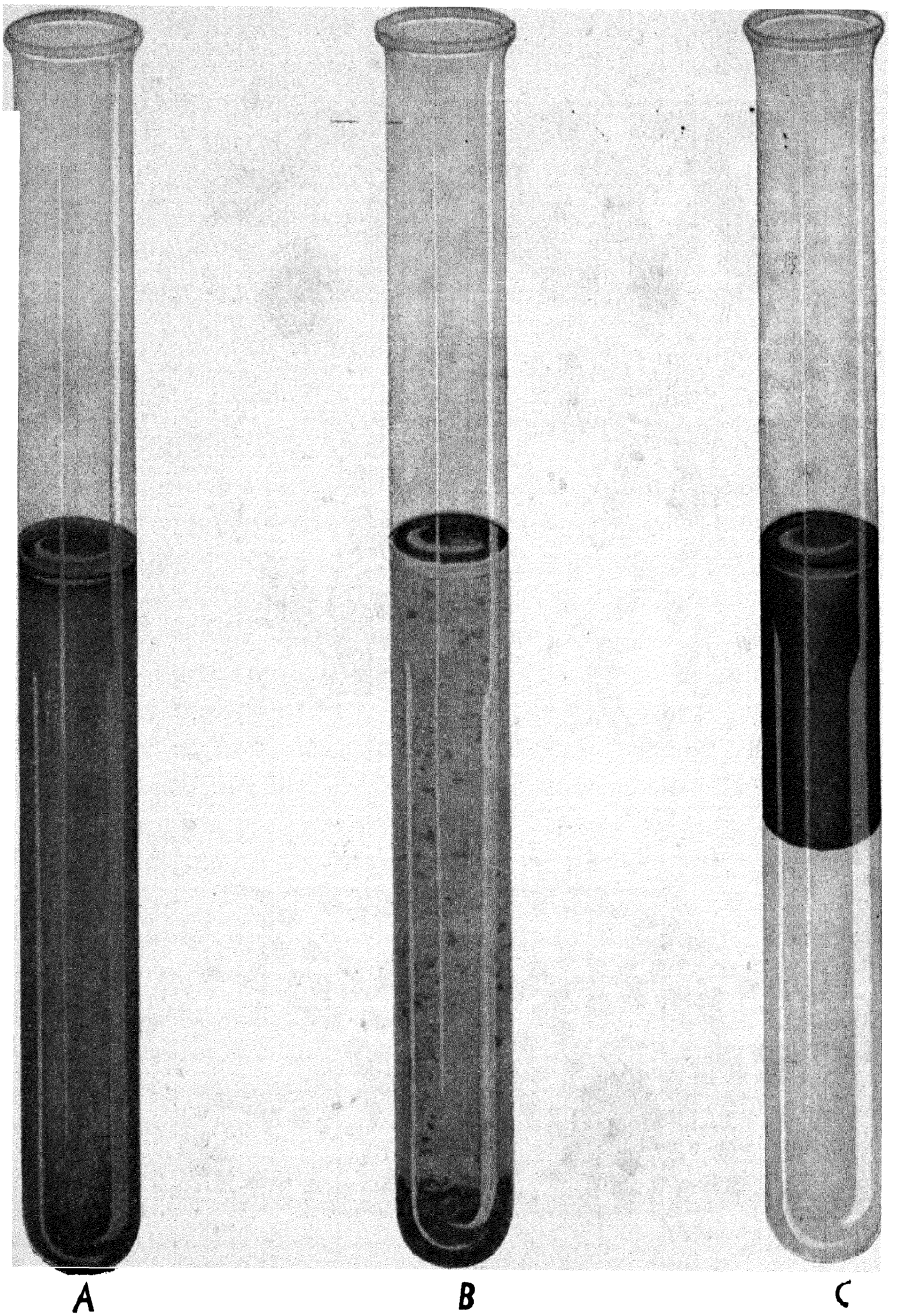


FIG. 1-2. Chlorophyll extracts in test tubes. *A*, alcoholic extract; *B*, the same after exposure to sunlight; *C*, alcoholic extract to which benzene has been added (see text for further explanation).

is not green, then it is only in the green parts, such as the leaves or green stems, that there is photosynthetic activity. The green color in plants is due to the presence of two green pigments, properly designated *chlorophyll a* and *chlorophyll b,* but usually referred to by the one term chlorophyll. Although a leaf looks green as if the green pigment were present throughout the whole material structure, this is not the case. A microscopic examination reveals the presence of the chlorophyll only in small dense protoplasmic bodies or *plastids,* called *chloroplasts,* embedded in the more fluid protoplasm or cytoplasm of the cells (Fig. 1–1). The shape, size, and distribution of these chloroplasts may vary in different kinds of plants, but they are commonly roundish or lens-shaped, very small, and lie in the protoplasm close to the cell wall. (In a way the plastid and the green pigments are independent of each other and yet they are not.)

Certain plants sometimes produce chlorophyll in darkness. Potatoes sprouting in a dark cellar grow long yellowish shoots. If a board lies on the grass for a while the grass loses its green color. In these cases the plastids are present but the green pigment is not. Light is necessary for the formation and existence of the chlorophyll. If a seed is germinated in total darkness the shoot does not develop chlorophyll. If living green plants are put into darkness and kept there they will gradually lose the chlorophyll which had been present. The blanching of celery is a good example of the loss of chlorophyll.

We can separate the chlorophyll pigments from the plastids by soaking green plant tissues in certain chemicals which will dissolve the chlorophyll. Chloroform, ether, benzene, acetone, and alcohol will serve the purpose. Common grain alcohol is most often used for laboratory experiments, and if heat is applied the extraction is hastened. Chlorophyll does not dissolve in water even if green leaves are boiled in it.

It can be shown readily that the alcoholic extract is not a simple compound. If benzene is poured slowly into a test tube partly filled with an alcoholic extract, and a few drops of water are added, there will be a separation (Fig. 1–2). The benzene will rise to the top and will be bluish-green, while the alcohol which remains below will be yellow. Chemical analysis has revealed that there are two pigments in the benzene, *chlorophyll a* and *chlorophyll b;* the former is blue-green and the latter yellow-green. The chlorophyll *a* and *b* are definite compounds and are always present in all green plants. The yellow color in the alcohol is due to pigments known as *carotenoids.* They are always associated with the chlorophyll in green tissues. They also occur in roots, flowers, and fruits in the absence of chlorophyll. They are the cause of the yellow color of carrots,

sunflowers, lemons, and oranges. The carotenoids are responsible for the yellow color of animal body fat, butter fat, and egg yolks. One of the carotenoid pigments (β carotene) is converted into vitamin A in the animal body.

There are two other facts about the alcoholic extract which can be discovered without difficulty. It is fluorescent, i.e., it looks green by transmitted light and reddish or brownish by reflected light. If some of the extract is divided between two tubes and one of them is exposed to sunlight for a short time, the other being kept in the dark, it will soon be evident that the one in the light has changed to a muddy brownish color, whereas the tube in the dark is unchanged. Light has broken down the green pigments. A similar destruction doubtless occurs in the living green tissues in the light, but so long as the formation equals the destruction they do not appear to change. Under the unfavorable conditions of the autumn, which prevent the formation of new chlorophyll, the green color does disappear and yellow and red colors prevail. The yellow color is due to the carotene pigments which were present but masked, and the red is due to the development of other pigments (*anthocyanins*) which were not present previously. The red pigments appear in the cell sap and are soluble in water. In some plants, such as coleus and red cabbage, the red pigments are present throughout the growing season and mask the green pigments which are also present. In some bacteria there is present a purple pigment which is chlorophyll-like and enables them to carry on photosynthesis. These plants which appear red or purple are exceptions to the general statement that only green plants carry on photosynthesis.

The first product of the photosynthetic process is a soluble sugar known as glucose, but in many plants this sugar is very quickly changed into starch. Food in the form of starch is insoluble in cold water. In the cells it exists as grains, easily visible with a microscope. The form and size of the grains vary in different plants (Fig. 1–3). Food analysts are often aided in their work by the identity of starch grains which they can determine by microscopic examination. At night the starch is changed back to sugar and is removed from the working cells and transported through the veins of the leaves to the stems and other parts of the plant body. Not all of the starch, however, may be removed from the green leaves during only one night. The rapidity of transportation varies in different kinds of plants and may vary in the same plant at different stages of development.

Since iodine turns starch a blue color it is possible to use it as a test for the presence of starch. In order that the blue color may show, green leaves

are first blanched by heating them in alcohol. When iodine is added to such whitened leaves not only can we detect the presence or absence of starch but by the depth of the blue color we can get a general idea of the amount of starch present. Tests have shown that young plants of sunflower, castor bean, common bean, and cabbage will remove all the starch from their leaves in one night. The common geranium must be kept in the dark two nights and one day (and corn three nights and two days) before all traces of starch are removed from the leaves.

In order to experiment with the manufacture of starch, the experimental plants should be placed in the dark long enough to drain them of their starch. They should not, however, be kept in the dark longer than necessary since that might cause the chlorophyll to break down.

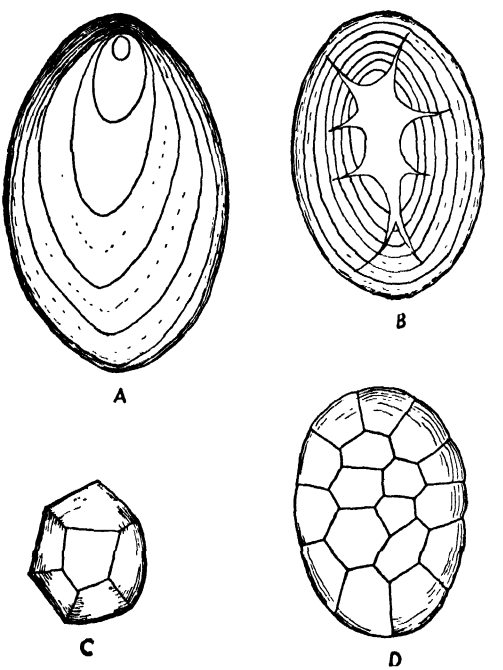


FIG. 1–3. Grains of four different kinds of starches. *A*, potato; *B*, bean; *C*, corn; *D*, oats.

One of our first experiments may be to determine whether chlorophyll is really responsible for the food-making process. A potted plant of some species which has variegated leaves supplies the material for the test. One of the geraniums used for borders of flower beds, sold under the trade name of Mme. Saleroi, is an excellent plant for this purpose. Chlorophyll is present only in the centers, there being a well-defined white margin to practically every leaf. If we take these leaves from plants that have been destarched by keeping them in the dark, remove the chlorophyll by heating in alcohol, and apply iodine, we will of course find no starch. Now if the plant is left in the light for an hour or even less and if leaves are then tested in the same manner, we find starch present in the center distributed exactly in the same area where the cholorophyll was located. There is no blue color in the white margin where the chlorophyll was lacking. Here is evidence that chlorophyll is necessary for photosynthesis (Fig. 1–4).

Relation Between the Raw Materials and Photosynthesis

The chemists tell us that the formula for the sugar, glucose, is $C_6H_{12}O_6$. Such a compound can be formed from CO_2 (*carbon dioxide*) and H_2O (*water*) with an excess of O_2 (*oxygen*) according to the following equation:

$$\text{Energy} + 6\ CO_2 + 6\ H_2O = C_6H_{12}O_6 + 6\ O_2$$

Starch originates from the glucose ($C_6H_{12}O_6$) by transformation. The formula is $(C_6H_{10}O_5)_n$. This means that there is a loss of water and that the combination $C_6H_{10}O_5$ is repeated an unknown number of times in the molecule.

While the above equation showing how carbon dioxide and water may be combined to form glucose looks simple, the actual process in the plant

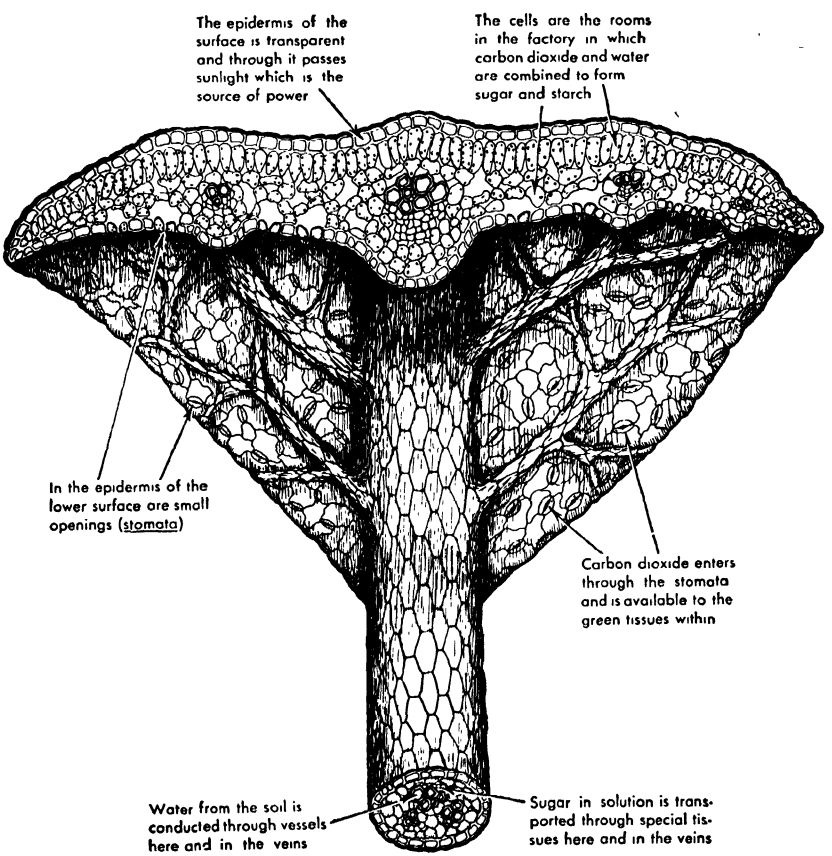


FIG. 1–5. A green-leaf photosynthetic factory. (Drawing by Louise Burpo.)

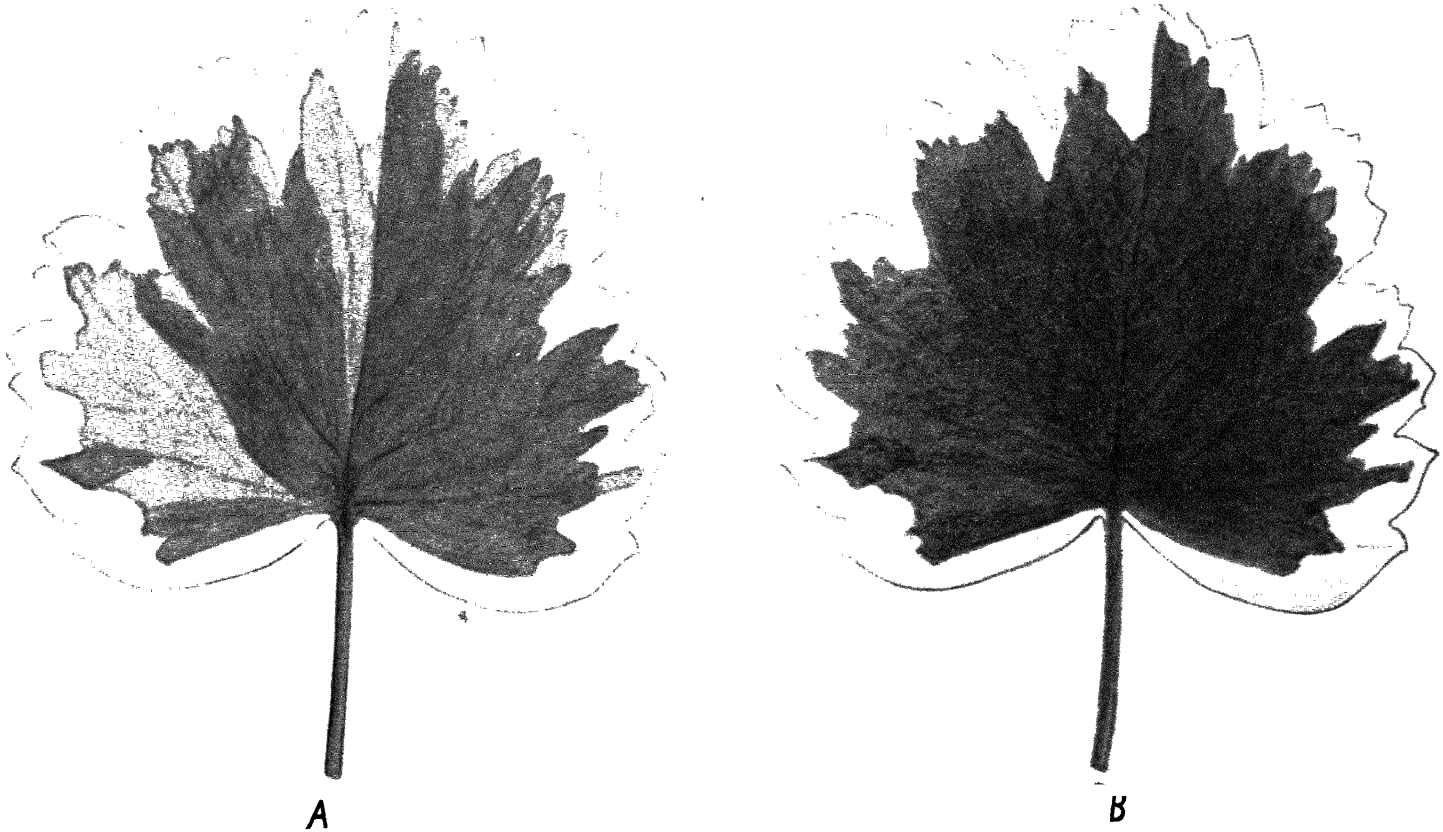


FIG. 1-4. Experiment showing the necessity of chlorophyll for photosynthesis. *A*, fresh leaf of a variegated geranium; *B*, the same leaf with the chlorophyll extracted and treated with iodine. Note that the starch pattern corresponds with the chlorophyll pattern in *A*.

is not simple. There is every reason to believe that the process is extremely complex. There has been much chemical and physiological investigation of the process of photosynthesis.

These facts are well established: (1) Chlorophyll and light are necessary; (2) carbon dioxide and water are the raw materials; (3) carbohydrates are formed and oxygen is liberated (Fig. 1–5). It is certain that for every volume of carbon dioxide used, an equal volume of oxygen is liberated. Although many theories have been advanced, the chemical reactions suggested for transforming the raw materials into the products (carbohydrates and oxygen) must be considered speculative. One of the recent theories is that chlorophyll actually combines with carbon dioxide and water as a first step; then there occurs a molecular rearrangement resulting in a complex compound of the nature of a peroxide. The carbon of this compound which originally came from the carbon dioxide is then reduced, possibly by a shift of hydrogen atoms from water to another chlorophyll molecule and then to the carbon, and glucose is eventually formed, probably with the aid of enzymes (substances manufactured by living protoplasm and effecting chemical changes). According to this theory, only the intermediate reaction is photochemical, the first and last reactions being purely chemical. This theory also makes chlorophyll play a larger part than absorbing light since it assumes that the chlorophyll combines chemically with the raw materials.

That carbon dioxide is necessary for photosynthesis is a fact which can be proved readily. The gas, when present in the air, enters the leaves through small openings (stomata) in the layer of surface cells (epidermis). Green leaves in an atmosphere devoid of carbon dioxide do not show any starch reaction. The results are conclusive. For the test (Fig 1–6), a gallon bottle with a fairly wide neck is used.

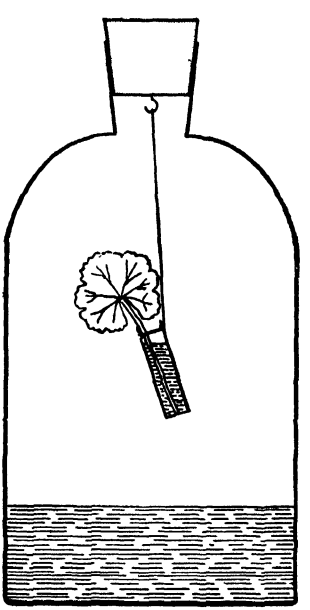


FIG. 1–6. Method of suspending a leaf in an atmosphere devoid of carbon dioxide. See text for explanation.

From a rubber stopper there is suspended by a wire a small vial in which a detached leaf may be placed in water to keep it fresh. In the bottom of the bottle is placed a solution of potassium hydroxide. This absorbs the atmospheric carbon dioxide so that the leaf suspended in the vial has no

supply of the gas. A second bottle is arranged in exactly the same manner, except that water which does not absorb the carbon dioxide is placed in the bottom of the bottle instead of potassium hydroxide. The leaves for both bottles are taken from the same plant, which was previously kept in the dark in order to make certain that the leaves will be starchless at the beginning of the experiment. If the two bottles are exposed to sunlight for an hour, or even less, and the leaves then blanched in alcohol and tested for starch, the leaf from the bottle with water gives a positive reaction and the leaf from the bottle with potassium hydroxide gives a negative reaction.

The discovery, made about the end of the 18th century, that the carbon in plants comes from the carbon dioxide of the air ranks as one of the important milestones in the progress of the natural sciences. It was by no means easy to come to the conclusion that an element making up half the dry weight of plants had such an origin. It was much easier to believe that the carbon and all the other nutrient substances were taken up by the roots from the soil.

It is not so easy to prove the necessity of water for photosynthesis. Since water is always present in the cell sap it would be difficult, if not impossible, to set up an experiment in which water was lacking. Only if the supply of water is so low as to cause wilting is the process of photosynthesis affected.

Relation Between Light and Photosynthesis

The placing of two plants in the dark until all the starch is translocated from the leaves and the keeping of one there while the other is exposed to light is a simple test to prove the necessity of light for the process of photosynthesis, although all the other factors are present.

By placing a screen over a portion of a destarched leaf (Fig. 1–7) it can be shown that light must fall directly upon the green tissue in order to have photosynthetic activity. A piece of tin foil placed over part of the surface will be found to prevent starch formation in the area beneath it.

It is a well-known fact that the rays emanating from the sun are not a simple form of energy. There is a distribution of rays from the infra-red through visible light to the ultraviolet. Ordinary light is a combination of the rays of the spectrum which are visible. But not all the rays of the visible spectrum are equally effective. Studies have shown that the red rays are most active and that the blue-violet rays are of next importance (Fig. 1–8). Of the total amount of light energy falling upon plants, it is estimated that only about 1 per cent is used in the process of photosynthesis. How-

ever inefficient this may seem to make plants as agents for the storing of energy, we must keep before us the fact that they supply in this way all the energy for themselves, for animals, and for man. The storing of radiant energy is the most important part of the process of photosynthesis.

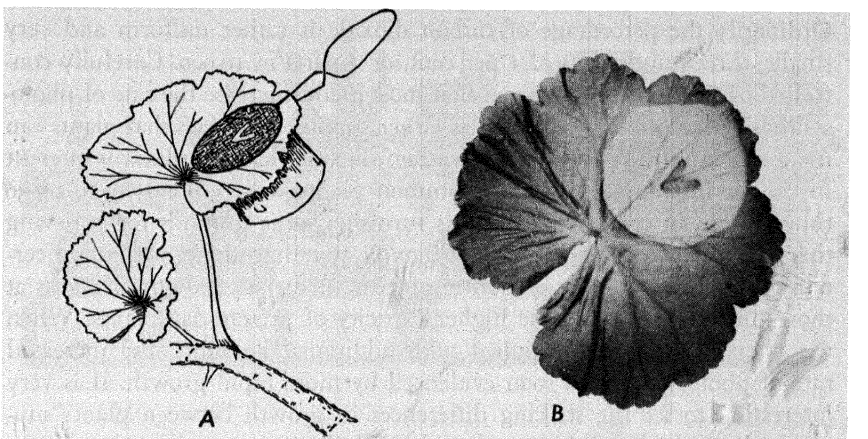


FIG. 1–7. Experiment showing effect of darkening an area of a green leaf by a light screen. The white of the darkened starchless area is in contrast to the blue of the areas exposed to the light. *A*, sketch to show method of applying screen; *B*, photograph showing result.

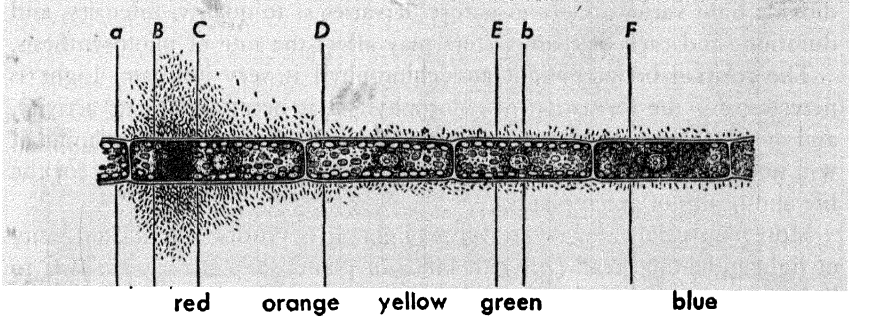


FIG. 1–8. Experiment showing the influence of the different rays of the spectrum on photosynthesis by throwing a spectrum on an algal filament. Since oxygen is liberated in photosynthesis the rate of photosynthesis may be estimated by the evolution of oxygen. Bacteria seek oxygen and are used as a test for its evolution. The greatest accumulation of bacteria is between *B* and *C*, the red region of the spectrum. (Adapted from Pfeffer.)

Conditions Affecting the Rate of Photosynthesis

It is estimated that the average rate of photosynthesis is about 1 gram of carbohydrate per square meter of leaf surface per hour. There are certain conditions which affect the rate in a very definite way.

One of the most important conditions affecting the rate of photosynthesis is the amount of carbon dioxide in the air. There are different sources of atmospheric carbon dioxide. It is released into the air by the respiration of plants and animals; from volcanoes and mineral springs; in the burning of coal, wood, and other fuels; and from the waters of the oceans and lakes. Ordinarily the percentage of carbon dioxide is rather uniform and very small—three-hundredths of 1 per cent, or 3 parts in 10,000. Carefully controlled experiments have shown that most plants increase the rate of photosynthesis perceptibly if furnished a larger supply. (The fact that plants can use a much higher percentage of carbon dioxide than is ordinarily present in the air is interesting.) Most common plants will respond to 20 to 30 times the usual concentration. This furnishes some grounds for believing that a larger percentage of carbon dioxide may have been present in certain geological ages, thus accounting for the luxuriant growth of plants at those times and also for the higher capacity of present-day plants. When the plant is artificially supplied with additional amounts, the increased rate of photosynthesis is soon evidenced by more rapid growth. It is very interesting to see the striking differences in growth between plants supplied with additional carbon dioxide and those grown in ordinary air, when all other conditions are kept constant.

Light affects the rate of photosynthesis, and unlike the supply of carbon dioxide light varies greatly in nature. It varies as to quality, intensity, and duration; and each of these factors may affect the rate of photosynthesis.

The relation between light and chlorophyll is very intimate. Light is necessary for the formation of chlorophyll, it is necessary for its activity, and at the same time it destroys chlorophyll. With these facts in mind it will not seem strange that light conditions are extremely important for the life and health of green plants.

Most plants flourish best in diffuse light. It is possible for the intensity of light to be too great. Different kinds of plants vary in their reaction to light intensity. Some plants can have noontime daylight reduced to 1/12 of its intensity before a decrease in photosynthetic activity occurs. Plants which endure shade can carry on some photosynthetic activity with low intensity. The Norway maple is capable of functioning when the intensity is 1/55 of noon daylight. The cherry, on the other hand, can stand a reduction of only 1/3 without interference with the rate of activity.

The daily duration of light may have an effect upon the growth of plants, particularly upon the development of flowers and fruits (Fig. 1–9). Many plants "attain the flowering stage only when the length of day falls within certain limits," some responding to short days and some to long days. These responses are attributable not to the effect of the quantity of light upon

food-making but rather to the number of hours. Other physiological processes may also be involved. Further reference to the influence of length of day is to be found in a later chapter where growth is discussed.

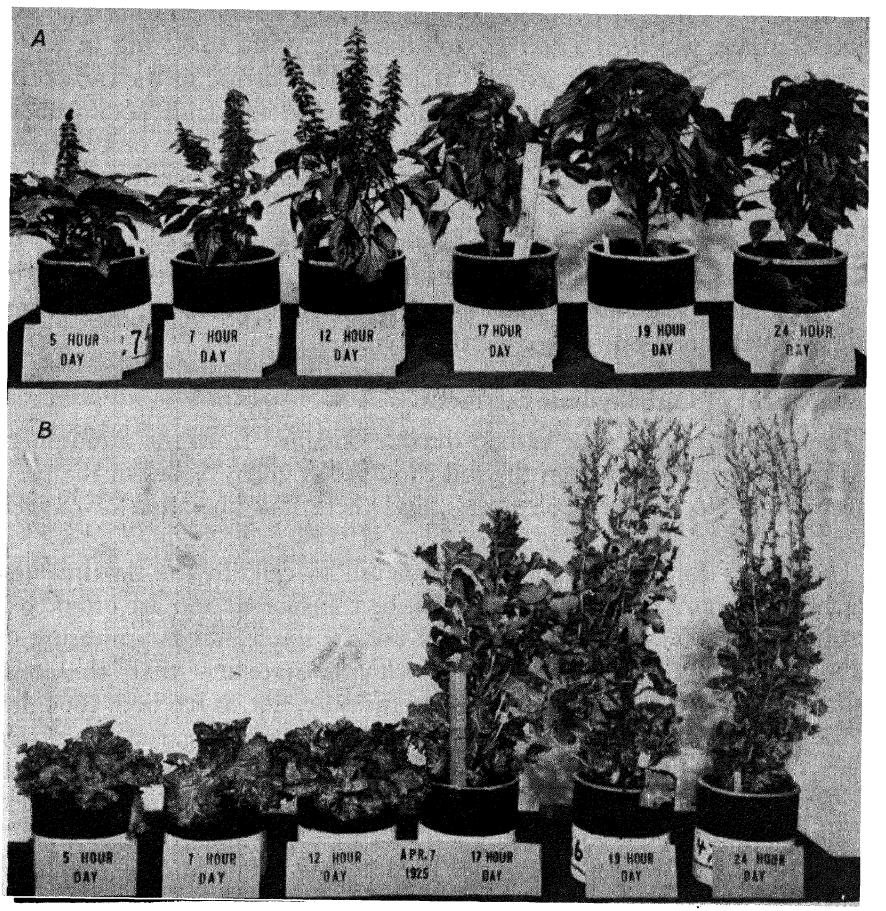


FIG. 1–9. Effect of length of day on plant growth. *A*, a short-day plant, scarlet sage; *B*, a long-day plant, lettuce. (Photograph by J. M. Arthur. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

Temperature is another condition which affects the rate of photosynthesis. The so-called cardinal temperatures—minimum, maximum, and optimum—vary with the species of plants. In some arctic species effective photosynthesis can take place below 0°C. In the laurel cherry the lower limit is said to be — 6° C. and the upper limit 45° C. The optimum for

many common plants is from 20°C. to 22°C. From experiments with the Irish potato the following data have been reported: In full sunlight carbohydrates formed at the rate of 2.1 milligrams per 100 square centimeters of leaf area per hour at a temperature of 5°C.; at 10°C. the amount increased to 6.3 mg., at 15°C. to 8.6 mg., reaching an optimum of 13.8 mg. at 20°C.; there was then a decrease to 8.8 mg. at 25°C., to 8.0 mg. at 30°C., to 5.7 mg. at 35°C., and to 2.9 mg. at 40°C. An increase in the carbon dioxide supply raised the optimum temperature in the Irish potato about 10°C. and the maximum at least 5°C. The photosynthetic process, generally speaking, is doubled for every 10-degree rise in temperature between 0°C. and 30°C.

The rate of carbohydrate synthesis may be affected by a deficiency in soil water. If the water supply is insufficient, lessened synthesis may be due not directly to a lack of water as a raw material, but rather to unfavorable internal conditions caused by the dryness.

Restatement of Carbohydrate Synthesis

The facts are these: The carbon dioxide obtained from the atmosphere and the water obtained from the soil combine in green tissues in the presence of light to form carbohydrates, and there is a liberation of oxygen (Fig. 1–10).

The sugars formed readily pass from cell to cell. In the daytime the sugars form more rapidly than they can be transported and are often converted into starch. While we ordinarily use the starch test as a measure of carbohydrate synthesis we must agree with the statement that "the accumulation of starch in the chloroplasts is a measure, not, as has been thought, of the working capacity of a leaf, but of the excess of sugar-making over sugar transportation." Starch can be made from sugar not only by the green plastids but also by colorless plastids, and this process may take place in the dark, as in potato tubers.

The rate of photosynthesis varies in different plants and in the same plants under different conditions. Ganong has estimated that an average may be 1 gram of carbohydrate per square meter of leaf surface per hour. This he says is enough in a season to cover the leaf with a solid crystalline layer of sugar 1 millimeter (1/25 in.) thick, and it requires as much carbon dioxide as is to be found in a column of air of the same area as the leaf and 2.4 miles high. However, the carbon dioxide actually used is never taken out of such a hypothetical column. Additions to atmospheric carbon dioxide are constantly being made from the soil, especially during rains. This carbon dioxide escaping from the soil remains near the ground be-

cause it is heavy; it thus forms the chief supply for plants. It is possible that the small amount of carbon dioxide available in the atmosphere usually operates as the limiting factor in photosynthesis. The quality, intensity, and duration of light, the temperature, and the water supply are other conditions affecting the rate of carbohydrate synthesis.

A recent writer has referred to photosynthesis as the packing of radiant energy into small parcels by the choloroplasts of the chlorophyll-containing plants. The packing of these parcels of energy, which he calls "foodstuff molecules," is referred to as one of the two fundamental reactions of life; the other is their unpacking. The packing reaction is performed only by chlorophyll-containing plant cells, while the unpacking reaction "is performed by all cells, whether of the plant itself, or of the animal which eats the plant, or of the animal which eats the animal that ate the plant." It must be emphasized that the unpacking process requires oxygen, which is constantly available in nature because the supply is replenished in the packing process.

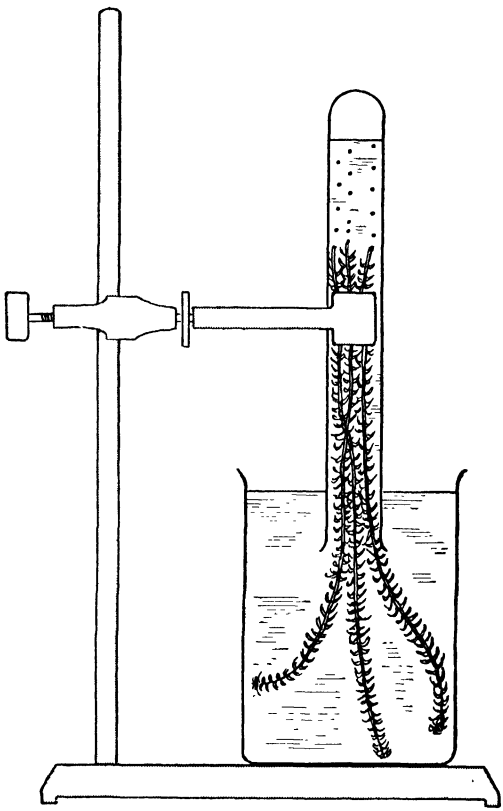


FIG. 1–10. Apparatus for the study of release of oxygen in photosynthesis. Shoots of some plant growing under water such as *Elodea* may be used.

FAT AND PROTEIN SYNTHESIS

The foods manufactured by plants are three: (1) carbohydrates; (2) fats, or fixed oils; and (3) proteins, nitrogenous in nature. We know a good deal about carbohydrate synthesis but not so much about fat and protein synthesis, yet our conception of plant nutrition would be incomplete indeed if we did not give some consideration to fats and proteins.

The fats, or fixed oils, are made up of the same elements as carbohydrates but in different proportions. The properties of fats and carbohydrates are not at all similar. The fats are relatively low in oxygen content. They are lighter than water and insoluble in it, but are soluble in ether and chloroform. We are familiar with fats and fixed oils as they are stored in such seeds as peanuts, castor beans, cotton, and corn, or as they are found in the commercial products expressed from such seeds. The fixed oils are excellent storage materials partly because of their light weight and partly because they contain a larger amount of stored energy per volume than carbohydrates. The so-called volatile oils, familiar to us for the fragrance they give to lemons, cloves, wintergreen, peppermint, etc., are different in composition and significance and are not to be regarded as foods.

Fat and Oil Synthesis

It does not seem probable that the synthesis of fats and oils is localized in any tissues, cells, or cell parts. Fats and oils are found to some extent in all protoplasm and it seems likely that it is a fundamental capacity of protoplasm to synthesize them. They are derived from carbohydrates by the protoplasm without the aid of light or chlorophyll. Specific enzymes are involved in the process. In some kinds of seeds, large quantities of carbohydrates are converted into oils while the seeds are maturing. Young almond seeds have been found to have 35 per cent carbohydrates and 2 per cent oil, as against 8 per cent carbohydrates and 46 per cent oil when old.

Protein Synthesis

In addition to carbon, hydrogen, and oxygen, proteins always contain nitrogen, usually sulphur, and sometimes phosphorus. The elements nitrogen, sulphur, and phosphorus are supplied from the soil, chiefly in the form of nitrates, sulphates, and phosphates.

The method of synthesis is uncertain and probably variable. The most important requisites are a supply of carbohydrates and available nitrogen. The green cells seem to be the chief seat of protein synthesis because the supply of raw materials is most adequate there. Carbohydrates are the basic substance out of which proteins are made. It is believed that the nitrates are first reduced to the ammonium form and that nitrogen is then incorporated with the three elements of the carbohydrates to form "building stones" known as amino acids. This is a step of great biological importance, since nitrogen is an outstanding constituent of the living protoplasm. The fact that green plants do not use free nitrogen of the air but utilize combined nitrogen from the soil accounts for the fact that nitrates are often the most

important constituent of fertilizers. Nitrogen scarcity in the soil is frequently the limiting factor in the growth and development of crop plants.

The final step in protein synthesis is the linking together of the amino acids, a step in which enzymes (substances capable of causing chemical transformations) are involved. This can be carried on in all parts of the plant, although regions where growth is most active may produce larger quantities. Proteins are so essential for the building up of the protoplasm that we may regard them as among the most important substances manufactured by plants.

Chemists recognize several different groups of proteins under such names as globulins, albumins, glutelins, etc. They will not diffuse from one cell to another until converted into amino acids by enzymes. The amino acids may be rebuilt into proteins after translocation to the growing parts or storage regions. Proteins are highly complex compounds with very large molecules. Gliadin, a protein of wheat, has the formula $C_{685}H_{1088}N_{196}O_{211}S_5$; egg albumin, $C_{696}H_{1125}N_{175}O_{220}S_8$. They exist in the cells sometimes as grains and sometimes as crystals. Their presence cannot always be made out well microscopically unless they are treated with reagents.

DIGESTION AND TRANSFER OF FOODS

Foods are synthesized in certain cells and frequently assimilated or stored in other cells. There are two reasons why foods must be moved from place to place within the plant body—one is to supply the cells which do not make food with their nutritional and respirational needs, and the other is to shift reserve materials to a place for storage. Carbohydrates are made originally only in green cells. They must be supplied to the cells lacking chloroplasts. It is evident that there must be a transfer of foods within the bodies of plants. We should know something about how this is accomplished.

Digestion

In order that foods may be assimilated, or transferred from tissue to tissue, or otherwise used, it is necessary that they be rendered soluble. These are fundamental biological processes. The reactions involved are *catabolic* in nature; i.e., they are the tearing-down processes of metabolism. The catabolic processes of making foods soluble are known as digestion.

The first foods manufactured in the leaves are the carbohydrates, sugar and starch. The higher foods are constructed from these by rearrangement

of their constituents or with additional materials. Sugar is soluble in water. Its molecules are comparatively small. Food in the form of sugar is readily transferable as such, while starches, fats, and proteins are not. We have learned that starch quickly appears in some leaves when conditions for photosynthesis prevail. But in order that starch may be made soluble it must be converted into sugar. This can be brought about by a type of chemical reaction known as *hydrolysis*. In this process there is a chemical addition of water. Such changes are effected by the activity of substances known as *enzymes*. The common enzyme in plants which changes starch into sugar is *diastase* (in reality not a single enzyme but several) and the process of conversion is called *digestion*. It is possible to demonstrate the digestion of starch in a test tube.

Diastase (of malt) can be purchased from any chemical supply company. Malt, which is sprouted grain, is a good source of diastase for the manufacturing chemist. When seeds are germinating, the enzyme is present and converts the starch into sugar. Starch paste can be prepared by putting starch into hot water. By adding a solution of diastase to a starch paste in a test tube the disappearance of starch can be proved by the iodine test. The appearance of sugar can be demonstrated by the use of a test with Fehling's solution.[1]

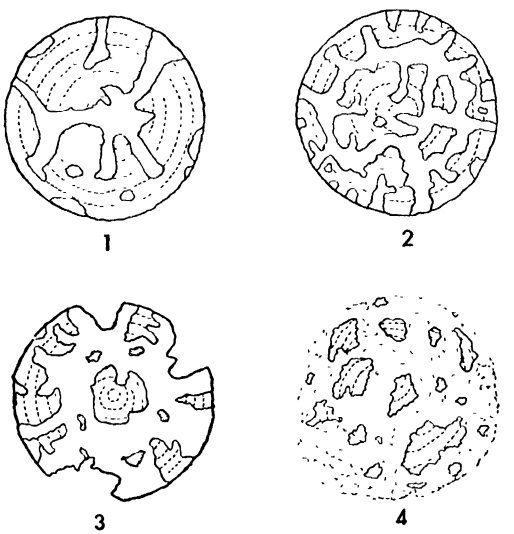


FIG. 1–11. Stages in the digestion of starch grains of barley. (After Strasburger.)

The digestion of starch grains can be observed under a microscope. They show gradual erosion. At first narrow canals appear which branch and enlarge until the grains finally become completely disintegrated (Fig. 1–11).

Starch must be digested in order to be moved out of the leaves where it first forms. It is transferred in the form of sugar. If not assimilated, starch

[1] Fehling's solution is a mixture of copper sulphate, sodium hydroxide, and sodium potassium tartrate (Rochelle salt). If glucose is present in a solution it can be detected by adding Fehling's solution and heating the mixture to the boiling point. The presence of glucose produces a yellow-red precipitate. The amount of red precipitate is a measure of the amount of glucose present.

may be reformed in some storage organ, such as stem, fleshy root, or seed. When foods are taken out of storage for new growth or for respiration, digestion must proceed once more. If reserve foods are in the form of fats or proteins they must be digested in order that they may pass from one cell to another and eventually be assimilated. The enzyme commonly associated with digestion of fats and oils is lipase. Proteins are digested by proteases and allied compounds.

Enzymes

A further word about enzymes is in order. In chemistry it is known that there are certain substances or agents called catalysts which are capable of hastening the rate of chemical reactions and yet appear unchanged at the end of the reactions. Enzymes are catalysts. They are produced only by living cells. They can, however, be isolated and separated from the living cells and are then capable of bringing about the same reactions as they do in the living tissues. Although they are produced by living cells, their activities are not dependent upon the life of the cell. They have been described as "the chemical tools of the living cells." The changes brought about by enzymes in organic substances are numerous and varied. We have shown how they are important to digestion. They are important not only to digestion but in most of the chemical changes that take place in living bodies. Not much is known of the chemical nature of enzymes. It is known that a very small quantity of enzyme can produce extensive effects. It does not seem too strong a statement to say that enzymes are fundamental to life.

The terms used to apply to specific enzymes are sometimes confusing. This comes about because there are a few old terms and a multitude of new ones, and, as a result, there is some overlapping. We referred in a foregoing paragraph to *diastase* as the enzyme concerned with starch digestion and added in parentheses "in reality not a single enzyme but several." Diastase is a collective term. In the conversion of starch into glucose there are likely several steps and several enzymes involved—amylase, dextrinase, and maltase. We used proteases in the plural to indicate that there are several. The proteases convert proteins into albuminoses and peptones. Lipase acts upon fats and oils, changing them to fatty acids and glycerin. This enzyme is able to reverse its action and bring about the synthesis of fats from fatty acids and glycerin. It is interesting that it can cause either synthesis or hydrolysis. It is believed that the water content of the tissue is a factor in determining its action. Some other enzymes may be mentioned. Sucrase reduces cane sugar (sucrose) to grape sugar (glucose) and fruit sugar (fructose). *Zymase* converts glucose and fructose into alcohol and water.

Zymase was first known in connection with yeast and was called a "ferment." *Cellulase* is an important enzyme in the fungi because it digests the cellulose walls of plant cells from which the fungi obtain their nourishment.

The Mechanism of Translocation

The movement of food in the plant body from the places of formation to the places of use and storage is known in plant physiology as *translocation*. When the insoluble foods are changed to soluble forms they are in condition for translocation. It is known that sugar in solution will move from one cell to another provided there are differences in concentration. Such a movement is called diffusion. Diffusion may account for much of the movement of sugar both in living cells and in dead conducting cells. If sugar, when moved into storage tissues, is converted into starch, the conditions for the continued entrance of the sugar into the storage cells is maintained. This is obvious when we keep in mind that in diffusion the sugar moves from the places of its higher concentration to places of its lower concentration. The conversion into a starch would lower the concentration of sugar and make possible the continued movement.

Later we will learn about special conducting tissues in plants. Everyone is familiar with the veins in leaves. These are expressions of bundles of elongated cells (called vascular bundles). These bundles are continuous throughout the roots, stems, and leaves. Some of the cells in these bundles function in the conduction of water and others in the conduction of food. The food-conducting elements are designated as phloem. They are living cells. Movements of the living matter (protoplasm) may be an aid. It seems probable that food may move in these phloem cells under pressure, which would help to account for the rapidity of its movement. It has been pointed out that in the course of a night all the food which was made the previous day may be translocated so that in the early morning the leaf may be free of food.

The phloem tissue is in the inner bark in woody plants. It is a well-known fact that removal of a ring of bark usually causes the death of trees. Death results from root starvation. All summer there is a constant movement of food downward in the inner bark for the nourishment of the parts below and for storage. If a wire or metal ring is clamped tightly about the bark, it is sometimes possible to see a swelling of the tissues just above. This results from overgrowth partially due to the stoppage of the downward movement of food. Sometimes food may be present in the wood. Thus the wood of maple trees is tapped and the sap contains sugar.

THE FOOD SUPPLY OF DEPENDENT PLANTS

Our discussion thus far has referred to the nutrition of green plants, i.e., plants with chlorophyll which synthesize their foods inside their own bodies. It is customary to call such plants *independent* plants. But there

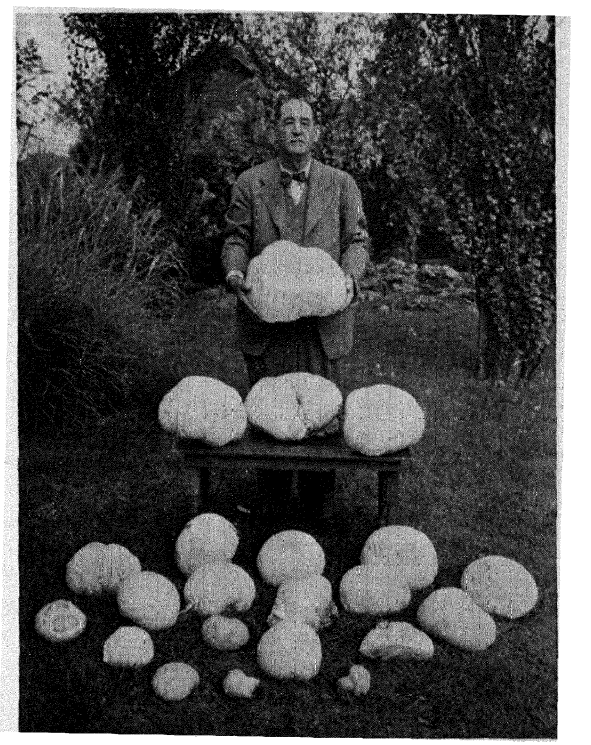


FIG. 1–12. Giant puffballs. These are chlorophyll-less saprophytes belonging to the group of plants known as fungi. (Photograph by A. B. Stout.)

are many kinds of plants which lack chlorophyll and hence cannot synthesize carbohydrates. They obtain their supply by absorbing them from some outside source. This means that they must directly or indirectly live at the expense of other organisms. On this account they are appropriately called *dependent* plants. There are two classes of dependent plants: *parasites,* which obtain their food from other living organisms, and *saprophytes,* which obtain their food from non-living organic matter or compounds. In the case of parasites we call the plant from which the food

is taken the *host*. Some parasites live within the body of their hosts. In any event they penetrate the host tissues in such a way that they can absorb food from the living cells. Saprophytes frequently live upon the dead bodies of other organisms. In fact it is due to the action of saprophytes that

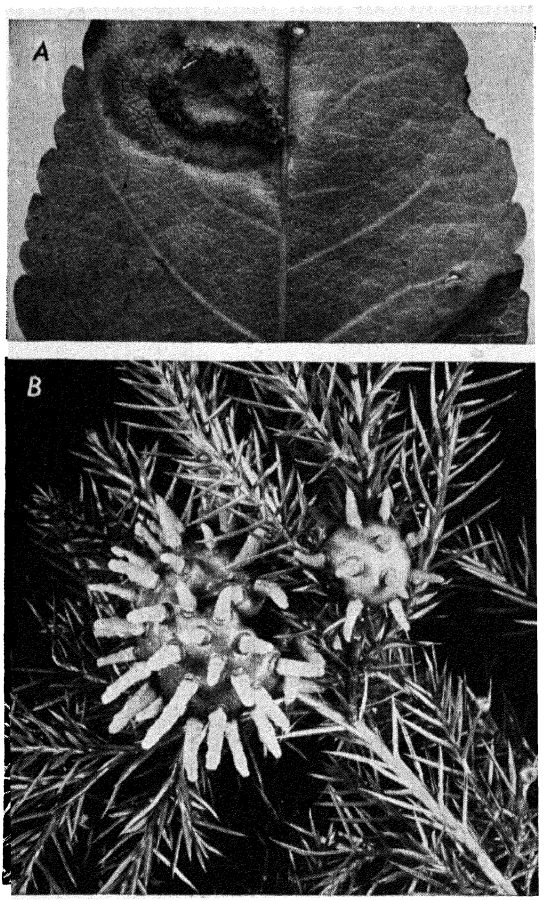


FIG. 1–13. Apple and cedar rusts. These are chlorophyll-less fungous parasites. *A*, as the rust appears on the under side of a crabapple leaf; *B*, the same fungus as it appears on galls on the red cedar.

dead organic matter undergoes decomposition and decay. As the saprophytes obtain their food they break down the complex organic substances and this constitutes decay. Our best examples of dependent plants belong to a great group known as the fungi, of which mushrooms, toadstools, and puffballs are well known (Fig. 1–12). These are saprophytes. Somewhat less widely known perhaps are such plant diseases as blights, smuts, and rusts (Fig. 1–13). Many people, however, are familiar with potato blight,

corn smut, and wheat rust. There are many more. These are caused by fungous parasites. Others are caused by bacteria. Not all of the saprophytes and parasites belong to these low classes of plant life, as evidenced by such plants as Indian pipe and dodder, which are flowering plants (Fig. 1-14). Saprophytes and parasites are able to digest, translocate, assimilate, and store food—they may synthesize fats and proteins—but they are not able to produce their own basic food from inorganic materials as are green plants.

FIG. 1-14. The Indian pipe, a chlorophyll-less saprophyte which is a flowering plant. (Photograph by L. O. Overholts.)

THE FOOD SUPPLY OF CHLOROPHYLL-LESS INDEPENDENT PLANTS

There are some kinds of bacteria which lack chlorophyll and yet are not parasites or saprophytes. Reference has already been made to the fact that they manufacture their food by a process which is a substitute for photosynthesis. These bacteria synthesize sugar from carbon dioxide and water without the energy of light. The energy necessary for this synthetic process is obtained through the oxidation of reduced iron, sulphur, manganese, or nitrogen. Since this synthetic reaction is accomplished through chemical energy instead of light energy it is called *chemosynthesis* in contrast to *photosynthesis*. Although chemosynthesis is dependent on oxidation it must not be confused with respiration. In respiration energy is released; in chemosynthesis energy is stored—it is comparable to photosynthesis, not to respiration. A few other kinds of bacteria, such as the purple bacteria, contain chlorophyll-like pigments which enable them to carry on photosynthesis.

CHAPTER 2

HOW PLANTS USE THEIR FOOD

(*Assimilation, Respiration*)

In the preceding chapter we described how plants obtain their food. We concluded that the materials which they take into their bodies are not food but merely the materials from which they make food. Their actual foods are the carbohydrates, fats, and proteins which they synthesize inside their own bodies. Accordingly foods for plants and animals are identical. The difference nutritionally between plants (green plants of course) and animals lies in the fact that animals cannot synthesize foods and must get their supply, directly or indirectly, from plants. It is a good thing that plants make more than they use. It is probably a safe general estimate that only three-fourths of the foods made by plants are used by them in their own growth and development, the other fourth being taken from them by animals for their nourishment.

Plant bodies contain a variety of substances. The living substance, protoplasm, the skeletal structures which support it, and many special substances are constructed directly or indirectly from foods. Foods are the source of the materials from which all the organic compounds are made. The transformation of food into protoplasm and other essential constituents of the living body is known in the biological sciences as *assimilation.*

In the preceding chapter emphasis was placed upon the fact that energy is stored in food. All living organisms, plants and animals, depend upon food as a source of energy. The process through which the stored energy of food is released and made available in the living body is called *respiration.*

With these two convenient terms it is possible to say that foods are used in assimilation as a source of building materials, and in respiration as a source of energy. Supplies of foods in excess of the immediate needs of assimilation and respiration accumulate within the plant. We frequently refer to the accumulation of food as the "storage of food." Storage food in green plants is the source of the food supply of most animals and of many

kinds of non-green plants. Assimilation, respiration, and storage must be considered if we would understand what becomes of the food which plants make.

ASSIMILATION

The actual living substance has long been called protoplasm. Huxley, the great English biologist, referred to protoplasm as "the physical basis of life." He used this as the topic for one of his famous essays. An important point that he made in this essay was that "all work implies waste, and the work of life results directly or indirectly in the waste of protoplasm." But he pointed out that happily protoplasm "has the capacity of being repaired and brought back to its full size after every exertion."

The Living Protoplasm

A part of the food supply of living things must go into the making of protoplasm, either to repair it and bring it back to full size, or to add to it. if growth is to take place. It is particularly the class of foods known as proteins which become incorporated into the protoplasm. It has been said that protoplasm is merely a complicated mixture of proteins together with mineral matter, water, and other compounds. It is, however, not generally accepted that we can regard protoplasm as a mere mixture of other substances. It must be regarded as a highly organized substance in itself.

Protoplasm is so important and so complex that its adequate consideration requires further treatment in a subsequent chapter. This brief presentation here is to bring out the point that one of the most important uses of food is to nourish the living protoplasm, even if it is true that only a small proportion of the total food synthesized by green plants actually has this function.

Skeletal Structures

In the higher animals we are familiar with the hard bony inner framework which supports the fleshy living substance, and in the lower animals with tough outer shell-like coats which protect internal living parts.

Many plants also have very real skeletons which are not only firm but tough, resistant, and in some cases extremely durable. We have only to think of the trunk of a tree together with its branches and roots to realize this (Fig. 2–1). Even leaves which may at first consideration seem soft and tender have a definite and effective system of veins. This can be realized when one sees leaves in which only the veins remain after the softer parts have disappeared (Fig. 2–2).

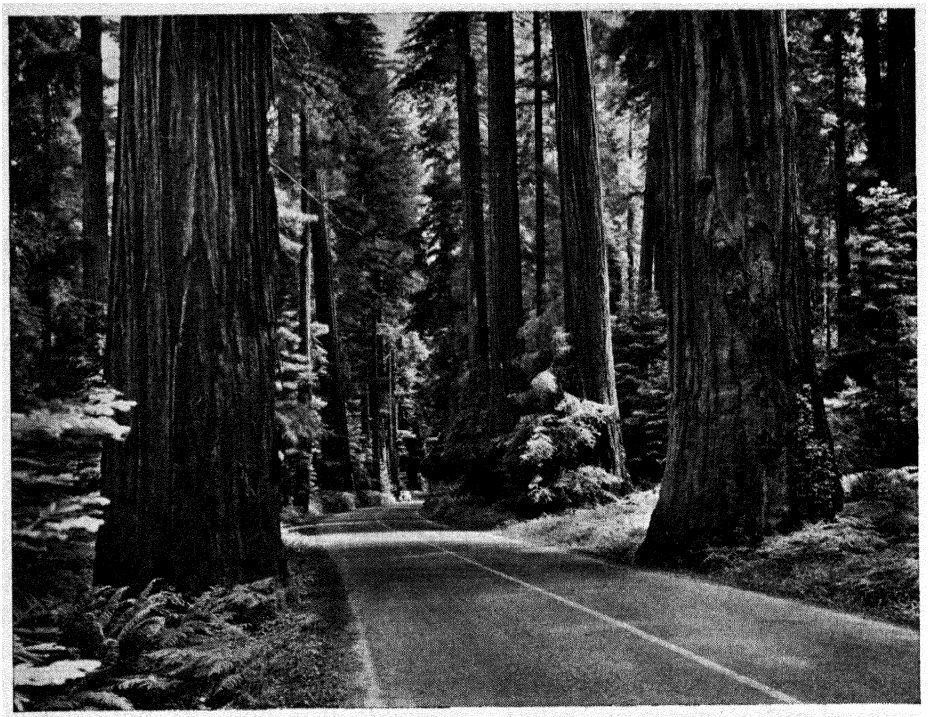


FIG. 2–1. Trunks of the giant redwoods, so massive that they reach heights of 350 feet, diameters of 30 feet, and so durable that they have existed for 2000 years. (Gabriel Moulin Photograph, courtesy Save-the-Redwoods League.)

FIG. 2–2. Leaf skeleton showing network of veins.

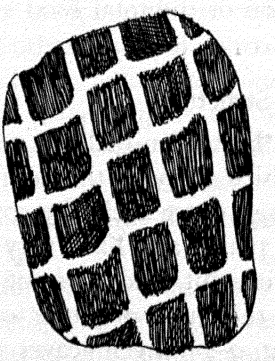


FIG. 2–3. The honeycomb (cellular) appearance of cork as copied from an illustration by Robert Hooke.

Nearly 300 years ago an English philosophical mechanic by the name of Robert Hooke discovered that bottle cork was made up of little separated compartments to which he gave the name cells (Fig. 2–3). Little did he realize the biological significance of his discovery, but it has long since been known that these spaces were originally filled with protoplasm when the cork was young and growing. Hooke used the term "cell" because he

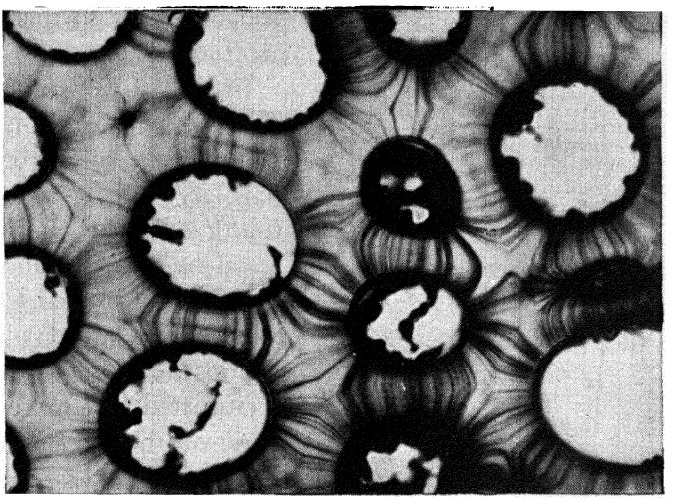


FIG. 2–4. Section of endosperm (food-storage tissue of seed) cells of persimmon, showing connecting protoplasmic threads through the greatly thickened walls. (Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

was impressed with the space, but now we think of the protoplasm together with the surrounding wall as the cell. However, we do sometimes use the term cell in the original sense as Hooke applied it. There are conducting elements and fibers in the woody tissues where the protoplasm finally dies and disappears, and yet we refer to the empty walls as cells. This cellular structure, with variations in the size and arrangements of the cells, is to be found in all plant parts as well as in the cork of the bark where first seen. The living unit of protoplasm, often called the *protoplast,* builds the wall around itself. A wall is a characteristic part of most plant cells. It is not an indispensable part of a cell. There are some plant cells and many animal cells without walls. The walls of plant cells do not completely separate the protoplasts; they are commonly penetrated by exceedingly fine channels through which pass delicate protoplasmic threads (Fig. 2–4).

The walls of these tiny units, cells, collectively form the plant skeleton. They are, therefore, a most significant structural feature of the plant body

(Fig. 2–5). Not only do they serve as a framework for mechanical support but they may serve equally well for the transportation of water and food. Elongated cells in a series form conducting strands when the walls have thin spots or perforations, especially at the ends where the cells are joined. In the woody portions of the stem the entire end walls of the cells in the series may dissolve and disappear so that real tubes are formed.

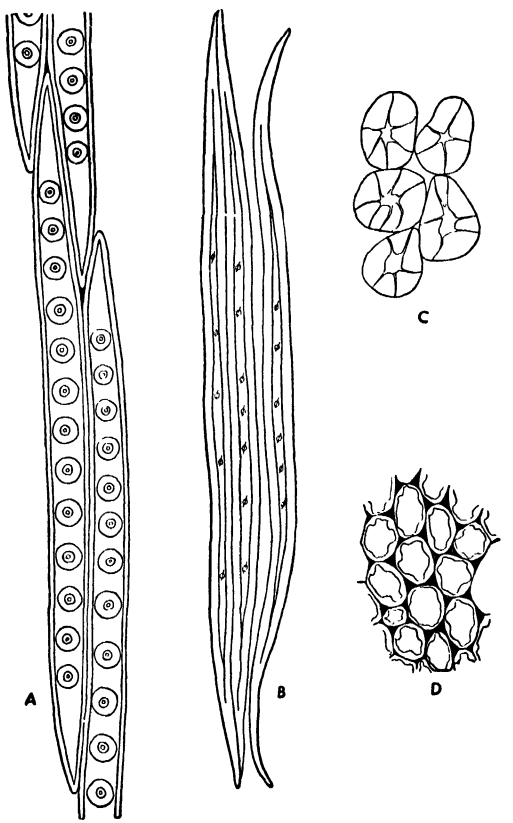


FIG. 2–5. Four important types of cells serving as mechanical elements. *A*, tracheids, from woody tissue; *B*, fibers possessing great tensile strength and flexibility; *C*, thick-walled cells known as stone cells which form supporting tissues in various parts of the plant body; *D*, collenchyma cells which provide strength and elasticity in young stems and leaves.

The chief constituent of the walls of plant cells is cellulose. With the cellulose other materials are usually associated. In young cells the walls are composed of cellulose and jelly-like (pectic) compounds. Chemically, cellulose is a carbohydrate made within the plant from sugar. It is estimated that more than one-third of the sugar made by a green plant is converted into cellulose. It is without doubt the most abundant plant material in the world. The chemist writes the formula for cellulose as he does for starch $(C_6H_{10}O_5)_n$, with the n representing a different value. The actual value of n is unknown for either starch or cellulose. Cellulose is not soluble in dilute acids or alkalies.

Cotton fibers are the nearest approach in nature to pure cellulose. Filter paper is a product consisting chiefly of cellulose. Cellulose is the raw material used in the manufacture of such articles as paper, celluloid, artificial silk, guncotton, and cellophane. The process of manufacture of these materials, and many others, comprises an interesting story.

Cellulose is definitely a structural material, but not the only one. We have

already referred to the fact that the young cells in growing parts have walls of cellulose and pectic compounds but that the composition of the walls may be altered by the addition of other substances as the cells grow to maturity. One of the substances added to cellulose walls is *lignin*. It is by the addition of lignin that wood is formed. Lignin makes the walls firmer and harder. The capacity of resisting stresses is increased in this way. The shell of a nut is also a good example of the development of hard tissue by lignification. An alteration of the opposite kind is the deposit of mucilaginous materials in the cell walls. It is well known that such seeds as those of flax and quince absorb water, swell, and become slimy because of the presence of gummy substances. Corky cell walls of bark are formed by the addition of *suberin*. The outer or epidermal cells of leaves are rendered waterproof by an external coating of *cutin*. Mineral compounds may occur in old cell walls in wood. The outer cell walls of grasses contain silica (a quartz-like compound) which gives them very great firmness. Tannins are often present in the bark of trees, from which they are extracted for tanning leather. Tannins, oils, and resins also occur in wood and are chiefly responsible for the colors of woods of commercial value.

Special Substances

Among many special substances is a group of non-nitrogenous compounds. They contain only the elements carbon, hydrogen, and oxygen. They are derived from the carbohydrates but differ from them in composition and functions. It is likely that only a small percentage of the basic sugar goes into their formation. Their functions are in some cases uncertain, but it seems that they may serve chiefly in the better adaptation of plants to their environment.

First may be mentioned the *essential* or *volatile oils*. These are not like the oils and fats which we have considered as foods. The volatile oils are aromatic or pungent. Lemon and clove oil are good examples. Other volatile oils, secreted by special glands, are responsible for the fragrance of flowers and fruits and serve to attract insects which effect pollination, or animals that aid in the dissemination of fruits and seeds.

Then there are the *organic acids* which occur in the juices of fruits and which are responsible for their tartness. Everyone is familiar with the citric acid of oranges and lemons. Malic acid occurs in apples, tartaric acid in grapes.

On the surface of some leaves and fruits there is noticeable a grayish or bluish coating. It can be observed on grapes and plums. This is due to the formation of a *wax*. Such a thick coating of wax forms on the fruits of the

bayberry that it is possible to collect and make it into candles which are highly prized as a novelty especially at Christmas time. These plant waxes are related chemically to the oils.

Under the term *resins* is included a variety of substances which are extensively employed in medicine and the arts. Like the essential oils, organic acids, and waxes, they are composed of carbon, hydrogen, and oxygen. In the plant body they accumulate chiefly in special ducts or passages. The best-known resin is a product of pine trees. Here it is called also rosin. It exudes in a semi-liquid form from the ducts in the wood when a cut or gash is made in a tree trunk. By distillation the crude exudation is separated into turpentine and the resin proper. The latter is used in soaps, ointments, and pharmaceutical plasters, and for sizing paper. Other well-known resins from evergreen trees are the balsam of the fir and the gum of the spruce. In most cases when resins are extracted from the plants which produce them they are mixed with essential oils. According to the amount of oil, which determines their behavior, they are classed as hard resins, soft resins, and gum resins. Rubber is made from the milky juice of certain temperate and tropical plants. The milky juice is called latex. This is a mixture of resins, gums, and other substances. Amber, which like coal appears to be a product of the mineral kingdom, is a fossilized vegetable resin. It is probable that amber was derived from extinct coniferous trees. Some chemists classify bitumen and asphalt as fossil resins.

It is not clear just what functions the resins serve in the physiological processes of plants. Some of them flow out of wounds in such a way as to suggest that they may serve as a protection to injuries. It does not seem likely that they ordinarily serve as food, although it is not improbable that they may do so under certain conditions.

Some of the glucose goes into the formation of a class of substances called glycosides. This term applies to certain compounds that are composed of sugars chemically combined with other substances. Some of them contain nitrogen in addition to the carbon, hydrogen, and oxygen. *Amygdalin* is probably the most familiar glycoside. It is the substance which gives the bitter taste to the seeds of almonds and plums. The peppery taste so common in the species of the mustard family (*Cruciferae*) is also due to a glycoside. *Coniferin,* found in the sap of coniferous trees, can be artificially converted into *vanillin,* which is the aromatic principle of vanilla. Some of the glycosides are poisonous. Such a one is *solanin* which is found in the potato family (*Solanaceae*). *Digitalin* is a poisonous glycoside in the leaves of the foxglove (*Digitalis*) which has a use in medicine.

There is uncertainty regarding the value to plants of a class of substances

known as *alkaloids*. Since many of them are bitter in taste and poisonous in nature they may protect the plants against destructive animals. Chemically, the alkaloids contain nitrogen and are related to, and doubtless formed from, the proteins. Among the more important alkaloids may be mentioned strychnine, from *Strychnos* beans; nicotine, from tobacco leaves; morphine, from poppies; caffeine, from coffee berries and tea leaves; cocaine, from coca leaves; muscarine, from a mushroom (*Amanita muscaria,* Fig. 2–6); and quinine, from the bark of the cinchona tree (Fig. 2–7). Some of these have large economic or medicinal uses.

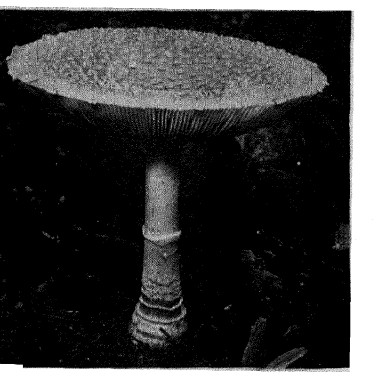


FIG. 2–6. *Amanita muscaria,* the mushroom which produces the poisonous alkaloid, muscarine. (Photograph by L. O. Overholts.)

Some of the plant food is used in the formation of pigments. The chlorophylls and carotenoids were discussed in Chapter 1, and reference was made to the anthocyanins. The latter pigments are the basis of the red colors of autumn foliage, of the red color of beets, and of the red and blue colors of flowers and fruits. The red color of some flowers is associated with an acid reaction, and blue with an alkaline reaction. This can be demonstrated by placing petunia flowers in ammonia or acetic acid. Other plant pigments which man has used as dyestuffs are haematoxylin, henna, indigo, litmus, and madder.

Other important substances synthesized within the tissues of plants are *enzymes, vitamins,* and *hormones*. Enzymes are necessary in digestion, as previously explained, and in practically all chemical transformations (metabolism) taking place in the living organism. Vitamins, known to be essential to animal life, are probably as essential to plant life. Hormones are substances which influence growth. All of these substances, although common in plants, are present in such small quantities that no substantial part of the materials within the plant body is required for their formation.

RESPIRATION

We have already indicated that when we are reviewing the various uses which plants make of their food, we must give a prominent place to a consideration of the way they get their energy from it, for this is one of the

important uses of food. It is a well-recognized fact that animals develop and expend energy. We associate activity with energy. Because plants do not move about and seem never to be active or to exercise force it is not a

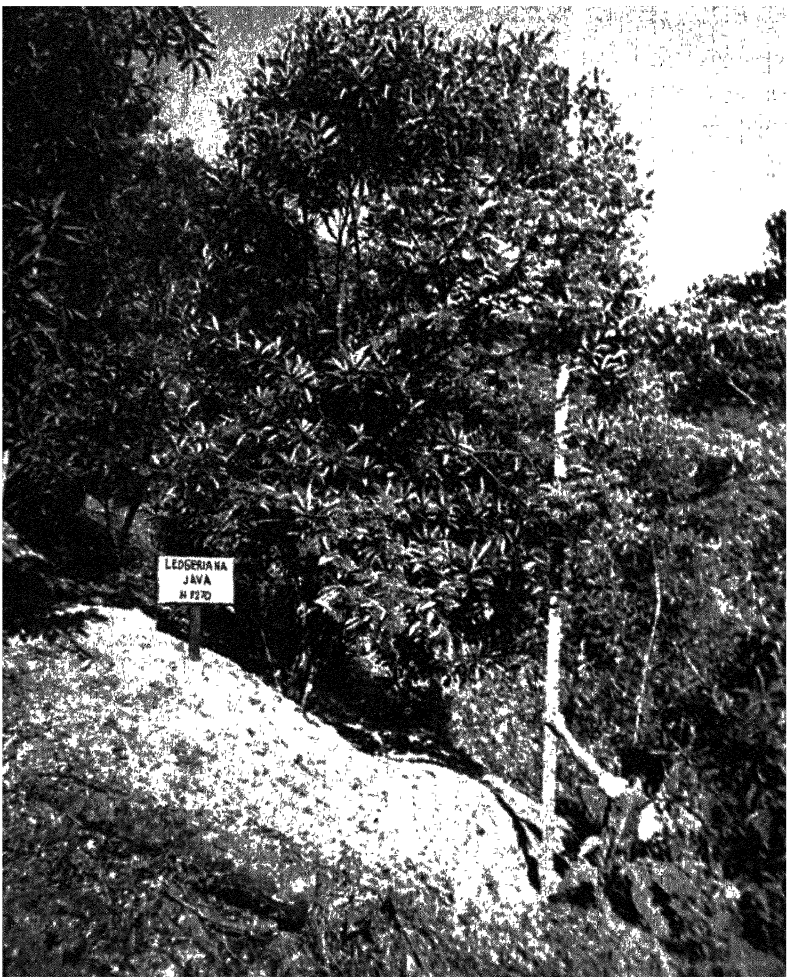


FIG. 2–7. Cinchona; the bark is the source of quinine. (Photograph by J. R. Shuman.)

generally recognized fact that they develop and expend energy. The Biblical saying, "Consider the lilies of the field, they toil not neither do they spin," is an expression of the concept that plants are passive beings.

Although plants do not move from place to place it can be proved that their parts move in a really energetic manner. It is because their motions

are so slow that we fail to appreciate them. Fortunately it is possible to magnify these actions so that we may get an entirely different impression. This can be done by taking what are known as time-lapse pictures on a film and then running the film in a moving-picture projector. We then see stem tips moving upward, nodding, and turning energetically about; roots penetrating the soil with curious twisting motions; flower buds opening and closing with jerky and often sudden movements; tendrils sweeping through the air until, striking a support, they grip it and pull the plant toward the support. Even without the aid of the movie camera we have all seen seedlings which have broken through the soil in a way to leave no doubt of a power within them.

And so we need have no hesitation in concluding that plants, as well as animals, carry on activities which require the expenditure of energy. This energy is made available through biological oxidation, the process called *respiration*. Ordinarily oxygen is taken into the living cells, with the result that substances, usually organic compounds, are broken down. The splitting of a carbon compound such as sugar releases energy; the energy was in the food molecules. A considerable portion of the food manufactured by plants is used as a source of energy. The original source of the energy is the sunlight which was locked up when the carbohydrates were manufactured in the process of photosynthesis. The *kinetic* (active) energy of light is stored in the food as *potential* (resting) energy. To be utilized, this potential energy must be reconverted into kinetic energy. All living cells are able to bring about biological oxidation "in such a way that energy is not liberated as heat but in some other more useful form." Combustion is a homologous oxidation process by which energy is similarly converted in non-living bodies. Combustion results in the release of energy principally as heat, but with the proper machinery this form of energy can be transferred into motion and made to do work. In living organisms protoplasm is the medium which transforms into motion and work the energy released by respiration.

Proof of Gaseous Interchange

The fact that animals must breathe in order to exist is so well recognized that no one asks for proof of it. But it required experimental investigation to prove that plants take in oxygen and give off carbon dioxide. A hundred and more years ago this question had been investigated and correctly interpreted. And yet some prominent workers long afterward expressed disbelief. The opposition held that it had been proved positively that plants take in carbon dioxide and give off oxygen (which they do in photosynthe-

sis) and that it was absurd to suppose that both processes could be carried on at the same time when one was the reverse of the other. But this is just what occurs. Of course both processes do not take place in all tissues and at all times simultaneously, but under certain conditions they do proceed together in the same cells. Green tissues alone take in carbon dioxide and give off oxygen, and then only in the light, whereas both green and non-green tissues in both light and darkness take in oxygen and give off carbon dioxide.

That oxygen is absorbed can be proved, but its demonstration is somewhat difficult. If seeds are germinated and grown for several days in a

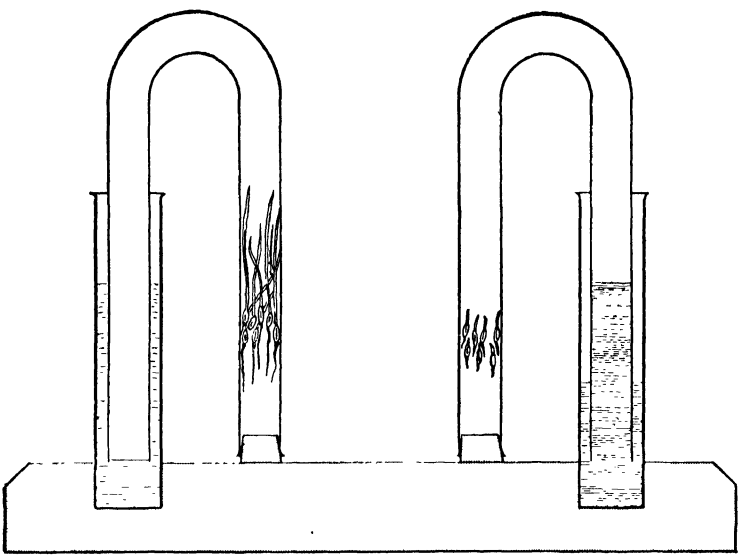


FIG. 2–8. Diagram of apparatus to show the necessity of oxygen for the respiration of germinating seeds. See text for explanation.

closed chamber, a chemical analysis reveals that oxygen has disappeared. If germinating seeds are placed in a closed chamber from which all the oxygen has been removed they cease growing immediately, whereas in a chamber with all conditions the same, except that the normal amount of oxygen in the air is available, they keep on growing normally for some time. In the first case the lack of growth indicates lack of energy, which is explained by the failure of respiration due to the absence of oxygen. To set up such an experiment two U-tubes can be used to advantage (Fig. 2–8). The germinating seeds (oats are especially good) are placed in some moist cotton near one end and that end stoppered. Some pyrogallic acid is pressed into the open end of the tube from which the oxygen is to be removed. If

care is taken, the acid will adhere to the glass and stay in place. This end can then be carefully lowered into a vessel containing potassium hydroxide. Pyrogallate of potash is formed and the oxygen is absorbed. Air pressure forces the pyrogallate up the tube so that it comes to occupy one-fifth of the space if all the oxygen is removed. The end of the other tube is placed in a vessel of water so that all conditions are exactly duplicated except that the ordinary oxygen of the air is present.

That living plants, or plant parts, give off carbon dioxide can be demonstrated by a simple method. The plant parts are placed in a wide-mouthed

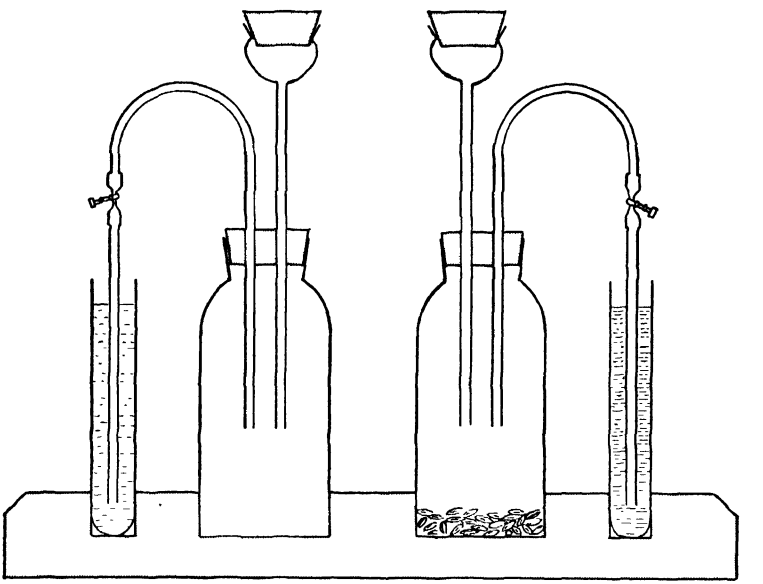


FIG. 2-9. Diagram of apparatus to show that carbon dioxide is given off in respiration. See text for explanation.

bottle (Fig. 2-9). Through the stopper is inserted a thistle tube and a U-tube which leads into a test tube containing limewater. A stopper should be placed in the thistle tube and the U-tube should have a short section of rubber tubing furnished with a clamp. In this way the bottle is airtight and can be left overnight or at least for several hours. If carbon dioxide is evolved, it is possible to detect it by its property of turning limewater milky. The gas in the bottle can be forced to bubble up through the limewater in the test tube by pouring water into the bottle through the thistle tube. If the limewater turns milky, carbon dioxide is present. By using a similar setup without the plant parts as a check it can readily be demonstrated that the carbon dioxide present in an equal quantity of air from an

empty bottle will not turn limewater milky. Any living plant parts will suffice for the experiment, but the best results are obtained when parts that are actively working are used; germinating seeds, opening flower buds, or growing mushrooms are good materials. If green parts are used it is well to keep the apparatus in the dark so as to avoid complications from photosynthetic activity.

Respiratory Mechanisms and Conditions

In ordinary respiration, which involves interchange of gases between protoplasm and the atmosphere, it is clear that the process can proceed in a simple manner with unicellular organisms, or with relatively simple multicellular organisms, whether they be animals or plants. But in larger multicellular bodies comparatively few cells are in direct contact with the air on the outside of the body and those that are so situated may be more or less impermeable. It follows that provisions for gases to pass back and forth between the atmosphere and the individual internal cells are very necessary. Most people are familiar with various mechanisms in animals such as gills, tracheae, and lungs. In the higher animals we can divide exchange of gases into two steps: (1) the interchange of gases in the lungs, and (2) a similar interchange between the body cells and the surrounding fluids. We also know that the higher animals do not wait for air to enter the lungs by its own circulatory movements but that the air is taken into the lungs and expelled rhythmically in the process commonly known as breathing.

There are no respiratory movements of plant parts. In the higher plants gases enter through openings in the epidermis (*stomata*) and through small areas of loosely arranged cells in the bark (*lenticels*). On the inside they pass through intercellular spaces. All gases diffuse from places of abundance to places of scarcity, and this purely physical process, known as diffusion, brings about the entrance and exit of gases to and from the plant body.

There are a number of conditions that affect the rate of respiration. Some of these conditions are internal factors and some are of an external nature. The age of the plant, its activity, the acidity of the cell sap, and the amount and concentration of respiratory materials may be mentioned among the internal factors. In dormant structures, such as seeds, buds, and bulbs, respiration proceeds feebly; but when growth is renewed it proceeds rapidly. Wherever tissues are growing actively the rate of respiration increases. If there is not an adequate supply of food, the rate falls.

Temperature has a direct effect on the rate of respiration. There is some respiration as long as there is life. At extremely low temperatures the rate is exceedingly low. As the temperature rises, the rate of respiration approxi-

mately doubles for each 10°C. rise until a maximum is reached. Light has an indirect effect on respiration; it is not necessary for respiration. We know that respiration proceeds at night, but in green tissues the rate is more rapid in the light. This may be due to the increased supply of carbohydrates as respiratory materials. The supply of oxygen is rarely a limiting factor in respiration since normally a great deal more is present in the atmosphere than is used. Some plants and plant parts continue to live and give off carbon dioxide in the absence of free oxygen. They carry on what is known as *anaerobic respiration*. This topic will be discussed later. The amount of water present has a direct effect on respiration. We have referred to the low rate of respiration in dry seeds. Increasing the water content increases the rate until a maximum is reached. Some chemical compounds, such as chloroform, ether, acetone, and formaldehyde, are toxic to plant tissue because of their effects on respiration. Strong doses may check respiration and cause death, but weak doses may act as stimulants increasing the rate of respiration, at least for a time. Diseases and injuries may act as stimulants to the respiratory process. Injuries under certain conditions are followed by increased growth resulting in the healing of the wound. The energy for the new growth is supplied by increased respiration.

The Chemical and Physical Aspects of Respiration

We have referred to respiration as a process inside of living cells in which oxygen unites with organic matter and breaks it down into simpler products. The chief products of this breaking-down process are carbon dioxide and water. The process goes on under the influence of respiratory enzymes called oxidases and is highly complicated. Carbohydrates disappear and carbon dioxide and water appear. Centering our attention on these end substances, we can express the reaction by a chemical equation, thus:

$$\underset{\text{Glucose}}{C_6H_{12}O_6} + 6\,\underset{\text{Oxygen}}{O_2} = 6\,\underset{\text{Carbon dioxide}}{CO_2} + 6\,\underset{\text{Water}}{H_2O} + \text{Energy}$$

This equation represents the complete respiration of glucose. As it stands, the volume of oxygen taken in is equal to the volume of carbon dioxide given off. For various reasons this is not always the case. But even if the process is not as simple as the equation would seem to indicate, the equation is correct for the two extremes of the process. Attention is drawn to the fact that this equation is the exact reciprocal of the one given in Chapter 1 as the photosynthetic equation.

Living organisms, both plants and animals, utilize atmospheric oxygen

in respiration. The constant respiration of organisms would eventually exhaust the available supply of oxygen in the atmosphere, were there not some means for releasing oxygen and making it again available for respiration. Such a means exists; it is part of the process of photosynthesis. Car-

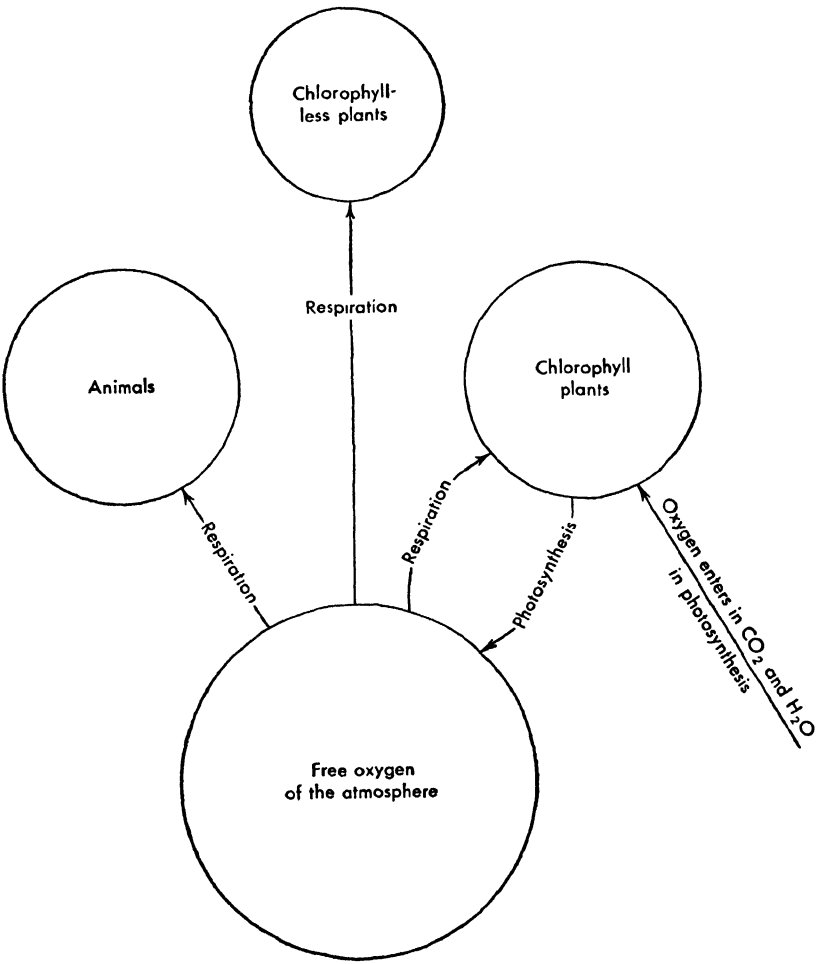


FIG. 2–10. Circulation of oxygen.

bon dioxide and water are formed in respiration; they are combined in photosynthesis to produce sugar with the liberation of oxygen. Through photosynthesis the supply of oxygen in the atmosphere is replenished. This is another way in which plant life is indispensable to all life. These facts are summarized diagrammatically in Fig. 2–10.

The respiratory equation indicates the release of energy. We have al-

ready emphasized that energy is the fundamentally important feature of respiration, and this fact must not be forgotten. Since the chemically similar process of combustion produces heat, the question naturally may arise whether or not this is true of respiration. The answer is that some of the energy released by respiration is in the form of heat. If soaked living seeds are placed in a thermos bottle provided with a thermometer through the stopper, the evolution of heat can be observed. If soaked seeds which have been killed by hot water are used for comparison, they will be found not to produce heat.

If the statement is correct that the source of the carbon released in the carbon dioxide is the solid material inside the plant, then it follows that respiration always results in a loss of weight. This is true and can be proved readily. Of course the growing plant gains in weight. This is the case because its addition of new materials by photosynthesis more than offsets its losses from respiration. To try an experiment, divide some seeds into two lots of equal weight and arrange them for growth in water cultures. Keep one lot in the dark and the other in the light. After a time those which have been in the dark will be long and spindly and will look larger than those which have grown in the light. But if the water is dried out of them and the dry weights are compared, it will be found that those grown in the light are much heavier than those grown in the dark. Those in the light have made added food, whereas the others have been losing without any additions and they weigh not only less than the seedlings grown in the light but actually less than the seeds from which they grew.

Anaerobic Respiration and Fermentation

We have already referred to the fact that plants which ordinarily require free oxygen for respiration may, when placed in an atmosphere devoid of oxygen, continue to live for a while and to liberate carbon dioxide. Physiologists call this *anaerobic respiration.* No oxygen is consumed. Energy is liberated but to a less extent than in respiration where oxygen is consumed, because the compounds yielded still contain much of the energy in the original compounds. In other words, the process does not result in complete oxidation. Carbon dioxide is formed. A common form of anaerobic respiration, or fermentation, is represented by the following equation:

$$\underset{\text{Glucose}}{C_6H_{12}O_6} = 2\,\underset{\text{Carbon dioxide}}{CO_2} + 2\,\underset{\text{Alcohol}}{C_2H_5OH} + \text{Energy}$$

The yeast plant regularly produces this effect in a sugar solution. This process is ordinarily called *fermentation* but it is actually the respiration of the yeast plant. There is a release of energy which is utilized by the yeast cells for their growth, carbon dioxide is liberated into the liquid, and alcohol is formed. When we use yeast in bread-making, our objective is the release of carbon dioxide which raises the bread. When we use yeast in the fermentation of grape juice our objective is the alcohol which is the secondary product. In neither case are we interested in the yeast plant itself except for the effects which it produces as it carries on its respiration.

Without doubt, alcoholic fermentation is the kind most familiar to us, but there are other sorts. Bacteria cause milk to sour and butter to become rancid. Carbon dioxide is produced in both, but the secondary products are lactic acid and butyric acid respectively. Fermentation is a less efficient method of obtaining energy than is ordinary aerobic respiration and yet it is the sole method used by many bacteria and fungi.

Decay of dead organic substances is in reality a form of fermentation brought about by bacteria and fungi. These organisms in their respiration break down complex substances into simpler ones until carbon dioxide and water are finally formed. Other products formed include other elemental substances and gases which are responsible for the odors that sometimes accompany the decay of organic matter. Bacteria which cause certain diseases produce their effects through poisons known as ptomaines. These bacteria act on the blood or body tissues in a manner similar to the way that yeast acts on sugar. They are carrying on respiration and obtaining energy. The ptomaines are products that are left over in these intramolecular rearrangements as alcohol is left over when yeast acts on sugar. It is a well-known fact that fermentation, decay, and certain phases of disease are caused by yeasts, fungi, and bacteria. In these processes simple organisms destroy organic matter and reduce it to carbon dioxide, water, and other elements from which it was originally formed. It is perhaps not so well known that these processes cannot be effected in any other way than through the activity of these organisms. It is surely not so well known that these processes are the results of the respiration of these organisms whereby they obtain their energy. In these organisms intramolecular respiration, which does not require free oxygen, is a complete substitute for ordinary respiration, which requires free oxygen.

STORAGE OF FOODS

In our discussion of the uses of food, we saw how food goes into the production of protoplasm, skeletal structures, and special structures, and how it is oxidized to release energy. But in many plants not all of the food made is used at once and directly in these ways. In fact most plants have both the capacity and the habit of making more food than required for their daily needs. As the surplus accumulates, it is stored. Some plants have special reservoirs or storage organs such as tubers, bulbs, fleshy roots, etc. Of course it must be clear that storage is not in itself a use of food but a method by which food is reserved in a place and in a form in which it is available for a future use. A large part of the foods which animals take from plants is in the form of stored or reserve food.

Since many plants exist in regions where conditions for food manufacture are favorable only part of the time, stored food must be utilized for respiration during the unfavorable season and must supply materials for the early growth in the next favorable season until new manufacturing parts are produced and brought into activity.

The amount of food stored, and the place and conditions of storage, are dependent upon the kind of plant. In trees great quantities of food are stored in the twigs, branches, trunk, and roots. In the spring there is a rapid movement into the unfolding buds. Many plants which do not have woody parts above ground but whose underground parts live over from year to year (perennials) have food stored in the roots or in specialized underground stems (Fig. 2–11). The thick root of the dandelion is a good example of root storage. The sweet potato is another. In the Canada thistle and the wild morning-glory underground stems are the storage parts. In lilies and hyacinths we speak of the structures as bulbs. Here the storage occurs in thickened leaf scales. The corm of the gladiolus is a thickened stem. In the common potato and the Jerusalem artichoke stems are the storage organs, for the tubers are but thickened and modified stems. In plants which live for only one growing season (annuals) food is stored in the seeds where it is available for the nourishment of the young seedling until the new green parts are producing a new food supply. In plants which live for two seasons, producing seed at the end of the second season (biennials), food is stored both in the overwintered roots and in the seeds.

All classes of foods (carbohydrates, fats and oils, and proteins) are found in storage organs. Starch is a common form of storage food. If we cut thin sections of a common potato and examine them under the microscope we find the cells packed with starch grains. If similar sections of the cotyledon

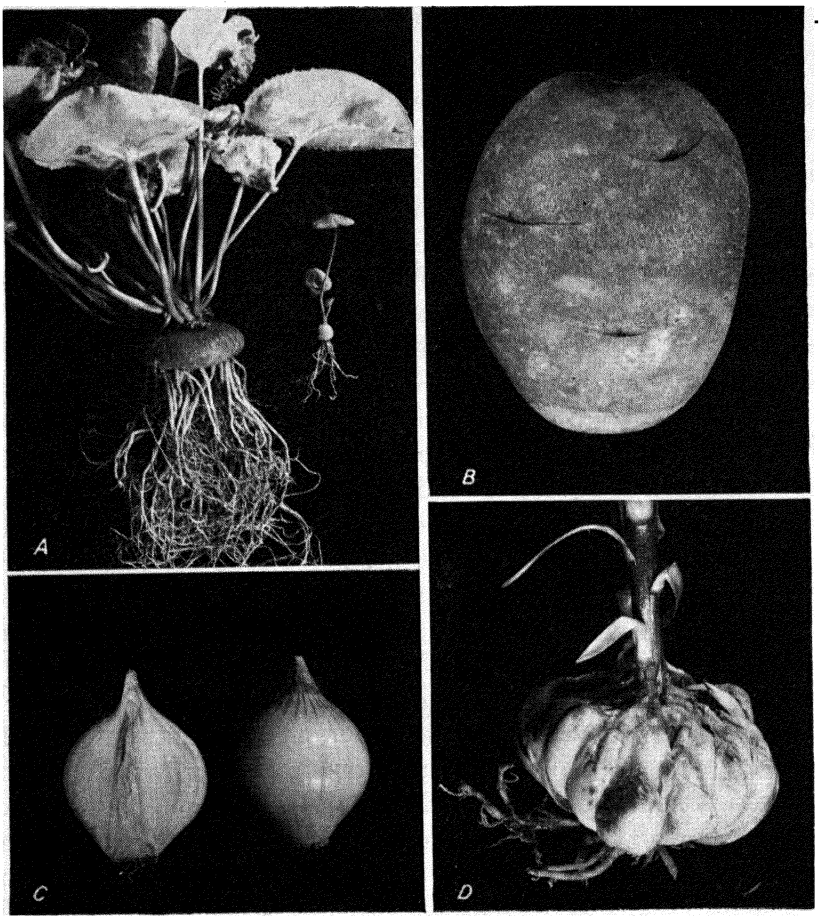


FIG. 2–11. Food storage organs. *A*, corm of cyclamen; *B*, tuber of potato; *C*, onions; *D*, lily bulb.

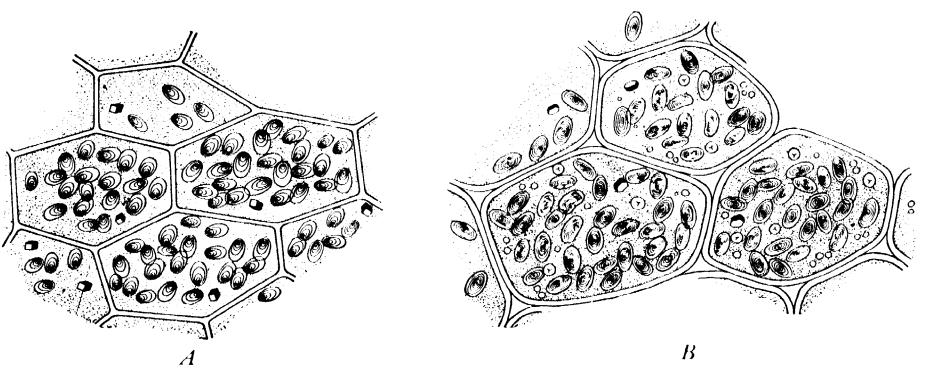


FIG. 2–12. Food storage cells. *A*, sections of cells of potato packed with starch grains; *B*, cells from the cotyledon of bean with starch grains, fat droplets, and protein granules. (Drawings by Vega Ihsen.)

(leaves of the embryo in the seed) of a bean are examined we find not only starch grains but also fat droplets and protein granules. Sugars are stored in many fruits, fats and oils in certain seeds, proteins in the grains. In some cases the walls of the cells become greatly thickened and serve as reserve food (Fig. 2–12). Here the composition is sufficiently different chemically from cellulose to be designated by the term hemicelluloses. They are found in such seeds as dates and coffee and in the nut of the ivory palm. They cause these structures to be very tough and hard.

CHAPTER 3

THE ORGANIZATION OF PLANT BODIES

(Protoplasm, Cells, Vegetative Organs)

It must be evident to the most casual observer that different kinds of plants vary greatly in form and size. Trees are large, usually with a strong trunk and branching crown; shrubs are smaller and branched but usually without any central trunk; and there are the countless smaller non-woody plants commonly called herbs. In addition there are mosses and liverworts and seaweeds which are recognized as plant life. We cannot escape the conclusion that the forms of these many kinds of plants are variable and diverse. At this point we are not concerned with an attempt to discover the causes of the variations in forms; but we should consider how great the variety of form really is, and how much the different kinds of plants have in common, although appearing so unlike.

It will be recalled that life is always associated with a substance long since known to students of biology as *protoplasm*. In the body of all living things, plant or animal, the real active living matter is the protoplasm. "The bodies of animals and plants are composed of protoplasm and its products." We come, therefore, to the realization that regardless of the form, size, or color of the body, all living things possess in common this basic material, protoplasm. Wherever there is life, there is protoplasm; "an organism is, in fact, an organized mass of protoplasm interacting with its environment." This does not explain what life is; it merely asserts that life is always associated with a certain kind of matter.

THE CELL

While it is true that life is universally associated with protoplasm we must guard against the conception that the bodies of living things always consist only of this substance. We also must avoid thinking of protoplasm as a solid or homogeneous mass. In its simplest condition it may be visualized as a thick, viscid substance something like the white of an egg. Within

the protoplasm may be included foreign particles, crystals, and droplets which are not part of the protoplasm but are completely surrounded by it.

If we examine under a microscope a drop of water containing some of the slime which collects at the bottom of fresh-water pools and similar locations, we may find a tiny moving animal form known as the amoeba.

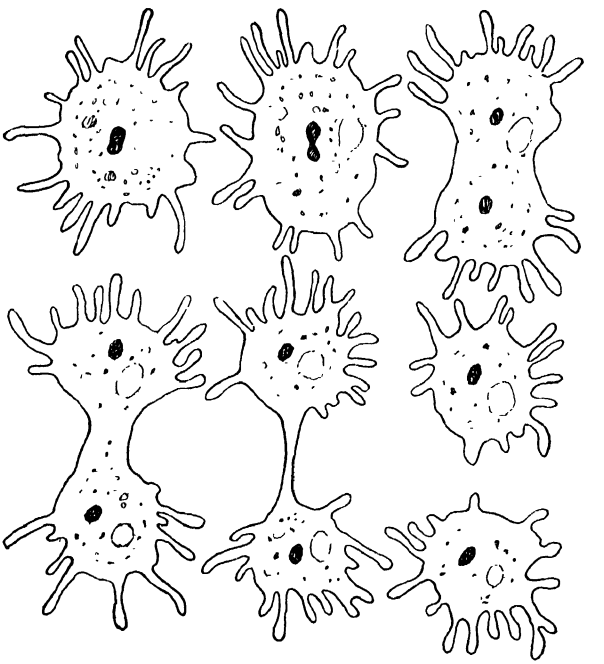


FIG. 3–1. An amoeba in several successive phases of division. (Redrawn from Woodruff.)

It is in reality nothing more than a little irregular particle of protoplasm. This simple organism is constantly changing its shape and its position. It does this by a kind of streaming motion. A projection forms on one side and much of the substance seems to stream into it. Then another similar projection appears and the streaming is continued. It is evident that the body is soft and semi-fluid, yet it does not mix with the water and always retains a well-defined outline despite the irregular shape. If we look carefully we can distinguish a denser globule within, which preserves its form no matter how much the shape of the protoplasmic mass changes; this is termed the *nucleus*. Foreign particles—usually minute fragments of an organic nature —are taken into the interior of the protoplasm. The amoeba increases in size. Soon a remarkable change may take place. A fissure may appear that keeps on developing until the amoeba is divided into two parts which

finally become completely separated so that two distinct amoebae result from the division of the one. The nucleus also divides, so that there are now two organisms in all respects like the original one (Fig. 3–1).

In their earliest stages the bodies of animals and plants, regardless of their larger size or later form, consist of a single minute particle of protoplasm more or less similar to an amoeba, except that it is rounded rather than irregular in shape. Soon this original particle divides into a number of parts which, instead of separating, as in the case of the amoeba, remain associated together to form a cluster or clump of minute particles of protoplasm. Each of these protoplasmic units is called a *cell.* A single cell constitutes the entire body in the smallest and simplest forms; a vast multitude of cells appears in the organization of the large and complex forms.

In the multicellular bodies, typical plant cells are separated by some intercellular substance and in addition each cell is surrounded by a relatively firm wall. The cells are thus rather distinctly separated from one another. The cell wall is a product made by the protoplasm. In contrast to plant cells, most animal cells are without walls, but they, too, are separated by intercellular substances. We have previously discussed cell walls and have pointed out how they form the skeleton of the plant. The earlier workers were much impressed with the discovery of the cellular structure of plant bodies. The cell walls were conspicuous as these workers carried on studies with the microscope. Not until the middle of the past century was it realized that the protoplasmic contents, and not the walls, were the real units of activity. While it is necessary to give attention to the structural features of cells, we can form proper concepts only by considering also the relation of the cells to the life process of the organism of which they are parts.

If we examine a thin longitudinal section of the tip of a root of a higher plant (a hyacinth root tip is especially good) with a magnification of about 450 diameters we find that it consists of nearly rectangular cells filled with protoplasm, and separated by delicate walls (Fig. 3-2). If the section has been stained and prepared according to the usual technique there will be clearly distinguishable in each cell a darker round body of comparatively large size. This body is the *nucleus.* Filling in the space between the nucleus and the wall is a lighter substance appearing more or less granular or reticulate; this is called the *cytoplasm.* The life of the cell depends on the interaction between these two components.

The observation of sections farther back from the growing tip, or in other parts of the plants where the cells are older, reveals that they are no longer filled with protoplasm. As the cells have enlarged there has not been a proportional increase in the amount of protoplasm and there are clear

spaces in the cytoplasm which look as if they were empty. These clear spaces are cavities called *vacuoles*. In life, the vacuoles are filled with a watery fluid, the *cell sap*. As the cells continue to enlarge, their whole central portion may be occupied by a single large vacuole. The cytoplasm then

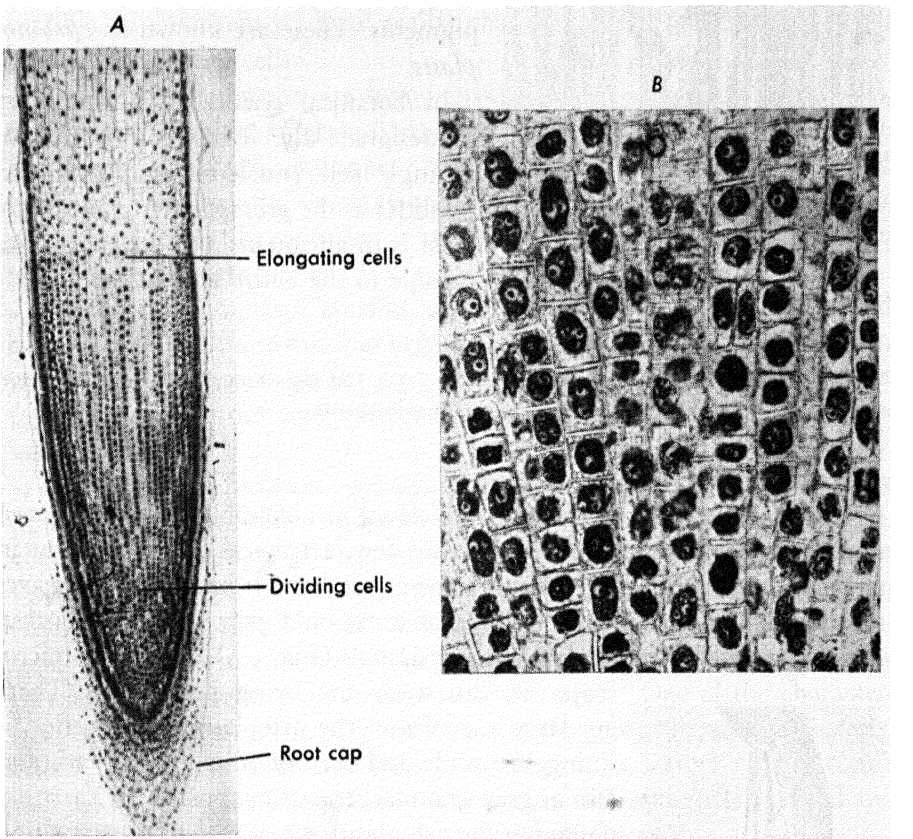
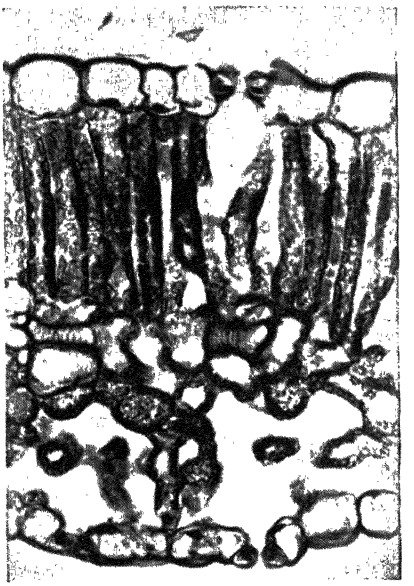


FIG. 3–2. Lengthwise sections of root tips. *A*, lower magnification; *B*, higher magnification showing the rectangular cells, walls, cytoplasm, and nuclei. (*A* reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

forms only a comparatively thin layer lining the cell wall and surrounding the nucleus. The nucleus is enclosed within the cytoplasm.

If a section through a living green leaf is examined we find in the internal cells a number of green rounded bodies, *plastids,* also suspended in the cytoplasm. These plastids contain the pigment chlorophyll and are known as *chloroplasts* (Fig. 3–3); they have already been described as the seat of photosynthetic activity. Other cells contain plastids which are de-



void of pigments. Such plastids are known as *leucoplasts.* Still other cells such as those in the petals of flowers and in the skin of fruits have plastids containing red, yellow, and other colored pigments. These are known as *chromoplasts.*

In botanical science it is customary to designate the living constituents of a single cell (nucleus, cytoplasm, and plastids) as the *protoplast.* A plant protoplast is to all intents and purposes comparable to the entire animal cell.

FIG. 3–3. Section through a leaf showing cells with chloroplasts.

The Protoplasm

If we remove some of the hairs which are so noticeable in the flowers of the garden spiderwort (the wandering Jew, a tropical plant common in greenhouses, is equally good), or some of the hairs from the young leaves of squash, and place them in a drop of water on a glass slide under a thin cover glass, we have a microscopic preparation (Fig. 3–4). Under the microscope we can study the living protoplasm. There are large vacuoles in the cytoplasm, but we find it lining the walls and surrounding the nucleus, and also as gray granular strands or threads. By carefully observing the cytoplasm, we may detect a streaming motion within it. Actually here within the bounds of the cell are movements comparable to those described in the amoeba. Sometimes there is a current in the layer along the wall. In other cells motion may be more noticeable in the strands. These strands or threads may alter their form, and as the movement continues, the position of visible granules changes; they are evidently transported by the flow-

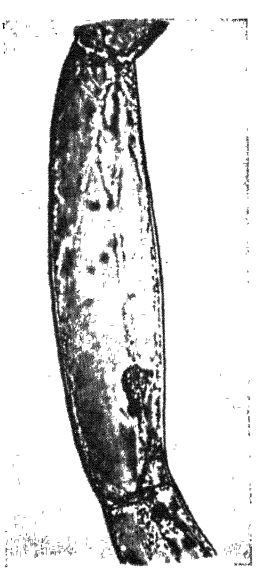


FIG. 3–4. Cell from stamen hair of the wandering Jew. When living cells are observed under the microscope a streaming motion can be seen along the cytoplasmic strands.

ing protoplasm. A similar preparation of a thin leaf of ditchmoss (*Elodea*) would show the chloroplasts in circulation. This streaming of the protoplasm within the cells is fascinating to observe. To most of us it seems a visible proof of its living condition. In many living cells there are no such streaming movements, or if any are present they are so slow as to be imperceptible. In any event we must realize that perceptible movements are not typical of all living cells.

Under the microscope the living protoplasm is usually inconspicuous, translucent, colorless or grayish, and appears more or less granular. The protoplasm of plastids may appear to be colored because of the presence of pigments. Ganong says, "A white-granular, slow-moving jelly; that is what protoplasm looks like, and that is precisely what it is . . . and try as one will, he can see little more." [1]

Physically, protoplasm consists of various interacting substances and compounds, both inorganic and organic, dissolved and suspended in water, which makes up 70 to 90 per cent of its weight. In the solid matter the protein content about equals in quantity the combined content of sugars, salts, and fats.

According to a foremost investigator, the laws of physics and chemistry dealing with pure liquids and true solutions are applicable only in a general way to protoplasm. In the words of this investigator, "Protoplasm is an intimate association of three distinct types of systems, a true solution, an emulsion, and a jelly. The salts and sugars in protoplasm are in true solution. The fats form an emulsion. The proteins exist as a jelly, which may be either very firm or fluid enough to flow freely." [2] One of the characteristics of protoplasm is the possibility of its undergoing changes in viscosity, that is, its capacity to change from a less viscous to a more viscous condition, and the reverse. The viscosity varies in the different parts of a cell and in the cell as a whole at different stages of development.

The chemical structure of protoplasm remains uncertain despite all the analytical studies. This is due to the fact that the necessary chemical laboratory procedures turn protoplasm into a substance quite unlike what it was when alive. We have said in an earlier paragraph that we must think of protoplasm not as a mere mixture of other substances, but as a highly organized substance in itself. However, it has been described as "a state of physical and chemical activity in a mixture of many different chemical compounds." Another writer lists thirty compounds that have been found

[1] W. F. Ganong, *The Living Plant*, Henry Holt & Company, Inc. Copyright 1913 by Henry Holt & Company.

[2] Reprinted by permission from *Physiology of Plants* by W. Seifriz, published by John Wiley & Sons, Inc. Copyright 1938 by William Seifriz.

in the protoplasm of one of the lower plants and ends with *undetermined matters, etc.* This will serve to emphasize its complexity. None of the substances or compounds listed are alive. Some workers believe that there is actually a living constituent which has not been identified. One says that "the essence of protoplasm is in the activity rather than the mixture." Ganong's account, although written several years ago, is still reasonable. He says, "Protoplasm, therefore, is probably composed chemically of two classes of materials; first, a very small amount of a distinctly living constituent, not yet identified, but consisting in the fibres, or the continuous substance of its physical texture; and second, a very large amount of various non-living substances, nutritive and other, which are under the control of the living constituent." [3]

While a majority of the known chemical elements have been found in protoplasm, only twelve are common: carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, sodium, calcium, magnesium, iron, and chlorine. Of these, the first four make up the principal part by weight. The most common of all compounds in protoplasm is water. It is a solvent for inorganic salts and for organic compounds. The gases present are oxygen and carbon dioxide. Protoplasm generally gives a neutral or an alkaline reaction. In the higher plants it coagulates at a temperature not much over 50°C. In spores and seeds where the protoplasm is in a dried condition it can withstand a higher temperature. The spores of some bacteria can withstand a temperature 105°C. without being killed.

The Cytoplasm

The soft protoplasm inside the wall and outside the nucleus is designated as the cytoplasm. It is a more or less tenacious semi-fluid. It coheres to the wall completely. The cytoplasm can be separated from the wall artificially by extracting the water from the vacuoles. When this is done it tends to assume a spherical form. The outermost part of the cytoplasm (periphery) is differentiated as a *plasma membrane.* This membrane plays an important role in the passage of water and dissolved substances.

The cytoplasm commonly encloses sap-filled vacuoles and one or more plastids. Other inclusions within the cytoplasm may be raw food materials, stored foods (starch grains, protein granules, oil globules), byproducts or wastes, and crystals.

Certain very small bodies called *mitochondria* or *chondriosomes* are present in the cytoplasm of both plant and animal cells (Fig. 3–5). Formerly they were frequently overlooked because the methods of preparing

[3] W. F. Ganong, *The Living Plant,* Henry Holt & Company, Inc.

microscopic mounts either dissolved them or failed to make them visible. They may be in the form of granules, rods, or filaments. Some investigators believe that they increase by division. Others think that they can arise

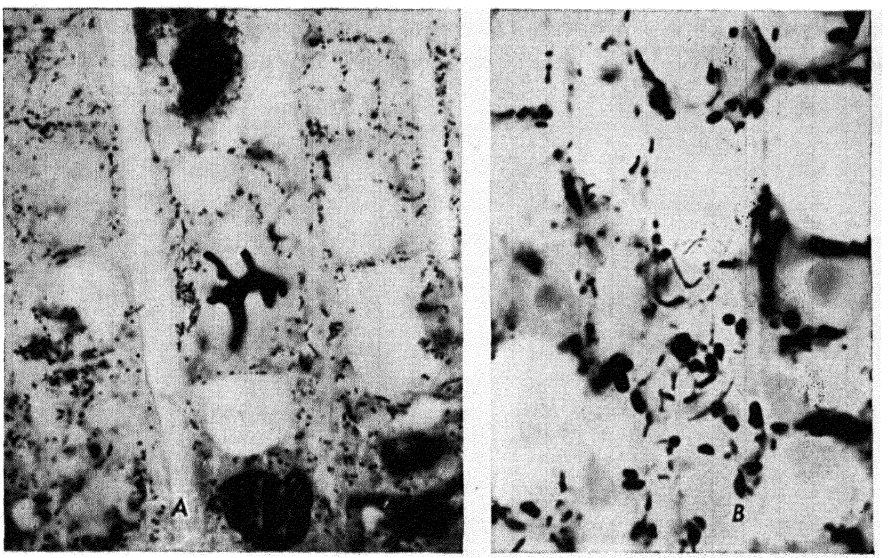


FIG. 3–5. Mitochondria in root tip cells. *A*, in narcissus, the mitochondria appear as small black bodies. The nucleus in the center cell is in a phase of division. *B*, in pea, the mitochondria are forming plastids. (Photographs by E. H. Newcomer.)

in the cytoplasm. There is some evidence to show that they are primordia for plastids and that they later become plastids. It seems probable that the so-called mitochondria are not a single type of body with similar functions but diverse types in both origin and function.

The Nucleus

An important part of the protoplasm of typical plant cells is the nucleus. The protoplasm of the nucleus is usually more dense than the cytoplasm and it also differs chemically from the cytoplasm in the proportion and complexity of its proteins. The nucleus is commonly globoid or ellipsoid in shape and is separated from the cytoplasm by a definite *nuclear membrane*. Within the nuclear membrane are three distinct substances, or structures, namely, the *reticulum*, the *nucleolus* (or nucleoli, if more than one), and the *karyolymph* (Fig. 3–6).

In microscopic preparations the *reticulum* frequently appears as a network of numerous crooked threads. Individual threads or units may not be identifiable in the network of the vegetative or metabolic condition of

nuclei. When nuclei divide, however, changes occur and separate units emerge which are called *chromosomes* (Fig. 3–7). From the facts gained from a study of dividing cells it is evident that the reticulum is a system of associated chromosomal threads. The chromosomes contain a substance

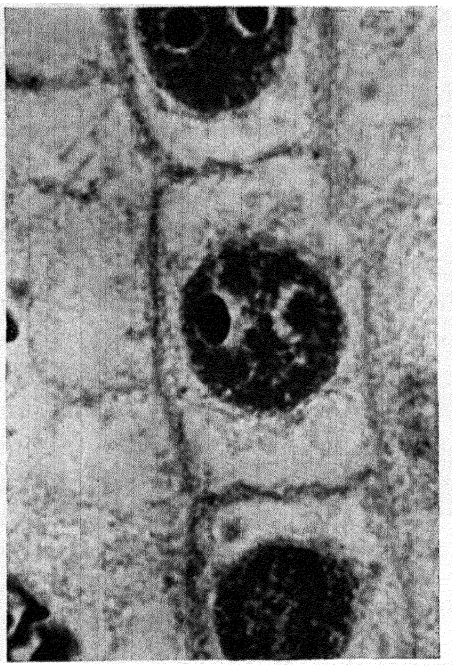


FIG. 3–6. Photomicrograph of a root tip cell of hyacinth. The nuclear membrane is indistinct; the reticulum and two nucleoli, surrounded a clear zone, are evident.

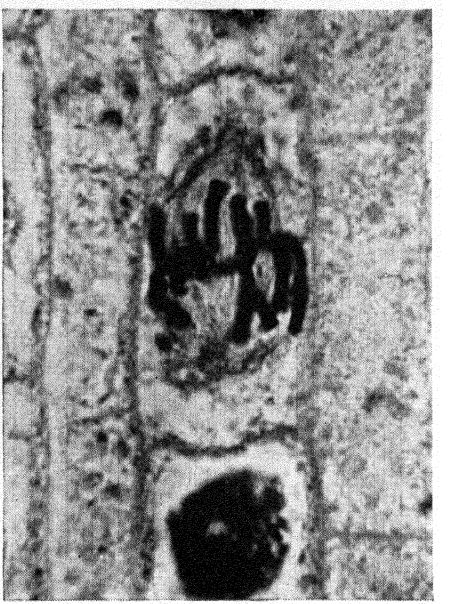


FIG. 3–7. A nucleus of a root tip cell of hyacinth in a phase of division, showing large well-defined chromosomes.

called *chromatin*. Genetic investigations have revealed the fact that they contain a series of basic factors (*genes*) which play an important role in the transmission of hereditary characters from cell to cell and hence from generation to generation. In later chapters further explanations of these important matters will be made.

Vegetative nuclei usually contain one or more *nucleoli*. In the living condition the nucleolus appears as a dull, usually roundish droplet. In prepared slides the nucleolus, as a general rule, appears as a dark staining body surrounded by a clear zone. At the time of nuclear division the nucleoli commonly disappear. The functions of the nucleoli are obscure. Some investigators believe that they are concerned with chromosomal development; others regard them as a reserve of protein material. The *karyolymph*

is a homogeneous substance which forms the larger part of the volume of most nuclei. It is also called the "nuclear sap."

The nucleus as a whole is regarded as the center of the internal physiological activities of the cell. Experiments have been performed in which certain one-celled animal forms (protozoa) have been cut into two pieces in such a way that one piece has the nucleus and the other piece is without it. The piece lacking the nucleus may move about for a time and respond to some stimuli but it gradually exhausts itself and dies. The bacteria and the blue-green algae do not have typical nuclei. In some of them there are materials whose reactions suggest a nuclear nature.

SURVEY OF VARIOUS TYPES OF PLANT BODIES

Large numbers of plants, which at first seem to be quite unlike, actually possess bodies with similar organization of their members. It is possible to determine points of agreement between seemingly different plants and thus simplify the problem. Those who have studied animals know that the vertebrates include a great variety of forms—fish, amphibians, reptiles, birds, and mammals. Yet in this diversity of structure there is a body plan. It is possible to build up a concept of an "ideal" vertebrate body. With this in mind attention may then be given to some of the modifications in the different groups. In like manner there is a "body plan" of the higher plants. Both outer form and inner structure must be considered. It will be best to begin with the simpler types of bodies and then proceed to the more complex ones.

Unicellular Bodies

The simplest form a plant body can have is that of a single spherical cell. There are many such simple plants (Fig. 3–8). A green growth often seen on the north side of trees or old fences consists of aggregations of simple spherical bodies of *Protococcus,* a green alga. Collectively these plants appear as a green stain. Individually the plants are single rounded small cells identifiable only under a microscope. They have firm cellulose walls, a single nucleus, and a dense relatively large chloroplast. These plants may appear as individuals; often, however, they adhere together in groups of two, four, or more cells.

Single plants of ordinary yeast, *Saccharomyces,* are also simple cells, but they are ellipsoidal in shape. They have a peculiar way of budding, and thus often appear to have an outgrowth at the end or side of a cell.

The bacteria, which are well known as the agents of decay and disease, are usually very small one-celled plants. The cells of the bacteria have a variety of shapes. In addition to spherical and ellipsoidal forms there are rod-shaped, filamentous, and spiral forms.

Diatoms are common unicellular plants that form the familiar brown coatings on sticks or stones in sluggish streams or slimy deposits on the bot-

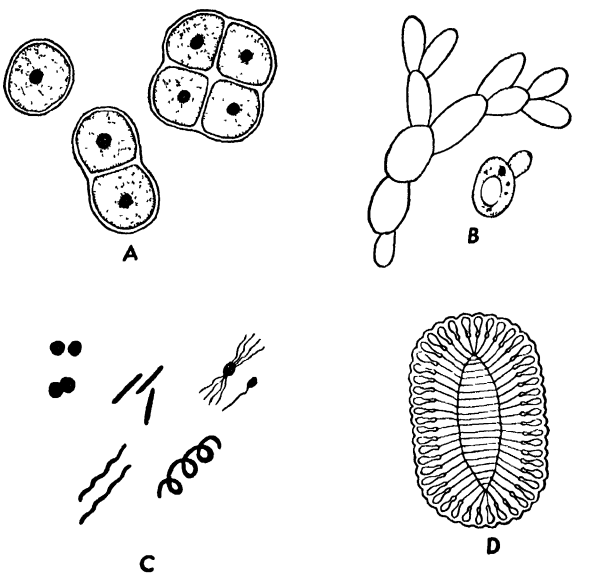


FIG. 3–8. Different types of unicellular plant bodies. *A*, *Protococcus*, a green alga; *B*, *Saccharomyces*, yeast; *C*, various kinds of bacteria; *D*, a diatom. See text for further explanation.

toms of ponds. The individual cells or plants are found in a great variety of forms, some being boat-shaped, others wedge-shaped, helmet-like, or fan-like. Some remain solitary, but others become associated to form bands, ribbons, or zigzag chains. The cells are covered by two glass-like valves, one of which fits over the other like the lid of a box. Because of the silica in them, these valves accumulate on the bottom of ponds and in the sea and in this way form beds of siliceous earth. Earth of this nature is the basis of some polishing powders and is also used as an absorbent in the manufacture of certain explosives.

The blue-green algae are simple one-celled plants that have certain features in common with the bacteria. Some of these algae are readily recognized as unicellular plants, but often the cells are more or less firmly joined together into rows, forming a thread or filament. The filaments

sometimes branch; and this feature, together with the fact that the various cells perform different functions, makes it possible to regard some of these forms not as colonies of individuals joined together, but as multicellular plants.

We have already referred to the plant *Protococcus* as consisting of a single individual cell. There are other related green algae in which the cells are united as definite aggregations or colonies. These colonies may be simple and composed of a few loosely joined cells to form flat discs, or they may consist of many cells in spherical or net-like forms. These aggregations of cells are considered colonies because all of the cells perform the same functions. Groups of cells, some of which are varied in character and perform certain functions not carried on by other cells in the group, may be regarded as constituting multicellular individuals. This brings us to the next stage in the consideration of plant bodies.

Multicellular Bodies of Simple Structure (Thallus Plants)

A simple type of multicellular body consists of cylindrical cells placed end to end to form a thread-like body or filament. The basal cell of a filament may be different in form and serve as a means of attachment. In such an aquatic filamentous green alga as *Ulothrix* (Fig. 3–9) we find this condition. The other cells of the plant are essentially alike, each containing a nucleus and a chloroplast, and are capable of manufacturing food and reproducing. The basal cell does not function thus but serves only to hold the plant fast to some object under water. This sort of cell differentiation is found to a far greater degree in higher plants

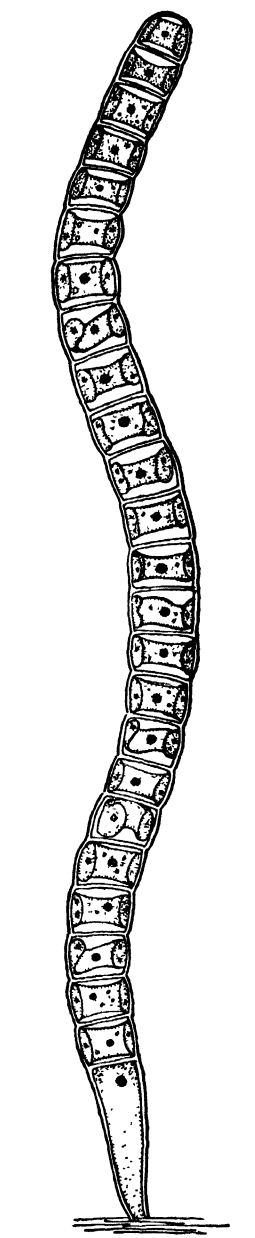
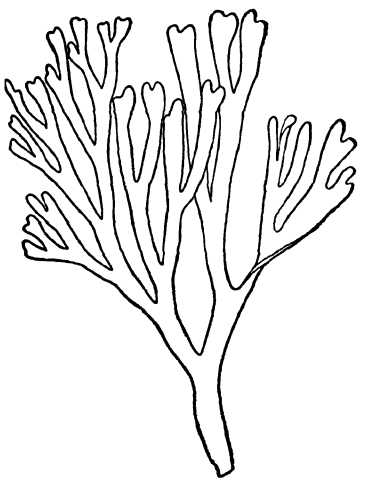


FIG. 3–9. *Ulothrix*, a multicellular plant body consisting of a simple filament. Note that the lowermost cell is modified to serve as a means of attachment.

where there are variations in cells that adapt them to the performance of many special functions.

In the marine green alga known as *Ulva,* division of labor among the cells is carried further by the cells at the base serving for attachment and those at the apex carrying on cell division or growth. Such a plant shows differentiation into base and apex. In the brown alga called *Dictyota* (Fig. 3–10), apical growth results from a large apical cell. Sometimes, following a division, two apical cells continue dividing and the result is a forked (dichotomous) branching.

In the brown and red algae, or seaweeds, there is a high degree of differentiation. The formation of an axis with lateral expanded branches makes many of them appear to possess stem and leaves and even roots. Although there is considerable internal cell differentiation, the resemblance to the higher plants in the formation and arrangement of their parts is chiefly external.



In the mosses and liverworts there is considerable external resemblance to the bodies of the higher plants. While some of them are simple and resemble the algae, others have stem-like and leaf-like structures which parallel the higher plants. But

FIG. 3–10. *Dictyota,* a brown alga, illustrating forked (dichotomous) branching. (After Oltmanns.)

in spite of the apparent variety of external form reached by these plants, their plant body does not attain the complex cellular organization of the higher plants and is called a *thallus.*

The simpler liverworts have a flat thallus which grows prostrate upon the earth (Fig. 3–11). By the division of the apical growing cell into two parts, already described in *Dictyota,* there are formed two growing points which produce a dichotomous branching. On the under side of the thallus numerous filaments (*rhizoids*) grow into the earth and serve both for attachment and for the absorption of water. The flat thallus is green. The upper cells bearing the chloroplasts are loosely arranged. Small pores permit a circulation of air so that the conditions for photosynthesis are provided. The lower cells do not develop chloroplasts and doubtless serve for food storage.

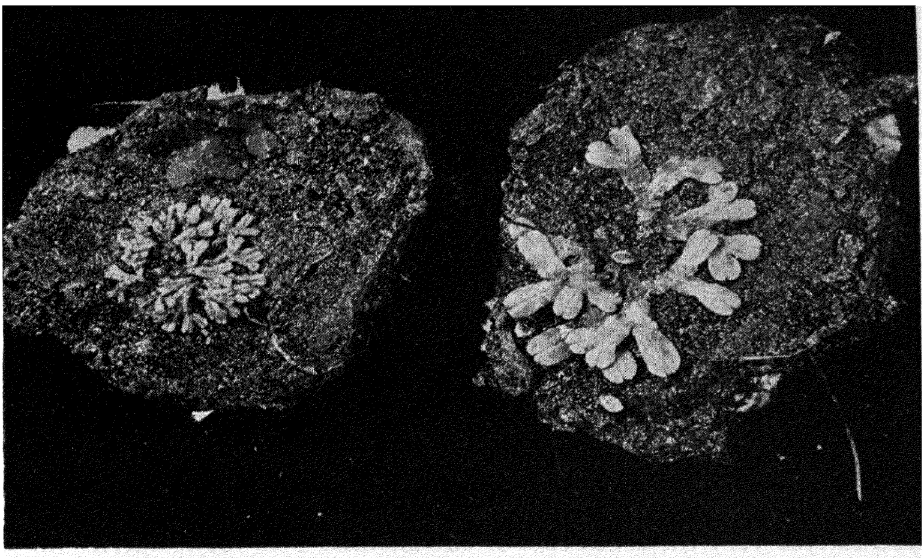


FIG. 3–11. One of the liverworts with a flat thallus which has forked (dichotomous) branching.

FIG. 3–12. Two plants of *Sphagnum* moss showing stem-like axis and radially arranged leaves.

The mosses generally have a stem-like axis with radially arranged leaf-like structures and root-like rhizoids below (Fig. 3–12). The cells show considerable differentiation. An advance over many of the liverworts is a central strand in the axis of some mosses which serves to conduct water. Although organs for absorption and conduction of water are present, they do not function effectively enough to permit moss plants to attain any considerable height. Many mosses are creeping forms and those that are erect rarely grow more than a few inches in height.

Multicellular Bodies of Complex Structure (Vascular Plants)

The vegetative body of ferns and seed plants consists of two main parts: a *green shoot system,* divisible into stem and leaf, which usually grows above ground, and a *non-green root system,* which nearly always grows underground. (See Fig. Introd.–1.) These two parts of the plant body are adapted to two very different sets of conditions. The *shoot* carries on photosynthesis where light and carbon dioxide are available in the atmosphere above, and the *root* absorbs water and minerals from the soil underneath.

Because of the similarity of organization of ferns and seed plants, it may be assumed that they have had a common origin and that their similarities are due to true relationship. However, our concern is not to trace out relationships but rather to become familiar at first with the main external and internal structures of the primary members of the plant body. After this, some attention must be given to the variations and modifications of these parts. Sometimes the modifications are so extensive as to result in one primary member assuming the character or functions of another.

The Shoot

Under the term shoot is included a stem and its leaves and flowers. The stem may be a simple axis or it may be branched. Branches develop from the upper angle between a leaf and the stem (*axil*). Therefore, the arrangement of branches is dependent upon the arrangement of the leaves. Leaves are always borne according to a definite plan.

Arrangement of Leaves. The places on a stem where leaves arise are called *nodes,* and the regions between the nodes are known as *internodes.* In some stems, such as the familiar bamboo, the nodes are prominent and easily seen even after the leaves have fallen or been removed. In many stems there is not much enlargement at the nodes, or other external evidence of their position except the presence of a leaf, or a leaf scar if the leaf has fallen. The term *phyllotaxy* is used to refer to the manner in which leaves are arranged on a stem axis. (See Fig. 3–13.)

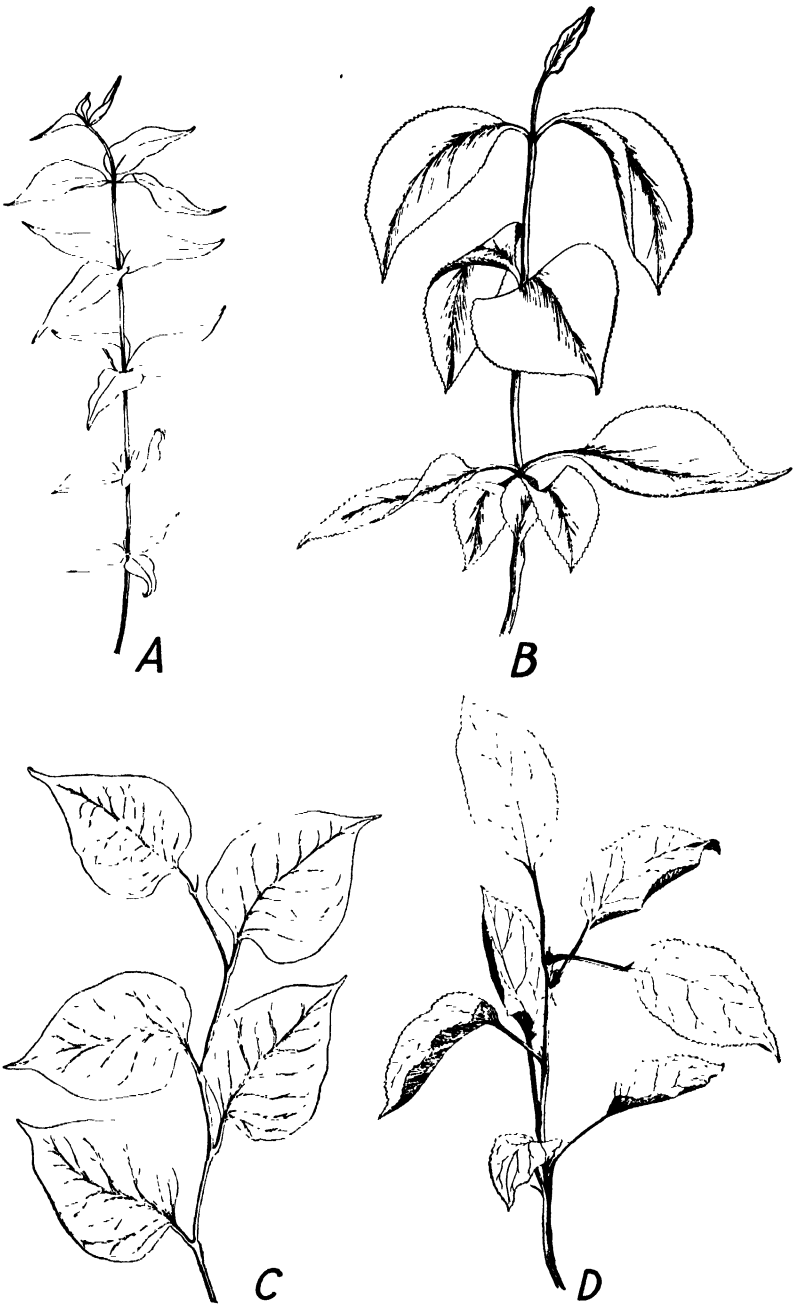


FIG. 3–13. Types of phyllotaxy. *A*, whorled; *B*, opposite; *C*, alternate with 1/2 arrangement; *D*, alternate with 2/5 arrangement. (Drawings by Elsie M. McDougle. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

In some plants a single leaf is borne at a node. This is called an *alternate* arrangement. In other plants there may be two leaves at a node, each on opposite sides of the stem. This arrangement is known as *opposite.* Some plants have three or even more at a node. These are known as *whorled* arrangements.

When leaves are alternately arranged the attachment at any node is not directly above that of the node below but to one side. The distance around the circumference between the attachment of two successive leaves varies in different plants but it is always uniform in the same plant. The greatest separation is one-half the circumference; it occurs in corn, iris, spiderwort, and basswood. Another separation is one-third the circumference; it is found in sedges and in white hellebore. A more common divergence between two successive leaves is two-fifths of the circumference; this is seen in apple, cherry, and many other trees and shrubs. Such an arrangement is a spiral one. The sixth leaf is above the first, the seventh above the second, and so on. Still other fractional divergences are 3/8, 5/13, 8/21, and 13/34. Here we have a new way of adding fractions, for it will be observed that in each fraction the numerator and denominator are the sums of those in the two preceding ones. The 2/5 arrangement follows the 1/2 and 1/3. It will also be noted that, in tracing the spiral, the numerator represents the number of turns around the stem in going from a leaf to one exactly above it. The denominator represents the number of leaves, or, to put it somewhat differently, the number of vertical rows of leaves on the stem.

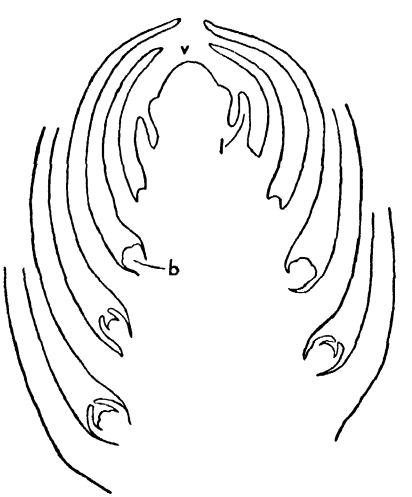


FIG. 3–14. Lengthwise section of the apex of a shoot showing the vegetative cone (*v*), the rudiments of leaves (*l*), and axillary buds (*b*).

Why there should be such systems of leaf arrangements is obscure, but it is obvious that definite and symmetrical arrangements do produce certain advantages. The distribution of the weight of the leaves is even, and if the stem is upright the leaves have equal opportunities for the utilization of light.

Buds and the Development of the Shoot. It has been pointed out that the term shoot includes a stem and its leaves. The apical end of the stem is the growing point. The actual apex is usually too small to be seen by

the unaided eye but when magnified it appears more or less cone-shaped and has been called the *vegetative cone.*

As the vegetative cone of the stem grows, the developing leaves appear first as little conical protuberances. The nearer the tip the smaller are these protuberances, and the farther away the better developed they appear (Fig. 3–14). Since the leaves farther back develop more rapidly than the embryonic stem which produced them, they come to overarch the vegetative cone. This vegetative cone thus protected is a *bud.* In other words, a bud is merely an undeveloped shoot.

New buds have their origin as protuberances in the axils of the embryonic leaves of the vegetative cone. By *axil* is meant the upper angle which the leaf makes with the stem. In its turn this axillary rudimentary growth develops into an *axillary* bud. These axillary buds, because they appear on the side of the stem, are termed *lateral* buds, in contrast to the bud at the upper end of the stem, which is called a *terminal* bud. Development of a terminal bud continues the growth of a stem in length; development of axillary or lateral buds causes a branching of the shoot. In contrast to the lateral and terminal buds which are always in fixed positions, some buds are in irregular positions. They may occur on roots, leaves, or on the internodes of stems. These are called *adventitious* buds.

Sometimes terminal growing tips continue the development of a shoot for a long time without the development of an outer covering of scales. As a means of protecting the vegetative cones from drying out they are usually invested during the resting period with tough scale-like leaves known as *bud scales.* These bud scales may be rendered more waterproof by gums, resins, or hairy coatings. In temperate latitudes the resting or dormant buds of the winter are always covered with scales. On many shoots in winter condition the lateral buds can be readily seen just above the leaf scars. Even most tropical plants must withstand a dry period; hence their buds are likewise protected by scales. When the scales of a (terminal) bud drop off they often leave characteristic ring-like scars about the stem. By means of these we can tell where the growth of one season begins and ends (Fig. 3–15). In woody plants in which the terminal bud lives through the winter it starts a vigorous growth in the spring. Ordinarily all of the lateral buds do not develop, but some of them may do so if the terminal is pruned off or if it is injured by insects or by frost. Lateral buds which do not develop may remain in position for a long time.

General Features of Leaves. Leaves vary so much in shape and size that it is difficult to make any statements that are generally descriptive of them. We may be safe in saying that green leaves are the most conspicuous parts

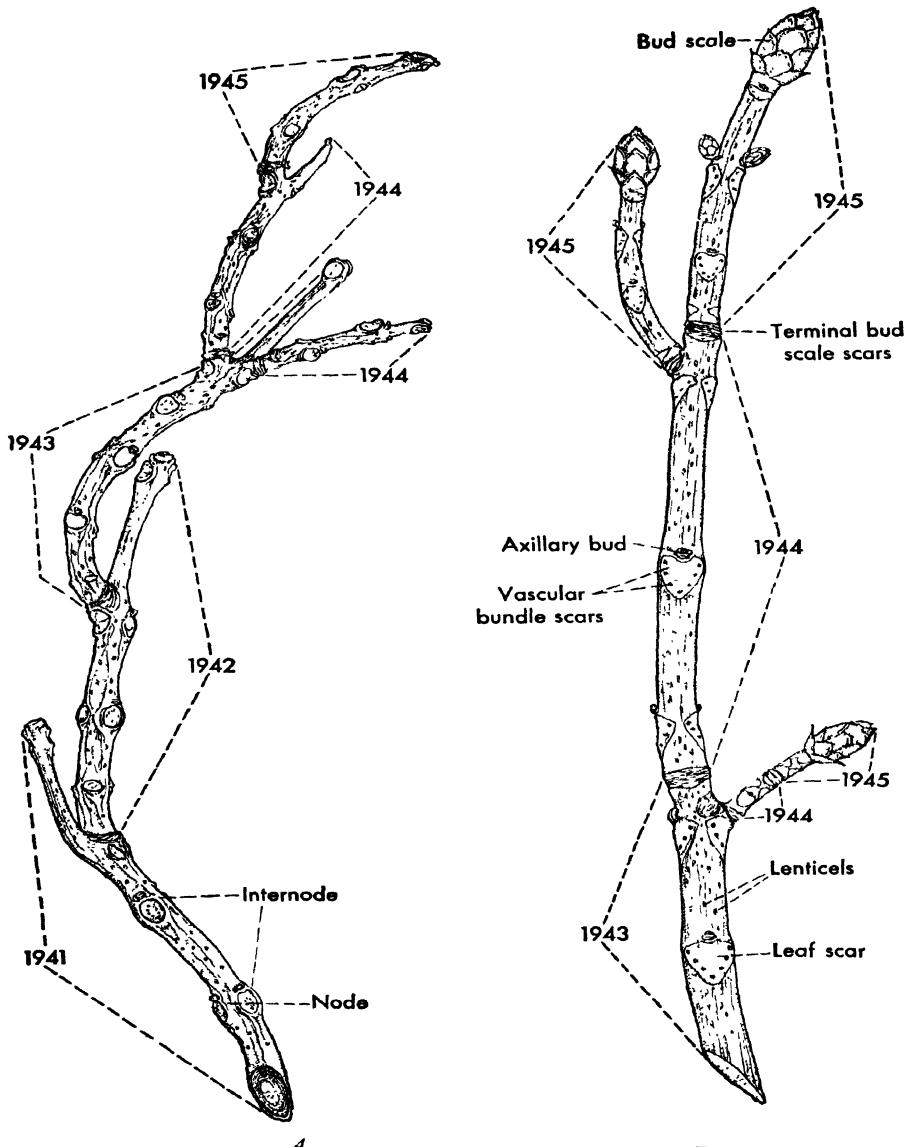


FIG. 3–15. *A*, shoot of catalpa showing continuation of growth by lateral buds; *B*, horse chestnut in which growth is continued by terminal buds.

of the vegetative plant body. We can agree that it is hardly an exaggeration to describe the green leaf as one of the most wonderful things in the world. The work which it does provides the store of carbohydrates, and the more complex nitrogen-containing proteins, on which practically the whole organic world subsists.

The great majority of foliage leaves are thin, flat organs. The flat expanded portion is the *blade*. The blade may be attached directly to the stem or it may be borne on a stalk called the *petiole*. Sometimes at the base of the petiole where it joins the stem there is a pair of appendages called stipules. A complete leaf consists of *blade, petiole,* and *stipules.*

Examination of leaves in good light reveals that there is an elaborate system of veins in the leaf blade. On the lower surface the larger veins project more or less to form definite ribs. In many leaves there is a central large vein or midrib from the petiole to the tip. This gives off strong lateral branches which reach nearly or quite to the margins. Between the lateral branches are smaller branches which are still further subdivided until slender veinlets ramify throughout the blade. The smallest veinlets can be seen better with the aid of a magnifying glass. The venation of a leaf may be best appreciated by observing one in which the softer tissues have weathered away, leaving only the skeleton composed of the veins (Fig. 3–16).

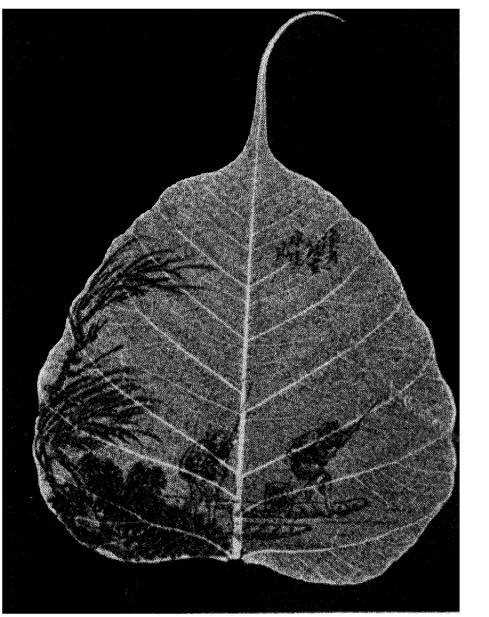


FIG. 3–16. Photograph showing the system of veins in a leaf—midrib, lateral veins, and network of veinlets. This specimen bears a scene painted by a Chinese artist.

The veins serve a dual purpose. The stronger ones form a mechanical framework and the whole branching system acts as a conducting system. The conducting is of two kinds, one for the distribution of the water which has come through the stem from the roots, and the other for the distribution of the food which is manufactured in the green cells of the leaves.

Leaves are often classified on the basis of their venation system. In general there are two sorts, *parallel-veined* and *netted-veined*. In the parallel type the large veins are about equal in size (except for a possibly larger midrib) and run more or less parallel from the base to the apex. These larger parallel veins may be united by smaller cross veins. We have already described a netted-veined leaf of the pinnate type—called pinnate because there is a prominent central vein with lateral branches on either side like the arrangement of the shaft and barbs of a feather. Another type of netted-

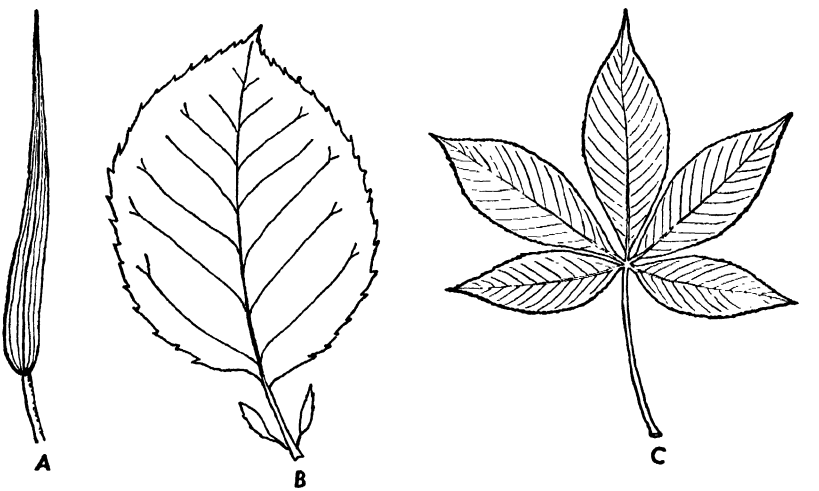


FIG. 3–17. Three types of venation. *A*, parallel; *B*, pinnate; *C*, palmate. The latter is a compound leaf, the others are simple. *B* is a complete leaf with blade, petiole, and stipules.

veined leaf is that known as *palmate*—called palmate because there are several equally prominent veins branching outward from the point of attachment to the petiole and resembling an open hand. (See Fig. 3–17.)

Reference has been made to the great variations in the forms of leaves. Variations may be due to the shape or length of the petiole. The petiole may be absent and the leaf is then said to be *sessile*. Whether stipules are present or not, their shape and size, if present, result in variations. But the greatest variations are found in the blades. Size, shape, margin, texture, and surface are all variable. This account cannot be complete enough to do justice to the subject, but we would fail if we did not present some variations.

To describe the shapes of leaves a good many terms are used by systematic botanists, who make it their business to write careful descriptions of plants. Here are some of the descriptive terms (see Fig. 3–18): *linear*

(narrow and elongate), *lanceolate* (lance-shaped), *elliptical* (oval), *ovate* (egg-shaped), *cordate* (heart-shaped), *peltate* (shield-shaped), and *sagittate* (like an arrowhead). The margins of the blades (Fig. 3–19) may be unbroken and are then said to be *entire*. Often they are toothed with the

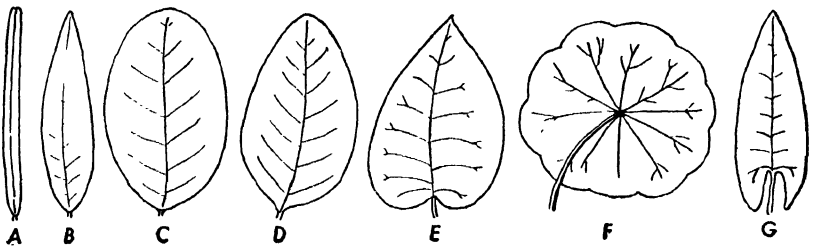


FIG. 3–18. A series of shapes of leaves. *A*, linear; *B*, lanceolate; *C*, elliptical; *D*, ovate; *E*, cordate; *F*, peltate; *G*, saggitate. (After Gray.)

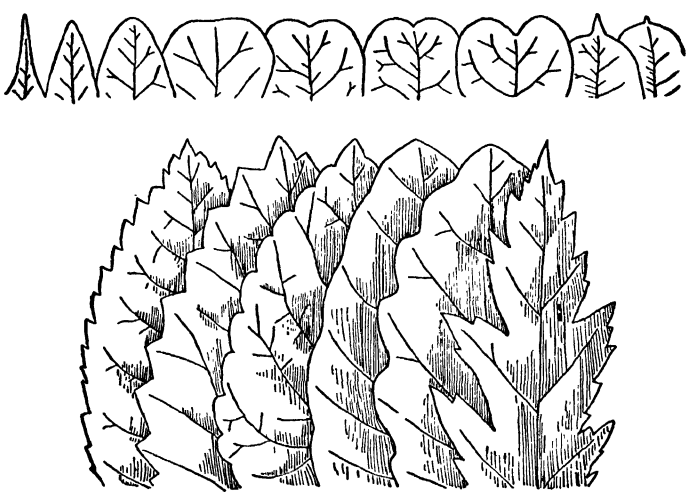


FIG. 3–19. Forms of the apex (above) and of the margins of leaves. (After Gray.)

teeth pointing outward, *dentate,* or with the teeth pointing forward, *serrate.* Or the margin may be *wavy* or *lobed* or *indented.* If the blade is in one piece even though deeply indented, the leaf is said to be *simple.* If the indentations are so deep as actually to divide the blade into separate parts (*leaflets*), the leaf is *compound.* Either the pinnate or the palmate leaves may be compound. A pinnately compound leaf has two rows of leaflets along a common axis (*rachis*). A palmately compound leaf has several leaflets radiating from the petiole. The number of leaflets in either type

may vary greatly. The leaflets in turn may be compound so that leaves may be twice-compound or even thrice-compound. A single leaflet of a compound leaf may resemble very closely in form a simple leaf of another plant, but it must be kept in mind that such a leaflet is not growing out of a stem and does not have a bud in its axil. The leaflets in turn may be variously shaped and the margins may be entire or broken as is the case in simple leaves.

The great variation of leaves in shape and margin has caught the interest of some literary folk. A poet has offered the fanciful explanation that originally "the leaves on the trees were as one; they were round, just as round as the sun" and he then proposes in further rhyme that the woodland spirit Pan carved them into strange figures by nocturnal clipping and snipping. He writes:

> One tree was entangled
> With stars five-angled—
> The sweet-gum, towering and gray;
> And another was spangled
> With ribbons that dangled—
> The sandbar willow today!
>
> Some were given a trim
> Of the merriest whim—
> Sassafras, tulip and haw,
> And some looked a bit grim
> As they swung on their limb
> For their edges were notched like a saw.[4]

The Root

Ordinarily the root is an underground structure and serves to attach the plant firmly to the soil. Other important functions are the absorption and conduction of water and dissolved soil minerals and the storage of manufactured foods. The root system may vary in appearance according to its adaptation for the performance of one or the other of these functions. We shall pay attention first to the form and structure of roots adapted to the usual functions of anchorage and absorption.

General Features of Roots. When a seed germinates, the primary root usually grows directly downward. If it continues as the principal root of the system it is termed the *taproot.* Secondary branches arise from the side

[4] From Paul Southworth Bliss, *How Pan Shaped the Leaves and Other Poems.* Copyright 1931 by Paul Southworth Bliss.

of the primary and these branches may in turn give rise to other lateral branches. Since roots do not have leaves and nodes, the lateral branches do not make their appearance at regular intervals up and down the parent root. The lateral branches do appear, however, at regular intervals around the parent root or, in other words, in longitudinal ranks or rows. There are in some roots four equidistant rows of branches, but the actual number of rows is dependent upon the internal structure of the parent root. A branch root has an internal origin and must grow through certain overlying tissue before it appears on the outside.

In some plants numerous adventitious roots develop about the base of the stem and there is no main root or taproot. Most grass plants have this sort of fibrous root system. In other plants there is a condition in real contrast to this, for there is not only a taproot but it is much enlarged for food storage, making the lateral branches seem very insignificant. Radishes and turnips have such fleshy taproots.

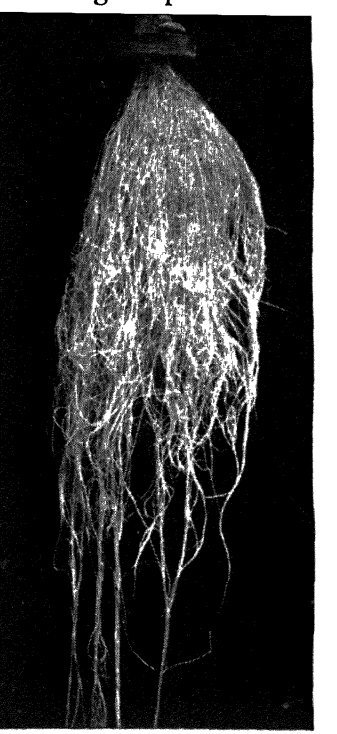


FIG. 3–20. Root system of a tobacco plant showing the extent of development. This specimen was grown in a water culture. It is difficult to obtain views of root systems of plants growing in soil because of the tendency of the smaller branches to break off in the process of separation.

The Structure of Young Roots. The expression "young roots" refers either to the short root of a seedling or to the tip portion of an older root system. Since roots have apical growth the tips are the younger parts. All the absorption of water takes place through these younger, delicate parts of the root system. When we learn how much water the roots of a large tree absorb from the soil in a day, it may seem impossible that it is all accomplished by the portions within a few millimeters of the tips, but this is the case. It is difficult to realize how profusely branched the root system may be and so we cannot appreciate readily how many young tips there are (Fig. 3–20).

The actual apex, or vegetative cone, of the young root is covered with a thimble-like protective layer of cells known as a *rootcap*. Since the growing tip of a root is forced through the soil as the root elongates, the rootcap

functions in a real way to protect the tender cells which it covers. The cap itself is worn away on the outside but it is renewed by new cells forming within so that it maintains itself as it is pushed downward. On the roots of most of our common plants the rootcaps can be seen only when magnified, but on aerial roots of some tropical plants they are plainly visible. The growing tip of stems is not sheathed with any structure at all similar to the rootcap.

To the unaided eye the small tip looks whitish for several millimeters and is in general cone-shaped. This region is the growth zone where cells are dividing and elongating. Just above this region there can be seen a narrow zone in which fuzzy whitish hairs radiate from the young root (Fig. 3–21). There is a multitude of these *root hairs*. Nearer the tip they are younger and shorter and farther back they are older and longer (Fig. 3–22). If seeds are sprouted in moist air

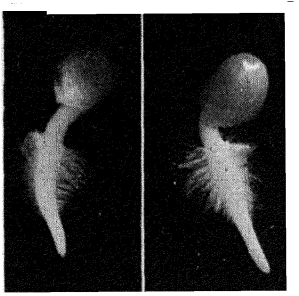


FIG. 3–21. Seedlings of mustard showing growing tip and root hair zone above.

between damp papers, the smooth tip and the root hairs can be seen as described. When roots are removed from the soil and washed, the hairs usually will be torn and injured because they are so delicate. Even those

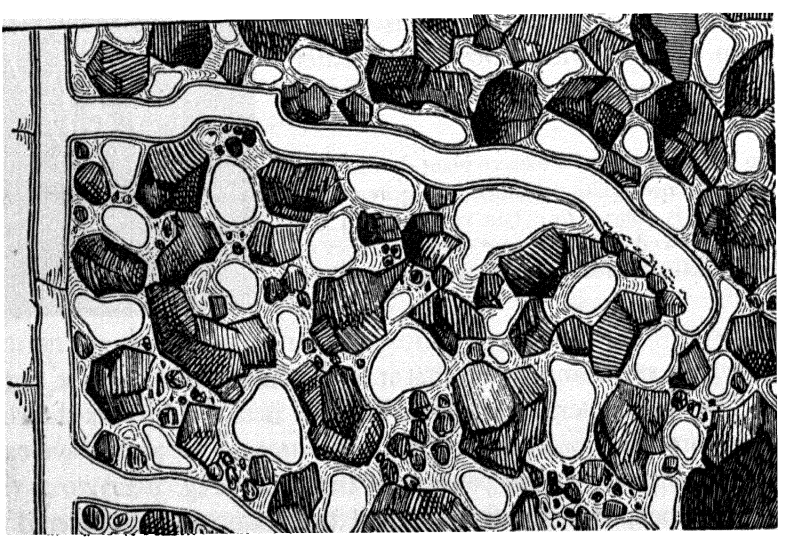


FIG. 3–22. Diagram of root hairs among particles of soil (darkly shaded), air spaces (white), and soil water (concentric lines). (After Sachs.)

grown between moist papers, as just suggested, must be examined promptly and carefully because a few moments in dry air causes them to collapse.

Dr. Oliver Wendell Holmes was much impressed with the activity of the roots of plants. In "Over the Teacups" he said, "A tree is an underground creature with its tail in the air. All its intelligence is in its roots. All the senses it has are in its roots. Think what sagacity it shows in its search for food and drink! Somehow or other, the rootlets . . . find every crack in the rocks where there are a few grains of the nourishing substances they care for, and insinuate themselves into its deepest recesses. . . . The next time you see a tree waving in the wind, recollect that it is the tail of a great underground, many-armed polypus-like creature. . . ." This figurative description places deserved emphasis on the importance of the root system.

CHAPTER 4

THE INTERNAL STRUCTURE AND DEVELOPMENT OF VEGETATIVE ORGANS

(*Anatomy, Growth*)

We have already considered the gross features of stems, leaves, and roots; but in order to understand how the whole living structure works we must learn about the inner organization of the parts. If we knew only that a house had in it living room, dining room, kitchen, bedrooms, and bath, but knew nothing of the furniture and equipment or how the rooms were connected, we would be in a poor position to know whether it was well adapted for the purposes of a dwelling. Likewise we must know how the organs of the plant are "furnished, equipped, and connected," if we wish to understand its activities.

TISSUES

The bodies of the higher plants are composed of countless numbers of cells. Microscopic examination of the apex of stems or the tips of roots (vegetative cones) reveals that all the cells are essentially alike in form and structure. But examination of the older parts of stems and roots reveals that the cells are not by any means all alike. The plant body is a complex structure composed of groups of cells called *tissues*. There are many different kinds of tissues, differing in the character of the cells and differing in the functions they perform. *Simple tissues* consist of groups of cells having essentially the same structures; *complex tissues* are composed of several kinds of cells. Tissues may be grouped as *tissue systems* on a functional basis.

Kinds of Tissues

We have referred to the cells in the apex of stems and roots. There are regions in which the cells are engaged in dividing and producing more cells (see Fig. 3-2). These apical tissues are undifferentiated or *embryonic* tissues. The botanical term for an embryonic tissue is *meristem*. Contrasted to these embryonic or meristematic tissues are the mature tissues. The plant

body consists chiefly of mature tissues. There are conductive tissues where the cylindrical cells are adapted to conducting water or distributing food. Other good examples are the strengthening or *mechanical* tissues where the cells have thick stout walls which give strength and support (see Fig. 2–5). In the leaves are *food-making* tissues where the cells are characterized particularly by green plastids.

Tissues may be designated by common names based on their functions. We have already referred to conductive, mechanical, and food-making tissues. There are also absorptive, storage, reproductive, and protective tissues. It should be understood that such designations are purely general and that they in turn may be subdivided. For example, conductive tissue for *water* is quite different structurally from tissue that is conductive for *food*. Also the kinds of cells which form the conductive tissue for water may be different in one kind or group of plants from those in another group of plants. Neither is it possible to look upon a tissue as devoted only or even chiefly to a single function. No method of classifying plant tissues has been proposed which is not open to some objection.

The meristem tissues give rise to the complex structure of the plant through division of their cells followed by enlargement and differentiation. A meristematic cell as it progressively differentiates may be only slightly changed or very greatly changed, depending upon the kind of tissue of which it becomes a part. Ordinarily tissues do not increase by division of their own cells but by additions from the cells of meristematic regions. Under certain circumstances some tissues revert to a meristematic condition and produce tissues quite unlike themselves.

It is a familiar fact that stems and roots may grow both in length and in diameter. The growth in length is brought about by apical or terminal meristems known as *primary tissues*. The increase in diameter is accomplished by the activity of meristems located laterally, and the tissues thus formed are *secondary tissues*.

To continue our considerations of the internal anatomical structures until we became familiar with all the possibilities and variations would carry us too far. But we must pursue our studies far enough to get a clear picture of how cells are grouped to form tissues and how tissues are grouped to form systems and organs. It is an excellent concept that "we may picture the healthy, living plant as a marvelously constructed body, in which there is a splendid division of labor, with all cells, tissues, and organs working in harmony." We should also come to realize that living organisms resemble each other not only in gross structure and function, but in microscopic structure as well.

Tissue Systems

Tissues are united in the body of a plant to form tissue systems. Stems, leaves, and roots are commonly referred to as the vegetative organs. A leaf is covered with a protective tissue, and has conductive and mechanical tis-

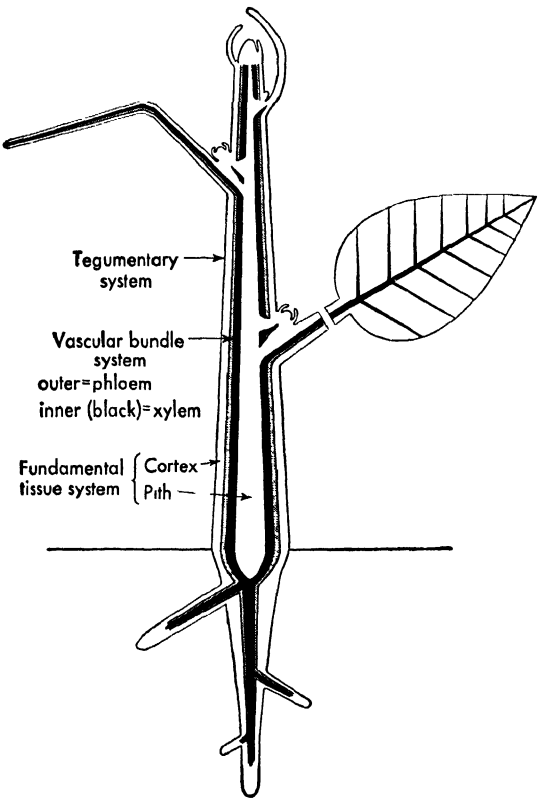


FIG. 4–1. Diagram showing arrangement of the three tissue systems.

sues in its veins, and food-making tissue in its softer parts between the veins. The protective tissue of the leaf is continuous with the protective tissues of the stem and root; the conductive and mechanical tissues of the veins of the leaf are continuous with and form part of a conductive and mechanical system in the stem and root; the food-making tissues of the leaf are continuous with and part of the basic internal tissues of the stem and root. Here may be distinguished three *tissue systems:* (1) the *tegumentary system* (protective), (2) the *vascular bundle system* (conductive and mechanical), and (3) the *fundamental tissue system* (chiefly nutritional but also mechanical); see Fig. 4–1. The fundamental system is enclosed by the tegumentary system

and traversed by the vascular system. This concise statement expresses the facts very well. From this general conception of the manner in which these tissue systems comprise the body of the plant, we may turn to the structural features of the organs, leaves, roots, and stems, in order that we may understand the particular parts they play in the life of a plant. Our conceptions can be correct and clear even if our considerations are too brief to be complete.

Leaf Tissues. The tegumentary system of the green leaf consists of a colorless single layer of cells called the *epidermis.* The function is distinctly protective. The soft internal cells would quickly dry out in the sun and wind if they were not protected. The outer walls of the epidermal cells are overlaid with a waxy material known as *cutin.* The layer of cutin is called the *cuticle.* The cuticle is not wholly waterproof but it is sufficiently impervious to the passage of water and water vapor greatly to reduce water loss from the interior cells by evaporation. The cuticle is continuous over the surface of the epidermal cells.

If the epidermal cells were close together without any intercellular breaks, water loss from within would be checked, but the passage of the atmospheric gases, carbon dioxide and oxygen, to and from the internal cells would be prevented. There are extremely minute openings in the epidermal layer called *stomata* (singular, *stoma;* the terms *stomates* and *stomate* are also used). A stoma is a slit-like opening between two special epidermal cells termed *guard cells* (Fig. 4–2), which permits movement of gases between the atmosphere and air spaces within the plant body. The guard cells differ from the other epidermal cells in their shape, structure, and contents. They are kidney-shaped or, as has been stated, they "may

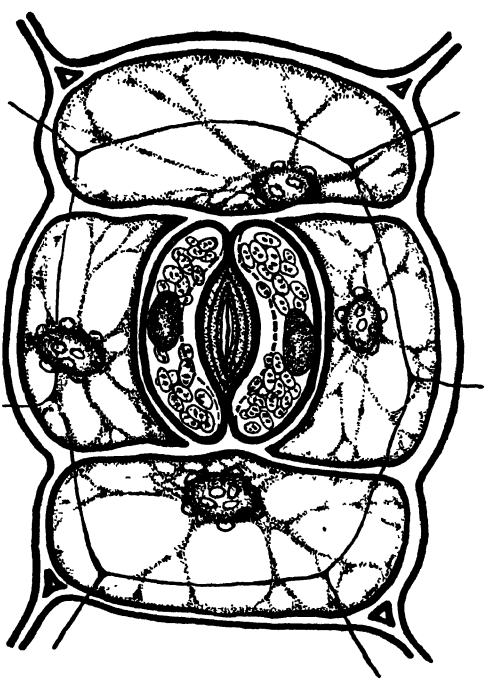


FIG. 4–2. Surface view of a stoma, with guard cells containing nuclei and chloroplasts, and neighboring epidermal cells containing nuclei, leucoplasts, and cytoplasmic strands. (Drawing by Louise Burpo.)

be compared with a couple of miniature sausages placed side by side, stuck together at the ends then pulled apart in the middle so that an oval space is left" between them. The walls facing each other are thicker than the remainder of the walls. The guard cells contain chloroplasts which are commonly lacking in the ordinary epidermal cells. Stomatal reactions are the indirect response of the guard cells to light (Fig. 4–3). In the light a series of chemical and physical processes are initiated which increase their volume, resulting in greater curvature and enlargement of the open-

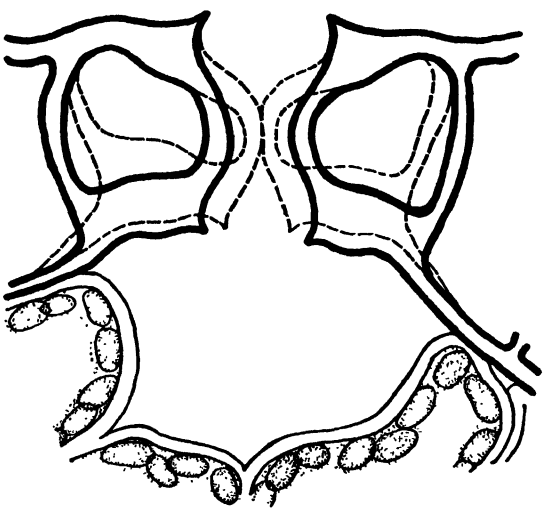


FIG. 4–3. Sectional view showing how the guard cells open and close the stoma through changes in shape.

ing. The opposite effects are brought about in darkness. Because these two special cells on the sides of the stoma thus vary the size of the opening they have received the name of *guard* cell. This is a brief description of what may be termed the stomatal mechanism. A good way to observe much of what has been described is to strip off a bit of epidermis, mount it on a glass slide in water under a cover slip, and examine it under a microscope. The under surface of a leaf of the Wandering Jew lends itself well to such a study.

As a rule more stomata are found on the under side of leaves than on the upper side and in some plants they are confined to the lower side. The number of stomata varies in different plants from a few up to 500 to 600 or more per square millimeter of surface. It is estimated that there may be an average of about 125,000 per square inch in many common leaves.

Hairs or scales, called *trichomes,* are characteristic of the tegumentary

system. The epidermal hairs may consist of a single cell, or they may be multicellular; either simple rows of cells or branched structures. Sometimes they are disc-shaped or star-shaped. The cells of some hairs retain their protoplasm; others die and become filled with air. Dead hairs are common on the leaves of many plants. The stinging hairs of nettles contain poisonous contents.

The internal fundamental tissue of a leaf is termed *mesophyll.* The cells have thin walls and numerous chloroplasts. The mesophyll is the great

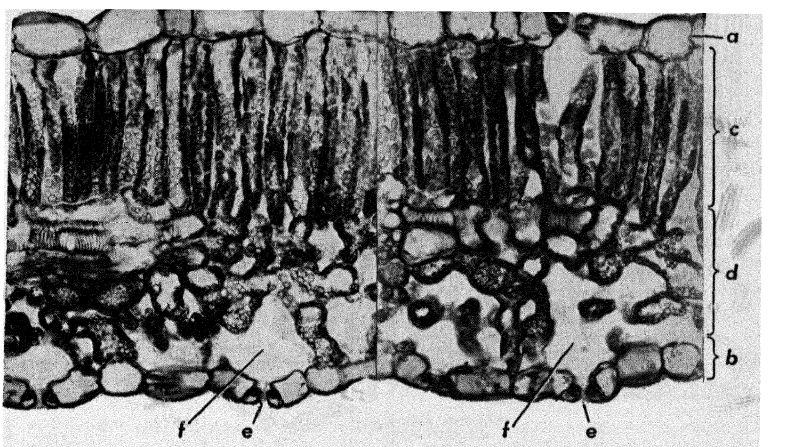


FIG. 4–4. Photomicrograph of a cross section of a leaf showing upper epidermis (*a*), lower epidermis (*b*), palisade layer (*c*), spongy mesophyll (*d*), and stomata (*e*), opening into intercellular air spaces (*f*).

food-making tissue. In many leaves the cells on the upper side are longer than broad and are arranged closely side by side in a palisade-like manner; because of this arrangement they have been called the *palisade layers.* The cells on the lower side are shorter and loosely arranged with many large intercellular spaces giving a spongy effect; because of this appearance they have been termed the *spongy layers.* These facts are brought out best by studying a cross section of a leaf prepared for microscopic examination (Fig. 4–4). In such a section it is possible to observe also how the stomatal openings communicate with the intercellular spaces which form a connected aeration system whereby every mesophyll cell is brought into communication with the external air. There is no apparatus for forcing a flow of air similar to the inhalation or exhalation of air in the lungs of animals. The passage of gases is a purely physical phenomenon resulting from the natural tendency of all gaseous molecules to diffuse, i.e., to dis-

perse from regions of abundance to regions of scarcity. When carbon dioxide is used by the mesophyll cells, its concentration in the intercellular spaces becomes less than in the outside air and some molecules pass through the stomata if they are open. If the stomata are closed, the

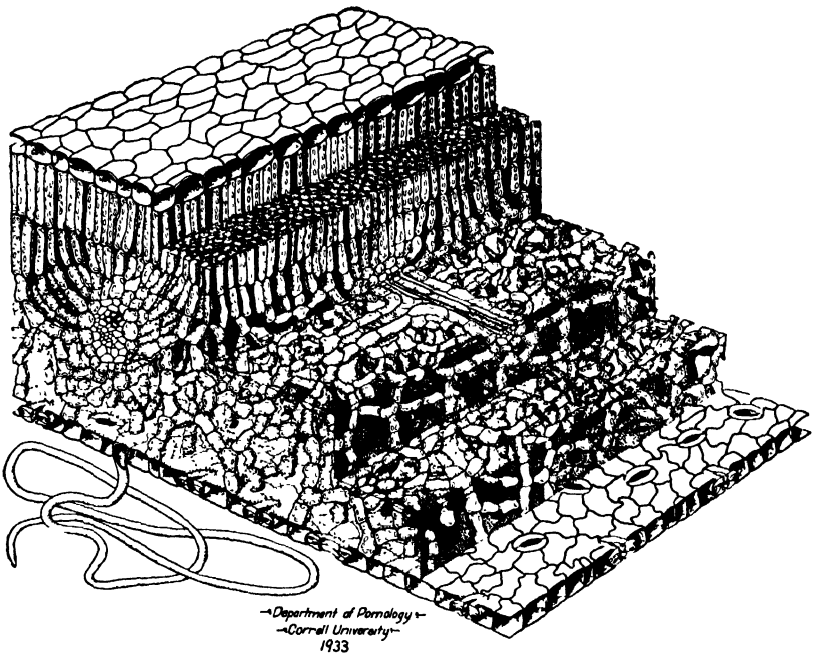


FIG. 4–5. Three-dimensional diagrammatic drawing of a portion of an apple leaf showing arrangement and interrelation of cells. Note that a vein is shown in cross section and also in lengthwise section; one elongated trichome appears growing from a cell of the lower epidermis. (Drawing, courtesy L. H. MacDaniels. From *Cornell Memoir 258*, Cornell University Agricultural Experiment Station.)

passage of the molecules is retarded or prevented. Ordinarily the stomata are open during the day and closed, or partially closed, at night.

In a cross section of a leaf it should be possible to gain a partial idea of the vascular bundle system, because the section nearly always cuts through a vein. Since the veins run in various directions we may find a place where a section parallels a vein and gives us a longitudinal view, or another place where it cuts across at a right angle and gives us a transverse view. Through a study of the two views (Fig. 4–5) it is possible to determine both the arrangement of the tissues and the character of the cells. A vein is in reality a single *vascular bundle* (Fig. 4–6). There are two kinds of conducting tissues, *xylem* (water-conducting) and *phloem* (food-conducting). The transverse view shows that these two tissues lie side by side, the xylem

FIG. 4–6. Section parallel to surface of leaf showing spongy mesophyll, branching veins, and bundle ends. Photograph by L. H. MacDaniels, From *Cornell Memoir 258,* Cornell University Agricultural Experiment Station.)

toward the upper side of the leaf, and the phloem toward the lower side. The xylem consists of elongated cells and tube-like vessels which may be called tracheary elements. These elements appear hollow because the protoplasmic contents have disappeared. The movement of the water to the mesophyll occurs chiefly in these tracheary elements. In the larger veins there are several parallel strands of vessels; in the smaller veins there are fewer strands. The walls of the tracheary cells frequently have thickenings which wind around in a spiral manner (Fig. 4–7). Breaking a petiole of geranium leaf and separating the pieces carefully will pull the spiral thickenings from the vessels so that they can be readily observed. Sometimes the thickenings are in the form of a network rather than a spiral. Vertical series of cells may be

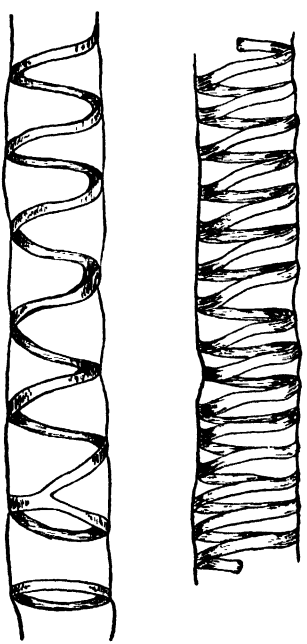


FIG. 4–7. Tracheary elements strengthened on the inside by spirals. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

joined in chains with the end walls missing or perforated so that they form tubes. Such elements are called *vessels* or *tracheae.* Individual elongated cells are called *tracheids.* As the veins become smaller by branching, the number of tracheary elements in them becomes fewer until the tips may be composed of a single tracheid (Fig. 4–8). The veins with their smaller and smaller branches penetrate all parts of the fundamental food-making tissue so completely that no mesophyll cell is more than a few cells away

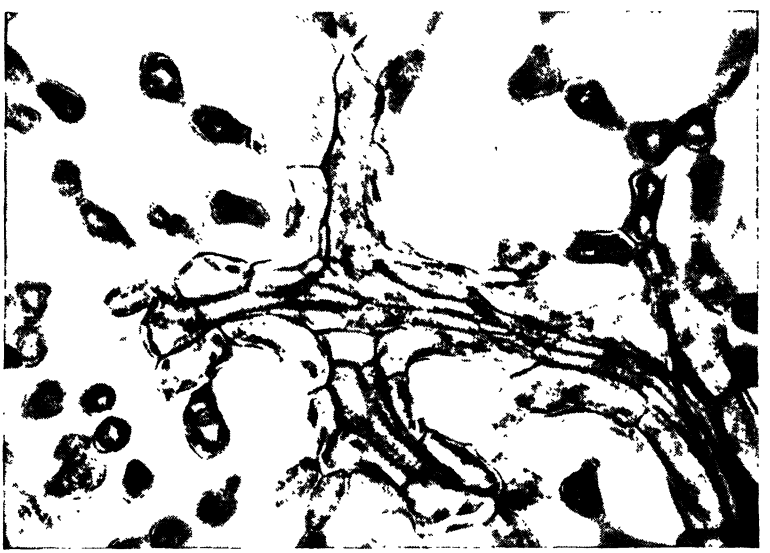


FIG. 4–8. The anchor-shaped bundle tip is an enlargement of a portion of Fig. 4–6. (Photograph by L. H. MacDaniels. From *Cornell Memoir 258,* Cornell University Agricultural Experiment Station.)

from a conducting element. This arrangement facilitates conduction of water to the photosynthetic mesophyll cells and provides an outlet for the sugars made by them.

The phloem, or food-conducting part of a bundle, has cells which are small in comparison with the xylem cells. They contain protoplasm and the walls are thin. More than one type of cell can be distinguished. The more conspicuous ones are elongated and arranged more or less definitely end to end in longitudinal rows. These cells form a series by the connection of their protoplasm through small perforations in thin areas which are called *sieve plates.* The cells are called *sieve tubes* (Fig. 4–9). Sieve plates are common in the end walls but may occur also in the side walls.

In the main veins there are usually mechanical tissues, in the form of fiber-like cells, surrounding the xylem and the phloem and called the

bundle sheath. The thickness of the sheath varies with the size of the vein. Sometimes a sheath is not continuous around the bundle and the fibers are restricted to strands on the upper and lower sides.

A petiole has an epidermis surrounding a considerable mass of fundamental tissue. There are usually several separate vascular bundles which are branches from the vascular system of the stem and continuous with the veins of the leaf blade. They are often arranged in the form of a semicircle as seen in cross sections or in the scars on the stem after the leaves have fallen.

Root Tissues. A transverse section of a young root taken from the region a little above the root hair zone, where the cells have all reached maturity, is excellent for the study of tissue arrangement. Here only primary tissues are present. This means that all the tissues are developed from the meristem of the root tip. Three regions comprising the three tissue systems, tegumentary, fundamental, and the vascular bundle, are readily recognizable: (1) the *epidermis*, (2) the *cortex*, and (3) the *stele* (vascular cylinder); see Fig. 4–10.

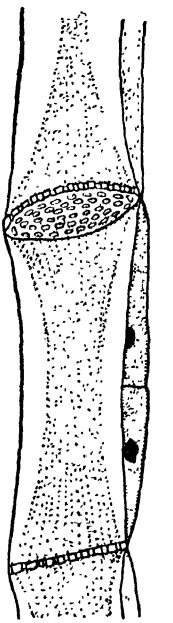


FIG. 4–9. A sieve tube of the phloem showing the end walls perforated to form sieve plates; the smaller cells on the right are companion cells.

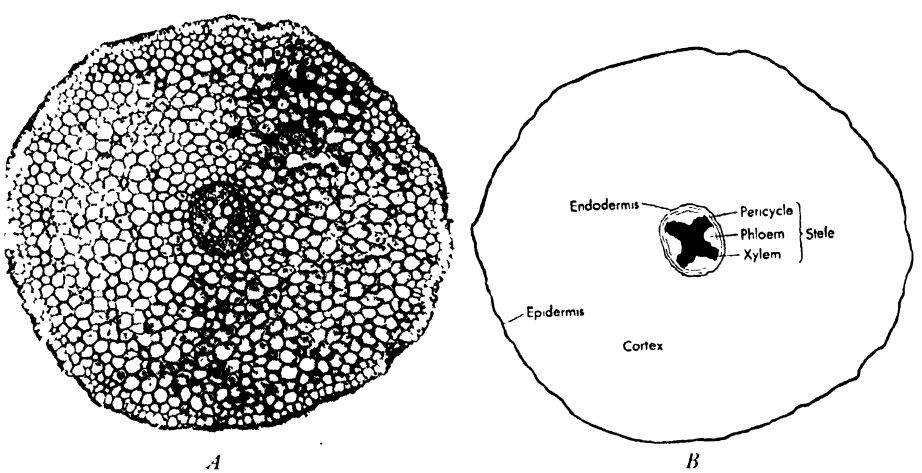


FIG. 4–10. *A*, photomicrograph of a cross section of root of *Ranunculus* (buttercup) above the root hair zone; *B*, diagram of same to show location of tissues.

The epidermis of young roots is a single layer of cells. From the epidermal cells just above the zone of elongation in the root tip root hairs develop. A root hair is a tubular outgrowth from the outer wall of an epidermal cell (Fig. 4–11). The hairs have thin cellulose walls. The hairs are short-lived, but as the older ones above collapse and die new hairs form below. Thus the zone of root hairs remains about the same width. As the root elongates, the root hair zone moves along at the same rate—it is always about the same distance back of the tip—so that new ground is being invaded constantly during the growing season. Because there are so many hairs in such a small zone a large absorbing surface is provided. It is estimated that the hairs increase the absorbing area from five to twenty times. It is through the root hairs that the chief supply of water and mineral salts is obtained.

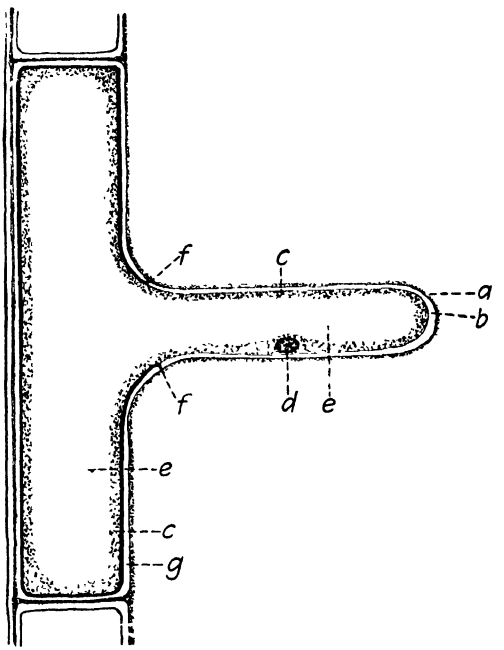


FIG. 4–11. Diagrammatic lengthwise section through a root epidermal cell showing origin and structure of a root hair; *a*, outer wall layer; *b*, inner wall layer; *c*, peripheral cytoplasm; *d*, nucleus; *e*, vacuole; *f*, point where root hair burst through the cellulose layer; *g*, cellulose layer. (Drawn by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

The cortex is an extensive region comprising most of the bulk of the root. The stele is centrally located and relatively small. The cortex extends from the epidermis to the *endodermis,* a definite sheet of cells, one layer thick, surrounding the stele. The cortex is composed of living colorless cells which are not greatly different from the cells of the meristem except that they are larger. They may be close together or sometimes they may allow considerable intercellular spaces. Such relatively undifferentiated cells as these in the cortex of the root are called *parenchyma cells;* they may be found in many regions of the plant.

The outermost layer of cells of the stele, or central cylinder as it is often called, is the *pericycle.* The xylem portion of the stele which is central in many kinds of roots appears in cross section to radiate like the points of a

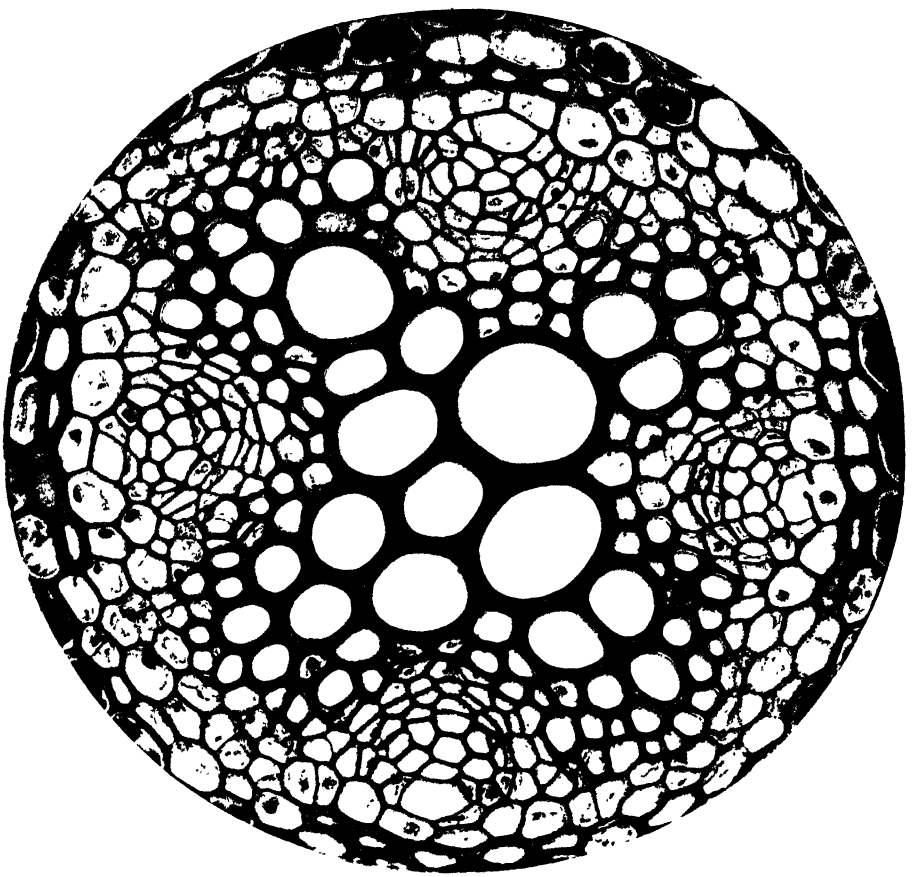


FIG. 4-12. Cross section of root of *Ranunculus* showing the stele, or central cylinder. The thick-walled red cells in the center forming a four-pointed star are the xylem; the thin-walled green cells between the xylem rays are the phloem. The thick-walled red endodermal cells form an interrupted ring near the margin; the thin-walled green cells just inside these constitute the pericycle. (Courtesy George H. Conant, Triarch Botanical Products.)

star (Fig. 4–12). The number of rays is variable. Between the rays of xylem lie separate strands of phloem. In some roots the central cells are parenchyma-like, and then the rays, or strands, of xylem are isolated. Water absorbed from the soil by the root hairs and epidermal cells must pass through the cortex to reach the tracheary elements within the stele. Branch roots arise in the pericycle from points opposite the rays and grow through the cortex (Fig. 4–13). Thus the central xylem of the branch

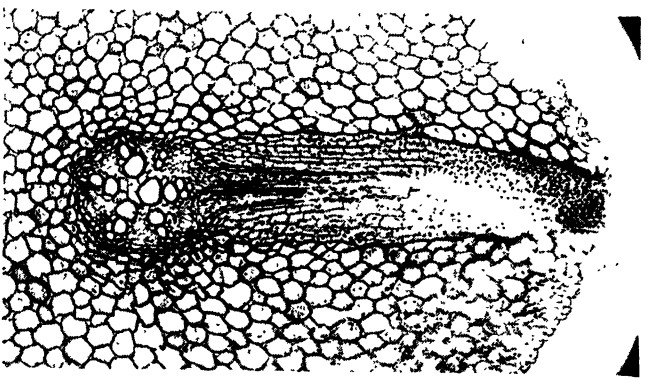


FIG. 4–13. Photomicrograph of a cross section of a root showing branch root originating from one of the xylem rays and growing through the cortex.

is connected to the xylem of the parent root and phloem is connected to phloem. In consequence there are as many vertical rows of branch roots as there are xylem rays in the parent root.

The discussion up to this point has taken into consideration only the distribution of primary tissues in the root. How the secondary tissues are added, thus bringing about secondary growth, is reserved for later consideration. At this time it is sufficient to know that secondary thickening is brought about by new cells produced by a lateral meristem called the *cambium.*

Stem Tissues. Stems vary greatly in the amount and arrangement of the vascular bundle system. A common type is characterized by vascular tissue arranged in the outline of a truncated cone. Within the cone the fundamental tissue is called the *pith* or *medulla.* The region surrounding the cone of vascular tissue is the *cortex.* Since the taper of the truncated cone is usually slight it may seem to be almost cylindrical. For this reason it is common practice to use the term "cylindrical" in describing the arrangement of the vascular tissue. In many herbaceous plants the vascular tissue is in the form of a more or less complete cylinder about a central

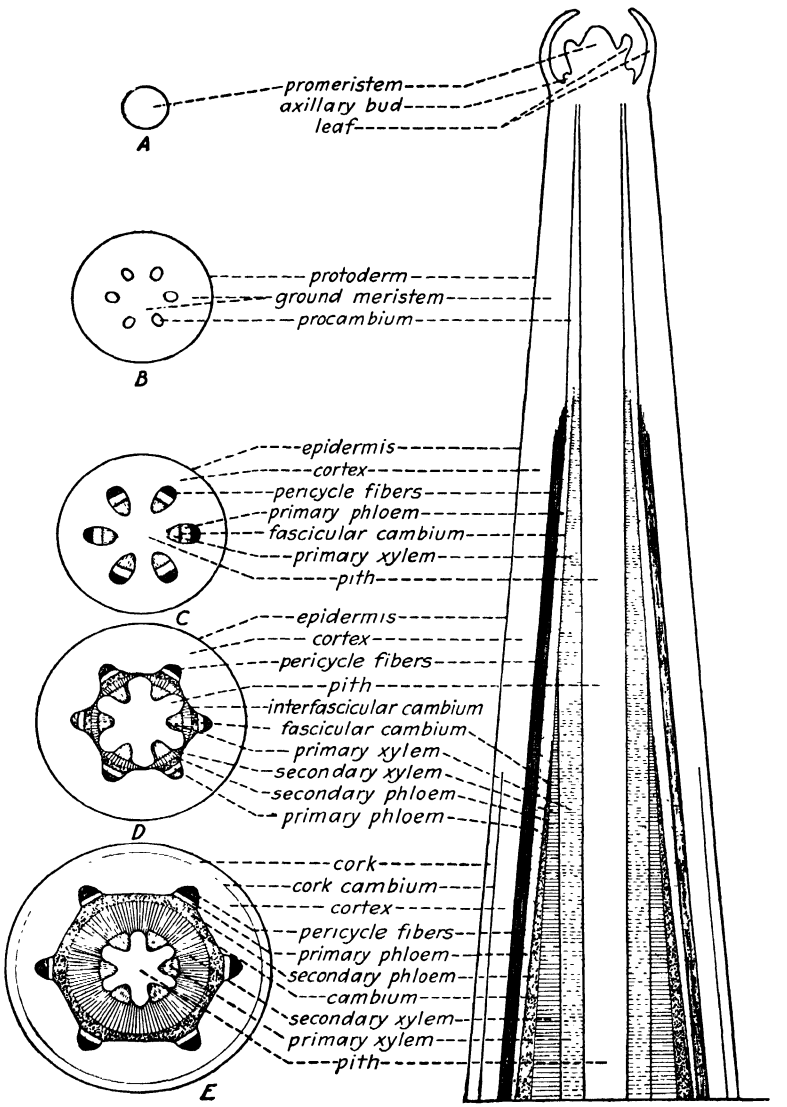


FIG. 4–14. Diagrammatic drawing showing the origin and arrangement of primary and secondary tissues in the stem of a dicotyledonous plant (modeled after a sunflower stem; lengthwise section at right, cross sections at different levels at left, *A–E*). (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

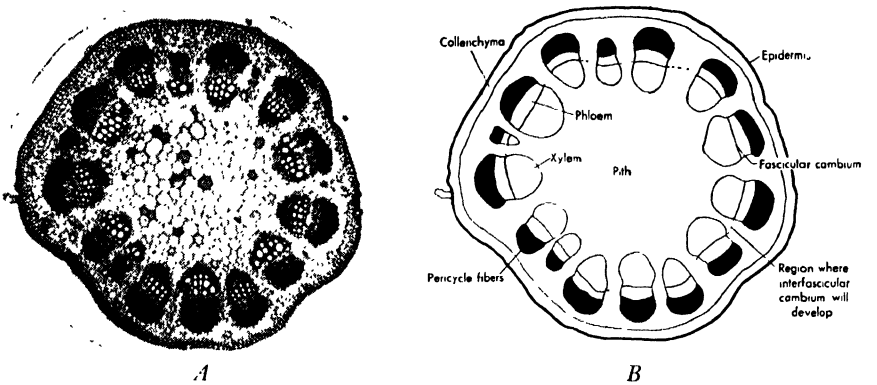


FIG. 4–15. *A*, photomicrograph of a cross section of a sunflower stem; *B*, diagram of same to show location of tissues.

pith and surrounded by a cortex (Fig. 4–14). In some young stems distinct bundles may be close together but separated by rays of parenchyma cells connecting the pith and the cortex. These regions are called *pith rays* or *medullary rays.*

Just outside the vascular bundles, between them and the cortex, is the *pericycle.* It is broader and less well defined than in roots. Often there are strengthening fibers, *sclerenchyma* cells, in the pericycle. In some stems these pericycle fibers are grouped on the outside of the phloem of the bundles, appearing as if they

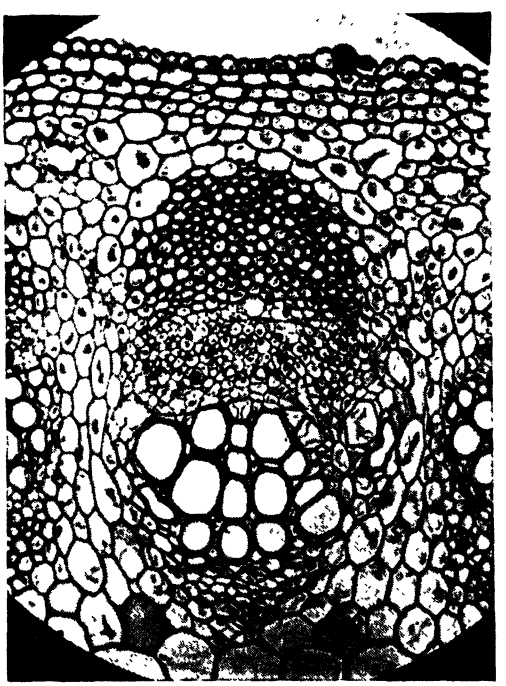


FIG. 4–16. Enlargement of one of the bundles from the preceding figure showing details of structure in the xylem, phloem, and fibers. Note also pith rays on either side of the bundle, and the strengthening collenchyma cells just within the epidermis.

were a part of the bundle (Figs. 4–15, 4–16). In other stems they are in a continuous layer around the vascular cylinder. A well-defined endodermis, such as is found in most roots, is lacking in many stems. If present it lies between the pericycle and the cortex.

In the kind of stem just described secondary growth ordinarily occurs as a result of cambial activity. This type of stem is characteristic of the great group of seed plants known as *dicotyledons.* Here belong many of our common herbaceous plants and trees with netted veined leaves. In another type of stem the bundles do not possess a cambium and are often scattered throughout the fundamental parenchyma; the limit of cortex, pericycle, and pith is indistinguishable. In many stems of this sort the central cells disintegrate, with the result that the stem becomes hollow, except at the node. This type of stem is characteristic of the group of seed plants known as *monocotyledons* (Fig. 4–17). Here belong grasses, lilies, and many plants with parallel veined leaves.

The epidermis of young stems is much like the epidermis of leaves. In general it consists of a single continuous layer of cells. Stomata are present

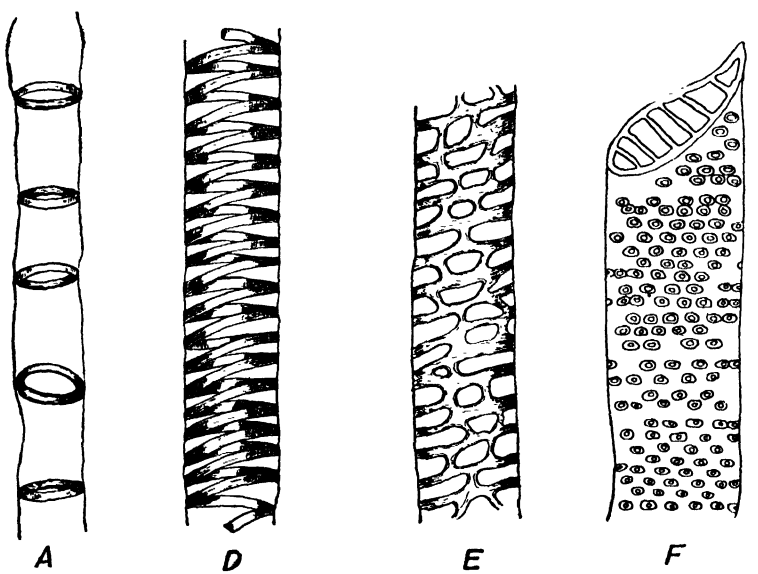


FIG. 4–18. Four types of conducting vessels. *A*, annular; *D*, spiral; *E*, scalariform; *F*, pitted with scalariform end wall. (Drawings by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

but usually much less numerous than in leaves. The outermost cortical cells are often thickened at the corners or angles and are called *collenchyma.* They function as strengthening tissue in young stems. The phloem of the bundles contains sieve tubes, smaller cells accompanying them known as companion cells, ordinary parenchyma cells, and sometimes also scleren-

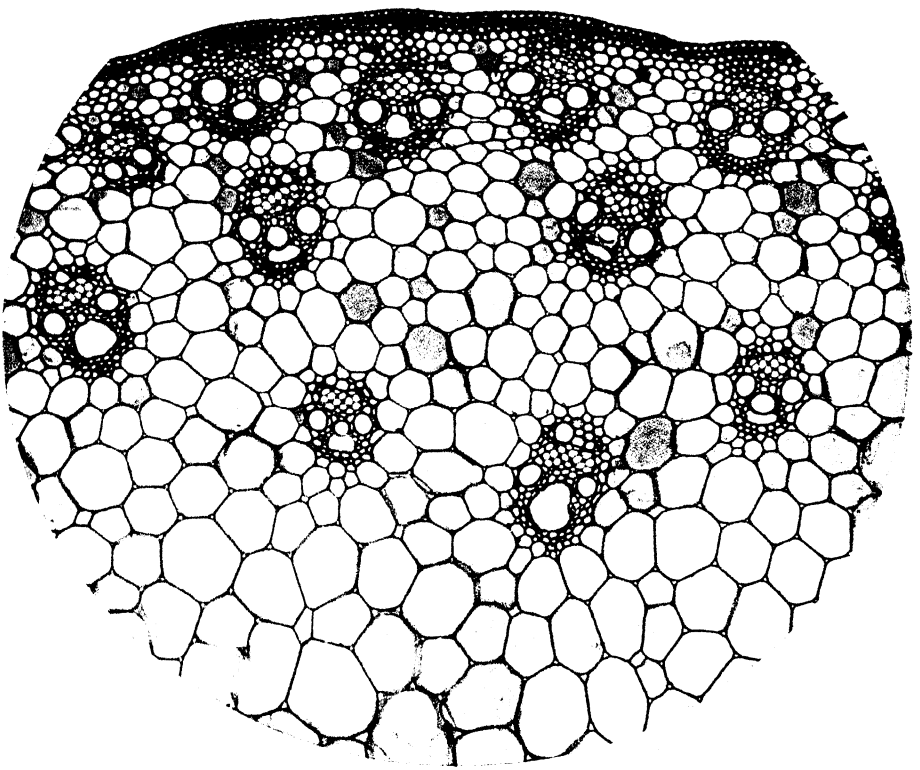


FIG. 4-17. Cross section of a monocotyledonous stem (corn) showing scattered bundles, pith, and the small cells, with thick lignified walls, which form a protective rind inside the epidermis. (Courtesy George H. Conant, Triarch Botanical Products.)

chyma fibers. The xylem is made up of tracheids, tracheae, wood fibers, and parenchyma cells. In the younger growth the vessels are usually of the annular or spiral types (Fig. 4–18). In the annular type there are thickened rings on the inside something like a barrel would be if the hoops were on the inside. These thickenings of various sorts in the walls of conducting vessels make them strong so that they will not collapse from outside pressure or internal tension. The spiral type is also common in young regions. In older regions the walls of the tracheae are frequently thickened but have thin areas or pits. Sometimes the thickenings are more or less crosswise and bar-like, giving a ladder-like appearance which has been called *scalariform*. The wood fibers are elongated and pointed, and have thick hardened walls. The walls of the cells of woody tissue consist chiefly of *lignin* which is added to the original cellulose. Lignin makes the walls firm and hard but does not interfere with the penetration and passage of water. The cells of the medullary rays and the pith are of the parenchyma type and function chiefly for food storage.

A concept of the distribution of the tissues in the stem and the character of the cells will be aided greatly by a study of the accompanying illustrations. Cross sections show the distribution best, but many cells must be seen in lengthwise view if we are to get an idea of their shapes and markings. Therefore, longitudinal sections or macerated tissues in which the cells have been separated are important for studies of the individual cells.

The Secondary Tissues

We have already referred to the familiar fact that stems grow both in length and in thickness. This may be equally true of roots although not so readily appreciated. The growth in length we call primary growth. It is brought about by cells added to the ends of stems or roots by the meristem at the stem tips and root tips. The tissues formed as these cells, which are at first all alike, differentiate into various kinds of tissues are called the *primary tissues.*

After growth in length has ceased, secondary growth begins by the addition of *secondary tissues* to the primary tissues. The secondary tissues are formed by a lateral meristem to which is given the name *cambium.*

The Cambium. A layer of cells lying between the xylem and the phloem called the *cambium* does not differentiate but remains meristematic. If the bundles are separate, the cambium of a bundle is called the *fascicular cambium.* Between such bundles, and continuous with the fascicular cambium of the adjoining bundles, there develops in the ray tissue what is aptly called the *interfascicular cambium* (Fig. 4–19). The fascicular

and the interfascicular cambium become joined to form a complete *cambium cylinder.* If we were to be exact, we could not use the term cylinder because stems and roots are not really cylindrical but taper upwards and downwards respectively. In cross sections the cambium appears as a circle. In woody stems the cambium region is easily recognized between the wood and the bark. The cambium cylinder (we shall continue to use that expression) consists of a single layer of cells, but in a cross

FIG. 4–19. Photomicrograph showing how the interfascicular cambium arises by tangential divisions of pith ray cells between the bundles.

section it may appear to be several layers in thickness because cell division goes on faster than differentiation. The cambium cells divide both tangentially and radially. The tangential divisions make possible the additional layers of cells. The radial divisions make possible additional cells in the cylinder, so that the added layers can be constantly larger, thus enabling them to reach around an axis which is constantly increasing in circumference.

The cambium cylinder develops two layers by tangential divisions (Fig. 4–20). If the inner layer enlarges and differentiates, additional xylem is formed. The outer layer remains as cambium and divides again. A repetition of xylem differentiation results in the formation of more xylem inside the cambium. But it is possible for the outer layer of divided cambium to mature into phloem. In such a case the inner layer remains

cambium. In this way cambium activity builds up a new layer of xylem over the preceding xylem and a new layer of phloem inside the preceding phloem. As a rule the differentiation is more often into xylem than into phloem so that the zone of secondary xylem is thicker than the zone of secondary phloem.

The Cork Cambium. Up to this point we have considered only the formation of secondary tissues in the vascular cylinder. Even if we cannot

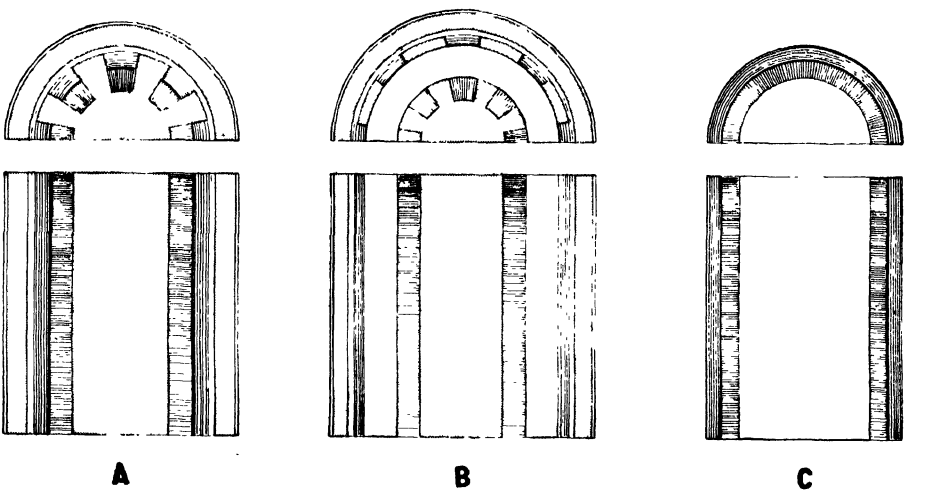


FIG. 4–20. Diagrams showing primary and secondary growth, *above* transverse sections, *below* longitudinal sections. *A*, the first-formed stem as it is built up by primary growth. *B*, secondary growth formed by cambial activity pushes apart the primary xylem and the primary phloem. In this diagram the space which the secondary growth occupies is vacant. *C*, the masses of secondary xylem and secondary phloem which really occupy the vacant space in *B*.

present the details fully, the fact will be recognized that there must be a secondary increase in the tegumentary system and in the cortical region to provide for the increasing diameter of the vascular cylinder. In woody plants the epidermis is replaced by a layer of brownish cork tissue derived from a lateral meristem called the *cork cambium* which arises beneath the epidermis. The cork cambium develops new layers of cork cells inside of the older cork layers, and may develop new cells (*phelloderm*) outside of the deeper-lying cortical cells. Thus is provided a protective coat which is capable of expanding so as to cover a stem or root that is increasing in diameter. The cork is waterproofed by the formation of *suberin* in the walls of the cells. As the epidermis is replaced by the cork, the stomata are replaced by *lenticels*. The cork functions in a manner similar to the epidermis by reducing evaporation of water from the inner tissues without preventing

the passage of gases. In a sense we may say that the lenticels are the successors of the stomata. A lenticel usually develops under a stoma and consists of a mass of loosely arranged cells with many air spaces through which gases diffuse readily. Lenticels are many-celled structures and often protrude above the surface of the bark so that they can be seen by the unaided eye. They are frequently conspicuous on young stems and their appearance and arrangement may be characteristic for a species.

The Vascular System. As the vascular cylinder develops from the cambial activity there are formed in the xylem and phloem not only the elements for upward and downward conduction, but sheets of cells which run crosswise in a radial direction. The height of the radial structures may vary from few to many cells. They are thin ribbon-like formations and there are many of them. In the xylem they are designated as *wood* or *xylem* rays and in the phloem as *phloem* rays.

The elements of the secondary xylem are provided either with transverse, slit-like, scalariform pits or with circular or oval pits. Wood fibers and wood parenchyma cells are also present. The walls of the fibers are much thickened and lignified. Sieve tubes and their smaller companion cells, fibers, and parenchyma cells are the elements of the secondary phloem. Ordinarily the secondary phloem is much like the primary phloem.

A study of cross-section diagrams is most helpful in gaining an idea of the arrangement of the different regions and the distribution of the various tissues.

When woody stems are cut either lengthwise or crosswise there are evident streaks which make them appear as if composed of layers. Concentric rings may be apparent in the end of a log, especially if it is cut smoothly and evenly. They are often so sharply defined as to be visible to the unaided eye. Doubtless many people call them annual rings without any clear conception of what the term means or without a real understanding of why they exist.

These rings represent different layers of growth. Since each layer is the growth of one year they may very properly be called *annual layers.* In cross sections these annual increments appear as rings (Fig. 4–21). By counting the number of rings in a cross section it is possible to tell the age of a stem, or of a tree if the section is taken through the trunk close to the ground. Under unusual conditions the number of rings may exceed the number of years. Destruction of leaves by insects or fire may stimulate midsummer growth so that there is a second formation of spring wood. In tropical regions where there is no climatic variation the periodicity of cambial activity is lacking in some plants and annual rings are not formed.

An interruption of growth, which might occur during a dry season, would bring about the formation of annual rings even in tropical plants.

But why does a demarcation appear so plainly between the growths of the different years? It is due to the fact that the structure of the cells in the early spring is different from that of the cells produced later. The terms *spring wood* and *summer wood* are commonly used for the growths

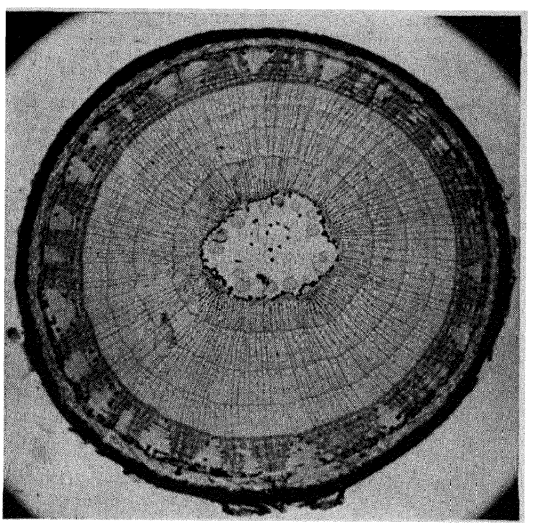


FIG. 4–21. Photomicrograph of a cross section of a four-year-old stem of *Tilia* (basswood) showing annual layers in the xylem (wood), and less evident, but still apparent, rings in the dark phloem surrounding the lighter xylem.

produced in these seasons. In the spring there is a large-celled soft growth which turns into a hard reddish growth in late season. At the end of a season's growth the cambium rests until the following spring. In tropical woods it may not be easy to tell one ring from the next, but in temperate climates the demarcation between the summer wood of one year and the spring wood of the next year is distinct.

The thickness of an annual increment varies with different seasons and in different plants (Fig. 4–22). Some trees grow rapidly, producing wide increments, whereas others grow slowly, producing relatively narrow rings. Slower growth usually produces harder wood. Even though large tubes may be formed in the spring, growth may be sufficient for the small heavy-walled cells of the summer growth to produce a solid hard wood. The appearance of the wood may be affected greatly by the character of the

wood rays. They form radial structures of varying prominence. In a lengthwise section they may show up conspicuously if the section parallels the radius fairly closely. Quarter sawed oak owes its effect to these wood rays.

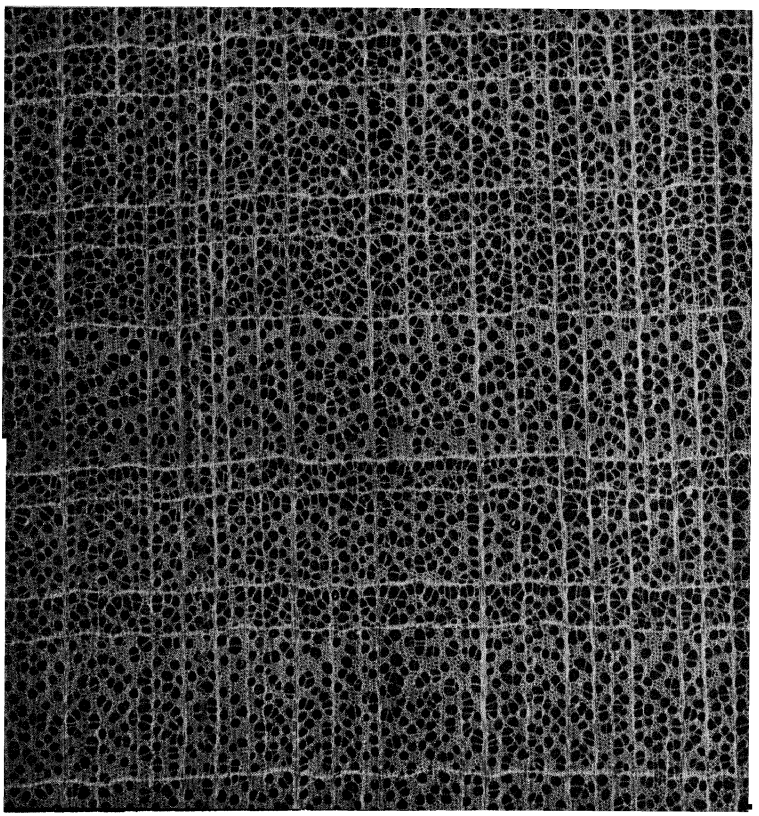


FIG. 4–22. Photomicrograph of wood of tulip poplar showing annual increments varying in thickness in different seasons. The large vessels are more or less evenly distributed throughout the growth of each season. (Photograph by D. A. Kribs.)

The so-called soft woods do not have a band of large tubes in the spring wood, but the cells are larger there and annual rings are evident. In the wood of these trees there are often present large intercellular canals which are resin ducts (Fig. 4–23). Many of the hard wood trees have such large conspicuous vessels in the spring wood that they appear as pores and the term *ring-porous* is sometimes used to describe such woods (Fig. 4–24).

Since the growth of trees is influenced by the conditions of the environment their rings record the effects of favorable and unfavorable years. Studies of old trees, such as the redwoods, have revealed the records of drought, rainfall, and sunspots for hundreds of years. These tree-ring

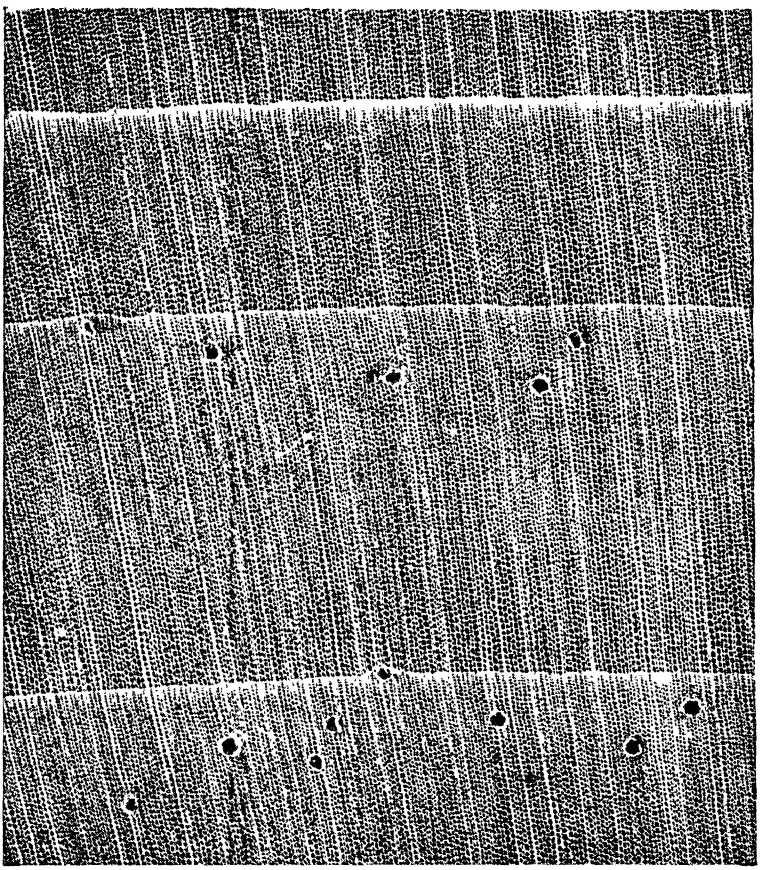


FIG. 4–23. Photomicrograph of wood of white pine. The cells are of rather even size except those at the outer part (upper in picture) of each annual increment. The large, dark, scattered openings are resin ducts. (Photograph by D. A. Kribs.)

chronologies, as they are called, make possible a historical study of climatic cycles. Such studies may lead to an estimation or prediction of future conditions. Tree-ring studies of pines have developed another important possibility—that of dating the age of beams in ancient ruins of cliff dwellings and other events in the history of ancient peoples. The rings tell a story of the time of building as to both the number of years involved and the order of building, facts of interest to anthropologists and archeologists.

For the relation of tree rings to climatic cycles and dating problems we are indebted to the work of A. E. Douglass.[1]

The secondary xylem makes up the greater part of the vascular system in many plants. In woody plants it constitutes the bulk of the entire plant

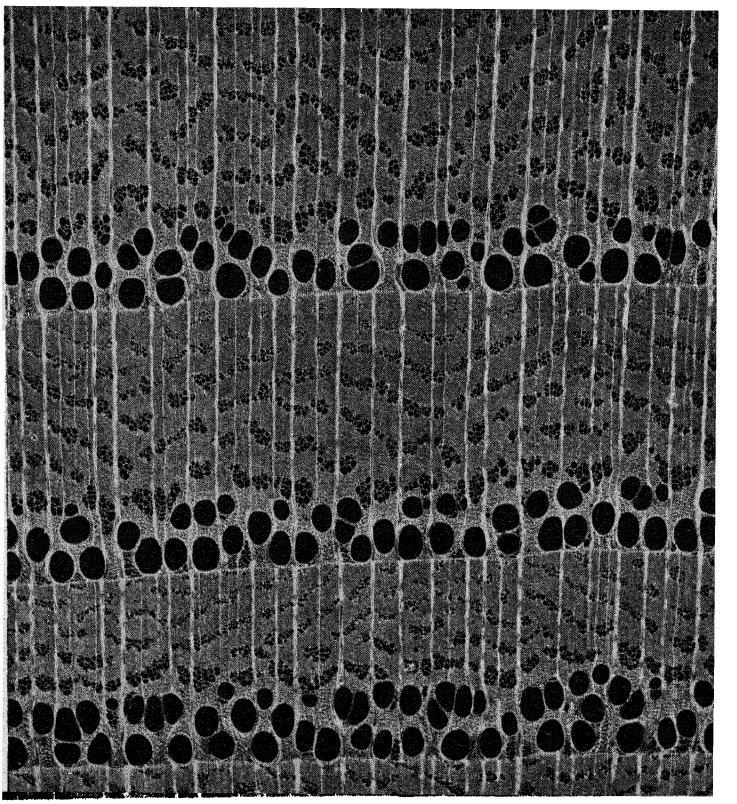


FIG. 4–24. Photomicrograph of wood of slippery elm. Large vessels appear in the spring growth forming what is known as ring-porous wood. (Photograph by D. A. Kribs.)

body. The wood and lumber of commerce is the secondary xylem of tree trunks. In the modern world wood is finding an ever-increasing use. Wood can be made into substitutes for wool and cotton. From it sugar and alcohol can be obtained. By impregnation and the application of heat and

[1] *Publications* of the Carnegie Institution of Washington, 1914, 1919, 1928, 1936; papers in the *Scientific Monthly*, 1925; *Nature Magazine*, 1928; and University of Arizona *Bulletin*, 1937.

pressure wood products can be made which have strength and durability approaching that of steel. Wood products are made into plastics which may be "lighter than aluminum, as transparent as glass, as soft as rubber, as flexible as lead." Wood is certain to be a substantial factor in the raw material market of the future.

In woody stems there are two well-defined regions, the *bark* and the *wood,* separated by the cambium. The bark in older stems may be differentiated into the *inner* and the *outer* bark. The inner bark is made up of active secondary phloem. The outer bark consists of dead phloem, the remains of the cortex, and layers of cork. On the stems of most shrubs and trees the outer bark cracks and may slough off.

Many roots increase in diameter in a manner which is similar to that in stems. Secondary growth results from the development of a cambium between the xylem and phloem. Woody roots of trees or shrubs show annual increments and have about the same structure and appearance as a stem of the same age.

We may summarize by saying that woody stems and roots increase in diameter by activity of two cambiums, one in the vascular cylinder and one in the bark. The cambium of the vascular cylinder might well be known as the vascular cambium but it is usually designated as *the cambium.* It adds new layers to the *exterior* of the wood and to the *interior* of the bark. The cambium of the bark is the *cork cambium.* It develops layers of cork within the epidermis and keeps on adding new layers within the old cork.

GROWTH

A seed germinates and the little plant (embryo) which was within the seed develops into a seedling (Fig. 4–25). The seedling increases in size, new branches and leaves develop, and later flowers appear. The enlargement of the trunks of trees and the extension of their branches, although gradual, are nevertheless familiar phenomena. These developments and increases in size are manifestations of growth. Growth usually results in an increase in weight, a change of form, and an increase in the size and number of parts. Spring is the season when growth is most evident; new seedlings appear on every hand, leaves burst from the dormant buds, and new branches develop. Most plants grow by repetition of similar parts, new leaves, new stems, new roots, and new flowers forming in succession. "The nature of growth has been as eagerly sought as has been the explanation of life itself."

The Factors Influencing Growth

Since growth is the result of several physiological processes it is affected by several factors, of which some are internal and others external.

Among the internal factors which affect growth are heredity, growth regulators, nutritional balance, and the interrelation of plant parts. The form, and to a certain extent the rate of growth, are determined by a group of factors inherited from the preceding generation. These inherited factors constitute heredity. An acorn is the fruit of an oak and in turn the acorn develops into an oak. The

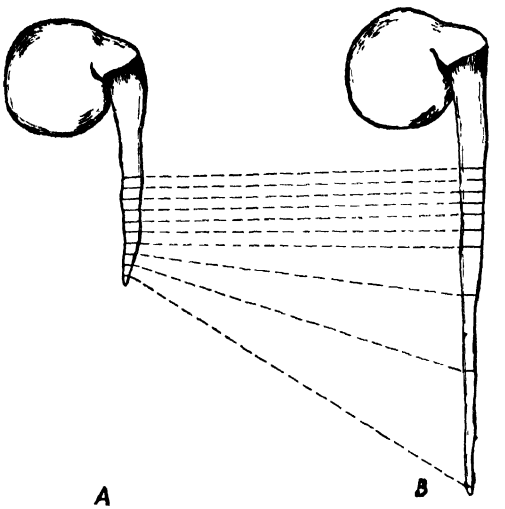


FIG. 4–25. Growing region of a root of a pea seedling. *A*, root marked into 1 mm. spaces. *B*, the same root 24 hours later. (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

embryo in the acorn inherits the capacity to become an oak and no conditions can cause it to develop into any other kind of tree. Heredity is a most important factor in growth and development.

For some years it has been known that there are glandular secretions in animal bodies which influence basic life processes. It is known that similar substances are present in plant bodies. Two terms have been used for these compounds, *hormones* and *auxins*. They are also called growth regulators or growth substances because of the influence that they exert on growth. In discussing hormones emphasis is frequently placed on the fact that they may be produced in one part of a plant and may control or influence a process in another part. The term auxin is generally used for those substances considered to be growth regulators. It should be emphasized "that they are used to condition the growth of the organism rather than to build its structure, as mineral salts, sugars, and proteins are used." In addition to the growth-stimulating substances naturally occurring in plants there are some substances, which are not plant products, that have more or less similar effects. Some of the synthetic hormones are used in practical ways. Indoleacetic and indolebutyric acids accelerate the growth of roots on cut-

tings (see Fig. 8–5). Naphthalene acetic acid or naphthalene acetamide is used for spraying fruit trees to delay the falling of fruit. The spray solution delays the organization in the fruit stem of a separation zone (abscission layer), the weak place where the fruit separates from the tree. Leaf fall, which is also effected by an abscission layer, is also retarded by the spray but for a shorter time than in the case of the fruit.

Vitamins are a group of organic substances known to have important effects on the growth and good health of animals. It is not certain how significant they may be in plant life and development. Since green plants synthesize them within their bodies, experimentation is difficult. Scientists are now discovering some of their functions in plants. It has been definitely proved that certain vitamins are growth substances for fungi and bacteria and also for higher plants. Vitamin B_1 is essential for root development. Vitamins are not classed as foods. They have been so regarded because animals get their supply of vitamins with their food.

The relative proportions of carbohydrates, fats, and proteins, or the nutritional balance as it is called, may also have much to do with growth. Abundance of carbohydrates may favor reproductive activity, whereas an excess of nitrogen may promote a vegetative but unfruitful development. The interrelation of plant parts is known to be important in the development of a plant. This is demonstrated by the removal of a part. If the end of a branch is removed some of the lower buds, which otherwise would have remained dormant, are stimulated into growth. It is a well-known fact that the shape of a fruit tree and also its tendency to bear fruit can be changed by pruning.

Among the best-known external factors affecting growth are light, temperature, and moisture, but there are many others. The supply of oxygen, mineral salts, and carbon dioxide is important; gravity, electricity, wind, insects, and diseases also may have a bearing on the form and rate of development.

Light is necessary for the formation of chlorophyll and for photosynthesis, and if insufficient for these processes growth is retarded or is not normal. Plants grown in the dark are yellow and spindly, and have undeveloped leaves.

Reference has been made previously (Chapter 1) to the effect of length of day on the growth of plants into a vegetative condition or a reproductive condition. Some plants, such as radish, lettuce, or hibiscus, bloom normally in midsummer and are called *long-day* plants. Others, called *short-day* plants, bloom in spring or autumn when the days are comparatively short. Most of the spring flowers and the autumn-flowering chrysanthemums,

asters, and ragweeds are examples of short-day plants. Some plants such as chickweeds, dandelions, tomatoes, and buckwheat respond to different lengths of day and bloom any time during the growing season. Chrysanthemums can be brought into bloom by being shaded in such a way as artificially to produce the effect of shorter days. Experiments have shown that some plants can be hastened into bloom in a shorter number of days than usual by lengthening the daily light period with artificial light. Some plants show obvious ill effects and even changes in form if subjected artificially to wide changes in the length of day. The influence of the length of the normal daylight period is of real importance in governing the time of planting of certain crops. It also affects the growing of greenhouse crops during the winter. In his recent book, *Plant Growth,* Yocum says the reason for length-of-day phenomena is not understood. "Much work," he writes, "has been done on the problem, studying such fields as nitrogen assimilation, temperature, stored food, and growth hormones, but at present the problem remains unsolved."

Temperature is a very important factor affecting the rate of growth. The range of temperature varies within the minimum (somewhat above freezing) below which no growth occurs, and the maximum (usually about 25°C.) above which no growth takes place. Between these is an optimum (around 30°C.) which permits the highest rate of growth. A rise in temperature from the minimum to the optimum increases growth. The range of temperature varies with different kinds of plants. Corn, for example, grows best on hot nights, whereas most ferns thrive under cool conditions. Even in the same plant the optimum temperature for root and shoot may be different. In starting bulbs, the bulbs are kept in a cool environment for root growth and moved to higher temperatures for later growth and flowering.

Water is so important in the growth of plants that much of the following chapter is devoted to its consideration. The relations of soils and of diseases and pests to plant growth are topics also discussed in succeeding chapters.

CHAPTER 5

THE SUPPLY OF RAW MATERIALS

(Absorption, Conduction)

The raw materials for which plants are dependent upon their environment are carbon dioxide, water, and certain minerals. Some of the facts about these essentials and their uses in the plant have been discussed in preceding chapters. Other facts about their mode of supply, their entrance, and their movements within the plants are significant and must be considered. These raw materials are constantly in movement or circulation in the environment—carbon dioxide in the air, water and dissolved substances in the soil. The plants remain fixed in one place; the widely distributed but not always abundant raw materials come to them. Although bound in the living plant bodies for a time, these materials are ultimately released and again made available to plants.

WATER RELATIONS

The bodies of both plants and animals contain a large amount of water. It is a safe general estimate that more than three-fourths of the total weight of either plant or animal bodies is due to water. There is considerable variation in different plants or plant parts. Woody parts may not contain more than 50 per cent water. Juicy fruits may have as much as 95 per cent, whereas dry seeds may have as little as 10 per cent. As a rule the young growing parts of a plant contain more water than the older parts.

The Uses of Water

There are several ways in which water functions in plant bodies, some of a physical nature and some of a chemical nature. Under ordinary conditions living cells maintain a certain internal pressure which causes a stretching of the plasma membrane (*cytoplasm* next to the wall) and, to some extent, of the wall. A cell in this condition of being distended by internal pressure is said to be *turgid*. It is the absorption of water which

maintains this essential condition of rigidity of the cells and tissues and prevents wilting. We have referred to the dryness of seeds—they may be so dry that they apparently are dead. One of the essential factors leading to a reawakening of seeds is water. Without water there is no growth. The stored food can be converted into soluble form only in the presence of water. Water is the medium in which the cellular reactions take place. It is water which serves as the solvent of the sugars and other substances. The required mineral salts of the soil can enter only when dissolved in water. Thus water is necessary both for the entrance of materials and for their movement from one part of the plant to another. Previously we learned that water and carbon dioxide are the essential raw materials in the formation of foods. They provide the elements hydrogen and oxygen which go into the making of carbohydrates. Water is therefore essential in the first step of the synthesis of organic matter from inorganic materials.

From these facts it can be seen how water is indispensable for permeating and distending the cells and how it serves for the formation, solution, and transportation of the various compounds in nutrition. On the other hand, while land plants retain and use a large amount of the water which they take up through their roots, they lose a still larger quantity through their aerial parts. The loss is chiefly through the leaves in the form of vapor as a result of evaporation.

Since water plays such an important role in the constitution and life of a plant it is evident that we must give attention to the processes involved in the entrance of water, its movement within the plant body, and its escape therefrom. Likewise attention must be given to the movement of materials dissolved in the water.

Absorption of Water

Plants which grow in the water do not require special absorbing structures. Land plants obtain their water from the soil and we find that they are provided with the means for absorbing soil water. The lower land plants, such as mosses and liverworts, have structures known as rhizoids. These plants usually grow in moist places and the rhizoids are chains of elongate cells which penetrate the soil to some extent but not to any considerable depth. The higher land plants absorb water through the roots. Root systems may be much branched and extensive. In our discussion of roots we referred to the fact that water is absorbed by the young and delicate terminal parts of the roots. It will be recalled that the absorbing surface of these young parts is greatly increased by a multitude of radiating *root hairs* just a little way above the root tip. These hairs are tubular

extensions of the epidermal cells and are the active water-absorbing parts of the root.

Our study of roots, stems, and leaves has revealed the presence of vascular bundles which are continuous from the region of the root hairs through the extent of the root and upward through the shoot and into the veins of the leaves. Water from the soil enters the root hairs, passes through the cortical cells of the root until it reaches the xylem ducts of the vascular bundles, and is conducted upward through them. Living cells in the stem or in the leaves in turn take water from the ducts. These living cells appropriate some of the water to their own uses. A considerable portion, however, evaporates from their walls into the intercellular spaces and eventually escapes to the atmosphere through the lenticels and stomata. Such is a brief statement of the water relations—water enters the roots, passes through the stem, some of it is assimilated, some of it is held in the living cells, and much of it escapes as vapor from the leaves. There is a current of water through the body of the plant from root hairs to leaves. These facts can be easily learned, but our troubles arise when we consider the physical forces which are involved and all the reactions which must take place. After we have done our best, there will remain some problems for which no wholly satisfactory solutions have been found. Nevertheless, we are justified in making the effort to get the facts before us and to interpret them as fully as possible.

Osmosis and the Entrance of Water

Root hairs present to soil spaces a wall lined with living protoplasm. The part of the protoplasm which lies next to the wall is the *plasma membrane*. The interior of the hair is a large vacuole filled with cell sap. This sap is a solution whose solvent is water which has been absorbed from the soil. The water has passed through the wall and through the living plasma membrane of the root hair. It is at once obvious that water cannot *flow* through the wall and through the membrane, but it does pass through in some manner. It does not pass through by mass movement but by molecular movement. Not only does water pass from the outside into the vacuole but it does so in such quantity that a water (hydrostatic) pressure is developed within the cell. The protoplasm is pressed with real force against the wall. Physiologists say that such a cell is *turgid* and they speak of the pressure of the cell content against the wall as *turgor pressure*. The movement of the water into the root hair is a physical process known as *osmosis*.

We may proceed by describing some simple experiments. If we tie a

membrane (parchment or pig's bladder), which is permeable to water, over the end of a thistle tube filled with a sugar solution (syrup) and then support the tube in a beaker of water, we have what may be called an *osmotic system* (Fig. 5–1). Shortly the sugar solution rises in the tube. If the membrane is more permeable to water than to sugar there will be a continued rise in the tube. If the sugar molecules pass through the membrane readily the rise soon subsides. Again, if instead of pure water in the beaker we use a sugar solution but with a lesser amount of sugar than is in the solution in the thistle tube, there will be a rise in the tube as before, but it will develop more slowly. We might tie a membrane into a small bag filled with a solution and place the bag in a dish of water. Solutes other than sugar may be used. If the bag were limp when placed in the water we would find that water soon enters it, making it swell

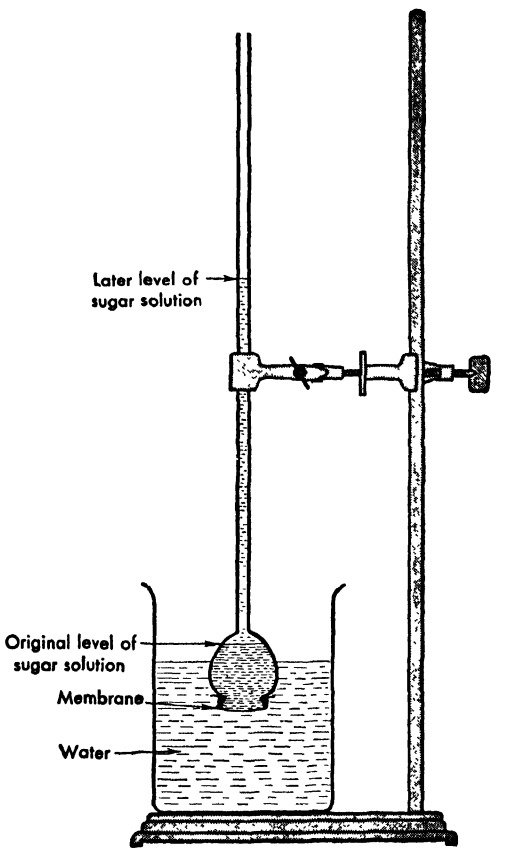


FIG. 5–1. An osmotic system; further particulars are given in the text.

from a definite internal pressure. In this bag we might have conditions similar to those in living plant cells. Whether this is the situation will depend upon the nature of the membrane used for the bag. Water passes readily through some membranes, but certain solutes do not. Membranes which differ in their permeability to different substances are said to be *selectively* or *differentially permeable*. The protoplasmic membrane of a living cell is an example of this type of membrane. Inorganic substances pass through it more readily than organic substances.

The facts are these: When water is separated from a solution (water plus a dissolved substance such as sugar) by a *selectively permeable membrane*

there is an excess movement of the water through the membrane into the solution. If two solutions of different concentrations are thus separated there is an increase in the volume of the solution of higher concentration at the expense of the solution of lower concentration. It is necessary that we analyze the preceding statement carefully lest we fall into an erroneous concept. We would doubtless all have a tendency to call a solution with *less* sugar the one of *low* concentration and a solution with *more* sugar the one of *high* concentration, and we would be correct if we are referring to the dissolved substance, sugar, as determining the *low* or the *high* of concentration. But if we are considering the water, the situation is reversed, for its concentration is *lower* in the solution containing *more* sugar and *higher* in the solution containing *less* sugar and still higher where there is no sugar, i.e., in pure water. The physical chemist tells us that there is a general law that gases and liquids and dissolved substances move from places where they are more concentrated to places where they are less concentrated, from where they are abundant to where they are scarce. In osmosis water behaves in accordance with this law of diffusion. A fuller account of diffusion is presented later in this chapter in the discussion of the entrance and movement of mineral salts.

We may try another experiment which will throw additional light on our problem. We have said that water enters the root hair through the protoplasmic membrane because the concentration of the water is less within the cell than it is in the soil water—the water moves to the place of its lesser concentration. We have reached the conclusion that the water is less concentrated within the cell because more dissolved substances are there. If now we reverse the situation and place around the root cells a solution which has more dissolved substances than the cell sap contains, water should leave the cell. We find this to be true. So much water may leave the vacuole that the protoplasmic membrane is no longer pressed against the cell wall, but withdraws from it toward the center of the cell. This contraction of the protoplasm in an active cell is known as *plasmolysis* (Fig. 5–2). If continued long enough the end result will be a rounded mass of protoplasm in the center of the cell.

It will be helpful to keep in mind that osmosis involves molecular movements. Everyone knows that water evaporates. The fact is that some of the water molecules on the exposed water surface leave the water and pass off into the air. There is no chemical change. The water molecules may be associated to form liquid or to form vapor. The tendency of the water molecules to escape into the air is known as vapor pressure. There are differences in the vapor pressures between pure water and solutions and be-

tween solutions containing different amounts of dissolved substances. Evaporation goes on faster from the surface of pure water per unit area than it does from the surface of a watery solution. The theory is that more water molecules are exposed per given area on the water surface than are exposed on the solution surface. That explains their more rapid escape. Now let us apply this to the separation of water and a solution by a membrane. Similarly there are more water molecules against the membrane

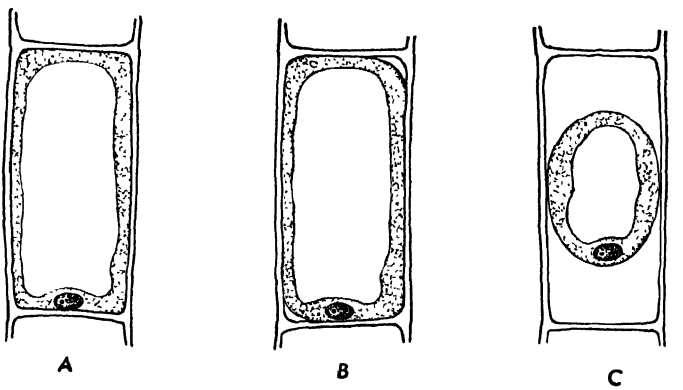


FIG. 5–2. Turgor pressure and plasmolysis in corn root cells. *A*, in water: The protoplasm is pressed with force against the wall and the cell is turgid; *B*, in 2.3 per cent potassium nitrate, showing slight plasmolysis; *C*, in 5 per cent potassium nitrate, showing a high degree of plasmolysis. (After Pfeffer.)

per given area on the water side than on the solution side (Fig. 5–3). Thus we see that the water molecules would enter the membrane at a more rapid rate from the water side than from the solution side. In turn the water molecules would leave the membrane at a more rapid rate on the solution side. The net result would be an excess movement from the water into the solution. The same reasoning applies to the separation of two solutions of unequal concentration. There are relatively more water molecules on the side of the weaker solution; hence the excess movement of the water is from the weaker solution to the stronger solution. The water is diffusing from the region of its higher concentration to one of its lower concentration. Of course the water molecules are moving in both directions but at a greater rate in one direction than the other; the end result is accumulation in the direction in which the rate is more rapid.

Restatement of Osmosis

Osmosis is a difference in the rate of movement of solvent molecules from opposite sides of a selectively permeable membrane separating two

solutions of different concentrations of the solvent. In plants the selectively permeable membrane is the peripheral layer of protoplasm (plasma membrane) surrounding living cells, and the solvent is water. Osmosis cannot be defined simply as "diffusion through a membrane." Osmosis

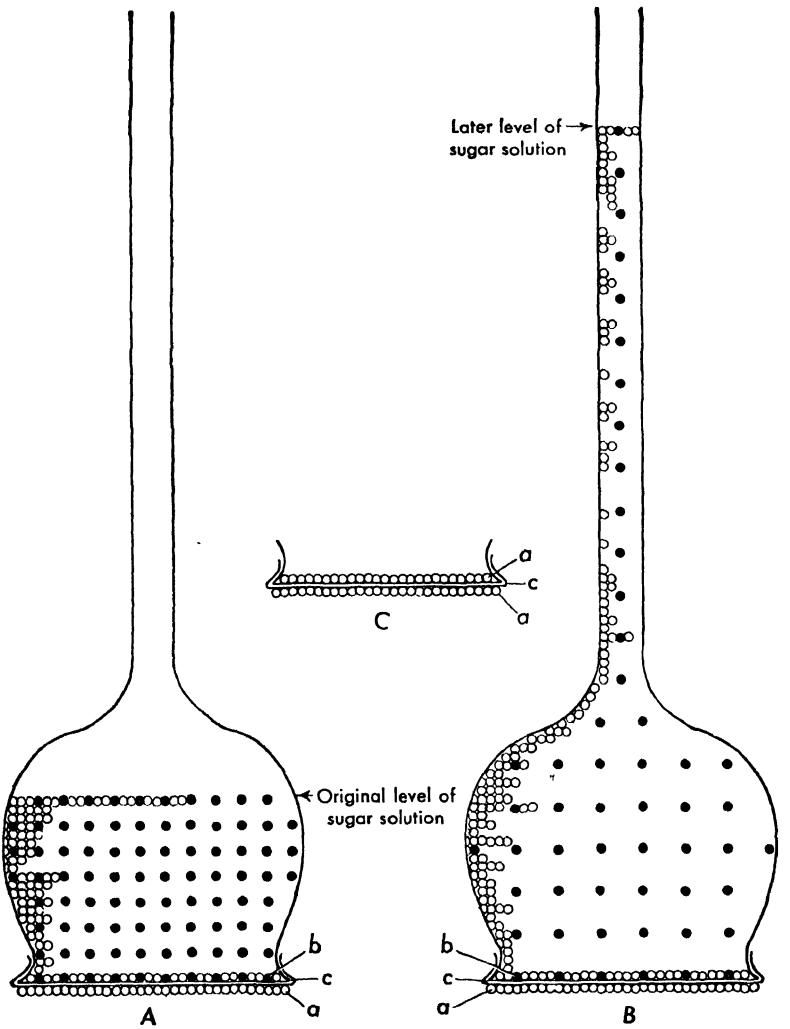


FIG. 5–3. Diagrams to illustrate osmosis. *A*, water molecules (*a*) on the outside of membrane (*c*) and water molecules (*a*) and sugar molecules (*b*) on inside of membrane. There are fewer water molecules in contact with the membrane on the inside; hence the water passes in more rapidly than it passes out, and the level of the solution rises as in *B*. Note that the sugar molecules become more widely separated. If equal numbers of water molecules are in contact on both sides of the membrane as in *C*, the movement of water molecules is the same in each direction and the level of the water will remain unchanged.

is a special case of diffusion which is a dispersal of material by molecular movement. In the dispersion of materials by diffusion everything moves from a region of abundance to a region of scarcity, so far as other features of the environment permit. When pure water is on both sides of a selectively permeable membrane the water molecules are diffusing through the membrane. In such a case the rate of diffusion from the opposite sides is the same; hence there is no osmosis. The phenomenon of osmosis appears only when there is an excess diffusion of water in one direction. The excess diffusion takes place when there is a difference in the concentration of the water molecules on the two sides of the membrane—or we might say when there is a difference of diffusion pressures on the two sides of the membrane. Water molecules are more abundant when there are fewer molecules of a dissolved substance (solute) present; hence the excess movement is always toward the solution having the higher concentration of the solute.

Living plant cells when mature are enclosed structures. The wall and peripheral protoplasm surround a large central vacuole filled with a solution of organic and inorganic solutes. When water, or a solution of lower concentration of solutes, is outside such a cell there is a movement of water into the cell. The volume of the solution in the vacuole is increased and the protoplasm is forced against the wall by the expanding vacuole. This pressure, which is the *result* of osmosis, is called *turgor pressure*. This should not be confused with *osmotic* pressure which is the *cause* of osmosis. Since osmosis is caused by the presence of solutes, and since the extent of osmosis is dependent upon the concentration of the solutes, the term *osmotic pressure* is used to refer to the maximum capacity of a solution to produce osmosis under perfect conditions. Osmotic pressure is a potential rating; *turgor pressure* is the actual pressure produced. If a solution outside a cell contains more solutes than the cell sap, water will move out of the cell faster than it moves in, and the protoplasm shrinks. In this condition the cell is said to be *plasmolyzed*. In a plasmolyzed cell the potential pressure of the cell sap is high, but there is no actual pressure; osmotic pressure exists but is not being expressed as turgor pressure under such a condition.

Osmosis is a process of outstanding biological significance. It is a factor in the entrance and distribution of water. The development of turgor pressure within cells is a feature of great physiological importance. The rigidity of the soft and succulent parts of plants is dependent upon turgor. Increase in the size of cells in growth is dependent upon the entrance of water by osmosis. Certain movements of plant parts are brought about by

changes in turgor. Osmosis and turgidity of cells are the basis of many processes which are fundamental to the development and behavior of the living plant.

Imbibition

It is believed that the prominent place given to osmosis in the entrance of water into the plant body is justified. Our account would not be complete, however, if we did not give consideration to *imbibition,* which plays a part in the absorption of water by living cells. A dry piece of gelatin absorbs water and shows the effect of the absorption by an increase in volume. Dry wood absorbs water—it will even absorb water from the vapor of the air—and there is frequently a noticeable swelling as is evidenced by the sticking of doors and windows in wet weather. The absorption of water by such materials as gelatin or the lignified cell walls in wood, with the accompanying swelling, is called *imbibition.* Dry protoplasm (as in seeds) absorbs water by the process of imbibition. There may be other substances in the cell which imbibe water. The forces involved in the swelling of substances in imbibition are a manifestation of the energy of diffusion.

The outer layer of the wall of root hairs is gelatinous material which causes the hairs to adhere to particles of soil and brings them into intimate contact with soil water. This gelatinous layer, and also the inner cellulose layer, absorb water by imbibition. Since imbibition brings the water into contact with the plasma membrane, it plays a role along with osmosis in the absorption of water from the soil by the root hairs.

Conduction of Water

We have already pointed out that water entering the root hairs passes through the cells of the cortex until it reaches the vascular system. The vascular bundles are continuous and unbroken, though much branched, from roots to leaves. There can be little doubt that there is a streaming, or mass movement, of water through the tracheary elements of the xylem. It will be recalled that there are two parts of a vascular bundle, the xylem and phloem. Age-old experiments prove that the principal movement of water is in the xylem, i.e., the wood (Fig. 5–4). If we take a twig, remove a section of the bark completely (this is known as girdling), and place the twig in water the leaves will remain fresh for a considerable time. Since the phloem was removed with the bark and only the wood (xylem) remains there seems no reason for doubting that the wood is functioning for the passage of water. But the converse of this experiment can be carried out by removing the wood and leaving only the bark. The result

is that the leaves soon wilt. The phloem either is lacking in capacity for water conduction or, at least, is inadequate.

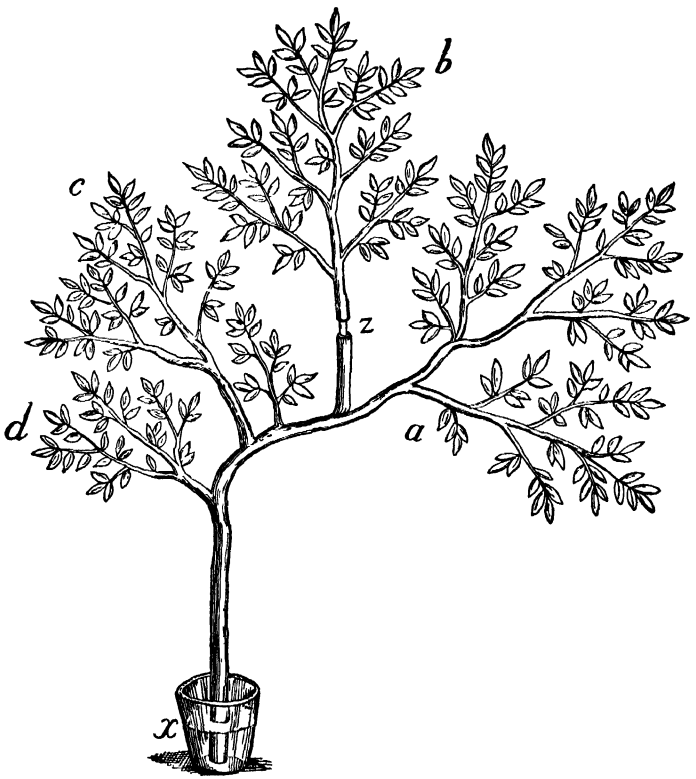


FIG. 5–4. Reproduction of an illustration by Stephen Hales in *Statical Essays: containing Vegetable Staticks; Or, an Account of some Statical Experiments on the Sap in Vegetables,* published in 1783. The following is his description of the experiments: "July 27th, I took several branches of *Currans, Vines, Cherry, Apple, Pear,* and *Plumtree,* and set the great ends of each in vessels of water *x* (Fig. 31.); but first took the bark for an inch off one of the branches, as at *z*, to try whether the leaves above *z* at *b* would continue green longer than the leaves of any of the other branches *a, c, d,*; but I could find no difference, the leaves withering all at the same time: Now, if the return of the sap was stopped at *z*, then it would be expected, that the leaves at *b* should continue green longer than those on the other branches; which did not happen, neither was there any moisture at *z*."

The determination that water is conducted by the xylem still leaves us with some interesting considerations concerning the mechanisms and forces involved.

The Transpiration Stream

Transpiration is the escape of water in the form of vapor from the aerial plant parts. A study of the quantity of water thus escaping, and of the

factors affecting the rate, comes later. At this point it is sufficient to understand that the release of vapor from leaves or green stems is a universal phenomenon in green plants. There is no counterpart of this process in animals. Perspiration is entirely different as to both meaning and method. Since quantities of water pass out through the leaves there must be a constant flow from the roots through the stems, and this has suggested the expression *transpiration stream* or *current*. It is generally agreed that the current ascends in the cavities of the xylem vessels and tracheids.

In transpiration, water evaporates from the mesophyll cells into the intercellular spaces and passes out through the stomata as vapor. The evaporation of water from the leaf cells lowers the amount of water in them. This furnishes exactly the proper basis for the passage of water from the xylem cells of the veins and veinlets to the mesophyll cells by osmosis. In other words, a deficiency of water in the mesophyll cells causes water to enter them from the xylem cells. The theory is that strong osmotic and imbibitional forces are involved and that a real pull or tension is exerted on the upper end of the water columns within the xylem elements. This is usually spoken of as the *cohesion theory* because it involves the cohesive strength of water. This theory asserts that a column of water has tensile strength and that if a pull is exerted on the top of the columns of water in the xylem tubes this pull can be transmitted along their whole length. Physicists say that an unbroken column of water possesses such tensile strength. According to this view, there is a pull causing an upward movement of water sufficient to balance the loss by transpiration.

If a shoot is cut from a vigorous plant and placed in water, no wilting takes place because water is drawn into the cut vessels. This shows that there can be an upward movement of water when no root is present. If the stem of a shoot is cut under water and inserted tightly in a glass tube filled with water, and if the lower end of the tube is inserted in mercury, there will be a rise of the mercury. With such a set-up it is possible to raise and sustain a mercury column to a height of at least 90 cm., which is more than could be accomplished by atmospheric pressure alone (76 cm.). Such an experiment demonstrates that there is a cohesion of the molecules of water and that transpiration does exert a pull in raising the column of water.

Although there have been many criticisms of the so-called cohesion theory, it constitutes the best explanation of the ascent of water in the plant body that has been offered. To a certain extent it is misleading to have so much emphasis on *cohesion*. According to the facts, *cohesion* of the water is only part of the mechanism which makes the movement possible. Even

if the water did cohere in the xylem it would remain stationary if there were not some *force* applied. The theory is that the force is a lifting or pulling force applied at the upper end. A lifting force is there. The rise of the water is made possible by cohesion, but in no sense is cohesion the cause of the movement. If we wished to place the emphasis on the forces concerned we would need to seek a different expression than cohesion theory, but to change a term is difficult even when we recognize that it is inappropriate.

It can be readily appreciated that such forces as atmospheric pressure, capillarity, and imbibition cannot account for the transpiration stream. It is inconceivable that atmospheric pressure can play a part because both ends of the xylem tubes are closed and it could not operate under such conditions. In any event water can be raised by atmospheric pressure only about 33 feet, whereas it must be raised ten or twelve times that to reach the tops of the tallest trees. Water does rise in very small tubes by capillarity, but in tubes the size of those in the xylem it would rise only a few inches, or at the most a foot or two. In capillary tubes many times smaller, the rise would be more significant. Imbibition has been offered as an explanation but is ruled out on the ground that its action is too slow to account for the movement of water at the rate it is known to ascend in trees. It seems fair to say that capillarity and imbibition are forces which may aid in maintaining the position of water but that they cannot account for its movement.

Root Pressure and Bleeding

If the stem of a vigorous plant is cut off close to the ground, water will flow after a time from the cut stem. When a glass tube is fastened firmly over the stump by means of rubber tubing the exuded water will rise gradually in the tube (Fig. 5–5). Under certain conditions it may attain a considerable height in the tube. By the use of a gauge it is possible to measure the pressure with which the water is exuded. Pressures sufficient to raise a column of water 20 or 30 feet are not uncommon; still higher pressures have been recorded. Sap may also flow from the cut or broken ends of twigs removed from trees in the spring. This exudation of sap is called "bleeding." It is well known that sap flows from maple trees when the trunks are tapped in the early spring. The century plant and certain palms are bled for sap which is used for making beverages.

The phenomenon of sap exudation from the cut stem when the entire top is removed has been called "root pressure" because it is obviously caused by forces operating in the roots. The fact that such forces are developed in the roots leads naturally to the suspicion that they may be responsible for the mass upward flow of water. If this were true the water

would be forced up by pressure from below rather than pulled up by lifting forces as previously concluded. There are numerous reasons why root pressure cannot be regarded as the cause of the ascent of sap. The most significant fact is that root pressure does not exist all the time. In fact, it is lowest when transpiration is the highest. By affixing a suitable apparatus to the trunk of a tree it has been determined experimentally that under certain conditions not only does sap not exude but that water actually flows into the tree. Such a lack of pressure could hardly exist if the sap were being forced up from below. The fact that cut branches, when placed in water, do not wilt is another indication that pressure from the roots is not necessary for sap ascent. It is also true that root pressure, even though sometimes of considerable magnitude, is still insufficient to force the sap to the tops of tall trees.

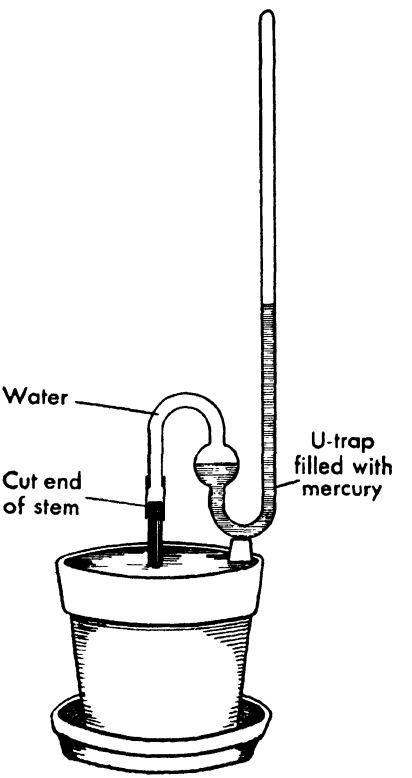


FIG. 5–5. Method of demonstrating root pressure. Water is exuded from the cut end of the stem, and the result of the pressure is evident in the rise of the mercury column.

Water Loss by Transpiration

We have called attention to the fact that a large proportion of the water which ascends through the stems of plants is lost by evaporation through the leaves. This escape of water vapor from plant parts is called *transpiration*. The chief loss is through the stomata and may be designated as *stomatal* transpiration, in contrast to the loss through the cuticle, or *cuticular* transpiration. Although cuticular transpiration may be significant, it is much less than stomatal transpiration, usually amounting to only 5 to 15 per cent of the total water-vapor loss. Theoretically, there would be no transpiration if a plant were growing in an atmosphere which was completely saturated with water vapor. Practically, such a condition does not often exist, unless it be in tropical forests, and it is therefore rare that transpiration entirely ceases. There are, however, wide variations in transpira-

tion depending upon both external and internal factors, and some attention must be given to both factors in order to gain a clear conception of what is taking place.

The really remarkable thing about transpiration is not its existence but its volume. It will be remembered that the green food-making cells within the leaves have thin walls and are filled with protoplasm and sap. If not protected by an epidermis and cuticle they would soon dry up and perish when exposed to the sun and wind. If protected so thoroughly that there could be no water loss at all, the cells would be functionless from the point of view of food synthesis and respiration. Inasmuch as there is provision for the entrance and exit of carbon dioxide and oxygen, this same provision makes possible the passage of water vapor. In other words, the same features which provide for photosynthesis and respiration provide also for transpiration. There may be some question as to whether transpiration has certain advantages or whether it is a necessary evil, but there is no question about its existence.

A large sunflower plant will transpire more than a quart of water on a warm day. A birch tree estimated to have 200,000 leaves is said to transpire 700 to 900 gallons on a hot summer day. It is calculated that an acre of such trees would give off in a growing season 3,168,000 pounds of water. Many careful studies have been carried on with potted plants in greenhouses where it is possible to make careful measurements. Ganong attempted to arrive at what he called a conventional constant, or a generalized average; his figures are 50 grams per square meter per hour (50 gm^2h) by day and 1/5 of this amount by night. Another interesting way to view the matter is to determine the amount of water given off by a plant while a certain amount of solid matter is being formed. It has been found that many plants give off 200 to 500 ounces of water for every ounce of dry solid matter produced. Some authors speak of the *water requirement* of plants. They refer to the number of units of water used for each unit of dry matter produced, and such figures can be cited: corn, 368; wheat, 513; potatoes, 636; cotton, 646; red clover, 453; ragweed, 984. After presenting these statistics it seems hardly necessary to say that the magnitude of the water requirement of plants is a matter of surprise to most people. It may be added that in general plants with lower water requirements are relatively drought-resistant.

Measurement of Transpiration

When we see wilted plants we are seeing evidence of an excessive water loss. Under ordinary conditions where there is no wilting we are unaware

of transpiration unless it is demonstrated by some means. There are several ways in which we may proceed. A fresh shoot covered by an inverted flask and held in place by a split cork, with the cut end in water, makes a good arrangement. Soon droplets of water condense on the inside of the

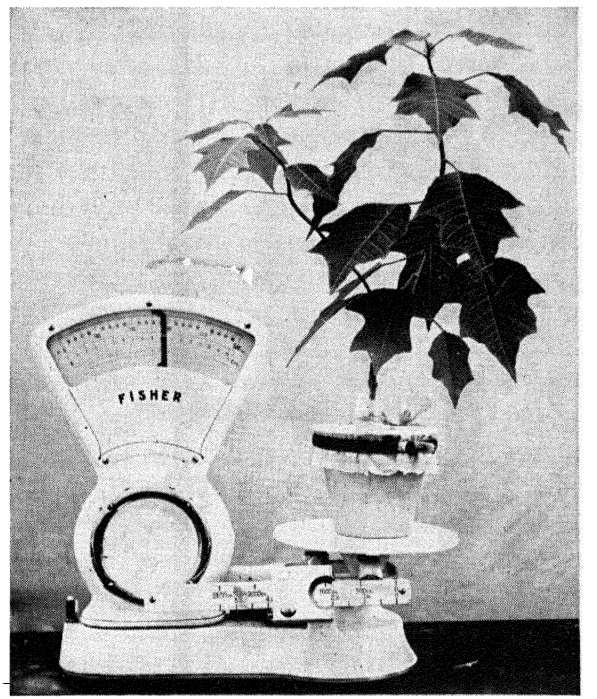


FIG. 5–6. Weighing method of demonstrating and measuring water loss by transpiration; further particulars given in the text.

flask. There can be but one conclusion—the air inside the flask has become saturated from the vapor transpiring from the leaves. A check may be provided by arranging in identical fashion a shoot which has had vaseline rubbed on the lower surfaces of the leaves.

There is a weighing method by which transpiration may be both demonstrated and measured (Fig. 5–6). A potted plant (fuchsia, geranium, or other greenhouse plant) is used. The pot is enclosed in an aluminum shell and the soil is covered with a sheet of rubber which is clamped to the shell and fastened closely about the stem; a bit of cocoa butter may be used here to form an airtight union. If weights are taken at intervals, a loss is noted which is properly attributed to transpiration. It is true that this experiment is subject to some errors from photosynthesis and respiration; but under

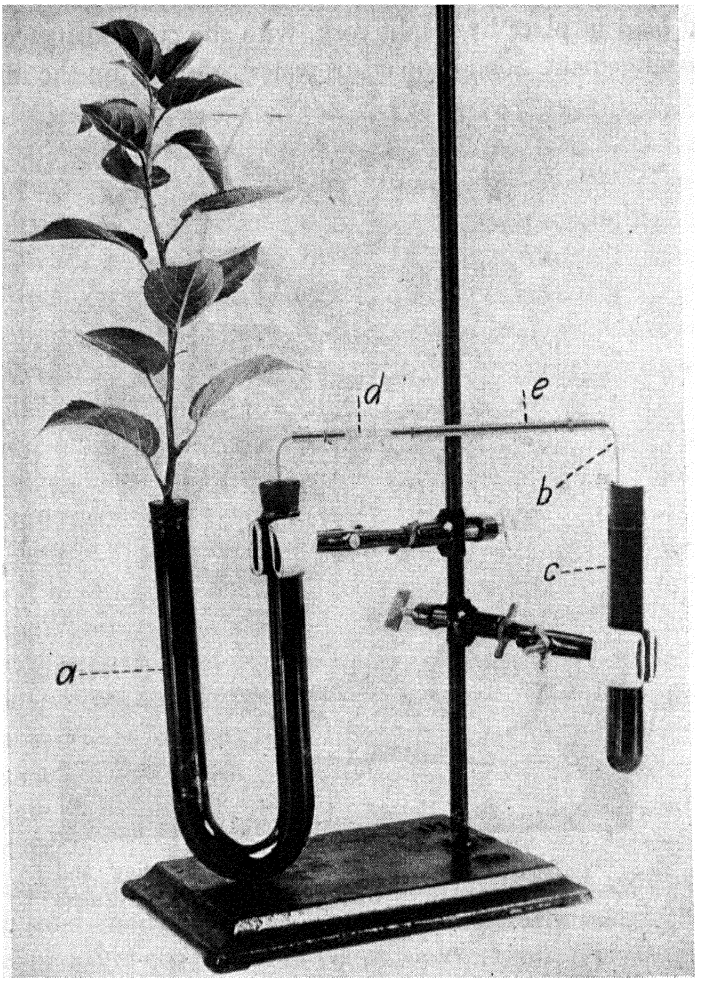


FIG. 5–7. Apparatus known as a potometer for measuring the rate of transpiration. A leafy twig is fastened through a rubber stopper into one arm of a U-tube (*a*) which is filled with colored water. A bent capillary tube (*b*) is lowered into the other arm of the U-tube until the water is forced out of the free end of the capillary tube. As water is transpired by the leafy shoot, air is drawn into the free end of the capillary tube. When a bubble of air has been drawn into the tube, the free end is lowered into a test tube (*c*) also filled with colored water. The rate of transpiration is determined by the time taken for the bubble (*d*) to move across a scale (*e*) fastened to the back of the capillary tube. To force the bubble back to the zero mark on the scale the capillary tube is pushed farther into the U-tube. The effects of light, darkness, air currents, and different temperatures on the rate of transpiration can be determined by the use of this apparatus. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

the usual conditions of the experiment, where the plant is kept in weak light, these are not significant. In this manner the variations in loss of weight between day and night or between warm and cold atmosphere can be compared. If the experiment is continued for several days, it may be necessary to add water to the soil; in such a case the weight readings must be adjusted accordingly. In some physiological laboratories this type of experiment is perfected so that the loss of weight is recorded on a revolving drum and a graph is obtained. If, then, on the same sheet are plotted contemporaneous graphs of humidity, temperature, and light, it is possible to see at a glance the relation of these external conditions to the physiological process of transpiration.

There are various other ways of studying and observing transpiration (Fig. 5–7). The important role played by stomata may be demonstrated by means of a color reaction. If filter paper is impregnated with cobalt chloride and dried, it is dark blue. It will change to light rose upon the absorption of water. Prepared paper strips may be applied to the upper and lower surfaces of a leaf and clamped in place by small glass plates (cover glasses). The turning of the color of the paper strips to a light rose is due to their absorption of water and hence is a proof of transpiration. If one side of the paper changes color more quickly, this is evidence of greater transpiration. It will be found that the color reaction takes place more quickly on the side of the leaf more abundantly supplied with stomata. In most ordinary plants it is the lower side. It is possible to carry out this experiment also to show that the reaction is more rapid when the stomata are open during the day than when closed during the night. It is also possible to show by this means that transpiration is more rapid in a given time from some plants than from others even though the external conditions are identical.

Factors Affecting the Rate of Transpiration

There are numerous external conditions which have a profound effect upon transpiration (Fig. 5–8). A combination of intense light, high temperature, dry air, and wind favors rapid transpiration sometimes to the point where wilting results even if there is ample soil water. The roots cannot, under such conditions, absorb water as fast as it is transpired. Light favors transpiration because it causes the stomata to open, thus permitting a free escape of the water vapor from the internal air spaces, and also because some of its energy is transformed into heat, which brings about a more rapid vaporization. Heat increases transpiration because of the physical fact that air at higher temperatures is capable of holding more vapor than air at lower temperatures. Humidity, or the amount of water vapor

in the air, is naturally an important factor in influencing the net rate at which moisture will pass from the plant to the surrounding atmosphere. Winds or air currents are significant because of their direct effect on the surrounding atmosphere. If the air immediately next to the transpiring surface is constantly changing, transpiration is increased. Barometric pressure is also a factor in determining the rate of vaporization of water. This

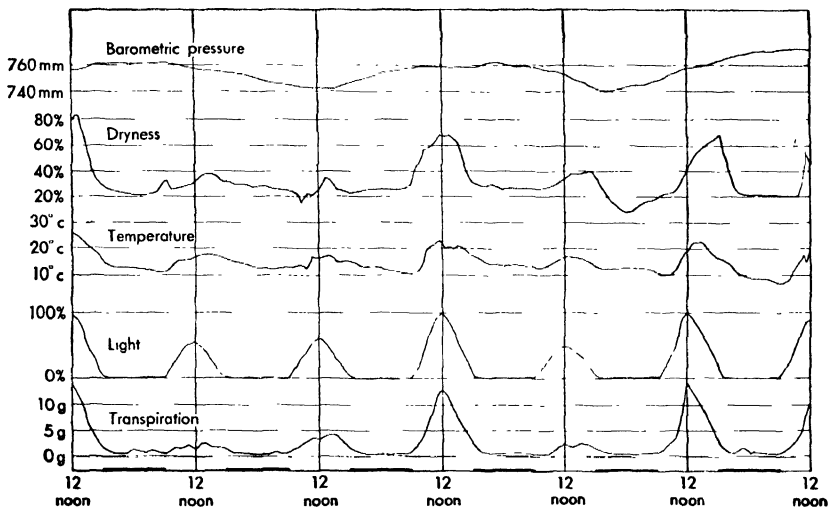


FIG. 5–8. Graphs showing correlation of transpiration with light, temperature, dryness, and barometric pressure. The graphs were plotted from data supplied by self-recording instruments, except for light which required a special method; the graph for dryness is an inverted graph of humidity. (Redrawn from *The Living Plant* by William F. Ganong with the permission of the publishers. Copyright 1913 by Henry Holt and Company.)

factor is not of importance in any given location but it does enter into the conditions between low and high altitudes. The effects of light, heat, dryness, and winds can be observed best in deserts where they prevail in a conspicuous manner. Under such conditions the ordinary broad-leaved plants do not survive; instead we find plants with reduced leaf surface and thick stems which serve as water reservoirs. Most cacti have spines which are modified leaves. Plants which possess combinations of characters that enable them to exist for a long time on a scanty supply of water are called *xerophytes* (Fig. 5–9).

This brings us to the point where we are able to conclude that the rate of transpiration is affected not only by external factors but also by structural features of the plants themselves. As already indicated, the size, shape, and arrangement of the leaves have much to do with influencing transpiration. The character of the epidermis, together with the cuticle, is impor-

tant. A double layer of epidermal cells, sunken stomata, a covering of hairs, and a thick waxy cuticle are features which reduce water loss. Xerophytic plants usually possess such characters. Sometimes transpiration is checked by a rolling or folding of the leaves. This is frequently seen in corn and other grasses.

A further word must be said about stomata and their relation to transpiration. Although the opening and closing of stomata are important factors in

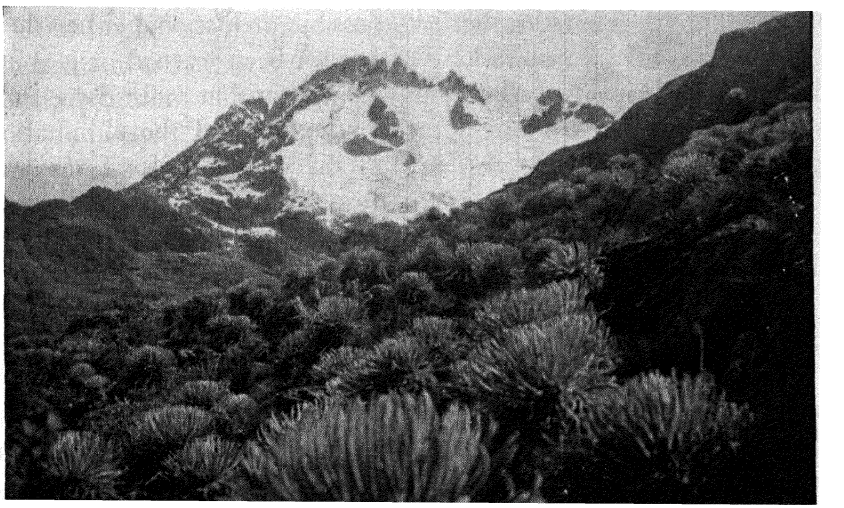


FIG. 5-9. Xerophytic vegetation at a high altitude in the Andes of Venezuela. The most characteristic plant is a bushy composite (*Espeletia*). The leaves and flowers are covered with a dense woolly coating of hairs.

modifying transpiration, their actions are influenced chiefly by the conditions concerned with photosynthesis. We would expect the stomata to be open during the time that light intensity is sufficient to carry on photosynthesis, and we find that this is the case. They are commonly closed at night. Under these conditions carbon dioxide is permitted to enter freely when its entrance is advantageous to photosynthesis. It seems impossible to escape the conclusion that the regulatory features of the stomata, if we are justified in using that expression, are associated with photosynthesis and not with transpiration. Certainly the stomata are open when the external conditions are best for water escape and closed when the conditions are least favorable for water escape. Beyond a doubt their movement is influenced more by light than by moisture conditions. It has been well said that stomata do not open to promote photosynthesis and do not close to conserve water.

This raises the question whether the escape of so much water is advantageous or disadvantageous. Some workers have believed that the passage of so much water through a plant has an advantageous effect on the salt supply. On the other hand trees in tropical forests, where transpiration is less, not only show no shortage of salts but are most luxuriant in their growth. It has been suggested that the regulation of temperature is a function of transpiration. We know that evaporation does reduce temperature and it is not impossible that this feature may be a real advantage. Seifriz, in a recent book, says, "There are but two possible deductions: either the true function of excessive transpiration has not yet been learned or it is an example of the inefficiency of nature." He points out that moist tissue surfaces make possible the absorption of carbon dioxide and the elimination of oxygen—but moist surfaces also furnish the condition for transpiration. His point of view, that the maintenance of one necessary condition may force wastefulness in another respect, seems reasonable.

Although we find it difficult to answer the question whether transpiration is useful or harmful to a plant, there are certain features about the water relations and water losses of plants about which there is no doubt. We know that plants must have a sufficient amount of water. Even slight deficiencies in the water requirement of crop plants will result in reduced yields. It has been asserted that in Ohio a variation of two inches of rainfall during July may be responsible for a variation in the value of the corn crop to the extent of $13,000,000. In fruit trees not only the quantity but the quality of the fruit is affected by drought. The available water supply is one of the important factors influencing the distribution of plants over the land surfaces of the earth. Temperature is also an important factor, but its effect is due to some extent to its influence on the relative amount of water. Even resistance to freezing (hardiness) is related to the condition of the water present in the tissue. The winter killing of unprotected crops, such as wheat, is due mostly to excessive transpiration rather than to the low temperature. Trees and shrubs which shed their leaves at the beginning of a cool or dry period are for the most part perfectly protected because the water loss by transpiration has been so enormously reduced.

Guttation

Our account would not be complete without a reference to *guttation*. We have emphasized that transpiration is the giving off of water in the form of vapor. Guttation is the secretion of water in liquid form. The secretion is not pure water but contains salts and other substances. Such exudation may be seen at the tips of grass leaves and around the margins

of the leaves of such plants as cabbage and nasturtium. Doubtless much of the wetness of the grass in lawns at night is due to guttation and not to dew. A fine demonstration may be arranged with seedling wheat plants grown in a pot (Fig. 5–10). If the soil is watered and the pot covered with a bell jar and placed in a dark cool place the droplets of water will be conspicuous. This suggests that guttation is greatest when the conditions for transpiration are poorest. Guttation seems to be a process of maintaining water movement when transpiration is ineffective. The water is exuded through special epidermal structures known as *hydathodes.*

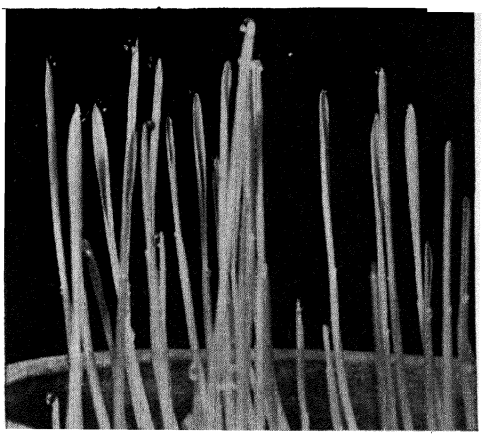


FIG. 5–10. Guttation in wheat seedlings grown in moist soil and covered with a bell jar. Drops of water appear at the tips of the leaves.

Water Storage

In connection with our consideration of water loss it is appropriate to make brief reference to some provisions for regulating the water supply through storage. Some plants actually catch and hold water in reservoirs or pockets formed by the leaves and later absorb it through hairs on the leaf surfaces. This is true of Spanish moss (*Tillandsia*) and other tropical bromeliads. They belong to a class of plants known as epiphytes, which grow upon trees without being parasites. Many epiphytic orchids absorb and hold rain water in a swollen sheath surrounding their aerial roots. In other epiphytic orchids, aroids, and ferns, humus material collects in receptacles formed by leaves or roots and holds water like a sponge until absorbed by the penetrating roots. In some plants popularly known as *succulents* there are specially developed tissues for the storage of water. The presence of mucilaginous compounds in these tissues is a factor in their water-retaining capacity. The leaves may be succulent, as in the house leek, or the stems may be the seat of storage tissues, as in the cacti. Sometimes the amount of water accumulating may be very great. It has been estimated that a specimen of giant cactus may contain as much as 30 tons of water (Fig. 5–11). The water in living storage tissues may be a part of the protoplasm, a part of the sap, or a part of the jelly-like compounds of the cell contents.

FIG. 5–11. Giant cactus (*Carnegica gigantea*) in which great quantities of water are stored in the thick stems. (Photograph by C. J. Chamberlain, courtesy J. G. Brown.)

THE MINERAL REQUIREMENTS

We know that certain mineral salts are necessary for the life of plants. This matter has been investigated in two ways. Plants have been chemically analyzed to determine what elements they contain. A more illuminative method of research has been through water cultures. Many plants will grow if their roots are immersed in water solutions. This fact has been known by plant physiologists for a long time and they have studied the

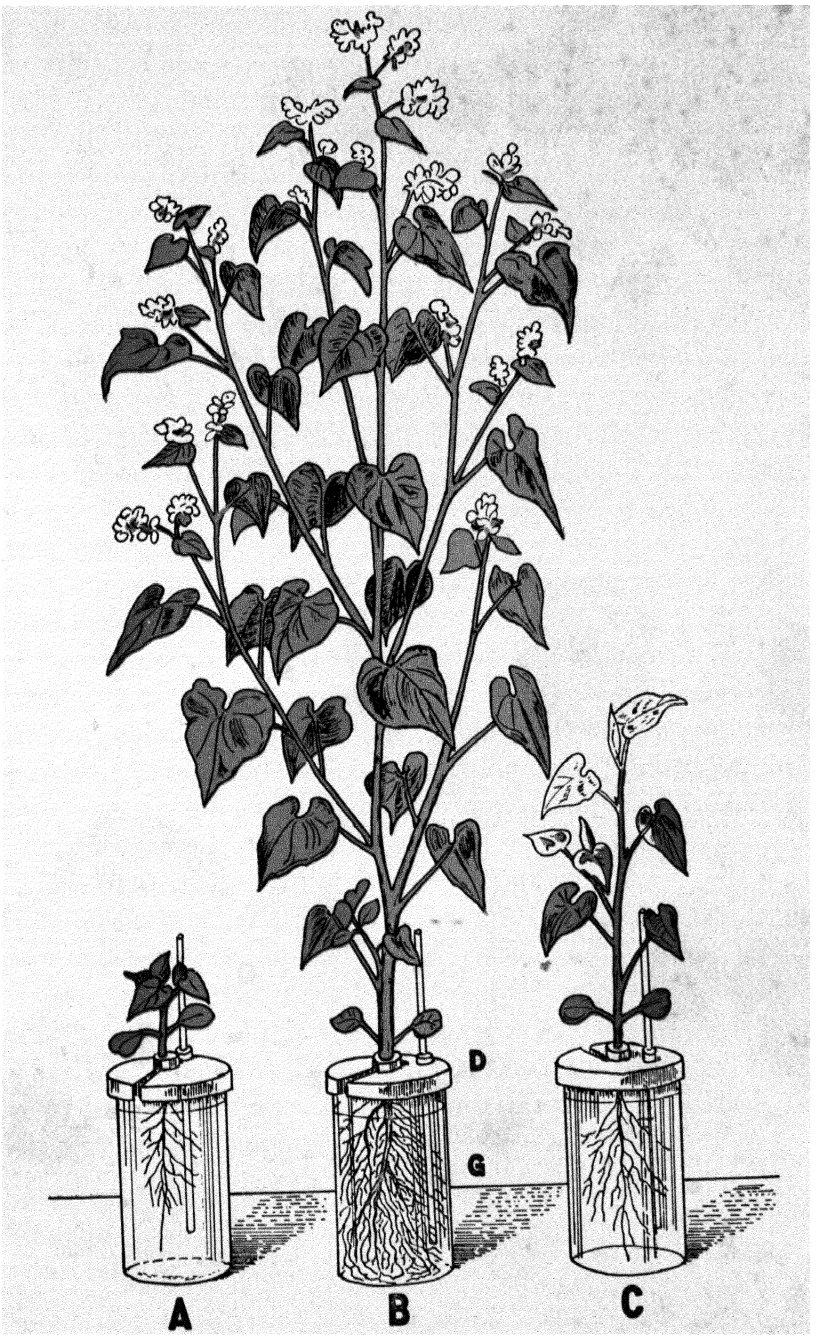


FIG. 5-12. Water cultures of Buckwheat; *A*, without potassium; *B*, in normal nutrient solution; *C*, without iron. The glass jars (*G*) contain the nutrient solution. The plants are fixed in the median opening of the porcelain lid (*D*) by means of a halved cork which was previously soaked in paraffin. (After Pfeffer.)

salt requirements of plants in this manner. In recent years certain workers have attempted to develop the water culture method to make it practicable commercially. Its use has been confined chiefly to greenhouses or to regions with a mild outdoor climate. Some success has been attained with such crops as tomatoes and potatoes.

The term *hydroponics* has been proposed for the art of growing crops by a water culture method. No soil is used, but gravel, sand, excelsior, straw, or peat moss may be provided as an anchorage for the roots. The novelty of a soilless method of growing plants has aroused considerable popular interest. Accounts appearing in the newspapers and magazines have caused many people to seek further information about a matter which appears to have such important possibilities. It seems unlikely that many crops can be produced economically in this way. The results thus far are promising for certain crops the marketable products of which are characterized by high water content. The culture of greenhouse flowers by hydroponics may also prove successful.

By growing plants in solutions of known compositions it is possible to determine their salt requirements (Figs. 5–12, 5–13, 5–14). With such a method the effect of the absence of one element can be learned. It is possible also to reach conclusions regarding the best chemical combinations. Nitrogen, sulphur, phosphorus, potassium, calcium, and magnesium are essential. Nitrogen, sulphur, and possibly phosphorus are constituents of proteins and protoplasm; magnesium is a constituent of chlorophyll. Potassium and calcium are primarily regulators of reactions; sulphur and phosphorus may be both regulatory and nutritive.

There are certain other elements which are essential but which are required in only small amounts. They are called minor or trace elements. Iron, copper, manganese, zinc, boron, molybdenum, and possibly also chlorine, sodium, and silicon are in this class. Altogether, forty-four elements [1] have been reported to occur in plants. When plants fail to obtain their needed supply of minerals, they do not thrive and may develop characteristic disease symptoms.

[1] These elements are as follows:

Aluminum	Chromium	Lithium	Potassium	Sulphur
Arsenic	Cobalt	Magnesium	Radium	Thallium
Beryllium	Copper	Manganese	Rubidium	Thorium
Borium	Fluorine	Mercury	Scandium	Tin
Boron	Gold	Molybdenum	Selenium	Titanium
Bromine	Hydrogen	Nickel	Silicon	Uranium
Calcium	Iodine	Nitrogen	Silver	Vanadium
Carbon	Iron	Oxygen	Sodium	Zinc
Chlorine	Lead	Phosphorus	Strontium	

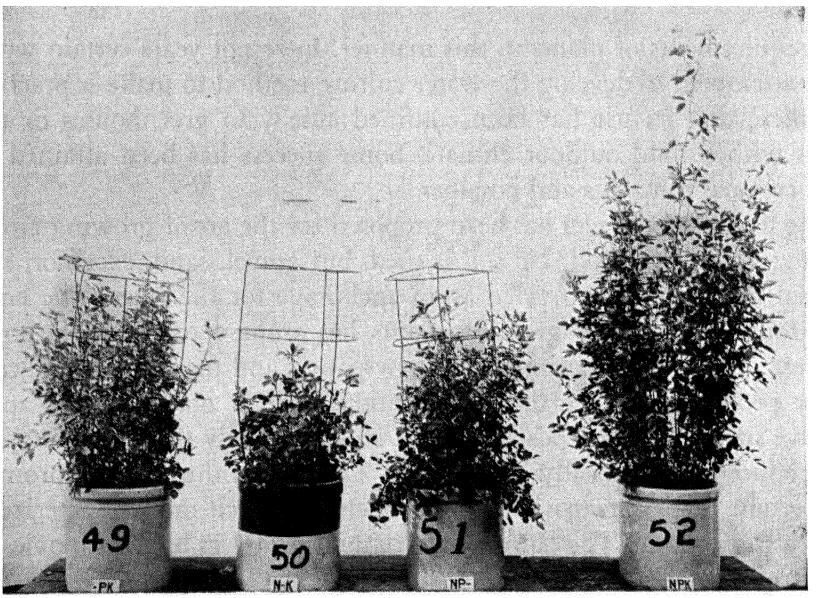


FIG. 5–13. Variations in growth because of the addition of minerals to the soil. The plant is sweet clover; the soil was the same for all jars. There was a notable response to the addition of phosphorus and potassium (49) and a still greater response to phosphorus, nitrogen, and potassium (52). (Photograph, courtesy E. E. DeTurk, from *Hunger Signs in Crops.*)

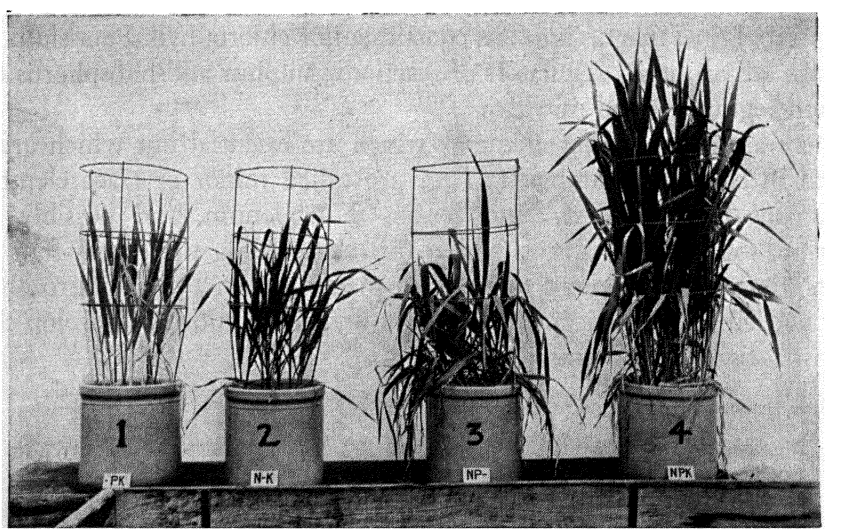


FIG. 5–14. Response of barley to the mineral elements, nitrogen, phosphorus, and potassium. Jar 4 received all three, the plants being healthy and vigorous; Jar 1 shows lack of nitrogen; Jar 2 lack of phosphorus; Jar 3 lack of potassium, plants having weak stems. (Photograph, courtesy George N. Hoffer, from *Hunger Signs in Crops.*)

The Entrance and Movement of Minerals

The mineral elements must enter the roots as salts dissolved in soil water. One of the physical processes involved in the absorption of minerals is diffusion, but many other complicated factors are involved. Diffusion is a physical process by which the molecules of a substance disperse. They may intermingle with those of another substance. One gas will diffuse into another. If a soluble substance is put into a solvent it will diffuse throughout the solvent. If we drop a crystal of some colored salt, such as copper sulphate, into a glass of water we can observe the diffusion by the color. The colored region, at first confined to the area about the crystal, continues to enlarge until finally the whole liquid becomes uniformly colored. The particles of the salt have moved from the place of their higher concentration to places of their lower concentration. In the end, the result is equal concentration throughout the whole solvent. The dispersal of material is brought about by molecular movement.

A crystal of a salt is a solid substance. Its molecules are held together by some force of mutual attraction. When a crystal is dropped into a liquid, such as water, the tendency of the molecules to hold together is reversed and replaced by a tendency to separate or spread as far apart as they can. The molecules may be separated into ultimate particles known as ions. The molecules and ions of a dissolved substance in a liquid are in constant motion and their mutually repellent movements cause them to diffuse from places of their greater to places of their lesser concentration. Certain types of membranes, when encountered, offer little or no resistance to the passage of substances dissolved in the water. However, the outer surface of the protoplasm, or plasma membrane, inhibits the free passage of some dissolved substances and therefore possesses to a greater or lesser extent the property of selective permeability. An important fact to keep in mind is that the permeability of the protoplasmic membrane is not constant but fluctuates with varying external and internal conditions. The root hair protoplasmic membranes in general permit the passage of many inorganic salts which are dissolved in the soil water. These salts move in the water by molecular diffusion. We must guard against thinking of their entrance by a movement of the water. The excess movement of solutes may be in one direction, while the excess movement of water is in the opposite direction. Temperature influences diffusion because it affects the rate of molecular activity.

Diffusion, however, is not the only process involved in the absorption of minerals. The life activity of the root hair cells—that is, their physio-

logical activity—probably plays an active part in absorption. If diffusion alone were involved, we should expect to find absorption of a particular mineral by a root hair only when its concentration was greater in the soil solution, since otherwise more of the mineral would be moving outward than inward. But we have reason to believe that a mineral can be absorbed even when there is more of it within the vacuole of the root hair than in the soil solution. The absorption of minerals is also affected by the acidity of the soil, by the presence of organic matter in the soil, by the general composition of the soil, and by other factors. This indicates that absorption of minerals is a physiological rather than a purely physical process.

Once the dissolved mineral substances reach the xylem they are conducted from the root to the leaves by the streaming, or mass movement of the water, in the dead tracheary elements. Their entrance into the living cells of the leaves involves the same physiological and physical processes as did their entrance into the root hairs.

THE CARBON AND NITROGEN SUPPLIES

In the synthesis of their foods green plants are constantly forming organic compounds in which carbon and nitrogen are bound. The available supply is not exhausted because there are means for releasing carbon and nitrogen from plant compounds and making them available for new syntheses. The courses followed by carbon and nitrogen are called cycles.

The Carbon Cycle

The utilization of the carbon dioxide gas of the air and water in the synthesis of carbohydrates by photosynthesis has been described in an earlier chapter. The entrance of carbon dioxide through the stomata and its movement through the intercellular spaces by diffusion also have been explained. When carbon dioxide is used in a cell in photosynthesis, its concentration within that cell is reduced; and, according to the laws of diffusion, more molecules will move into the cell than out of it, until the concentration is equalized. Through respiration, the carbon which is built into compounds by photosynthesis is returned to the atmosphere—the respiration of the plants themselves, respiration of animals which consume them, and respiration of the saprophytes which bring about decay after their death. Through combustion of plant and animal materials carbon dioxide is also released into the atmosphere. A diagrammatic representation of the circulation of carbon in nature is shown in Fig. 5–15.

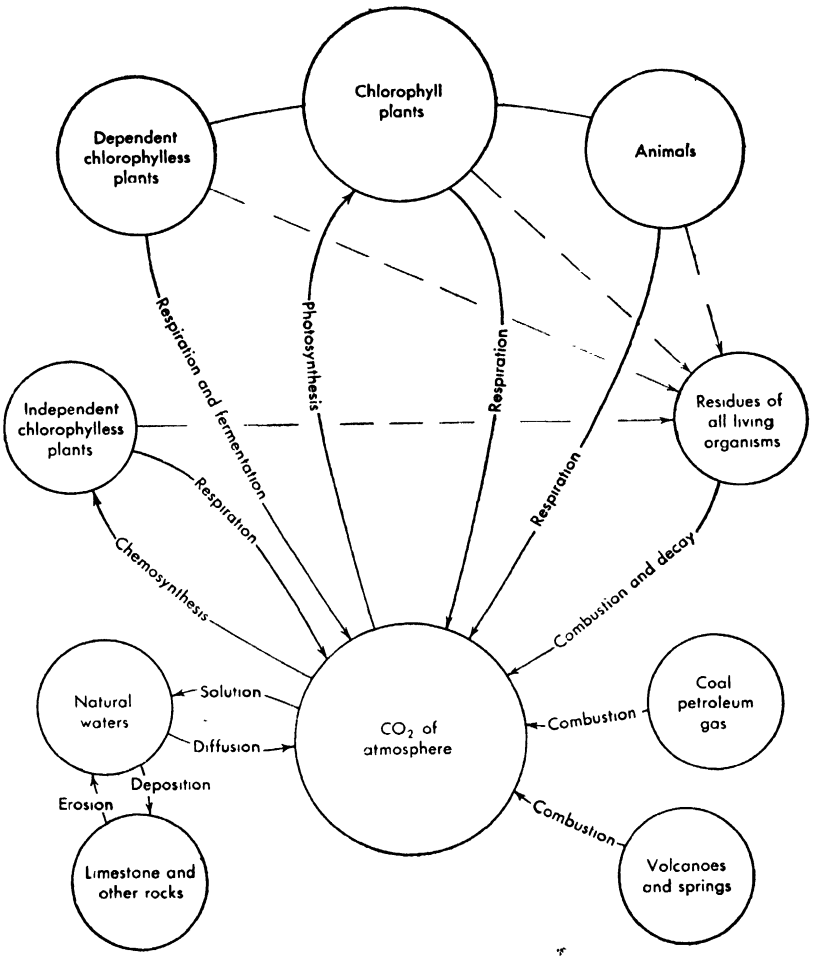


FIG. 5-15. The circulation of carbon dioxide in nature.

The Nitrogen Cycle

Nitrogen is essential for the synthesis of proteins and related compounds which are the principal constituents of protoplasm. Green plants obtain their nitrogen from nitrogenous compounds in the soil. The majority of plants absorb most of their nitrogen in the form of nitrates, although nitrites, ammonium salts, and organic nitrogen compounds may also be utilized. Nitrogen does not occur in the rocks from which soils are formed, and its presence in the soil is indicative of other sources. With the death of plants, or through the waste and death of animals, nitrogenous compounds reach the soil as organic residues. Saprophytic organisms, bacteria and fungi, decompose organic matter in the soil and in a series of reactions con-

vert it into ammonia, nitrites, and nitrates. Other bacteria add to the soil nitrogen supply by combining free nitrogen of the atmosphere with other elements to form organic nitrogenous compounds by a process known as nitrogen fixation. Fixation may be brought about by saprophytes which

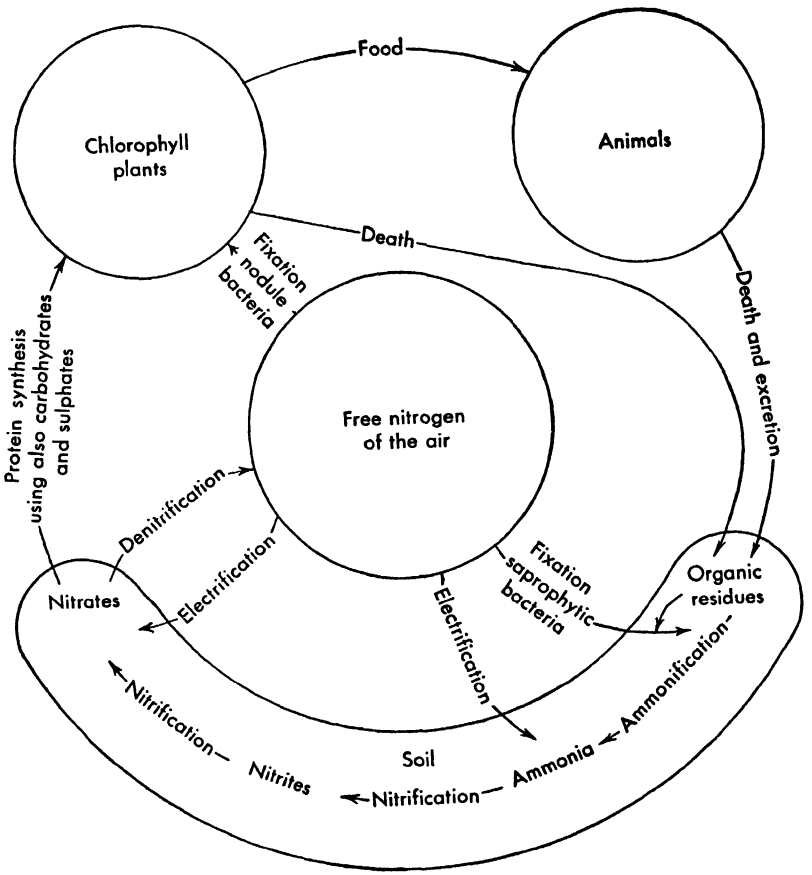


FIG. 5–16. The nitrogen cycle.

utilize dead organic matter, or by bacteria which live in nodules on the roots of members of the legume (pea) family. Indirectly, through the action of the nodule bacteria, atmospheric nitrogen is fixed and thus brought into the organic nitrogen cycle by legumes—clovers, alfalfa, peas, beans, vetches, and others. Some atmospheric nitrogen reaches the soil through rain water during electrical storms. Man has developed an artificial method of fixing atmospheric nitrogen by electrification. This has become of importance in the manufacture of commercial fertilizer. As the quantity of

nitrates in most soils is small, all means of increasing the supply are important. The complete relation of nitrogen to plant life involves a series of reactions some of which take place in the cells of soil organisms and some in the cells of the higher plants. A diagrammatic summary of the interrelations of the various events is presented in Fig. 5–16.

CHAPTER 6

REACTION OF PLANTS TO THEIR ENVIRONMENT

(*Irritability, Adaptedness*)

We have considered how plants manufacture food, how they obtain water and raw materials, how they derive energy, and how they build up their bodies. These are chemical and physical processes by virtue of which the life of an individual plant is maintained. These metabolic processes are primarily internal in nature but they are all more or less dependent upon external conditions. In order that the internal processes may proceed advantageously the vegetative parts must be favorably adjusted to their immediate surroundings. It must be evident that the external conditions and materials, such as heat, light, water, and salts, are not always uniformly distributed in the environment. If the separate leaves, stems, and roots could react so that they might adjust themselves to the most favorable positions, the advantage to the plant would be obvious. Fortunately for the plant, just such a capacity of reacting to external stimuli is inherent in it; it is called *irritability*. Plants not only possess such a property but manifest it to a high degree of efficiency. Our account would be incomplete indeed if we did not give consideration to the interesting and important phenomena which are included under this topic.

IRRITABILITY

Much of what is said here can be found in some presentations under the heading of *movements*. There is a reason why we may discuss the same things under the heading of *irritability* or of *movements*. Living things in adjusting themselves to the environment, i.e., in reacting to a stimulus, frequently give evidence of the response by movements. These may involve the organism as a whole or only parts of it. Of course, there are types of reactions other than movement which are not visible. We have chosen to direct attention to some of the stimuli which are responsible for causing plants to assume the positions they do, to point out how they react when

the conditions change, and to consider the ways in which the movements come about.

Response to Gravity

Ordinarily roots grow downward and shoots grow upward. Obviously this is advantageous because the roots are then in the soil where they can obtain water, and the shoots with their leaves are in the air where they are in the light. But, as we shall see, it cannot be the water which effects the downward growth of the roots, or the light which effects the upward growth of the green shoots.

As regards position we must be more specific in our statements. It is true that roots grow downward, but only the main or tap root assumes a vertical position. The branch roots assume a fairly definite angle with respect to the up-and-down axis of the main root. The same is true of stems. The main stem is vertical, the branches come off at an angle. The main axis of plants growing on a hillside is not at right angles to the surface of the ground but is vertical or upright. The branch roots and stems also show the usual angular relation to the main axis. In the search for an explanation of this situation even a brief consideration will suggest that the one force in nature which acts in up-and-down lines is gravity. We would seem justified in suspecting that gravitational force is the stimulus which is responsible for the positions taken by the roots and shoots. Much evidence can be had to confirm this hypothesis.

When a seed germinates, the young root emerges and turns downward and the stem turns upward regardless of the position of the seed. Even if the embryo in the seed is upside down the result is the same. The general term for such a response to a stimulus is *tropism*. The specific response to *gravity* is known as *geotropism*. Since the roots grow toward gravity they are said to show *positive geotropism*. Stems grow away from gravity and hence show *negative geotropism*. Lateral branches of either roots or stems growing at oblique angles or horizontally are said to show *diageotropism;* later branches growing in various directions and more or less disregarding gravity may be described as showing *plagiotropism*.

If we take a rapidly growing young seedling of some large seed, such as Windsor or scarlet runner beans, and place the tap root in a horizontal position, the root tip will turn downward. After a few hours the curvature will be complete and the tip will be pointing directly downward (Figs. 6–1, 6–2). Such an experiment may be set up by using a small box with a glass side. The box can be filled with damp sphagnum moss and the seedling can be placed close to the glass so that its position is readily observ-

able. Variations can be tried by arranging the straight tap root at various angles other than vertical. It is possible to record the original position by marks made on the outside of the glass with a wax pencil or with India ink and a fine brush. It will be observed that regardless of the original position the tip will be pointing downward after a few hours. Careful observation will reveal that the curvature is near the tip and that as the curvature has been brought about the root has been elongating. The elongation can be detected readily by the distance of the tip beyond the mark on the glass. But there is a still better way to check on the region of the curvature and its relation to the elongation. Small black dots of India ink can be placed equidistant (1 mm. is a good distance) on the white root before it is placed in position (Fig. 6–3). It will be found that the dots separate only in the region just back of the tip. It is in this region of elongation that the curvature has taken place.

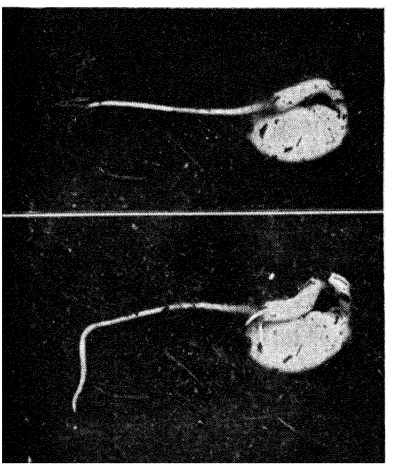


FIG. 6–1. Geotropism in young roots of bean seedlings; above, root placed horizontally; below, showing growth and curvature after a few hours.

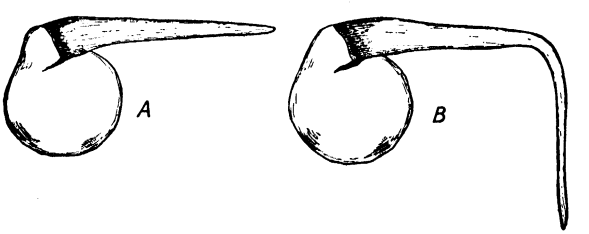


FIG. 6–2. Geotropism in roots of peas. *A*, root placed horizontally; *B*, the same root 24 hours later. (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

These observations should lead to the conclusion that curvature is correlated with growth. But we must inquire more particularly into the mechanism of the bending. We have concluded that growth is the motive force. But if the growth were of a normal or usual nature the tip would be pushed forward in a direct line with the axis of the root. But the growth is not of the usual sort when the root is placed in any position other than a vertical

one. There is then a differential growth, i.e., a more rapid growth on one side than the other. Since the root is stimulated to faster growth on the upper side than on the under side it is swung around so that its tip is directed downward.

In this connection there is another experiment which should be tried. If a straight tap root is placed in a horizontal position in such a way that it can be rotated slowly (this can be done with an instrument known as a clinostat which rotates by clockwork) there is no curvature; there is growth in a horizontal line. The revolving prevents the stimulus from acting on the root in a one-sided manner. If there is one revolution in about fifteen minutes all sides are equally exposed to the stimulus of gravity and we may say that the stimulus of gravity is neutralized so far as effecting a curvature is concerned.

It is possible to replace gravity with another force. We may continue to use our young seedlings for this experiment. By placing them on a

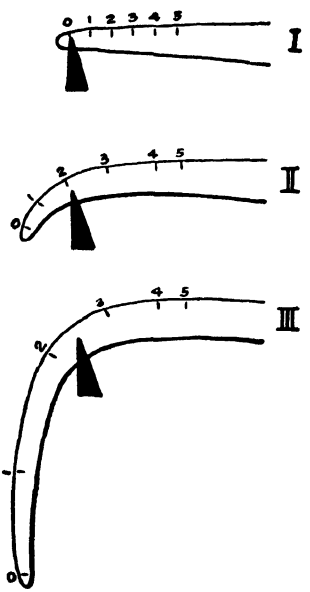


FIG. 6–3. Diagrams showing that geotropic curvature is in the region of elongation; further particulars given in the text. (After Sachs.)

rapidly rotating vertical disc, or wheel, it is found that the roots turn away from the center of the disc, and the shoots toward the center. In this arrangement the response is to centrifugal force and not to gravity. If the disc is revolving in a horizontal plane the force of gravity still operates and the result is an intermediate adjustment effected by the influence of centrifugal force and gravity combined. The actual position of plant parts is often the resultant of the effects of one or more stimuli.

Thus far we have centered our attention on the positive geotropism of roots. By choosing rapidly growing young stems negative geotropism may be observed and studied. For such studies potted plants may be used to advantage, and a comparison may be made with practically all the facts brought out in the root experiments. The stems turn upward, not in their lower nodes where elongation is complete but in the upper nodes where growth is still going on (Fig. 6–4). There is also a response on the part of the leaves brought about by bending of the petioles. If the plant is turned so that the main stem is in a horizontal position and is left in that posi-

FIG. 6–4. Negative geotropism in stem of coleus which was placed in a horizontal position. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

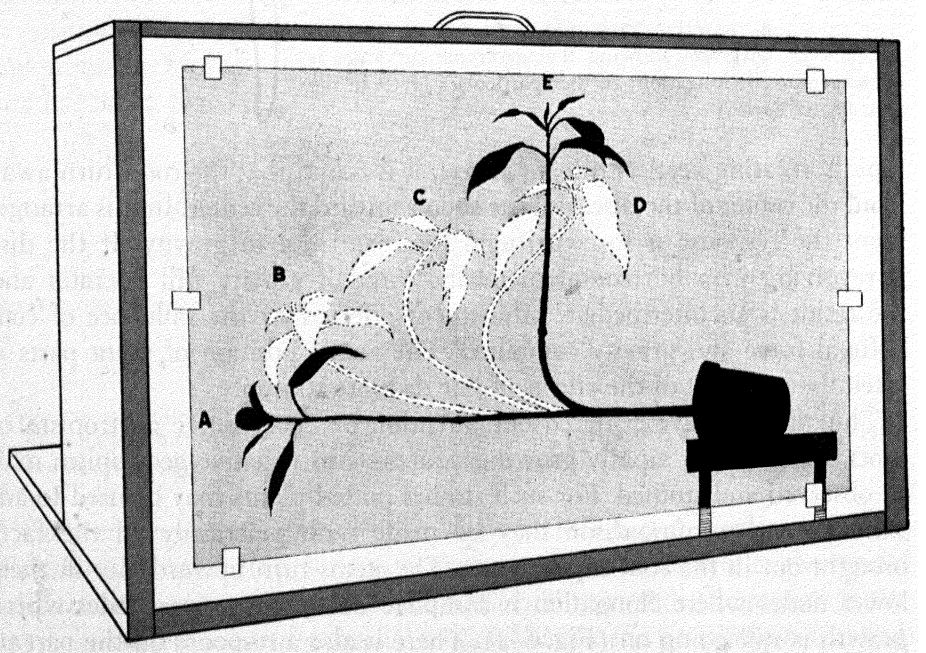


FIG. 6–5. Phases (*B–E*) of geotropic curvature in a shoot of *Impatiens* from horizontal position (*A*), shown by shadowgraph method described in text.

tion for several hours the curvature becomes complete and is evident at a glance. The change of position may be observed as it is going on, by arranging the plant so that it casts a shadow on a paper in such a manner that tracings of the shadow can be made (Fig. 6–5). With the aid of silhouettes

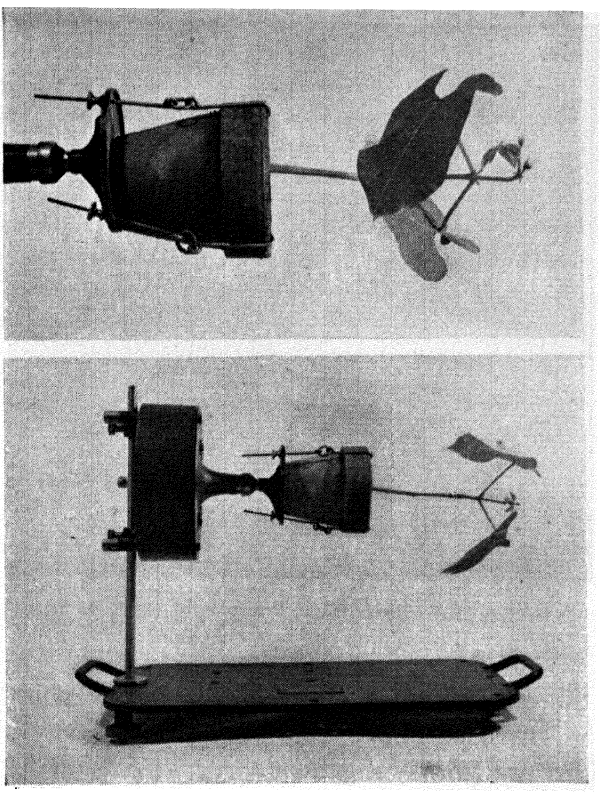


FIG. 6–6. A young bean plant in a horizontal position on a clinostat. There is no curvature below because of the rotation; above there is a curvature which took place after the rotation was discontinued.

it is possible to watch the gradual progress and to record how much takes place in a given interval. The rapidity of the reaction is generally a matter of surprise. If a shoot is placed in a horizontal position on a clinostat (Fig. 6–6) there is no curvature as long as the rotation is continued, but it takes place quickly if the rotation is stopped.

It is possible that the reader may wonder why we have not referred to the possibility that light is a factor in the upward growth of the shoot. Light does produce effects upon the growth of green shoots and hence must be discussed. But if we wish evidence that it is gravity and not light which

causes shoots to assume their upright position, we may obtain it by germinating seeds in the dark. We find that the shoots grow upward in the dark just as they do in the light (Fig. 6–7).

We have used the expression that the force of gravity is responsible for roots growing downward. But it must be understood that gravity does not

FIG. 6–7. Bean seedlings grow upright whether in light (left) or in the dark (right). (Photograph by L. O. Overholts.)

actually pull the roots downward. Gravity is also responsible for stems growing upward. Perhaps no one would think that gravity could push the stems upward because gravity is generally regarded as an attracting rather than a repelling force. We must think of gravity merely as a *stimulus.* The effect, or response, is produced by *growth.*

When a horizontally placed root or stem responds with a curvature it is believed to be due to an unequal distribution of auxin. Auxin moves downward and becomes more concentrated on the under side. Since higher concentration promotes growth in stems the increased growth on the lower side causes the stem to bend upward. Higher concentration apparently re-

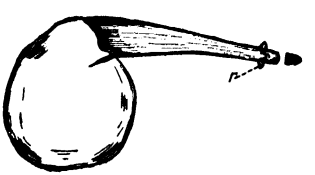


FIG. 6–8. The growing tip of a root has been removed; note failure to respond to gravity and the development of secondary roots (*r*). (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

tards root growth and the greater growth on the upper side causes the root to bend downward. If the tip of a root is cut off there is no geotropic response (Fig. 6–8).

Our discussion has been confined thus far to the reactions of the higher plants to gravity. The simple vegetative parts of some of the lower plants would not seem to be subject to gravity, but if they grow flat on the ground and have distinct upper and lower sides (dorsiventral form) this is in itself a form of geotropic orientation. The fruiting branches of mosses and liverworts exhibit negative geotropism. The fructifications of many fungi show distinct geotropic responses. Ordinary mushrooms and toadstools are negatively geotropic, but many of the bracket fungi growing out of the sides of trees and logs form a definite angle with the downward direction of gravity and hence are diageotropic.

Response to Light

Much space has been devoted to geotropism. Gravity is the first stimulus to which a young plant is subjected and throughout the life of the plant it remains a predominant factor, but its influence is often modified by light. The growth response to light was formerly called *heliotropism,* but later workers have preferred the term *phototropism.*

Without doubt everyone is familiar with the fact that house plants placed near windows grow toward the light. The expression that plants "are drawn to the light" is sometimes heard. In these cases we are speaking of the stems and leaves. The stems and also the petioles show curvature, so that the leaf blades are more or less at right angles to the light from the window. It is interesting to compare a plant which has been grown in a greenhouse, where the light comes equally from all sides, with one grown in a window (Fig. 6–9). Even better than a window-grown plant is one grown in a dark chamber with only a small opening on one side.

On the greenhouse plant the main stem is upright; the branches, if any, radiate at fixed angles; and the leaves assume the positions determined by their origin from the stems. In this specimen it is evident that the type of plant and gravity have determined its form. In the specimen in one-sided illumination both gravity and light are influential and the final effect is a resultant of the reactions to these influences.

In the same way that we neutralized the effect of gravity by rotation we may neutralize the effect of light. By putting our plant on the clinostat all sides will be equally exposed to the light stimulus and no curvature results.

Study of a plant which has reacted to a one-sided source of light will

reveal that the curvature of the stem is in the upper internodes. It is certain that the response to light is brought about by growth and takes place only in the growing parts. In the older parts where elongation is complete there is no change of position. The positive phototropism of stems has usu-

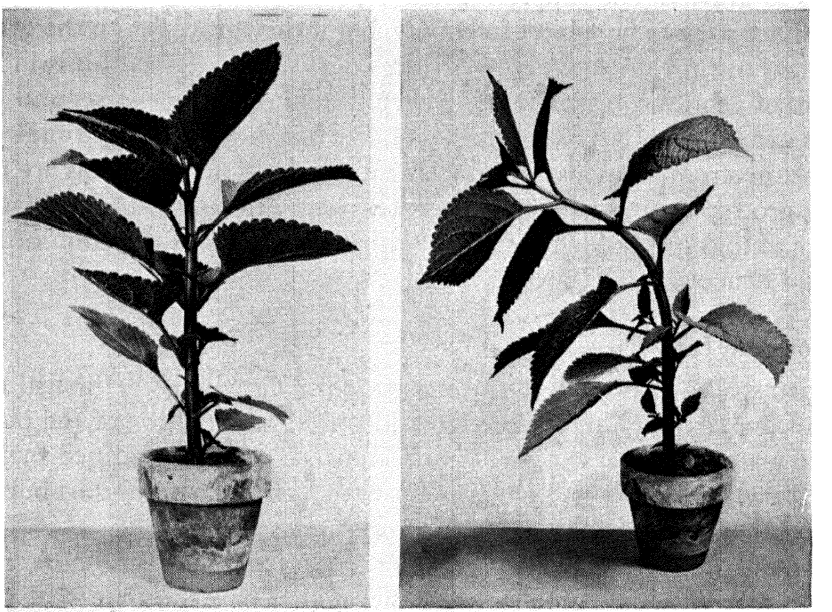


FIG. 6–9. A coleus plant which was kept in a uniformly lighted greenhouse (left) and then for several days in a chamber lighted only from one side.

ally been explained by the fact that light retards growth. Accordingly, the side of the stem toward the light would grow more slowly and the stem would curve toward the source of light because of the more rapid growth on the opposite side. It does not seem possible that such a simple hypothesis is sufficient to account for all the effects of phototropism. Mustard seedlings grown in water cultures and placed in a dark chamber which admits a beam of light from one side show a positive response of the shoot and a negative response of the root to the light stimulus. In the root the tissues grow faster on the lighted side, just reversing the situation in the stem. In both stems and roots the auxin moves away from the lighted side. Since this condition retards growth on that side in the stem and accelerates it in the root, the effects are opposite.

Some headway has been made in determining the region of perception of the light stimulus. It appears to be near the tips of parts, even though the region responding is farther back. For such studies Italian millet seed-

lings have been grown in the dark until they are about one inch high. Upon being exposed to one-sided illumination they bend at a rather sharp angle about 2/5 of an inch from the tip. This locates definitely the region of response. But if the tips are covered with tiny caps of tinfoil to a distance of 1/5 of an inch there is no response. From this it is concluded that the perceptive region is in the tip since there is no response when it is cov-

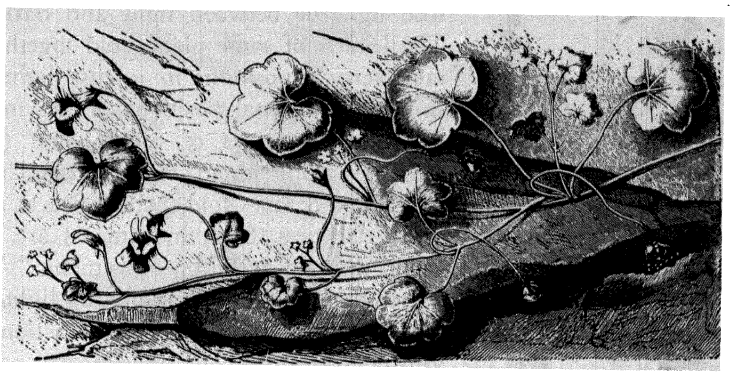


FIG. 6–10. Flower stalks of Kenilworth ivy, which bring the seed capsules into position for showing positive phototropism at first and a negative reaction later, dropping their seeds into clefts in the rocks. (After Kerner.)

ered even though the responding region is left exposed. There seems to be no doubt that a stimulus may be perceived in one location and the adjustment take place at another.

The phototropic sensitivity of organs may vary according to certain external influences or according to their internal stages of growth and development. The intensity of the light as well as the quality may be responsible for variations. Some plants in weak light react positively but will react negatively if the intensity of the light is excessive. Traces of coal gas as an impurity in the air affect phototropic responses. The flower stalks of Kenilworth ivy (*Linaria cymbalaria*) are at first positively phototropic, extending into the light and away from the rocks or walls upon which the plant is growing. After pollination they become negatively phototropic, elongating and turning backward. By this reversal the seeds are likely to be deposited in crevices or other favorable locations (Fig. 6–10).

It is generally accepted as a fact that many green plants do not need and cannot use all the energy of light that falls upon them in the summer. In some plants the position of the leaves becomes changed from a plane transverse to the more intense rays of midday to a plane more nearly parallel to these rays. There are two plants, one a wild lettuce (*Lactuca scari-*

ola) and the other a rosinweed (*Silphium laciniatum*), whose leaves in such an adjustment take more or less north and south directions and are commonly known as "compass plants" (Fig. 6–11). In contrast to such plants as these whose leaves show a permanent adjustment to the light rays are plants which exhibit temporary adjustments either between intense and diffuse light or between light and darkness. The leaflets of some plants fold together or take vertical positions in intense light and shift to horizontal positions in less intense light. Many plants of the legume (Pea) family—among them clover, peas, beans, senna, and acacia—fold their leaflets at night or in darkness. Such movements are commonly known as "sleep movements." They are responses to the stimulus of light, but the movement is not a growth reaction and so is not a tropism. The movement is accomplished by a change in the turgor pressure of the cells at the base of a leaflet and at the base of the petiole. They assume the usual positions in the light. In the so-called sensitive plant (*Mimosa pudica*) mechanical

FIG. 6–11. Arrangement of leaves in a "compass plant," the one on the right showing the north and south adjustment. (After Kerner.)

shock, as well as darkness, will bring about a folding of the leaflets and drooping of the leaves (Fig. 6–12). Some flowers close at night. It seems probable that temperature as well as light is influential. The opening and closing are accomplished by osmotic mechanisms and not by growth.

In some plants where many leaves grow close together there is an obvious shifting of positions so that the leaf blades tend not to shade one another. Such an arrangement is accomplished by the bending and elongating of the petioles and may be observed on many trees. Good examples may be seen in wall climbers such as the various kinds of ivy. Such even placements of leaves have suggested the term *leaf mosaic* (Fig. 6–13).

There are certain responses to light which are included under the term *phototaxis*. Here belong the movements of free cells or of bodies such as chloroplasts within cells. There are some unicellular aquatic plants which

swim about by the aid of whip-like protoplasmic strands called flagella. There are also reproductive bodies such as zoospores of certain algae which are motile. In the dark such free-swimming bodies and cells frequently move about in all directions in an apparently aimless fashion. When illumi-

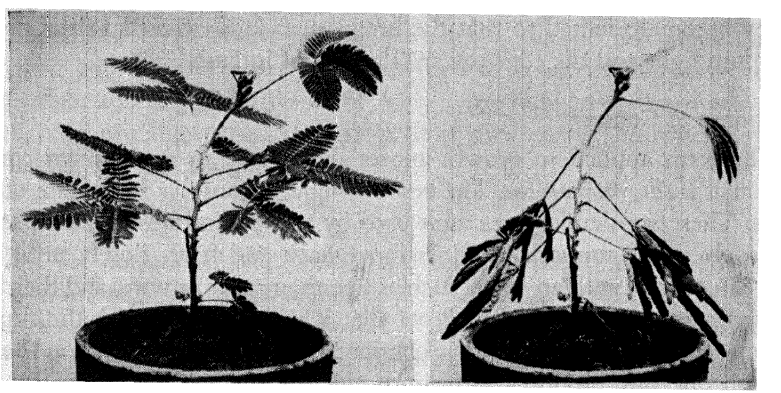


FIG. 6–12. The sensitive plant, *Mimosa pudica.* The folding of the leaflets and the drooping of the leaves as shown on the right may be brought about by mechanical shock or by darkness.

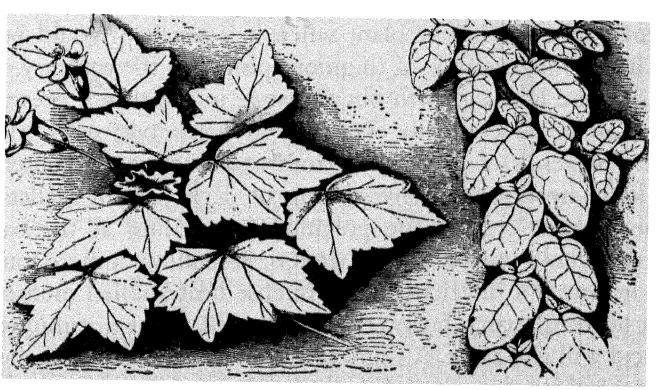


FIG. 6–13. Leaf mosaics, left a begonia, right a fig, both growing on a wall. (After Kerner.)

nated from one side only, a definiteness of direction is evident. They may move either toward the light or away from it. The advantage of zoospores of green algae reacting positively to the light is obvious since in this way they come to rest and establish themselves where the stationary adult will develop in the light. It is said that zoospores never come to rest if kept in

total darkness but keep on swimming continuously until exhausted. It should be added that other factors such as chemical substances and gravity affect free-swimming cells. Within cells chloroplasts are carried along passively by protoplasmic streaming, but they also move independently and arrange themselves within the cell in response to the conditions of light. They become oriented so that the broad surface is exposed to the rays of medium light and the edge toward the rays of intense light.

Response to Contact

The term applied to growth movements made in response to contact or touch is *thigmotropism*. The best example to consider is the case of tendrils. These are slender structures used by many climbing plants to secure themselves to a support. Tendrils move back and forth slowly until they come in contact with an object such as a stem or stake or wire, and then they make several turns around it. Proof that it is the contact with the support which acts as the stimulus can be obtained experimentally. Tapping the tendril on one side produces a turning and its progress can be observed. A quick contact will cause the tendril to bend, but it will straighten in case the contact is not continued. If the contact is maintained, a complete winding about the object results.

Anyone who has seen the prompt folding of the leaflets and drooping of the leaves of the sensitive plant when it is touched would be likely to think of it as a fine example of thigmotropism. On the contrary, the motor mechanism here is not growth but a change in the turgor pressure of certain cells (as we have already explained in connection with "sleep movements"). The result of a stimulus from a contact can be observed, as it travels along, by the successive closing of each pair of leaflets. Finally, when the impulse reaches the pulvinus (a swelling at the base of the petiole), the whole compound leaf droops. Sometimes a mere touch on the terminal leaflets is a sufficient shock. Intense heat applied momentarily by passing a burning match below the leaflets will act as a stimulus. A small drop of acid will also serve. A slight touch on the under side of the pulvinus will cause a sudden drooping of the leaf. After a time recovery ensues. The significance of these reactions is a mystery. They do not seem to be in any sense advantageous adjustments.

There are other reactions of plant parts to contact which do, however, have obvious advantages. Some insectivorous plants move in such a way as to capture insects which alight upon them. In the Venus's-flytrap the two halves of the leaves fold together quickly, thus catching and holding the insect. The contact is achieved by bristles on the upper surface of the leaves. In the sundew there are glandular hairs which secrete sticky drops that

serve to hold the insect. Slowly the leaf margins and hairs bend over the insect until its body is rather well overtopped by them. After the digestible parts of the insect have been absorbed, the glandular hairs unbend and assume their original positions. There is a reasonable question whether the movements of the leaves and hairs are due to a contact stimulus, because it is said that foreign bodies such as particles of dirt do not excite movements. In addition, there are some flowers with stamens that snap vigorously when touched. The result of such a mechanism is the dusting of pollen on the bodies of insect visitors. It is then carried to other flowers and brings about cross-pollination.

Response to Moisture

Roots are commonly very responsive to moisture. The movement in which moisture is the directive influence is known as *hydrotropism*. Under ordinary conditions gravity and moisture would act on roots from the same direction. To study the effects of moisture it is necessary to set up an arrangement so that the directions of the two stimuli are separated. There

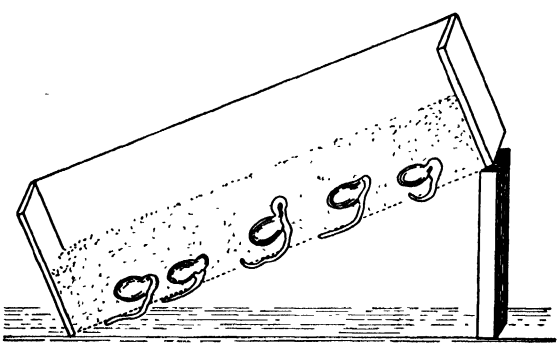


FIG. 6–14. Arrangement for testing whether roots grow in the direction of moisture. (After Osterhout.)

are various ways in which this can be done. We may take a flat box with a wire mesh bottom, fill it with damp sphagnum, and set it at an angle of about 45 degrees (Fig. 6–14). Seeds germinating in the sphagnum will push their roots through the wire mesh. If the roots responded to gravity they would grow downward; but the influence of moisture is stronger, as is evidenced by their growth along the surface of the wet moss. The advantage of the response of roots to moisture is obvious.

Response to Chemical Substances

A growth response directed by a chemical substance is known as *chemotropism*. Roots sometimes show positive chemotropism through growth

toward a supply of mineral salts. Sometimes they grow away from chemical substances, thus exhibiting negative chemotropism. The growth of roots toward places of favorable air conditions in the soil is a phase of chemotropism sometimes called aerotropism. Water plants with floating leaves will elongate the petioles if necessary for the leaves to come to the surface. This is another example of aerotropism. The growth of pollen tubes from the stigma to the egg through the pistil of the flower is believed to be a case of chemotropism.

The movement of free-swimming cells such as the male reproductive cells (sperms) is without doubt directed to the female cells (eggs) by chemical substances. A response of this type by a moving cell is called *chemotaxis*. Under certain conditions it may be negative.

ADAPTEDNESS

As we have described the structures of plants and their organs the thought must have occurred to the reader more than once that many of these structures are peculiarly fitted for the functions they serve. Many of them seem remarkably well suited to carry on their work in the environment and under the conditions in which they exist. The fitness of plants to their surroundings, i.e., the quality of being adapted, is here called *adaptedness*. A further consideration of the suitability of some plant structures to their uses and their environment is worth while. It will be evident that structures and behavior are in many instances advantageous.

Different theories have been advanced to account "for the origin of the obvious harmony between plants and their surroundings." In these days it is no longer believed that plants were created with the structures and behavior that they now have. It is generally agreed that their characters have been evolved—are the result of evolution. The attainment of characters which place a species in a more advantageous relation to its environment is known as *adaptation*. Adaptedness is being used in the sense of a state or quality; adaptation has long been used in the sense of a process of development.

Fitness of Plants for Food Synthesis

One of the foremost activities going on inside the bodies of green plants is concerned with the synthesis of foods. There are four essentials for these processes—light, carbon dioxide, water, and certain salts.

Of these four essentials two, light and carbon dioxide, are in the atmosphere; and two, water and salts, are in the soil. The higher plant body

has two primary parts: one, a green shoot, suited to the atmosphere, and the other, a colorless root, suited to the soil. The green shoot catches the light and admits the gas, carbon dioxide, from the atmosphere. The colorless root provides for the entrance of water and of the salts dissolved in it. The shoot and root are each well fitted for its share of the operations. We have but to recall the usual flat leaf in order to appreciate that in this way a large surface is exposed to the light. Since light cannot penetrate far into the tissues the spreading of the green coloring matter, chlorophyll, through the cells of a thin flat structure like a leaf blade insures a maximum exposure of the chlorophyll. We have only to refer to the structure of a stoma, and to the number and distribution of the stomata, to recall the way in which this mechanism serves to admit carbon dioxide from the air. We must remember that it is during the time that light energy is transmitted to the chlorophyll that photosynthesis can proceed, and therefore it is at this time that carbon dioxide must be available. We must not forget that light is the agency, even though indirectly, which causes the stomata to open.

Turning to the root, we find the root hair well suited to the entrance of soil water and minerals, and the great number of hairs provides for a large absorbing surface. If we keep in mind the fact that the root hair zones move forward slowly as the growth ensues we see how new regions are constantly being invaded, thus making more likely an adequate supply of minerals.

Through the relations between the four food-making essentials—light, carbon dioxide, water, and minerals—and the food-making processes we can understand how it is possible for plants to remain rooted to a spot. We have only to pause for a moment to realize that these essentials are in more or less constant circulation in nature. They come to the plants and the plants are able to remain in fixed places and yet obtain nourishment for themselves. Here we have a great contrast with animals, which must go in search of their food. The fixity of plants makes possible an extension of their bodies in a manner not found in the animal forms, which must move about and in which compactness of body is the rule. The extension of the plant body through its branching makes more certain the obtaining of the four essentials when they are not in abundance or when not available all the time.

If attention has not been drawn to the fact that most plants have radial symmetry there will be no difficulty in appreciating the fact. This type of structure means a symmetrical arrangement of parts about a central axis. This is a suitable arrangement because the circulating food essentials ap-

proach the plant equally from all directions and the plant parts radiate evenly in all directions. Most animals have bodies with bilateral symmetry —right and left sides—and an anterior and posterior end. With this kind of body plan their parts face in a particular direction as they move about, an obvious advantage in their search for food.

Adaptedness of Leaves to Functions Other than Photosynthesis

We pointed out in an earlier chapter that leaves are organs growing from the side of a stem which, in the majority of cases, have buds in their axils.

FIG. 6–15. A series of bud scales and leaves of the buckeye showing gradations from typical scales to typical leaves. (Redrawn by permission from *Textbook of General Botany* by Wilfred W. Robbins, published by John Wiley & Sons, Inc.)

We also stated that leaves vary so much in shape and size that it is difficult to make any statements that are generally descriptive of them. Then we proceeded to describe a green leaf consisting of blade, petiole, and stipules. Such green leaves comprise the foliage of plants and they perform the photosynthetic function.

But there are structures wholly or in part unlike the usual foliage leaves which must be recognized morphologically as leaves because of their origin, development, and relationship to stems, buds, or shoots. Our consideration would be incomplete if we did not give attention to some of the unusual forms of leaves.

Most people are familiar with the winter buds as they occur on trees and shrubs. The buds are covered by *bud scales* which serve to protect the growing parts within from drying out. The bud scales are attached to the stem and are actually a form of leaf. They are sometimes called *scale leaves.* The outer scales are often tough and hard in texture and brownish in color. They are frequently resinous. If a bud of the buckeye is dissected

(Fig. 6–15), the outermost scales have no characteristics of foliage leaves, but the inner ones have small leaf blades at their apices. The scale itself is a modified petiole. In some plants the stipules are the bud coverings. This is the case in the tulip tree (*Liriodendron tulipifera*). There are cases where a bud becomes much enlarged through a development of thick fleshy scale

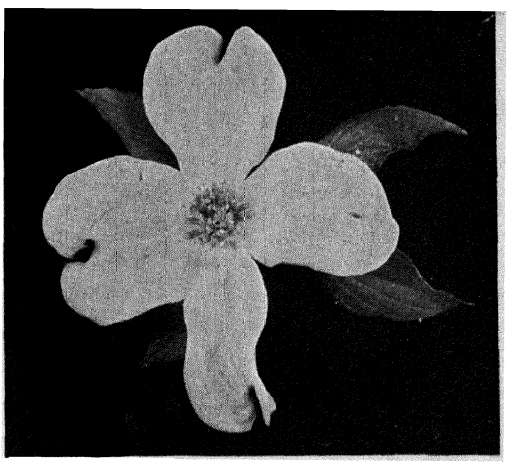


FIG. 6–16. A flower cluster of the dogwood (*Cornus florida*) surrounded by four conspicuous white bracts which appear like the petals of a single large flower. (Photograph by L. O. Overholts.)

leaves or leaf bases which serve for food storage. This is the situation in the onion, the hyacinth, and many similar species. Such structures are commonly subterranean and are called *bulbs,* but their bud-like nature is evident. Scale leaves are present on other subterranean structures such as rhizomes, tubers, and corms, but in these it is the stem which is fleshy and serves for food storage, the leaves being usually reduced and scale-like and having little if any function.

Other leaf forms found in flower clusters are termed *bracts* or *bracteal leaves.* The expression is often used that a bract subtends the flower, which means that the flower is in the axil of the bract. The bracts may be green and more or less foliage-like but are sometimes otherwise colored. In the brilliant Christmas poinsettia (*Poinsettia pulcherrima*) the real flowers are inconspicuous and the red showy parts are bracts. In the dogwood (*Cornus florida*) the bracts are white or pinkish and are grouped below the flower cluster in a way to appear like the petals of a flower (Fig. 6–16).

A flower is a shoot, and its parts—sepals, petals, stamens, and carpels—

are sometimes called the *floral leaves.* In form, the sepals and petals are more leaf-like and the stamens and carpels less leaf-like. The sepals are often firm and green, more or less resembling the bracts. The petals are

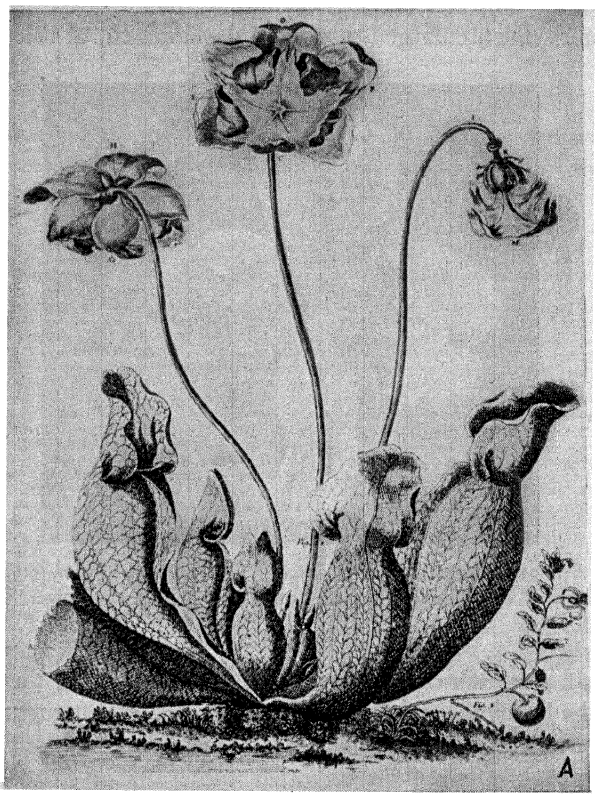


FIG. 6–17. The pitcher plant (*Sarracenia purpurea*), an insectivorous plant growing in bogs. The leaves are hollow receptacles or "pitchers" which hold water. Insects are trapped in the pitchers, their bodies disintegrate, and the digested constituents are absorbed by the plant tissues. (From *Elements of Botany* by Benjamin Smith Barton, one of the first textbooks of botany published in the United States [1803].)

usually delicate and variously tinted with pigments other than chlorophyll. The stamens and carpels are reproductive in function; and despite their difference from leaves in form and function, their manner of origin is fundamentally similar. We shall return to a fuller consideration of flowers in a later chapter.

An interesting modification of foliage leaves is found in the pitcher plants. In these the leaf blades are tubular and since they hold water they

are commonly called *pitchers*. There are several different kinds. They are bog plants. The pitchers serve as insect traps. Insects fall into the water, drown, and are digested by the plant. The pitchers also possess chlorophyll; therefore, in these plants there are two ways of securing nourishment. In the pitcher plant of the eastern United States (*Sarracenia purpurea*) the leaves are really pitcher-shaped and are usually partially filled with water and dead insects (Fig. 6–17). In the southern species (*S. flava*) the leaves

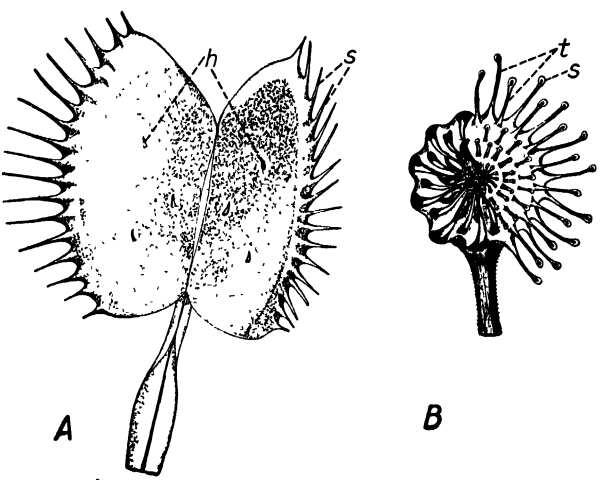


FIG. 6–18. *A*, leaf of Venus's-flytrap showing sensitive hairs (*h*) and marginal spines (*s*); *B*, leaf of sundew (*Drosera rotundifolia*) showing glandular tentacles (*t*) with secretions (*s*) at their tips. The tentacles on the left side have bent over a small insect. (Drawings by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

are long and trumpet-shaped. In California there is another kind (*Darlingtonia*) in which the upper end has a helmet-like hood over the mouth of the pitcher. In the tropics of the Orient there is a still different form (*Nepenthes*). In it the leaf base is expanded and blade-like; this narrows into a slender stalk from the end of which hangs the pitcher with a hinged lid. The elongated petiole-like part between the base and the pitcher sometimes twines like a tendril. This species is often called the East Indian pitcher plant. It is frequently grown in greenhouses. In a water plant called bladderwort (*Utricularia*) some of the leaflets develop into little bladder-like cavities with valvular lids which trap small water animals. We have referred previously to two other insectivorous plants, Venus's-flytrap (*Dionaea*) and the sundew (*Drosera*). In the former the two halves of the leaves fold together to trap the insect, and in the latter there are glandular hairs or tentacles which do the trapping (Fig. 6–18).

In our discussion of thigmotropism (response to contact) we referred to *tendrils* and pointed out how they twine about and cling to a support.

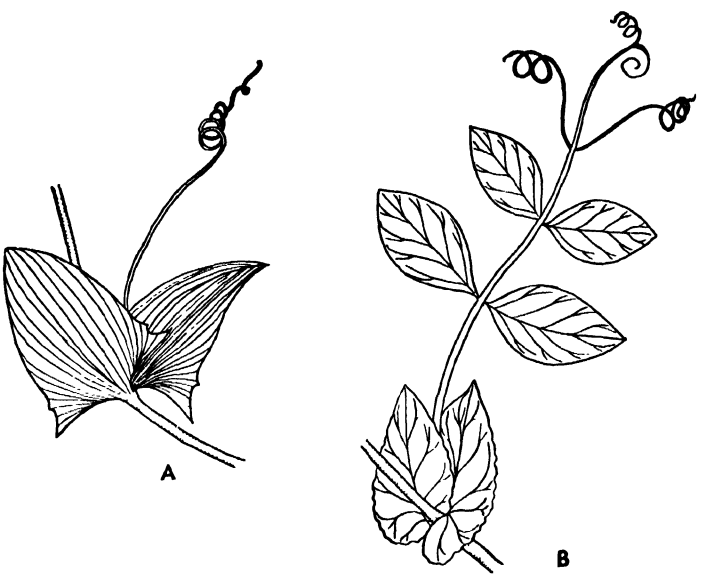


FIG. 6–19. Two examples of leaf tendrils. *A*, *Lathyrus Aphaca*, yellow vetchling. *B*, *Pisum sativum*, common pea. See text for explanation.

Tendrils are tough cord-like structures. Tendrils may be transformed leaves, or parts thereof. We shall see later that there are also stem tendrils. In the yellow vetchling (*Lathyrus Aphaca*) the tendril represents the whole blade and the photosynthetic functions are performed by the large stipules. In the garden pea (*Pisum sativum*) there are several tendrils on a single leaf (Fig. 6–19). The tendrils are modified leaflets. In the carrion flower (*Smilax herbacea*) there are two tendrils at the base of the petiole

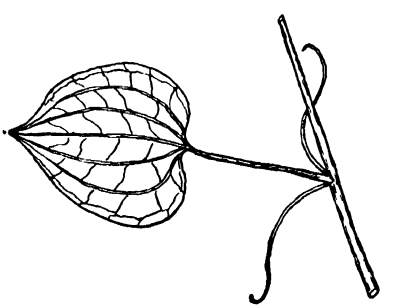


FIG. 6–20. Stipules as tendrils in the carrion flower (*Smilax herbacea*).

in place of the stipules (Fig. 6–20). In the virgin's bower (*Clematis*) there are no true tendrils, but climbing is made possible by the twining or clasping of the leaf stalks.

Special leaf forms may occur as *spines* or *thorns*. If a spine subtends an

axillary bud or shoot its leaf nature is at once evident. This is the case in the barberries. In young plants of the common barberry (*Berberis vulgaris*) all gradations from an ordinary leaf with spiny margins to a triple spine occur

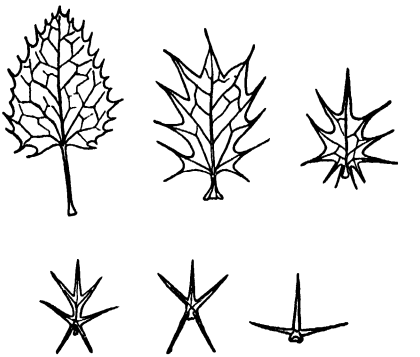


Fig. 6–21. Leaves of common barberry (*Berberis vulgaris*) showing gradations from an ordinary leaf with spiny margins to one consisting of a triple spine.

from the base of the stem toward the tip (Fig. 6–21). The thorns of the black locust (*Robinia*) are stipules; this is evident from their position (Fig. 6–22). Stems or shoots also may be reduced to thorns. Not all thorns and prickles are metamorphosed leaves or shoots. They may be merely surface outgrowths of the bark as in roses and gooseberries; these are called *emergences*. The significance of spines seems rather uncertain. Many writers have said that they serve for protection against herbivorous animals. Doubtless in some cases they are of advantage in this way, but in many cases it is impossible to see how they serve any purpose.

Foliage leaves in some plants serve as reproductive organs. In the ferns they bear the spores. But they may also play a part in vegetative reproduction. In the bladder fern (*Cystopteris bulbifera*) bulblets develop on the under side of the leaves. The bulblets drop off and germinate on the ground, thus starting new plants. In the walking fern (*Camptosorus*) a bud forms at the tip of the leaf and develops into a plant when it comes in contact with the ground (Fig. 6–23). In the higher plants reproduction from leaves is rare but it does occur. The so-called life plant (*Bryophyllum*) of the tropics, frequently grown in greenhouses and residences, produces buds in notches along the

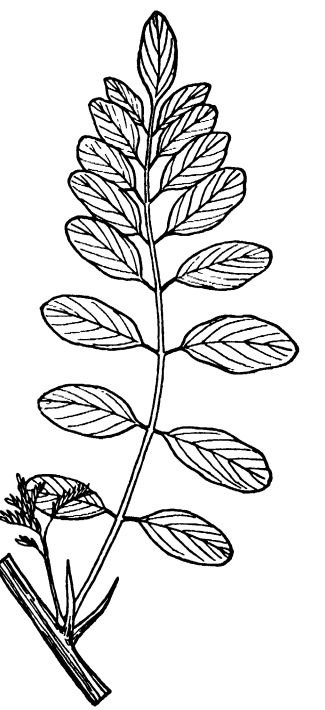


Fig. 6–22. Thorns of the black locust (*Robinia*) which are stipules.

FIG. 6–23. The walking fern (*Camptosorus*), with new plants growing from the tips of leaves.

FIG. 6–24. Leaf of life plant (*Bryophyllum*), with new plant developed from a bud in a notch in the margin.

leaf margins (Fig. 6–24). These develop into new plants when the leaves fall to the ground or even when still attached to the plant. All gardeners are familiar with the fact that the begonia and sansevieria can be propagated from leaf cuttings. Buds form as soon as the leaf pieces are placed in the soil.

Adaptedness of Stems to Special Functions

Generally the stem is an aerial structure bearing foliage leaves and flowers; the combination constitutes the *shoot*. If unbranched, the stem is

typically a vertical axis, although in some plants it may trail on the ground and in others it may twine or climb along a support. If the stem is branched, there may be formed a crown in which the leaves are carried upward and

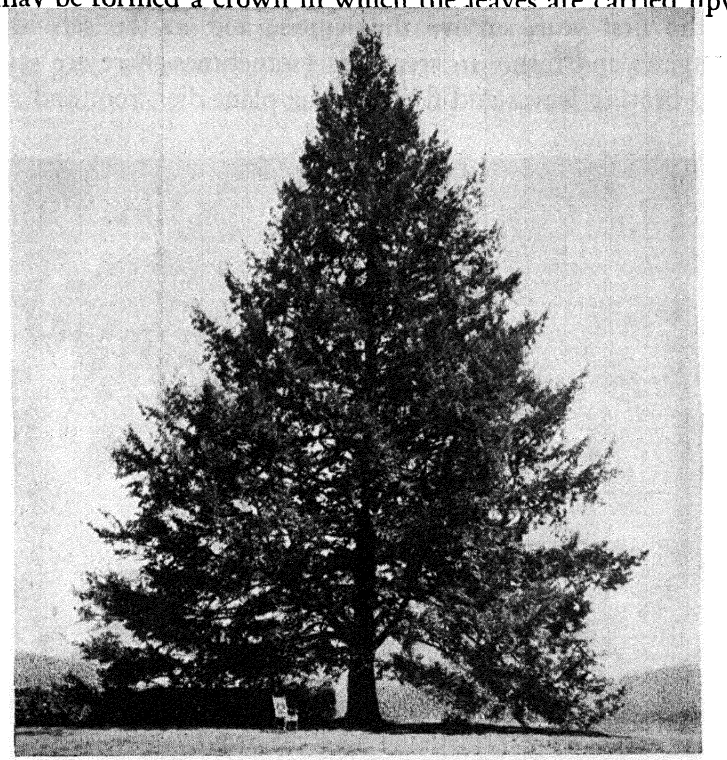


FIG. 6–25. The typical conic outline of an evergreen tree, the hemlock (*Tsuga canadensis*). (Photograph by Charles F. Jenkins.)

outward. Stems are concerned chiefly with the bearing of leaves and flowers. Their tissues are mostly mechanical for support and conductive for the transfer of water and food.

As a rule it is the character of the stem which determines the form of the plant body. Plants with woody stems which continue growth year after year are *trees* or *shrubs;* plants with stems which do not survive more than one season are *herbs.* Of course, these distinctions are arbitrary but they are convenient. Gradations between them are common. If the trunk of a tree extends to the top, the general outline is conic, as in most evergreens (Fig. 6–25). This is obviously an advantageous shape for photosynthesis. If the trunk branches and rebranches in a divergent manner, the shape may be ellipsoid, spheroid, or vase-like (Fig. 6–26). Loss of the lower branches results in a main trunk with a crown of branches and twigs.

Shrubs usually retain all their lateral branches so that they are bushy from the ground upward.

In some herbs the stem does not elongate much at first and the result is a rosette-like cluster of leaves. So-called *biennial* herbs produce this sort of growth the first year, survive the winter, and in the second year the stem elongates and forms an erect axis (sometimes there are several erect branches) bearing leaves and flowers. The plant dies, root and all, after it

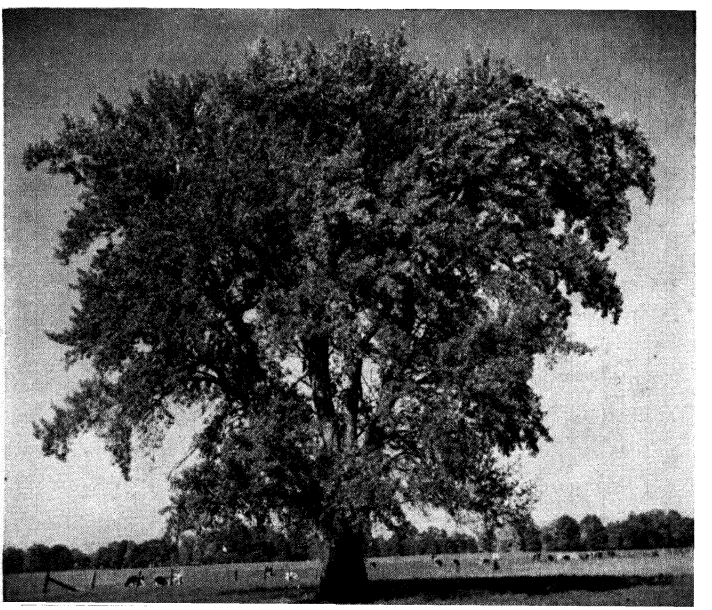


FIG. 6–26. The vase-like outline of a tree with divergent branching, the silver poplar (*Populus alba*). (Photograph supplied by Griffith Asplundh.)

has ripened its seed. Beets and radishes are good examples. The advantages are in favor of food synthesis the first year and of reproduction the second year.

An interesting deviation is to be seen in some plants in which the shoots develop only reduced leaves while the stems are flat and blade-like and take on the photosynthetic functions of foliage leaves. Such flattened shoots which resemble leaf blades are called *cladophylls*. The so-called "smilax" of florists is a good example. This is in reality a species of *Asparagus* and not a *Smilax*. The cladophylls are very leaf-like, but even a cursory examination reveals that they are stems arising in the axils of scale leaves. The centipede plant (*Muehlenbeckia*), commonly grown in greenhouses, has flat green stems with evident nodes (Fig. 6–27). Reduced leaves occur

at the nodes and branches arise in their axils. In the European butcher's-broom there are ordinary cylindrical branches and also cladophylls that are very leaf-like. They are especially curious because they bear on their upper faces a flower cluster in the axil of a bract, which though small is a genuine leaf (Fig. 6–27).

The green parts of most cactus plants are stems, and the spines represent leaves. These succulent stems take over the food-making functions of

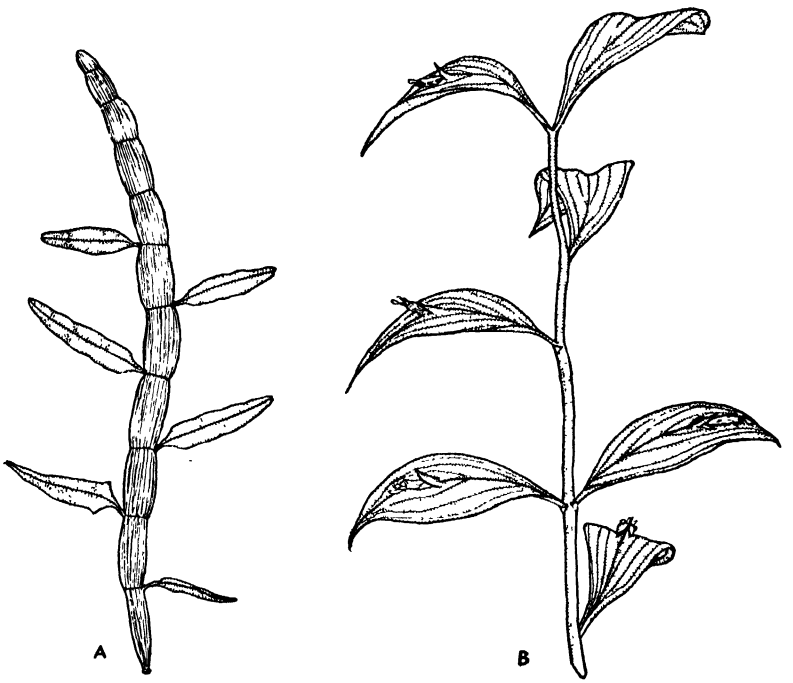
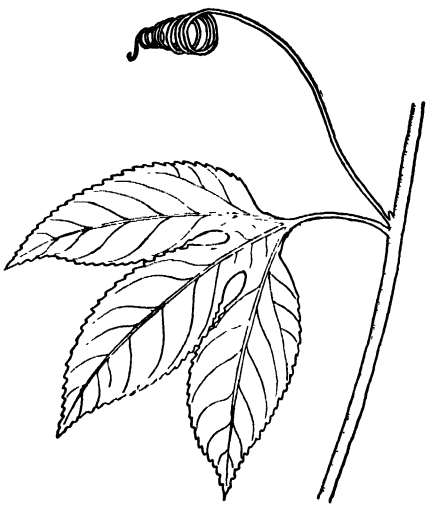


FIG. 6–27. Two examples of the adaptedness of stems to photosynthetic functions. *A*, the centipede plant (*Muehlenbeckia*); *B*, the butcher's-broom (*Ruscus*). See text for explanation.

foliage and they serve also for the storage of water. In these and other desert plants the green stems afford a sufficient green surface without danger from excessive transpiration. These characters enable them to live successfully in dry places.

We have discussed leaf tendrils as climbing organs. There are also stem tendrils. The function of the two types of tendrils is the same but morphologically they are different. In the passion flower (*Passiflora*) the stem nature of the tendril is evident since it arises in the axil of a leaf (Fig. 6–28). In the grape the tendril appears to arise opposite a leaf because it is a continuation of the main stem which is pushed aside by the shoot development that is continued by the axillary bud. The uppermost tendril shows its

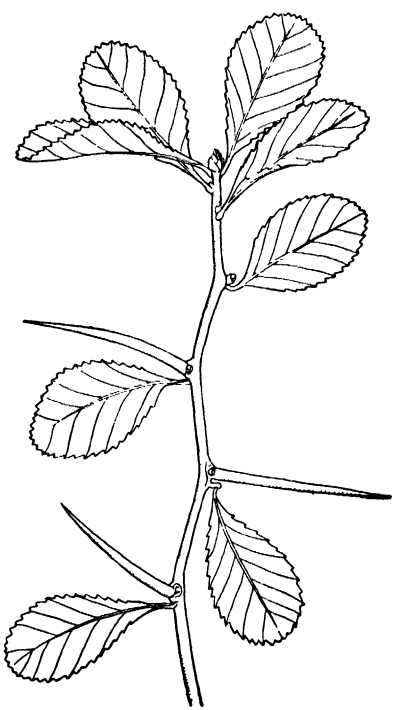


terminal nature until the axillary bud next to it develops into a shoot. The branched tendrils of the gourd family (including melons and cucumbers) are interpreted as specialized shoots —the basal portion the branch and the terminal portion a leaf. In the Virginia creeper (*Ampelopsis*) the tendrils affix themselves to smooth surfaces by dilated adhesive tips (discs) which adhere very firmly.

In the same way that there are leaf

FIG. 6–28. Stem tendril in the passion flower (*Passiflora*). See text for explanation.

tendrils and stem tendrils there are also leaf thorns and stem thorns. Those arising in the axils of leaves are easily recognizable as stems. They may be simple or branched, slender or stout, but are always hard and pointed. Sometimes they develop to large size as in the honey locust (*Gleditsia*) where they are often triple or compound. Stem thorns are well known in the Osage orange (*Maclura pomifera*) and in the hawthorns (*Crataegus;* Fig. 6–29).



Thus far we have been discussing aerial stems. Our consideration would not be complete if attention were not called to subterranean stems. The most stem-like of underground stems is the *rhizome*. It is by means of rhizomes that many herbaceous plants are able to live through the winter. A rhizome may appear more or less root-like; in fact, a term sometimes applied is *rootstock*. Rhizomes can be distinguished from roots by their nodes where scale leaves and axillary buds are borne. A good example of a rhizome is Solomon's-seal

FIG. 6–29. Stem thorns in the hawthorn (*Crataegus*).

(*Polygonatum biflorum*). It grows horizontally through the soil, sending up an aerial shoot each year. When the aerial shoots die at the end of a growing season they leave a sunken seal-like scar in the fleshy tissue which accounts for the common name. Many sedges and grasses have rhizomes. Functionally, rhizomes serve for both storage and vegetative extension. *Stolons* are closely related to rhizomes but grow along the surface of the ground and hence differ from rhizomes in not being subterranean.

In a few plants like the common potato and the Jerusalem artichoke (*Helianthus tuberosus*), the terminal portions of the rhizomes become much swollen and form special storage structures known as *tubers*. The "eyes" of the potato are axillary buds. It is a well-known fact that sprouts grow from them. The subtending leaves are so much reduced that they are scarcely recognizable except on very young tubers. There is also a terminal bud.

The *corm* is a bulb-like underground stem. It is a short, thick, rounded storage stem, sheathed with thin leaf bases. It differs markedly from a typical bulb with which it is commonly confused. The bulb has a very small stem development and food storage occurs in thickened leaf bases. Typical examples of corms are to be found in the crocus and in the gladiolus.

Adaptedness of Roots to Special Functions

Roots are typically underground organs serving primarily for anchorage, absorption, and conduction. In some plants the roots perform other functions and they are not always subterranean.

Many tropical orchids grow not on the soil but perched on the branches of trees or on rocks. They grow aerial roots which are quite different from underground roots. These aerial roots are covered with a whitish, thick, spongy layer of cells (*velamen*) which absorb and hold water that may be available from rain, drainage, or dew (Fig. 6–30). Such epiphytic orchids are frequently cultivated in greenhouses. Some of these aerial roots of orchids develop chlorophyll and in such cases they take on the food-making function of the foliage.

In another form aerial roots assume the function of anchorage, which makes climbing possible. Such roots grow from the side of a stem, sometimes in great abundance, and serve well to fasten the plant to a wall or other support. They are not positively geotropic but grow chiefly in a horizontal plane. Such roots are not absorptive. Good examples are to be seen in the climbing hydrangea, poison ivy, and English ivy. In the tropics climbing figs grow long woody roots which clasp stems of other plants

in a tendril-like manner. When they are developing they are thigmotropic in that they respond to contact with a support.

In addition to their typical underground root system some plants develop

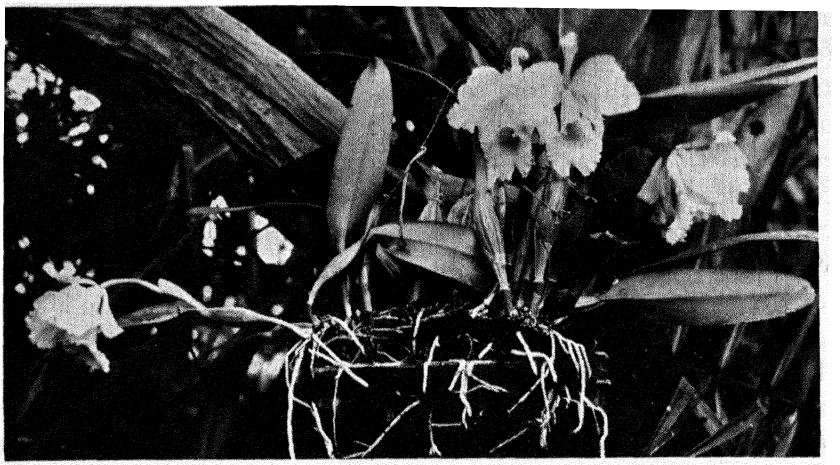


FIG. 6–30. A species of orchid (genus *Cattleya*), showing whitish aerial roots which are covered with a spongy layer of water-absorbing cells (velamen). (Photograph by Paul F. Shope.)

FIG. 6–31. Prop roots in the screw pine (*Pandanus*).

roots above the ground which grow into the ground and serve as braces or supports. They are termed *prop* roots. The most common example is to be seen in corn plants. These roots originate on the nodes nearest the surface of the ground and run diagonally into the soil. In a tropical plant called the screw pine (*Pandanus*) prop roots are so numerous and so

strong that they furnish more support than does the main stem (Fig. 6–31). In other tropical plants, such as certain palms and the mangrove, prop roots are conspicuous. Most people have heard of the banyan tree of India. A single tree may have an enormous spread (sometimes several acres) made possible by the development of hundreds of prop roots which arise from the horizontal branches and grow downward to the ground. Some species of figs come to have such roots in a slightly different manner. The

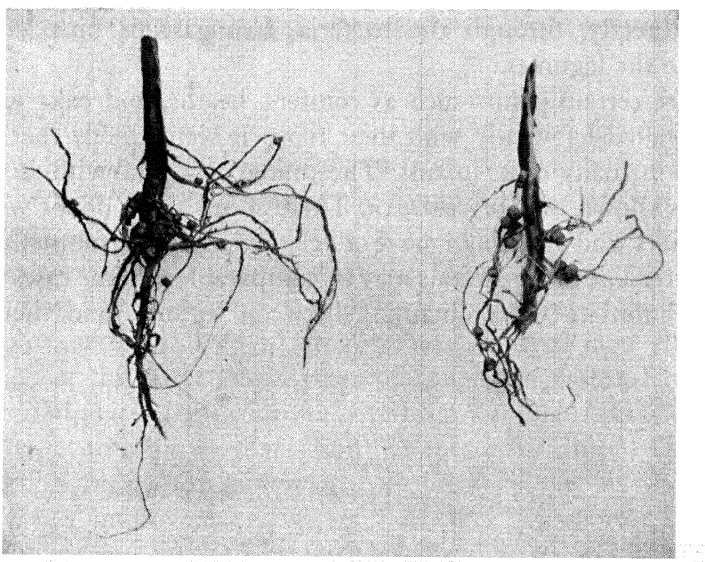


FIG. 6–32. Nodules on roots of soybean.

seeds germinate on the branches of trees well above the ground. Aerial roots grow downward and eventually reach the ground, and the plant becomes strong and independent. Often they envelop and strangle the tree upon which they began development and hence are called strangling figs.

Perhaps the most curious absorbing organs are those belonging to parasitic plants such as the dodder (*Cuscuta*). Special outgrowths called *haustoria* develop on the sides of the stems of such parasites. They penetrate the stems of the parasitized plant (host) and absorb nourishment from the vascular bundles. There are other plants which attach themselves by haustoria to the roots of their hosts. Such plants may be wholly or only partially parasitic.

Roots of plants of the legume (pea) family are characterized by enlargements known as *nodules* (Fig. 6–32). They are produced as the result of a reaction between the root tissues and certain bacteria which gain access

through the root hairs. Some authors refer to the relation between the bacteria and the leguminous plants as reciprocal parasitism. These bacteria have the capacity to use the free nitrogen of the air, a capacity not possessed by green plants such as legumes. The bacteria obtain carbohydrates from the legumes and build up nitrogenous compounds utilizing nitrogen from the air. The legumes in turn take up the nitrogenous compounds. The incorporation of free nitrogen into the bodies of the bacteria is known as *nitrogen fixation*. It is a process of great importance in the organic world. Indirectly, through the bacteria, free gaseous nitrogen is made available to the legumes.

There are certain plants such as conifers, heaths, and oaks which have fungi associated habitually with their roots. It seems likely that such relations exist in many other plants. The union of a root with its fungus is commonly known as a *mycorrhiza*. There seems to be doubt whether the higher plants and the fungi have a relationship of a mutually advantageous nature. The interrelations may be comparable in some cases and under some conditions to those obtaining between legumes and their tubercle bacteria.

CHAPTER 7

THE CULTURE AND PROTECTION OF PLANTS

(*Cultivation, Diseases, Pests*)

It is a generally accepted fact that plants have changed through the ages. The changes in plants may be considered from two points of view. In the first place there are the alterations in plants which take place in nature, i.e., from natural causes. These are considered under the topic of *evolution.* From various evidences we know that the history of natural changes in plants is a most ancient history. It goes back millions of years, runs down to the present, and is still going on. We have reserved later chapters for consideration of the alteration of plants through the past ages.

In the second place, great changes have been wrought in plants by man. Man has sought to improve plants and has succeeded. Improvements may be of two kinds, *individual* and *racial.*

By *individual* improvements we refer to those which can be brought about by culture and through protection from diseases and pests. According to one definition, "Cultivation consists in giving plants such conditions of space, nourishment, and freedom from enemies as will permit them to develop to the highest degree that their internal capacities will allow." If we accept this statement it will be plain that cultivation produces better individual plants and hence better crops. But cultivation alone will not produce better races because the good effects of it are not transmitted to the next generation.

Through selection and breeding, improvements which are *racial* may be brought about. By this we mean that the improvements are transmitted from generation to generation. The alteration of plants by breeding is the subject matter of a later chapter.

In the present chapter we are concerned with the *individual* improvement of plants and crops through cultural methods. Before we come to the marvelous effects which modern culture accounts for, some reference to ancient culture and our debt to it is in order.

There can be no doubt that the origin of the civilization of mankind is

inseparably linked to the cultivation of plants and to the domestication of animals. When primitive peoples gave up a nomadic life and settled down to care for crops and herds, the first steps toward civilization were taken. They began to establish homes while waiting for crops to grow. There was time for the consideration of community life. Thus we can see the truth of the statement that "it was farming that created society, and it is farming that sustains it today."

We are indebted to E. D. Merrill for the following statement about the origin of agriculture:

> The importance of the establishment of agriculture in relation to the progress of mankind cannot be overlooked. It was probably the most significant single advance in man's development. It should be borne in mind that at the dawn of recorded history every basic food plant now grown was already in cultivation and every domestic animal was already in domestication. It is true that modern man has greatly improved both cultivated plants and domesticated animals, but he has not added a single species to those domesticated by his remote ancestors. We thus owe a tremendous debt to numerous unrecorded individuals, who in remote ages, long before man prepared permanent records, selected from the wild and adapted to their needs through domestication the plants and animals which gave them a permanent food supply and hence paved the way to the development of civilization. So long ago did this happen that these pioneer agriculturists were forgotten long before recorded history commences, for the beginnings of agriculture among all early peoples are lost in mythology.[1]

We must agree that the history of man's domestication of plants is only partially known. We do know that many of our cultivated plants exist in a wild state and their origins are not mysteries. Corn (maize) and wheat, however, have not been found in a wild state and we do not know the nature of their ancestral forms. Our knowledge of the general regions where most of the cultivated food plants originated is fairly definite. From Eurasia have come the cereals (wheat, rye, oats, rice), cabbage, onion, carrot, asparagus, soybean, lentil, and many fruits (apple, pear, plum, cherry, apricot, grape, orange, peach, banana, coconut). From the western hemisphere have come corn, cotton, potato, tomato, sweet potato, cassava, cacao, common and lima beans, tobacco, squash, pumpkin, peanut, and pineapple. These are of course very incomplete lists. Apparently there was no interchange of plants between the Old and the New World prior to the time of Columbus.

[1] E. D. Merrill, "Crops and Civilizations," *Bulletin of the Torrey Club*, **60**: 323–329, 1933.

IMPROVEMENT OF PLANTS BY CULTURAL PRACTICES

After farming began, man must soon have discovered the value of certain practices in the growing of his crops. We are still discovering new facts about crop management, soil fertility, and related factors which are bringing about increased production. The potentialities of improvement are great, but the practical difficulties are many; hence the realization of the highest results is not attained with the frequency and definiteness that would seem possible. Our treatment of cultural practices must necessarily be brief. It is possible only to review some of the principles involved.

Seedbed Preparation

It is generally agreed that a well-prepared seedbed is essential for the best results in crop production. The good farmer knows that good crops cannot be grown on poorly prepared fields. Field practices for seedbed preparation ordinarily include plowing and harrowing, and may involve rolling or compacting the soil. Time, depth, and method of plowing are important. The benefits of good seedbed preparation are derived from improving the physical condition of the soil, bringing about aeration within the soil, conserving moisture, and turning under organic matter. Proper preparation before planting is essential for the reception of the seeds, for penetration of the roots, and for the development of the soil organisms that play a part in soil fertility.

Although the plow has been acclaimed "for at least one hundred and fifty years as a great instrument of civilization and of man's welfare," a recent book entitled *Plowman's Folly* challenges the theory of the fundamental benefits from the extensive use of the old-fashioned plow. Many publications have devoted editorials to the subject. Briefly the "case against the plow is that it turns over and buries all protective mulch on the surface of the earth and leaves the soil exposed and bare to the burning sun and invites destructive erosion by wind and water." It is proposed to use discs, disc plows, or some sort of tillage implements which break up the soil, "leaving a mulch on the surface or chopped into the surface." There are conditions of soil and climate where the practice has merit, but there are many conditions where such tillage is impractical and the plow must retain its place.

Seeding

Farmers use the term *seeding* to refer to all methods of planting field crops regardless of whether seeds or vegetative parts are used. The cereals

are propagated from seeds. Potatoes, sugar cane, and some grasses are propagated from vegetative parts. Seeding practices vary with the kind of crop. Corn, potatoes, and cotton are planted in rows far enough apart

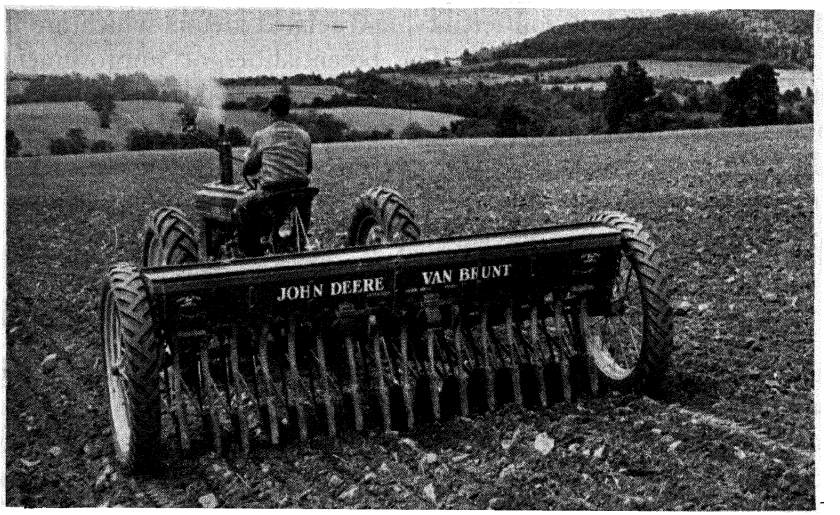


FIG. 7–1. Planting wheat. (Photograph, courtesy John Deere, Moline, Illinois.)

to admit the passage of cultivators. Wheat and oats are usually drilled in close rows (Fig. 7–1). Clovers and grasses are often broadcast. Tobacco and tomatoes are started in seedbeds and transplanted into the field. If seeds of poor quality or low germination are used it is the practice to increase the rate in order to obtain good stands. Thicker seeding, however, must not be regarded as a practice that justifies the use of inferior seeds. The climate and season have an important bearing on the time of seeding. Winter wheat must be sown early in the more northern regions and progressively later southward. The range of optimum dates varies from September 1 to as late as October 15. Depth of seeding is determined mostly by type of soil and by moisture conditions. With some plants the use of the crop is important in governing the seeding practice. Soybeans to be used for hay may well be in close drills like small grains, but if to be harvested for seed they are better sown in wide drills to permit cultivation.

Cultivating

The term *cultivating* is used specifically to include the operations of loosening or stirring the soil about growing plants (Fig. 7–2). *Tillage* is usually used in a broader sense to refer to all soil operations including

seedbed preparation. Cultivating the soil is practiced because it increases production. Its effects are brought about chiefly through weed destruction, moisture conservation, nutrient availability, and soil aeration. With some

FIG. 7-2. Cultivating corn. (Photograph, courtesy John Deere, Moline, Illinois.)

crops special forms of cultivation are used. In cultivating potatoes it is common practice to ridge the rows. In the cooler moister regions the ridge system is preferred.

Soil Productivity

It is a well-established fact that there are a number of soil conditions which have an effect upon plant growth. Among the more important factors are the chemical reaction of the soil, the content of organic matter, and the supply of mineral requirements.

Under certain conditions soils may develop an excess of acidity. Although the causes of soil acidity are not fully understood, the general method of treatment is the application of lime. The practice of applying lime to the soil is an ancient one antedating the Christian era. The commercial forms of lime commonly used are burnt lime, hydrated lime, ground limestone or ground shells, and marls. Although calcium predominates, some magnesium is usually present in all these forms. Practical agriculturists do not speak of lime as a fertilizer. Without doubt liming the soil frequently makes the use of fertilizers carrying nitrogen, phosphorus, and potassium more profitable. Soil acidity may be indicated by the abundance of certain

weeds and wild plants such as sorrel, wild daisies, poverty grass, dewberries, paintbrush, corn spurry, the bent grasses, and plantain. All crops do not respond alike to the use of lime; clovers and other leguminous crops are greatly benefited (Fig. 7–3).

The organic matter content of soils is important. It influences the physi-

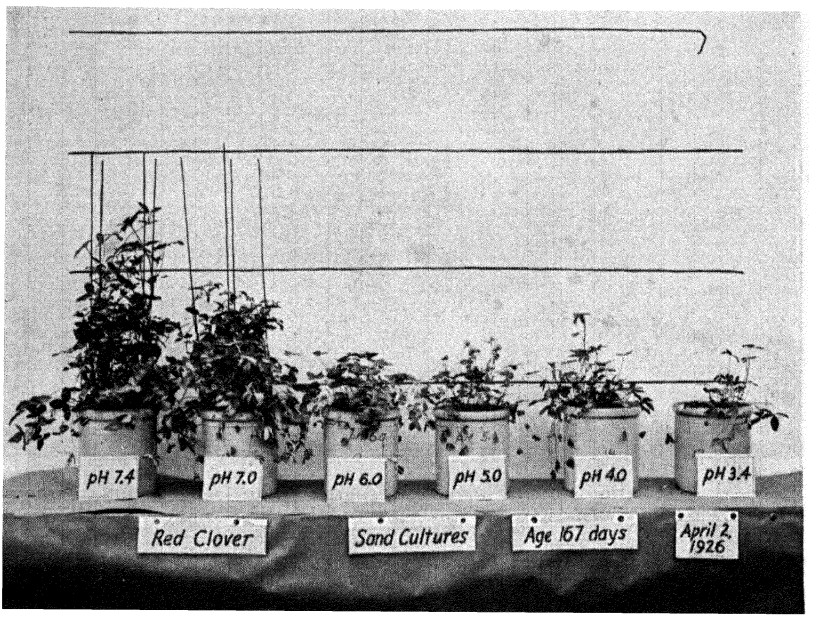


FIG. 7–3. Comparison of growth of red clover in soil of different reactions. Neutral (2nd from left) and slightly alkaline (extreme left) show good growth; increasing the acidity (left to right) produces poor growth, with symptoms similar to those of calcium deficiency. (Photograph, courtesy of E. E. DeTurk, from *Hunger Signs in Crops.*)

cal condition of the soil, its water-holding capacity, the temperature, and especially the bacterial processes which affect the availability of the mineral salts. So-called green manures are often used as a source of organic matter. They are crops which are plowed under (Fig. 7–4). In this way large amounts of organic matter are added to the soil. Sometimes crops are grown only for furnishing green manure, but more often they serve first for pasture, for hay, or for cover crops. Various legumes, vetch, sweet clover, cowpeas and soybeans, and the cereals oats, rye, and sorghum are used. The practice of green manuring is common in orchards.

Barnyard manure is also a source of organic matter. Early agricultural literature shows that the value of barnyard manure for increasing soil productivity has long been recognized. The results vary in different locali-

ties, with different types of soils, and with the various crops. Most of the common field crops react favorably to the use of barnyard manure. It produces results directly through the elements it contains and indirectly through its beneficial effects on the bacterial content of soils. Manure is high in nitrogen and potassium but relatively low in phosphorus. Its

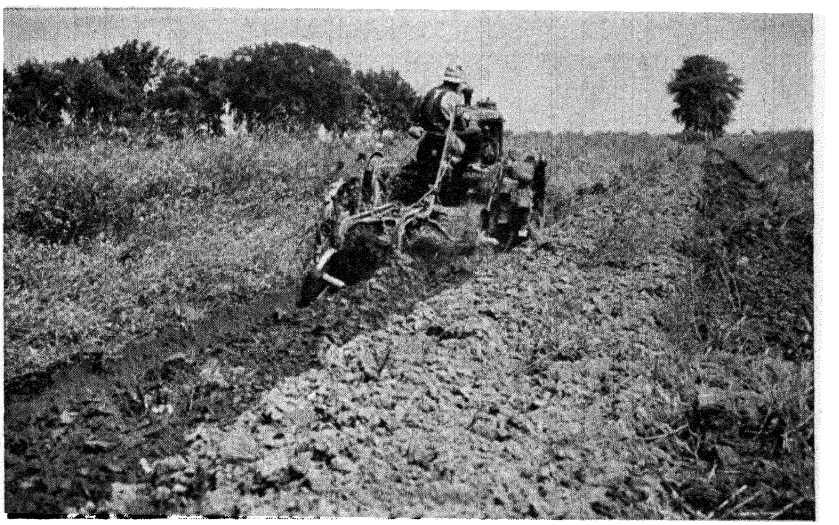


FIG. 7–4. Plowing under dense growth of sweet clover as a source of organic matter in the soil, an important step in supplying plant nutrients for subsequent crops. (Photograph, courtesy G. N. Hoffer, from *Hunger Signs in Crops.*)

efficiency is frequently augmented when supplemented with phosphate fertilizers.

Nitrogen, phosphorus, and potassium are often supplied to the soil in the form of commercial fertilizers (Figs. 7–5, 7–6). According to statistics of the U. S. Department of Agriculture, the average annual consumption of fertilizers in the decade 1921 to 1931 was approximately 7,000,000 tons. The success attained from applying commercial fertilizers is linked with a number of factors. Among these may be mentioned the type of soil, nature of the crop, and climate and weather conditions. By no means will fertilizers always overcome unfavorable growing conditions. Where the season is short and early frosts are likely, fertilizers are an aid in hastening maturity even if they do not increase the yields. Some of the sources of fertilizer material are superphosphate, ground bone, raw rock phosphate, sulphate of ammonia, nitrate of soda, dried blood, tankage, cottonseed meal, muriate of potash, and sulphate of potash. There is no doubt that com-

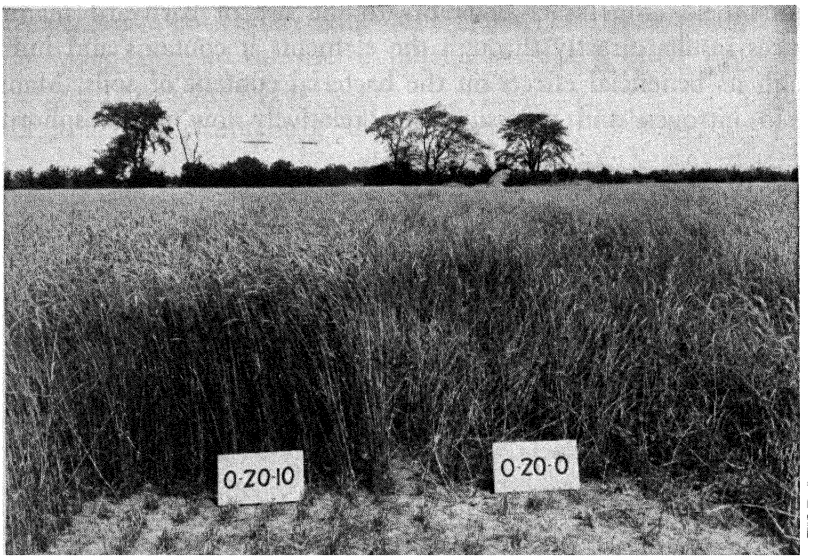


FIG. 7–5. Effect of fertilizers on wheat. Plants to right, fertilized with phosphate only, have weak stems and tend to lodge; plants to left, fertilized with mixture of phosphate and potash, produced strong stalks. This demonstration was made in a field where the potash of the soil had become depleted by successive crop removals and the continued use of phosphate only as fertilizer. (Photograph, courtesy E. E. DeTurk, from *Hunger Signs in Crops.*)

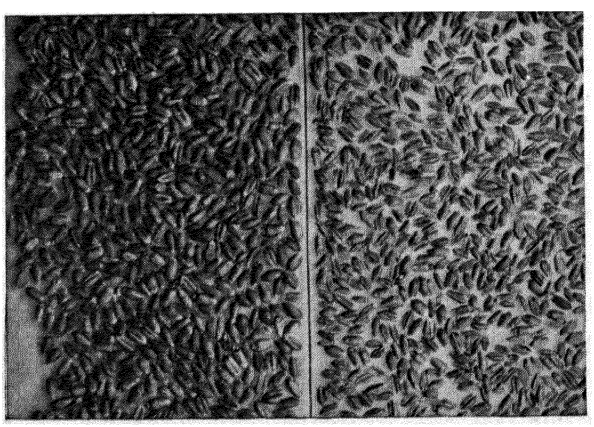


FIG. 7–6. Effect of fertilizer on the plumping of wheat kernels. Those on the right from plants receiving phosphate only; those on the left from plants receiving phosphate and potash. (Photograph, courtesy E. E. DeTurk, from *Hunger Signs in Crops.*)

mercial fertilizers when properly used do produce results. In 1934, at the Maine Agricultural Experiment Station, 1500 pounds of fertilizer on potatoes gave an increased yield per acre of 198 bushels; 2000 lbs., 296 bu.;

FIG. 7–7. Potato vines in field with well-balanced fertilizer, free from any nutrient deficiency, showing fine foliage and growth (above); the yield from this field (below). (Photograph, courtesy H. A. Jones and B. E. Brown, from *Hunger Signs in Crops.*)

2500 lbs., 315 bu.; and 3000 lbs., 352 bu. (See Fig. 7–7.) The method of applying the fertilizer to the soil is dependent upon the character of the crop; the best time depends upon the rotation.

Crop Rotation

When land is kept in one crop season after season, production usually decreases. This may be due to fertility depletion, development of diseases and pests, or a combination of these and other factors. It is generally true that a one-crop system is not desirable or profitable. A haphazard system of changing crops is usually also unsatisfactory. Crop rotation has been defined "as a more or less regular recurrent succession of different crops on the same land."

Many instances could be cited which prove that rotation increases crop yields. At the Missouri Agricultural Experiment Station after continuous culture of corn for thirty-one years the yield per acre was 19.6 bu., whereas the yield in a corn, oats, wheat, clover rotation was 52.5. In the twenty-ninth year of continuous culture for wheat the yield was 0.2 bu. as against 30.0 bu. in a corn, oats, wheat, clover rotation for the same year. In Ohio the average yield for corn grown continuously for twenty years was 15.47 bu., as compared with 34.93 for corn in a three-year rotation.

In addition to increased yields other direct results of rotation are better control of weeds, diseases, and insects. Indirect results are economy of labor, protection of the soil, and distribution of the risks of crop failures.

Crop Adaptation

Our account would not be complete if some reference were not made to the adaptation of crops to the regions of production. Most crops have both climatic and soil requirements and will not be productive beyond the regions suited to them. Cotton is grown in the southern states, for a long growing season with hot days and nights is required. Oats produce best in cooler areas where the rainfall is plentiful. The Great Lakes states produce most of the oats. Potatoes also do best where the weather is cool and moist. They can be grown southward in the early spring or in the autumn, thus avoiding hot summer weather. Corn is at its best where the rainfall is plentiful and the nights warm. Although corn is grown in every state the maximum production is in the upper Mississippi valley. Wheat has a wide range. Winter wheat will stand freezing winter temperatures if that season is not too prolonged. Spring wheat can be grown in the more northern areas. Tobacco is dependent upon certain soil types for the best development of quality and aroma. It will thrive under a considerable range of climatic conditions. In the United States, the states of North Carolina, Kentucky, Tennessee, and Virginia produce 80 per cent of the entire crop. Fine tobaccos are grown in the tropics. Rice is a tropical crop which is dependent upon an abundant supply of water. Sugar cane can be grown only in tropical or subtropical areas. It is well known that citrus fruits will not stand freezing temperatures. On the other hand apples will not thrive in any but temperate zones. Hay and pasture grasses do better in the cooler regions. It is at once evident that successful agricultural production is governed particularly by climatic conditions. Where crops are not naturally adapted "they must be grown on the richest land, given good cultivation and treated indulgently in many ways."

PROTECTION OF PLANTS FROM DISEASES AND PESTS

Farmers have long been familiar with the fact that diseases and pests attack their crops. The effects on the crops are manifest both by decreased yields and by the quality of the crops. Who has not heard of smutty corn,

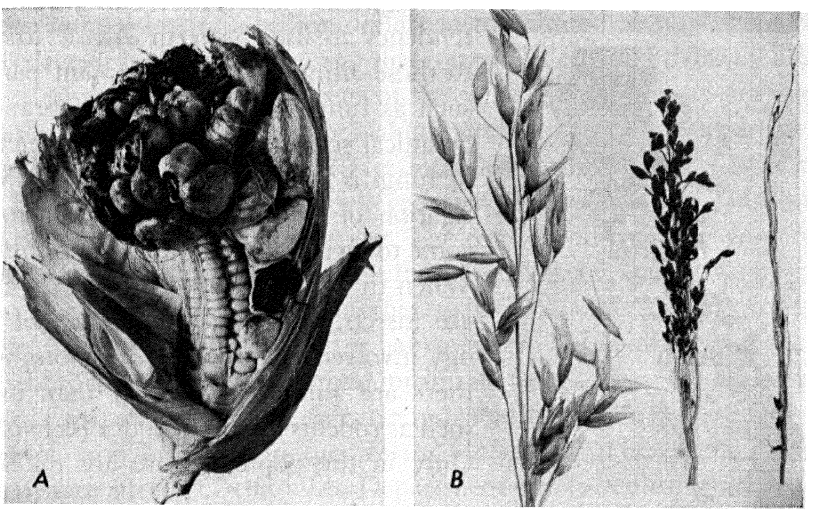


FIG. 7–8. *A*, corn smut. *B*, oat smut (healthy panicle at left).

scabby potatoes, and wormy apples? (See Fig. 7–8.) The problems of diseases and pests are by no means new. They were recognized by the ancients centuries ago. The Bible speaks of scourges and enemies of the grain crops. In the English text the word "mildew" appears. It is practically certain that the reference is to those fungous diseases that we now call "rusts." Not only are our food crops subject to diseases and pests but likewise our forest trees and all sorts of ornamental plants. White-pine blister rust (Fig. 7–9), Dutch elm disease, and Japanese beetles have been much in the news these past years. In the case of the annual food crops it is true that yield and quality of the crop are matters causing concern. In the forests and with other perennial plants the life and growth of the plants may be threatened, thus menacing a large investment.

It should be pointed out that wild plants of all sorts are attacked by diseases and pests. Many of the fungi and insects which do damage to cultivated plants can be traced to their wild hosts. The conditions of cultivation may render plants more susceptible; the massing of plants in fields

and orchards is particularly conducive to the spread of diseases and pests. And when we consider how certain crops are concentrated in immense areas, as is fruit in the Shenandoah valley or wheat in the Dakotas, we understand how plant troubles may develop to epidemic proportions.

In the broadest sense we might refer to all plant troubles, whether caused by plant or animal parasites or by unknown agencies, as diseases. But in practice such simplicity must be sought in vain. There has grown up a tendency to use the term *disease* to apply to those ailments caused by plant parasites such as fungi and bacteria. The branch of botanical science concerned with the study of fungi is known as *mycology*. The investigation of diseases and their control has come to be included under *plant pathology*. When the organisms responsible for injury are insects, the particular branch of zoology involved is known as *entomology*. But there are animal pests other than insects, such as rodents and nematodes (eelworms). Only in the popular sense are mites and spiders classed as insects. There are also maladies known to be caused by filtrable *viruses*. They are infectious in nature but without known visible causative organisms. The virus which causes tobacco mosaic is considered by many investigators to be a protein.

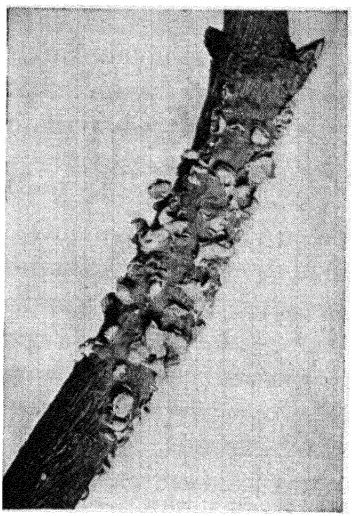


Fig. 7–9. White-pine blister rust.

This review reveals the fact that we have no unified system of dealing with plant troubles. It would be convenient from a practical point of view if consideration of all plant troubles were included in one department of science regardless of cause. Problems of control necessitate knowledge of the life history and life habits of the causal organisms. We must have the cooperation of mycologists (students of fungi) and entomologists (students of insects)—and we must use these terms in the wider rather than in the stricter sense. If treatments include application of chemicals to the plants, then the knowledge of chemists is involved. A comprehensive term is needed. In a wider sense than it is now used we might consider all morbid conditions of plants under one heading, viz., *plant pathology* or *phytopathology*. Plant medicine and plant hygiene do not appeal as acceptable terms. *Plant protection* has been used by an English author

(Martin) and since the procedures are chiefly preventive rather than curative this terminology has merit.

Importance of Protecting Plants

It is a fair question to ask how important it is to protect plants from diseases, insects, and other pests. It has been estimated that plant insects cause an annual loss of a billion dollars in the United States. There was a serious development of stem rust in this country in 1935. The survey showed that the rust destroyed 12 per cent of the wheat in Kansas, 15 per cent in Nebraska, 30 per cent in South Dakota, and as much as 60 per cent in North Dakota and Minnesota. The total loss in the country was more than 125,000,000 bushels. It is believed that the cereal rusts cause world losses of half a billion dollars a year. The cotton boll weevil is responsible for annual losses amounting to more than $150,000,000.

The facts may be stated in another way. According to a government bulletin, 4000 cases of treatment for oat smut resulted in an average increase of 4.6 bushels per acre. The total profit in these cases, involving about 400,000 acres, was $1,197,722. We are indebted to Whetzel for putting the matter of crop losses in another form. He states, "The estimates of the plant disease survey of the U. S. Department of Agriculture indicate that approximately one bean in every dozen, one peach in every eight, one bushel of Irish potatoes in every twelve, and one bushel of wheat in every ten, are destroyed annually by diseases in these crops."

There are known instances in which the entire agricultural industry of a region has been changed on account of plant diseases. Coffee was once the main export from the island of Ceylon. About seventy years ago a rust fungus attacked the coffee trees there. In spite of all efforts to mitigate the disease it gradually increased in virulence, and planters were obliged to give up coffee growing and take up other crops. In certain sections of Delaware, Maryland, and Michigan peach growing was all-important, but a disease known as yellows brought about the almost complete abandonment of that crop. In the ten-year period 1910 to 1920, the acreage of sugar beets in one Idaho county dropped from 8682 to 490 on account of the disease known as curly top.

Stakman writes that "plant pathologists and entomologists are often ridiculed for their allegedly extravagant estimates of damage caused by diseases and pests. But anyone who has seen the devastation caused by epidemics of black stem rust of wheat and other small grains, by late blight of potatoes, by grasshoppers and by many other diseases and insects must be profoundly impressed with the magnitude of the financial losses, the

tragic consequences to farmers and the far-reaching sociologic and even political implications of such crop catastrophes." [2]

The Methods of Plant Protection

How is it possible to protect plants from diseases and pests? The botanical and zoological sciences have gone a long way toward answering this question. The methods are more or less complex and they are often interdependent and overlapping. It is therefore difficult to enumerate and separate the procedures involved. Realizing that the difficulties of an analytical presentation are great, we are nevertheless attempting for convenience the schematic arrangement shown in the accompanying diagram, in order to emphasize the main principles of control measures.

Applied[a] *methods* of protecting plants from diseases and pests involve:

- *Safeguarding the host,* dependent on:
  1. Use of resistant varieties.
  2. Coating with chemicals to prevent or deter attack.
  3. Use of external factors to reduce liability of attack.
  4. Quarantines, inspection, and other legislative measures.
- *Combating the parasite,* dependent on:
  5. Destruction of parasites by chemical treatments of plant, seed, or soil.
  6. Destruction of parasites by physical or mechanical means.
  7. Use of external factors to reduce activity.
  8. Eradicative measures.

[a] The term *applied* methods is used here to contrast with *natural* conditions. Applied methods are under the control of man and are dependent upon him for their application and success. There are natural conditions, such as climate, topography, and natural enemies, which check parasites without dependence upon man for their operation and success.

1. *Use of Resistant Varieties*

The ideal method of disease and pest control is the utilization of resistant varieties. In nature plants exhibit variations in the resistance they offer to their parasitic enemies. The more resistant ones survive. Resistance is a heritable character. There is at work a natural selection of those plants which inherit resistance.

Man has made use of this natural process and through selection and breeding has produced resistant strains and varieties. A more appropriate place to discuss what he has done to bring about racial resistance to enemies

[2] From *The Scientific Monthly*, copyright 1937 by The Science Press.

is in a later chapter which deals with breeding. Man has used his knowledge of heredity to breed better plants. Speaking generally, "better" means larger yields, more desirable quality, and resistance to diseases and pests. Because the subject of resistance is treated under breeding our discussion here is brief.

The practical application of our knowledge of resistance is one of the most promising methods of plant protection. Not much has been done to develop plants that are resistant to insects. There is evidence that varieties of cereals show variations in their resistance to these pests. Some varieties of corn resist attacks by chinch bugs. More headway has been made with the development of resistance to fungous and bacterial parasites. The growing of wheat and other cereals has been greatly benefited by the breeding of varieties for resistance to rust and smut. Outstanding results have been obtained in producing sugar-cane varieties resistant to mosaic, a disease caused by

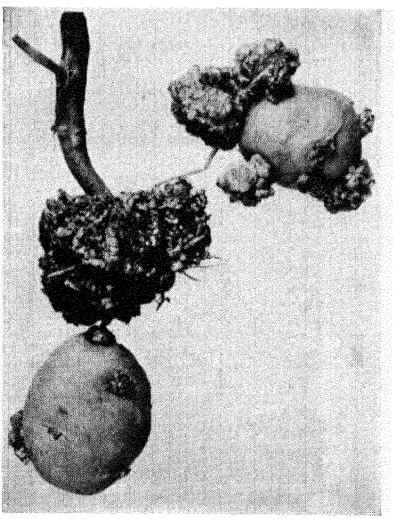


FIG. 7–10. Potato wart disease.

a virus. Potato wart is a very serious disease which attacks and distorts the tubers (Fig. 7–10). Some varieties are not only resistant but wholly immune. It may be safely said that the resistance method of disease control has met with some success in all types of crops, but much remains yet to be accomplished.

2. *Coating with Chemicals to Prevent or Deter Attack*

Poisonous substances used to coat the plant surface are chiefly directed against insects (called *insecticides*) and against fungi (called *fungicides*). The early history of insecticides is not known. The application of fungicides in which copper is the active agent appears to date from an accidental discovery by a Frenchman, Millardet, working in the region of Bordeaux in 1882. He sprayed a mixture of lime and copper sulphate on grapes to discolor them in order to discourage stealing, and noticed that the plants thus treated were not attacked by diseases. With this discovery an important epoch in plant protection had its beginning. The lime-copper sulphate

fungicide became known as *Bordeaux mixture.* When leaf surfaces are covered with a film of Bordeaux mixture many kinds of fungous spores will not infect them on account of the toxic action of the copper. This fungicide is still the most effective control for the downy mildew of grapes. Its use as a spray for Irish potatoes is well known (Fig. 7–11). It is used on many crops against a variety of fungi. There are now various other fungicides which contain copper in some form as the active agent. Sulphur is also a

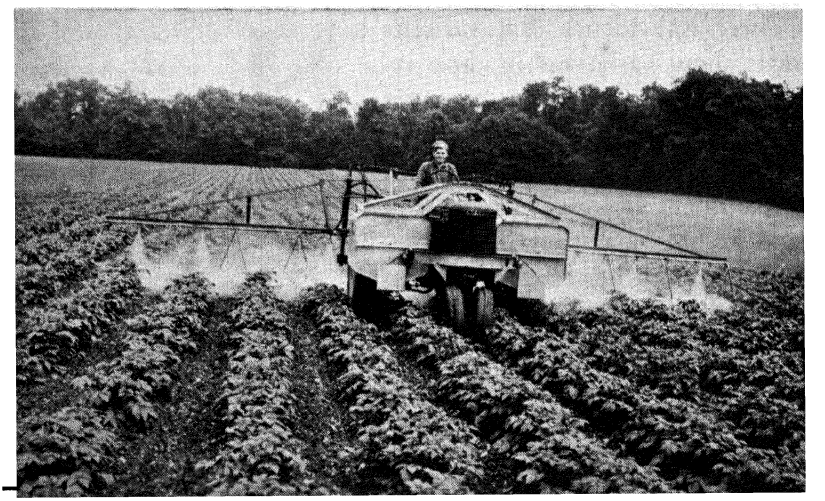


FIG. 7–11. Spraying potatoes.

valuable fungicide. Its possibility for this purpose was known as early as 1821, although its value was not appreciated for a quarter of a century. Its modern use dates from about 1905. *Lime sulphur* is a commercial name for a mixture of lime and sulphur. The mixture is widely used as a preventive spray for the control of apple scab.

Insects which chew the leaves and plant parts can be controlled by stomach poisons. The most widely used stomach insecticides are the arsenicals—Paris green, lead arsenate, and calcium arsenate. The potato beetle began spreading from its original home in Colorado about 1850. In fifteen years it had spread all over the eastern United States and southern Canada. It became so serious that it threatened the potato industry. Paris green proved to be the successful means of control. Today calcium arsenate is more commonly used in potato spraying.

Insecticides and fungicides may be applied in liquid form as solutions, suspensions, and emulsions; or they may be applied in dry form as finely divided powders. It is essential that they be effective against the enemy

toward which they are directed and that they cause no injuries of importance to the host plant. In some cases the margin of safety between the concentration that is effective and yet not injurious is wide. In other cases considerable research is necessary to find the best balance between control and injury. Such factors as dilution of the mixture, amount applied, and method of application enter into the problem of injury.

Much progress has been made in the manufacture of equipment for applying insecticides and fungicides to plants. There is a variation from

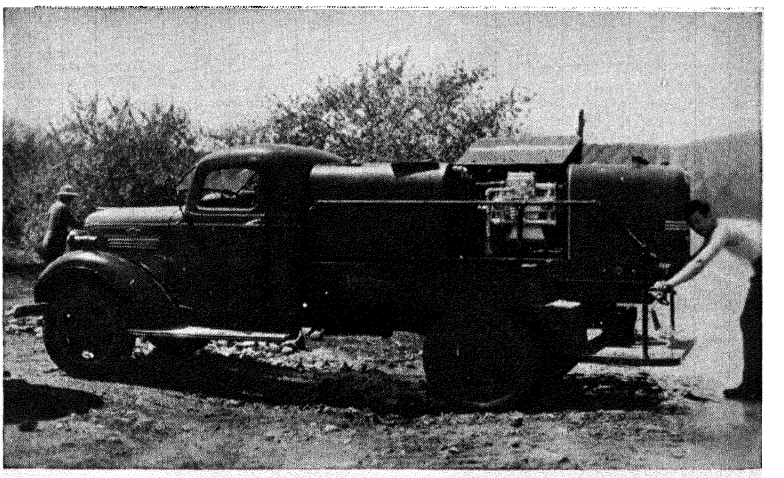


FIG. 7–12. Power sprayer used in orchards.

hand apparatus up to large power machines (Fig. 7–12). It would take us too far afield to consider the various kinds of sprayers and dusters. The essential requirement is the treatment of the surface of the plant "in such a manner as to give a uniform covering with the least expenditure of power, labor, and material possible to produce this result." Maintenance of good pressure is necessary for the best results in spraying. Large sprayers used in vineyards and orchards must develop pressures of 200 to 500 pounds per square inch. With potato sprayers the best results are secured when the pressure is kept between 300 and 400 pounds. A so-called speed sprayer has been developed which does not produce the spray by pressure but by the action of propellers or fans (Fig. 7–13). Most spray ingredients are diluted with water as a "carrier." Some of them are soluble in water, but others are insoluble and suspensions or emulsions are formed. When the ingredients are not soluble in water, an *agitator* to keep the finely divided particles evenly distributed is a necessary part of a sprayer. Sometimes special substances known as *spreaders* are added to the spray mixture to

cause it to spread over the sprayed surface more quickly and uniformly. Soaps, oils, and casein are used as spreaders.

The actual application of the spray is made from a rod or hose equipped

FIG. 7–13. A speed sprayer in action.

FIG. 7–14. Orchard spraying with gun.

with a suitable nozzle. Spray nozzles are of many sorts. They must be constructed so as to deliver a fine mist that will cover the foliage. To spray trees, spray guns and brooms are provided (Fig. 7–14). They have one or more adjustable nozzles enabling the operator to regulate the spray stream.

Timing the applications of sprays is an important consideration in disease and insect control. It is necessary to apply them so that the host is coated at the time the insects appear or when the fungous spores are being distributed. Applications must be repeated at intervals to replace loss from weathering and to cover new growth. For the convenience of growers definite annual spraying programs are developed for certain crops. Such programs are called "Spray Calendars." They may be based in part on the seasonal development of the

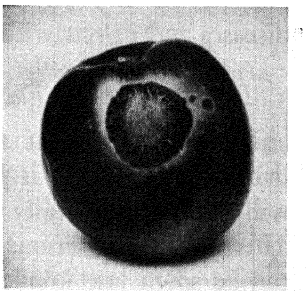


FIG. 7–15. Showing the damage to the apple fruit by the fungous disease known as scab.

plant. For example, an Apple-Spray Calendar may call for spraying as follows: *Delayed Dormant,* when leaves of blossom buds are out ¼ to ½ inch; *Pre-Pink,* when first tint of red shows in the central flower cluster; *Pink,* when majority of cluster buds are separated; *Petal Fall,* when most of the petals have fallen; *Cover Sprays,* three or four in number, the first 14 days after Petal Fall, and the others 14 days apart. For potatoes the recommendations are to apply the first spray as soon as the rows can be followed, later applications being made as often as necessary to keep all new growth covered. In the early season this means weekly applications, but later the period can be lengthened to 10 days.

In practice, fungicides and insecticides are frequently combined for application. Time and labor are conserved in this way. In the apple program fungicides are directed against scab (Fig. 7–15), frogeye, fruit spot, bitter rot, blotch, sooty fungus, and

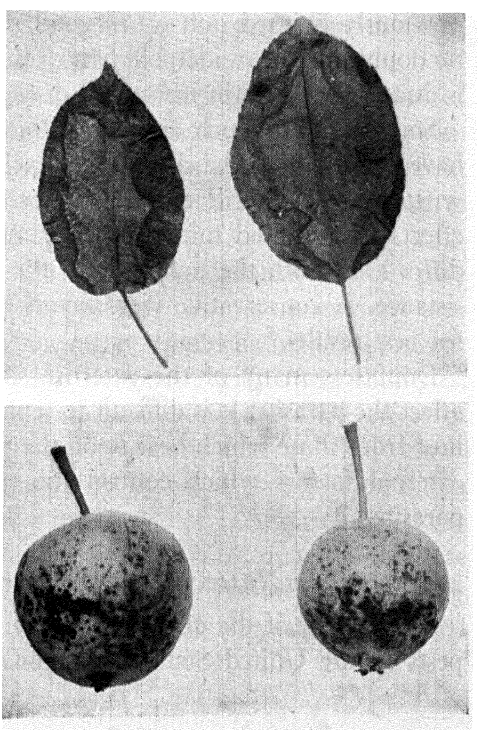


Fig. 7–16. Spray injuries to apple foliage and fruit.

other diseases. Insecticides are included against scale insects, codling moth, curculio, red mite, red bug, aphids, bud moth, leaf roller, and others. Sometimes a fungicide and two insecticides are mixed together for a single application. Much research is necessary to ascertain the best dilutions and proportions of fungicides and insecticides to secure effective control of diseases and insects without causing injury to foliage and fruit (Fig. 7–16).

3. *Use of External Factors to Reduce Liability of Attack*

There are a number of external conditions which have a bearing on the liability of attack. It is possible to take advantage of the conditions which will reduce the liability. A good example is to be found in the Hessian fly. This insect does serious damage to cereals, particularly wheat. The wheat can be sown late in the fall after the flies have emerged, laid their eggs, and died. It is authoritatively stated that "there are many years when a difference of a few days in the time of seeding will make the difference between a good crop and a very poor one, all because of the difference in the amount of infestation by the Hessian fly."

Other cultural practices aid in reducing attacks of insects. One of these is crop rotation. When crops of the same kind are grown in the same fields year after year the conditions are favorable for insect development. As previously pointed out, other good reasons favor crop rotation. There is no doubt that a considerable part of the increased production from rotation is due to reduction in insect and disease injury.

Soil conditions such as temperature, moisture, and supply of fertilizers have effects upon the degree of attack in some instances. Much has been written about the ill effects of excess nitrogen manuring and the good effects of increased mineral manuring (phosphate and potash). Opinions differ as to both the manner and the extent to which fertilizers affect resistance. A conservative view favors balance in the fertilizer constituents for best results.

Doubtless many of the external conditions which affect the crop also affect the parasite. It is difficult to separate the factors which bear upon the host from those which bear upon the parasite. In a later section we refer to external factors which control the spread, number, and activity of the parasite.

4. *Quarantines, Inspection, and Other Legislative Measures*

The history of the origin and spread of some of the serious diseases and pests in the United States is suggestive of what might be accomplished

by quarantine laws if they could be effective. The white-pine blister rust and the Dutch elm disease came into this country from Europe. The chestnut blight is believed to have been introduced from the Orient. Entomologists tell us that half of the serious insects with which we have to contend are imported. A few of them are the cotton boll weevil, codling moth, Hessian fly, European corn borer, and Japanese beetle.

The chief carriers of pests and diseases are the plants themselves. As a safeguard against the importation of new pests and diseases practically all countries have quarantine laws prohibiting or restricting the importation of plant materials. The laws may specifically prohibit plants or plant parts from certain regions because of the danger of parasitic organisms. Some countries provide an inspection service for all or certain plants, thus attempting to intercept diseases or pests at the port of entry. The United States maintains such a service through the Bureau of Entomology and Plant Quarantine of the Department of Agriculture. In some cases it is difficult to detect diseases even though the inspection be most thorough.

All our states now have regulatory laws preventing the entry of certain plants unless they have been inspected, and in some cases reinspection must be made at the destination. Nursery stock cannot be shipped interstate in the United States unless accompanied by a certificate of inspection declaring it free from pests and diseases. Such regulatory measures serve to check the spread of parasites but do not entirely stop their distribution.

Other legal enactments are concerned with enforcing the application of control or clean-up measures. The state of Massachusetts enforces the control of the gipsy and browntail moths. There are also state and national laws standardizing insecticides and fungicides, and making it necessary to label them properly as to content and efficacy.

There is no general agreement on the role that quarantines should play in insect and disease control. Some are opposed to them as unnecessary and undesirable. Others believe every possible effort should be made to prevent the promiscuous interchange of parasites between regions and countries. Objections are raised on the grounds that quarantines have the effect of trade barriers and so may come to have economic and political consequences. Retaliatory measures may be set up by other countries or states. The state of California has been active in the use of quarantines. A committee studying the efficacy and economic effects of plant quarantines there reached the conclusion that they "serve a useful purpose in preventing or delaying the spread of pests and diseases, provided they are maintained within reasonable and economic limits."

5. *Destruction of Parasites by Chemical Treatments of Plant, Seed, or Soil*

Some insects such as aphids, scale insects, and leaf hoppers have piercing mouth parts and suck their food from the plants. Such insects are not affected by the stomach insecticides used to coat the surfaces of plants. To destroy them contact poisons are used. Insecticides of this sort may be used in either liquid or dust form. They are not applied to plants in advance of attacks as preventives but are applied so that they will come in full contact with the insects. Insects not covered are not killed. Death of the insect is due to a poisonous action or to the clogging of the breathing tubes. Numerous contact insecticides are in use. Some of them are plant products and some are inorganic compounds. Nicotine, pyrethrum, and derris are the more important organic compounds. Nicotine is extracted from tobacco; it appears on the market as 40 per cent nicotine sulphate or under the trade name of "Black Leaf 40." Pyrethrum is prepared from the dried flower heads of a plant by that name. Derris and related compounds come from the roots of several leguminous plants. Rotenone is the name now used for the active principle of derris root extract. Other important substances are lime sulphur, oils, and soaps.

A new insecticide, DDT, came into prominence during World War II. Not only has there been much public excitement about this new product, aroused by stories of its remarkable use by the army and navy, but the entomological profession has shown its enthusiasm. A committee of entomologists has issued this statement, "We feel that never in the history of entomology has a chemical been discovered that offers such promise to mankind for relief from his insect problems as DDT." The designation DDT is derived from the chemical term "dichloro-diphenal-trichloroethane." The reaction of insects indicates that it is primarily a nerve poison. Experiments to date indicate that as a dust or spray it is promising against a variety of insect pests destructive to potatoes, fruits, vegetables, seed crops, and forests. More research is needed to reveal its qualifications and limitations and to determine its effects upon plants and soils.

Most fungicides are used as protective or preventive measures. We have explained how applications in advance of an attack serve to prevent fungous infection. There are some cases in which fungicides will kill by contact a surface fungus that is already established. Lime sulphur is used in this way for the control of powdery mildews. Eradicative or contact fungicides are used in the treatment of seeds to free them from fungous spores. Formaldehyde is used against bunt or stinking smut of wheat. Good results are obtained by treating various vegetable seeds with eradica-

tive fungicides before sowing them (Fig. 7–17). Copper, sulphur, and mercury compounds are used. Much progress has been made in the development of organic mercury compounds for seed disinfectants. A considerable number of diseases are effectively controlled by these products. To be successful the treatment must kill the fungi without materially injuring the

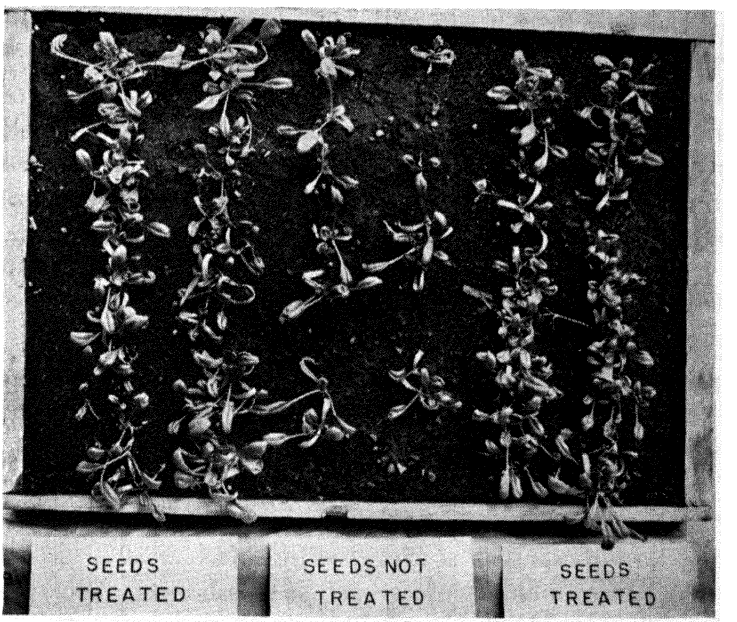


FIG. 7–17. Results of treating spinach seed with an organic fungicide.

seed. The margin of safety between avoiding seed injury and killing the fungi may be very narrow, and recommendations for the dilution and length of treatment must be followed carefully.

Insects are sometimes killed by fumigants, which are poisons in the form of gases. This method is frequently used against insects in greenhouses and mushroom houses, and for treating nursery stock, stored grains and seeds, and other plant products. When fumigants are used with live plants great care is necessary to prevent injury. Hydrocyanic acid (generated by the action of an acid on a cyanide) is the most extensively used fumigant. Extreme caution is necessary as it is one of the most deadly gases known. The risk to human beings and animal life other than insects must be constantly kept in mind. Carbon bisulfide and nicotine are other fumigants. The burning of tobacco stems in greenhouses is a common practice.

Under some conditions both insects and diseases can be controlled by

their destruction in the soil. Paradichlorobenzene is commonly used in the soil about the roots of the trees for killing the larvae of the peach-tree borer. Soil treatments are most useful in greenhouses, hotbeds, and outdoor seedbeds. Soil used in such places sooner or later comes to harbor harmful organisms. It is difficult to obtain new soil for greenhouse use that is not already infested with organisms causing such diseases as damping-off of seedlings, and various root rots and wilts. Heat treatments of the soil are most generally employed, but when growers are not equipped for those methods, chemical treatments may be applied. Formaldehyde is one of the best chemicals because it is effective against nearly all soil fungi and bacteria when properly applied. Copper carbonate and organic mercurials are also used. Liming the soil has been found to be a reliable method of controlling club root of cabbage.

6. *Destruction of Parasites by Physical or Mechanical Means*

The grubs of some insects burrow into the bark and wood of trees at the base of the trunk. They are called borers. For the apple-tree borers about the only successful remedy is digging or probing them from their burrows. Sticky bands are often placed around tree trunks to combat climbing insects. The destruction of insects or of egg masses by hand is sometimes practicable. Furrows or trails of heavy oils have been used as barriers against crawling insects such as army worms. Mechanical devices are sometimes employed for catching insects such as grasshoppers. Such mechanical processes as plowing and hoeing frequently play a part in the control of soil pests, especially if carried out at the right season.

Partial soil sterilization by heat, known also as soil pasteurization, is a common physical method of pest and disease control in greenhouses and seed beds. We have referred in an earlier paragraph to the need of destroying harmful organisms in the soil. It should be understood that there are many beneficial soil organisms. Complete sterilization might do as much harm as good. Partial sterilization by steam can be accomplished in a manner that will inactivate many of the harmful organisms without injuring most of the beneficial ones or without greatly altering the amount of soluble salts. Heating with electric elements has proved satisfactory for small batches of soil.

Heat may be applied to seeds to free them from insects. Insects which attack stored grains can be killed by heat treatment. Mills and elevators are often equipped to clean grain in this way. There are also heat-treating machines on the market. Loose smut of wheat is perpetuated by an internal infection of the grain. It has been found that the embryo of the

wheat kernel will stand a temperature that is high enough to kill the fungus. A hot-water treatment of the wheat kernels can be carried out successfully.

7. Use of External Factors to Reduce Activity of the Parasites

There are certain cultural practices which tend to reduce the activities of pests. Clean cultivation during the egg-laying periods of some of the crop insects, or plowing at times when they are in the larval condition, is recommended. The destruction of crop residues may be an important factor. A clean-up of corn stalks and refuse is one of the means of fighting the European corn borer.

Man has found out through his study of entomology that the insect enemies of plants may in turn have their enemies. Many may play a part in the biological struggles which are constantly taking place. And so it comes about that we have the possibility of biological control methods for plant pests. It is well known that many birds feed on insects. Encouraging the development of insectivorous birds is one of the methods of biological control. Less well known is the fact that insects prey on one another. The possibility of reducing the activities of plant-feeding insects by introducing their insect enemies is well established. The cottony cushion scale of citrus fruits was introduced into California from Australia and spread with such rapidity that it became a serious threat to the citrus industry. The insecticides then in use did not control it. A few years later the introduction of the Australian lady beetle solved the problem. Many other examples could be cited. There seems to be no question about the beneficial results achieved by the introduction of insects to check other insects.

It is also known that there are fungi which are parasitic on insects. Attempts to use fungi as biological control agents for plant insects "by their introduction into localities where they are absent, have never met with the success of the *insect versus insect* work." The possibility of using fungi as enemies of disease fungi has not been overlooked, but practical results are lacking.

8. Eradicative Measures

Most of the measures for protecting plants discussed thus far are designed to keep pests and diseases under control. The possibility of excluding parasites by quarantines has also been discussed. There remains for consideration the question whether it may be possible not only to reduce and restrict plant enemies but even to eradicate them.

Entomologists and plant pathologists have long recognized that there is

a possible place for eradication in the fight against plant diseases and pests. In recent years the public has come to realize the dangers from the establishment of new plant diseases and pests, and authority and funds for some eradication programs have been made available. Two extensive projects have been carried out in Florida, one with the Mediterranean fruit fly and

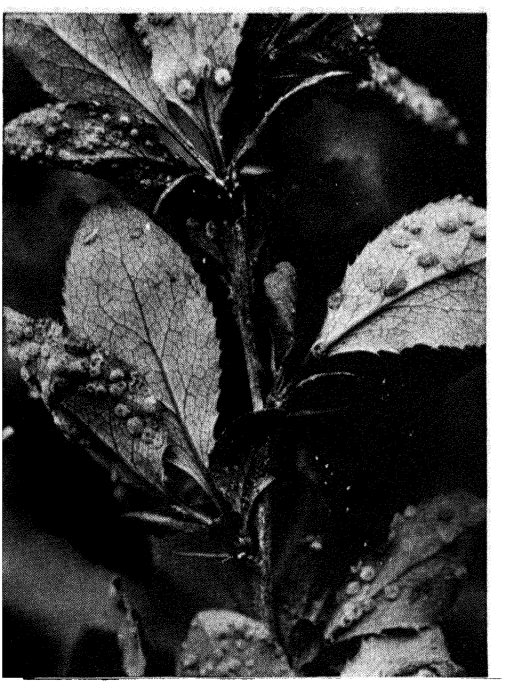


FIG. 7–18. Black stem rust of wheat as it appears on the barberry. (Photograph, courtesy U. S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.)

the other with citrus canker. Apparently both pests have been eradicated. Whether such programs should be undertaken can be determined only after thorough consideration from biological, economic, and sociological points of view.

There are some remarkable parasites which require two separate kinds of hosts for the completion of their life cycles. A considerable number of the plant rusts behave in this manner. Black stem rust of wheat and other cereals has the common barberry as an alternate host (Fig. 7–18). Apple rust has the red cedar as an alternate host. White-pine blister rust has gooseberries and currants as alternate hosts. The eradication of the alternate hosts has proved a valuable aid in controlling such diseases. On this point

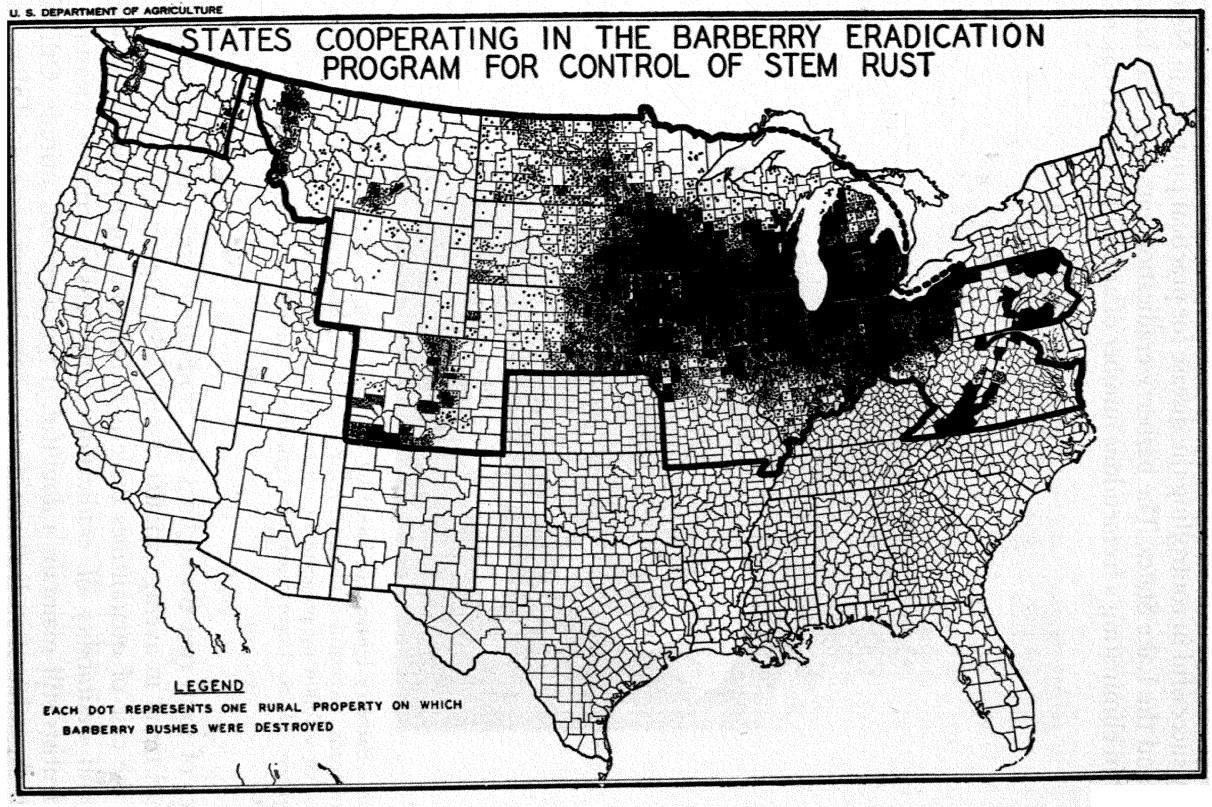


FIG. 7–19. Map showing the extent of the barberry eradication program in the United States (self-explanatory). Similar programs have been carried out in other countries. (Courtesy, U. S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.)

Stakman writes: "The white-pine blister rust campaign was not successful in completely eradicating the disease from the United States but it has been eminently successful in controlling the disease for practical purposes in New England and the Lake States. The barberry eradication campaign has been successful in eliminating a tremendous number of annual local and regional

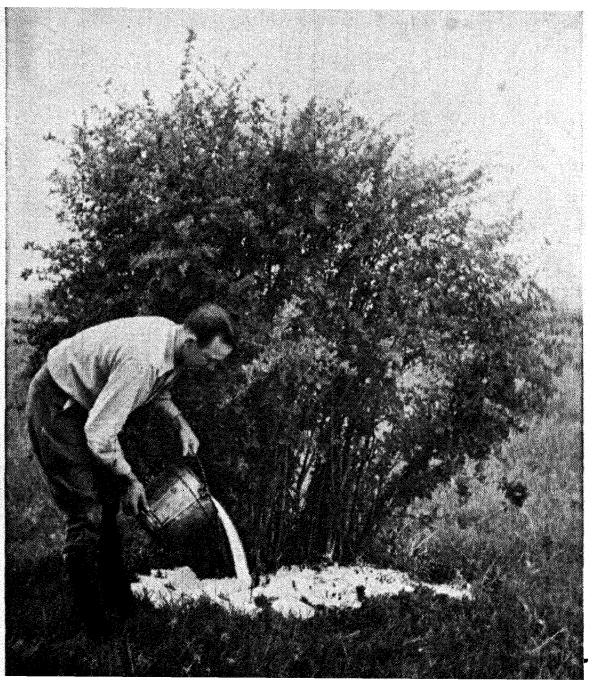


FIG. 7–20. Barberry bushes are killed by the application of salt. Since plants are produced from seeds, successful eradication must provide not only for destruction of all existing bushes but a follow-up program in succeeding seasons to destroy new plants. (Photograph, courtesy U. S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.)

epidemics of stem rust throughout the eradication area and in causing a downward trend in average annual losses." (See Figs. 7–19, 7–20.)

As in the case of quarantines there is a difference of opinion as to the efficacy and desirability of eradication campaigns as control measures. Many scientists still maintain a doubtful, if not skeptical, attitude. Others believe in the value of such campaigns as control measures even if they do not completely eliminate the pests or diseases.

PART II

THE PERPETUATION OF LIFE

(*Racial Preservation*)

CHAPTER 8

THE FORMATION OF NEW INDIVIDUALS

(*Reproduction*)

The manifestation of life is through the individual; the perpetuation of life is through the race. If we would understand life we must study individual maintenance and racial preservation.

Whether they be plants or animals (including man), individuals must obtain food, must elaborate it into living substance and utilize its energy, must adjust themselves to their surroundings, and must be able to survive the attack of pests and diseases. Nutrition, assimilation, respiration, adjustment, and protection—upon these the existence of the individual organism is dependent.

The duration of the life of individuals is limited. This is a familiar and fundamental fact. Death ensues sooner or later. The decayed remains of plant and animal bodies form an important part of the soil. Obviously if life is to be perpetuated there must be replacement of old individuals by new individuals; this is brought about by the process of reproduction. No scientist today believes in the spontaneous generation of living things as we know them. All existing individuals are descended from preexisting ancestral forms. As life has marched on, there has been "an unbroken continuity in the chain of living things."

Reproduction is a vital process which must be exercised to continue life from one generation to another. Reproduction in plants and animals is fundamentally similar both in meaning and in method. The great apparent differences are in external features connected with differences in habits of life. The central fact in reproduction is the formation of new individuals capable of growing into kinds essentially like those which produced them.

METHODS OF REPRODUCTION

The processes of reproduction in the plant kingdom are varied; and although they seem to be numerous, they are ordinarily grouped in two main categories. The simpler of the two categories is *vegetative reproduc-*

tion; the other is distinguishable as *sexual reproduction.* In vegetative reproduction certain cells or cell bodies are separated from the body of the parent and develop directly into a new individual without undergoing any further reactions. In sexual reproduction two kinds of reproductive cells called *gametes* are formed which initiate further development after their fusion with each other. Neither kind of gamete undergoes further development by itself; but when there is opportunity for a reaction between them known as gametic union, a series of events follows that may include a cycle in which two generations alternately occur. In many plants the vegetative mode is adequate to secure the reproduction and multiplication of the species, and yet the sexual mode occurs in the majority of plants, both simple and complex.

The occurrence of the sexual method in plants in which the vegetative method is sufficient for the perpetuation of the species, and its establishment in early evolutionary history, suggest that the gametic method may bear an important relation to the welfare and preservation of plant species. The significance of sexual reproduction is not easily apparent. The reason for its widespread existence must be not merely to bring about reproduction, but to answer some purpose not attained by the vegetative method.

One theory holds that sex "exists not for the sake of formation of offspring but for giving it a more certain and better start in life." When two gametes, which inherit characters from two independent lines, unite to develop a new individual there is a possible new combination of characters. Accordingly the significance of sex lies in the fact that it multiplies individual variation. It is well to keep these suggestions in mind in giving further consideration to the subject of reproduction.

There is an intimate relation between cell division and reproduction. Whenever an individual cell divides to form two new cells, it performs the function of reproduction. The result of cell division may be the growth of an individual body or the restoration of its wasted tissue. When an individual is a single cell, cell division followed by separation results in reproduction. The fundamental basis of reproduction is cell division. As ordinarily applied, reproduction means the production and development of new and independent individuals. Separation from the parent is necessary if independent offspring are to be formed. The formation of a branch is not reproduction so long as the branch remains attached; but if it is separated and becomes rooted, this constitutes reproduction.

The unit which is formed and separated to begin the development of a new individual is frequently a single microscopic cell, and one or two

parents may be involved. A reproductive cell—a spore or the united gametes—possesses all the capacities for the formation of a complete individual. The development of a highly organized adult body from such a small initial mass of protoplasm is an extremely interesting and amazing phenomenon. The formation and detachment of the reproductive protoplasm are accompanied by both the vigor and the organization that enable it to develop into a new individual manifesting both the general and the special characters of the preceding generation. As has been pointed out, the vegetative and growing body eventually dies, even though the general conditions of life continue to be favorable; but "racial vigor is periodically renewed in each generation."

Many times offspring do not find suitable conditions for their development. There may be great mortality. It is not sufficient that one individual be able only to replace itself. To insure mere replacement of old individuals there must be the possibility of starting several to many offspring, so severe may be the conditions under which they must develop. There is usually provision for possible multiplication. Sometimes the provision is lavish and yet there may be no appreciable increase in the number of mature individuals. It has been estimated that a poplar tree may produce 28 million seeds. Such fungi as toadstools and puffballs produce spores in quantities sufficient to defy calculation. According to estimates, a single large puffball may produce several trillion spores. It could be that the world would be filled with these fungi in a short time if even a small percentage of the possible offspring reached maturity. Actually so many perish that even such a remarkable provision for multiplication often results in a species just holding its own.

The formation, separation, activity, and multiplication of reproductive bodies are fundamental features of reproduction. The many kinds of living organisms differ more or less from each other in the ways in which these essentials have been met. The significance, however, is the same for all, and in general there is more similarity than difference in their fulfillment.

VEGETATIVE REPRODUCTION

Reproduction by the vegetative method occurs generally throughout the plant kingdom. This is the most direct method by which new plants can come into existence. The vegetative mode of reproduction takes on various aspects in the different groups of plants. In the higher plants the parts which give rise vegetatively to the new individuals are multicellular in

structure. In the lower plants single cells may bring about reproduction. Whether the cells which serve for vegetative reproduction do so as groups or singly, they may or may not have a special form and method of develop-

FIG. 8–1. After a stalk of the banana plant has produced a bunch of fruit, it dies; in the meantime suckers have arisen from the rootstock to take its place. (Photograph, courtesy of the Department of Agriculture and Commerce, Puerto Rico.)

ment. The condition of importance is the separation of the part, whether multicellular or unicellular, from the parent so that new individuals come into existence. The separation may occur naturally or may be promoted by man.

Special Vegetative Structures

Many flowering plants reproduce through special vegetative structures such as suckers (Fig. 8–1), tubers, bulbs, or corms. Rhizomes are under-

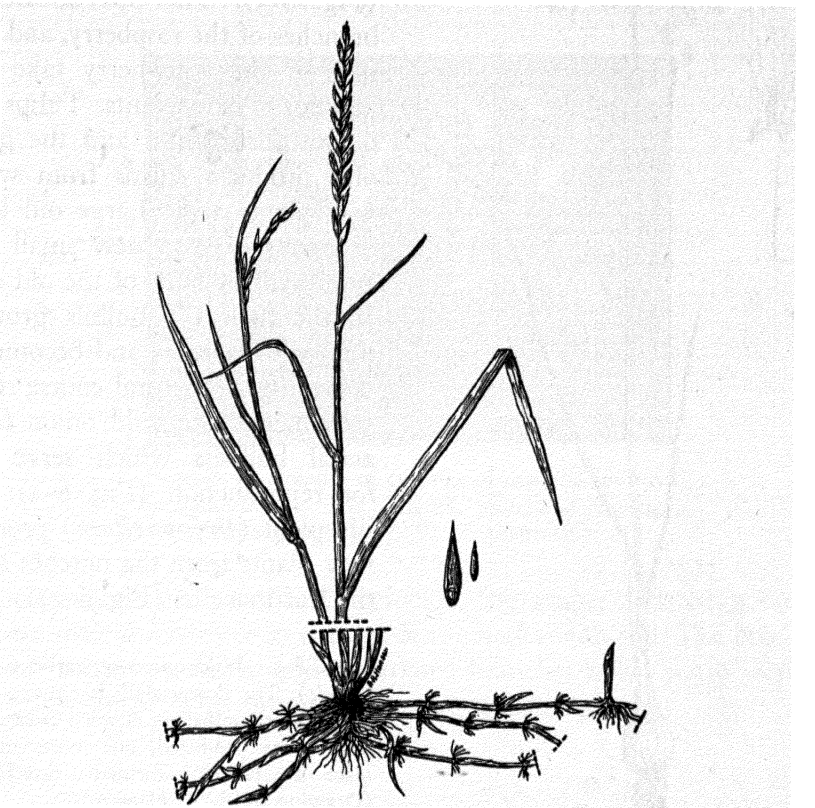


FIG. 8–2. Showing the origin of aerial shoots from buds at the nodes of the creeping rootstocks of quack grass (*Agropyron repens*). (Drawing by A. A. Hansen.)

ground stems which elongate each year by the growth of terminal buds. From the nodes of rhizomes, roots and aerial shoots (Fig. 8–2) develop and become separate plants by the death of the connecting parts (internodes). Grasses, ferns, and many other plants multiply in this manner. In the potato the tips of rhizomes develop into

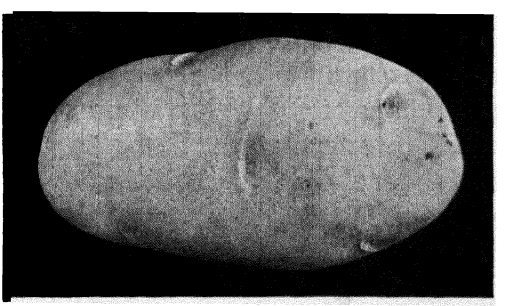
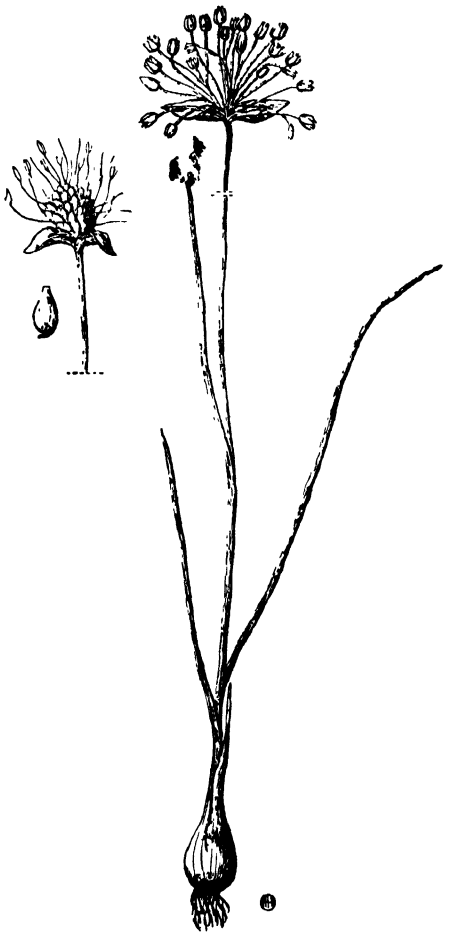


FIG. 8–3. Tuber of potato showing the buds (eyes) from which new plants develop.



fleshy tubers. When planted after a rest period, new plants develop from the buds (eyes) of the tuber (Fig. 8–3). The tips of arching branches of the raspberry, and runners of the strawberry take root and form new plants. Tulips and onions form bulbs and the gladiolus produces corms from which new plants arise. Large old bulbs or corms develop new small ones from axillary buds of the old ones. In the tiger lily bulbils grow in the axils of leaves and become detached in the natural course of development. The wild onion forms aerial bulblets which serve well for reproduction (Fig. 8–4). The life plant (*Bryophyllum*) produces new plants from the notches along the leaf margins (Fig. 6–24).

FIG. 8–4. Wild onion or garlic (*Allium vineale*). The flower stalk is crowned with one or more umbels of flowers. Occasionally flowers are produced, but more often in place of a flower is formed a tiny bulblet. (Drawing by A. A. Hansen.)

Cuttings

Man brings about vegetative propagation among many cultivated plants by taking advantage of these natural methods. The techniques employed by him may involve stems, leaves, or roots. Parts of these organs cut from a plant and partly buried in moist sand or soil frequently become rooted and produce new plants. Stem cuttings are frequently made from the geranium. New roots form from a spongy outgrowth of the cambium formed at the basal end of the cut stem. Willow twigs when placed in soil grow roots from the buried nodes, and branches from the buds above ground. In this way separate plants are readily produced. Some kinds of plants do not initiate adequate roots at the cut surface of a stem. In a number of such instances the application of growth-promoting substances

results in a successful rooting of the cuttings (Fig. 8–5). Some nurseries are now using this method commercially for hard-to-root cuttings. It has been found that there is a great advantage in such a method because cuttings with many roots develop faster than those with only a few roots. The stems

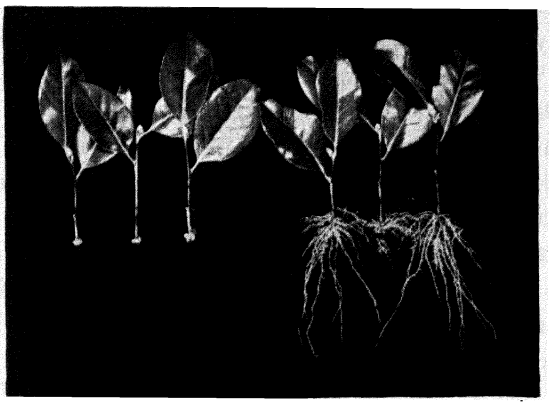


FIG. 8–5. Rooting of cuttings of camellia induced by indolebutyric acid (right); untreated cuttings (left). (Photograph by P. W. Zimmerman.)

of some plants, such as the honeysuckle, the grape, and the gooseberry, are bent over and covered at the tips or the nodes with soil. The production of roots is thus promoted and the rooted branches may then be separated and transplanted. This process is known as layering.

Grafting

Grafting is an artificial method of propagating cuttings which do not root readily. In this process, a cutting from one plant is attached to the stem or root of another plant, so that the two grow together to form physiologically a single plant. The cutting is known as the *scion,* and that to which it is attached is the *stock*. Ordinarily such unions are possible only between plants which are closely related. One variety of apple may readily be grafted upon another variety. Plums, peaches, and apricots may be grafted one upon the other. In practice, there are several different methods of inserting the scion. In all of them, care is taken to have contact between the cambial regions of the stock and scion. The cutting which is used as a scion retains its identity just as if it were rooted in the soil. Budding is a special form of grafting in which the cutting is a bud instead of a twig. The bud, which is left attached to a small piece of bark, is inserted under the bark of the stock.

Clones

The various kinds of vegetative reproduction, whether occurring naturally or at the hand of man, may annually give rise to multitudes of new individuals in the group of flowering plants. The new individuals are in all respects inherently like the parent plants from which they have been separated. They are, in fact, merely isolated parts of the original plant and possess all of its characters. The situation is readily understood when vegetative propagation by cuttings is considered. The new individuals are as much alike as are the branches of the plant from which the cuttings are taken. A group of individuals of common vegetative origin is called a *clone*. In several cultivated plants all the individuals, wherever they are growing, collectively constitute a clone, because they are perpetuated only by vegetative propagation. This is true among varieties of potato, grape, pineapple, and many ornamental plants. Although new individuals propagated vegetatively may be strong and capable of flowering and fruiting, they often require several years of growth before maturity for such production is reached.

FIG. 8–6. A liverwort plant (*Marchantia*) showing cups on the upper surface containing gemmae, special vegetative reproductive bodies.

In Liverworts and Mosses

In some groups of plants, such as the liverworts and mosses, vegetative reproduction may be accomplished without the development of special structures. By a system of branching, large colonies are produced. Separation of such colonial groups may be brought about in various ways, thus resulting in the establishment of new individuals or new colonies. On the other hand, in some liverworts special vegetative reproductive bodies known as *gemmae* are produced. In the liverwort *Marchantia* (Fig. 8–6) these gemmae are green biscuit-shaped bodies arising in cup-shaped outgrowths on the upper surface of the plant body (*thallus*). New plants are formed by growth and development of the gemmae. When conditions are favorable, *Marchantia* multiples abundantly in this way.

In Algae and Fungi

In the bacteria and certain algae, the individual consists of a single cell. These cells divide into two cells and when they become separated reproduction has been accomplished. In such instances it is obvious that reproduction is brought about by a simple division of the vegetative body followed by separation.

Other algae, and many fungi, have comparatively simple vegetative bodies, but they consist of many cells permanently joined. In these the regular division of vegetative cells results in the growth of the multicellular body. In such instances, increase in the number of individuals may be brought about by a modification of the ordinary process of cell division in which special cells, or cell groups, are formed and detached. The cells which become detached and serve the purpose of vegetative reproduction are known as *spores*. Most spores are single cells; some have thin delicate walls and others have thick hard walls. Spores in some plants are produced by cells which functioned previously as vegetative cells; in other plants they are formed in special organs or on special branches. Receptacles in which spores are produced are commonly called *sporangia*. Spores produced on the aerial parts of plants are usually distributed by air currents; those produced by water plants usually are able to swim by means of the movement of thread-like extensions called *cilia*. With either method of distribution many spores are not likely to arrive at places suitable for growth. Their production in great numbers makes it probable that some will find the proper conditions.

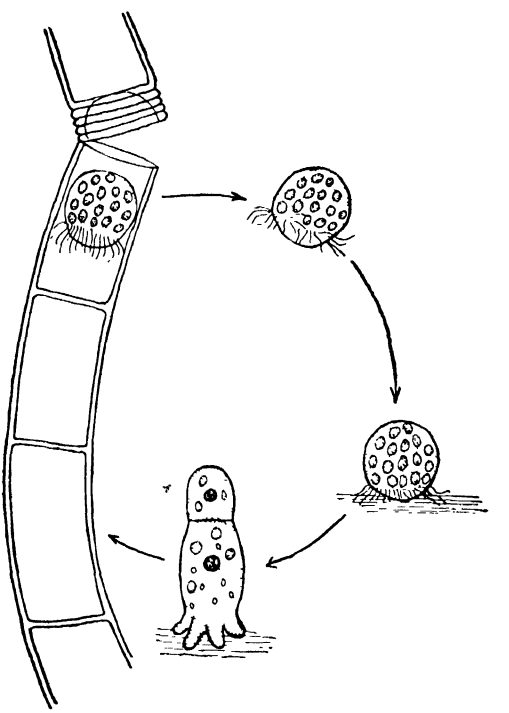


FIG. 8–7. Vegetative reproduction in the green alga (*Oedogonium*). The protoplast of a vegetative cell develops into a zoospore, which later escapes and grows into a new plant.

Algae are lower plants that usually grow in water. Some algae consist

of a simple chain of cells holding together end to end, thus forming a thread or filament. *Oedogonium* is a filamentous, unbranched green alga. The cells cling together firmly. In vegetative reproduction the living content of a cell (protoplast) becomes detached from the wall and forms a rounded body within the confines of the wall. A circle of cilia develops at one end and the vegetative protoplast has been transformed into a spore.

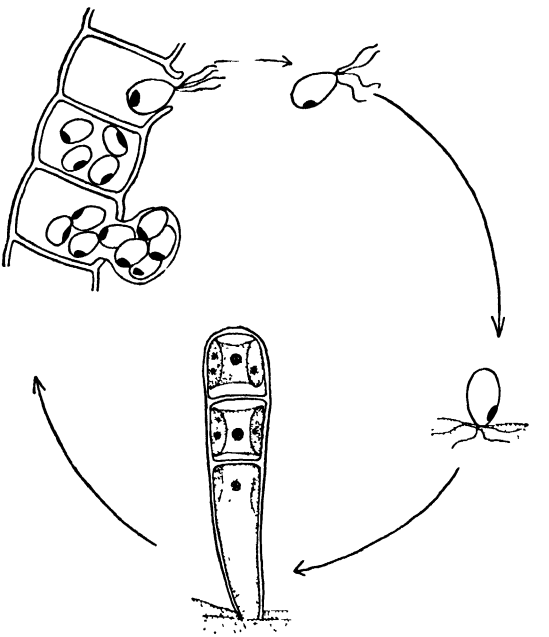


FIG. 8–8. The formation of zoospores in the green alga, *Ulothrix;* see text for explanation.

Later the wall splits and the spore escapes and swims about. Presently the spore settles down, withdraws its cilia, forms a new wall, and by divisions builds up a new chain of cells—a new individual (Fig. 8–7). The escaped protoplast, called the spore, does not differ from the other protoplasts, which do not escape, in capacity but rather in opportunity, for apparently all the vegetative cells with the exception of a few at the base are capable of behaving in a similar manner. Spores which swim by cilia are known as *zoospores,* because their behavior is suggestive of some of the simple animals. They are often produced not singly but in numbers, and for this reason they are also called *swarm spores.* In another filamentous green alga, *Ulothrix,* a vegetative protoplast may divide to form 2, 4, 8, or 16

daughter protoplasts, each of which rounds up, forms cilia, and becomes a spore (Fig. 8–8). Here the term swarm spore is appropriate. Each spore has four cilia. The spores escape through a pore in the side of a vegetative cell wall and after swimming about for some time come to rest and develop into new filaments by division and growth.

Among the fungi are to be found many examples of spores which are scattered by the wind. Fungi belonging to the group known as the powdery mildews appear during the summer and autumn on the leaves of various plants, producing a characteristic powdery appearance. A common mildew (*Microsphaera*) lives on the leaves of the lilac. The vegetative filaments (collectively known as the *mycelium*) grow on the surface of the leaves and send some branches into the interior of the leaves. Other branches of the mycelium grow outward from the leaf surface. By successive cell division a chain of spores is produced by these branches (Fig. 8–9). Fungous spores forming in this manner are called *conidia.*

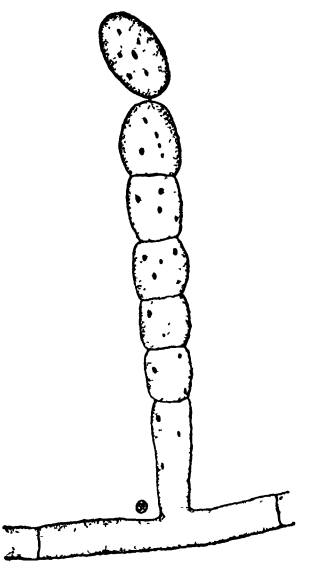


FIG. 8–9. Vegetative reproduction in a mildew. A mycelial branch is dividing into a chain of conidia. (Drawing by Edna S. Fox. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

They are easily detached and distributed; and since they start growth at once, they are responsible for the rapid spread of the mildew to other leaves during the growing season. Other fungi reproducing vegetatively in conidia are the blue-green molds. In some of these (*Penicillium*) the conidia are borne in chains at the ends of much-branched filaments (*hyphae*). In others (*Aspergillus*) a filament ends in a spherical swelling from which radiate many branches bearing chains of conidia.

In many plants reproduction is effected through the separation of single cells, sometimes combinations of cells, from the vegetative body. They may be transformed vegetative cells or they may have a special form and method of development. Regardless of the manner of production, cells which serve the purpose of vegetative reproduction are called spores. They are propagating units which grow directly into new individuals.

SEXUAL REPRODUCTION

Some one-celled forms and other simple colonial plants are not known to produce gametes. Most plants, however, both lower and higher, produce special cells called *gametes* which unite in pairs. The union of two cells to form one cell is itself the opposite of reproduction, but it is the initial step of a development which results in reproduction. In the majority of organisms, both plants and animals, the gametes which fuse are different in size and structure; in some plants and in most animals there are also physical differences between the individuals producing them. These physical differences are sexual differences recognized as maleness and femaleness. The type of reproduction which includes the union of the gametes, and the sequence of events which follows, is therefore called *sexual reproduction.*

The cell formed by the union of two gametes is called a *zygote.* The gametes have equal numbers of *chromosomes* in their nuclei. It is evident that gametic union results in a double number of chromosomes in the zygote. There is always a subsequent process—this is the reverse of

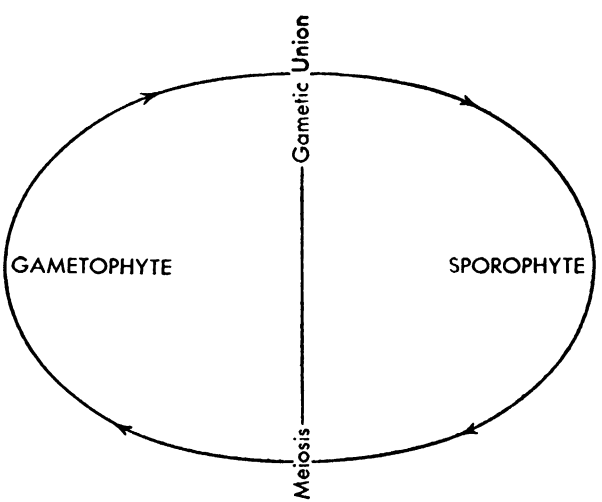


FIG. 8–10. Diagram of alternation of generations.

the union—which results in the restoration of the single number of chromosomes. This process is known as *meiosis* (a term meaning "lessening"). In the higher plants the zygote grows into a vegetative generation, all the cells of which have a double number of chromosomes until meiosis occurs. The reproductive units resulting from meiosis are single cells called

meiospores. The meiospores develop into a vegetative generation which is unlike the vegetative generation produced by the zygote, in which all the cells have the single number of chromosomes. The life cycle, therefore, includes two vegetative generations. When the gamete-bearing generation (gametophyte) gives rise through the zygote to a meiospore-bearing generation (sporophyte), and this gives rise through its meiospores to a gamete-bearing generation, there is an *alternation of generations* (Fig. 8–10).

An account of the principal events in sexual reproduction must include consideration of the gametes and their differences, the zygote and its behavior, the production of meiospores, and the alternation of generations. Ordinarily there is a definite sequence of developments and it is necessary to understand the order of the processes and of the production of the various structures. To do this it is best to learn what happens in certain selected plants without attempting to give attention to the deviations from the usual sequence which may occur.

The Formation of Similar Gametes

A simple type of sexual reproduction takes place in a filamentous green alga, *Spirogyra,* which is commonly called a pond scum. The vegetative body is a filament composed of cylindrical cells placed end to end. In this plant gametes are protoplasts which previously carried on vegetative functions. When conditions are right for sexual reproduction, usually in the spring or autumn, pairing of the gametes takes place between adjacent cells of parallel filaments. The union of the gametes is made possible through a tube which develops between opposite cells (Fig. 8–11). Each cell wall of a pair grows a projection. The projections meet and the walls at the point of contact are absorbed so that a tube leading from one cell to the other is formed. The protoplast of one cell shrinks and becomes detached from the wall, and a little later the other protoplast behaves in a like manner. These contracted protoplasts are gametes. The gamete which formed first migrates through the connecting tube into the other cell cavity. There the two protoplasts unite to form a zygote, the union involving both cytoplasm and nuclei. This union of two gametes into one structural and functional unit is the basis of sexual reproduction. When the two gametes are similar in size and structure the process of union is known as *conjugation.*

In *Spirogyra* the zygote develops a thick wall and is resistant to freezing and drying. By the disintegration of the walls that enclosed the gametes the zygote is eventually set free. After an interval of several weeks—or it

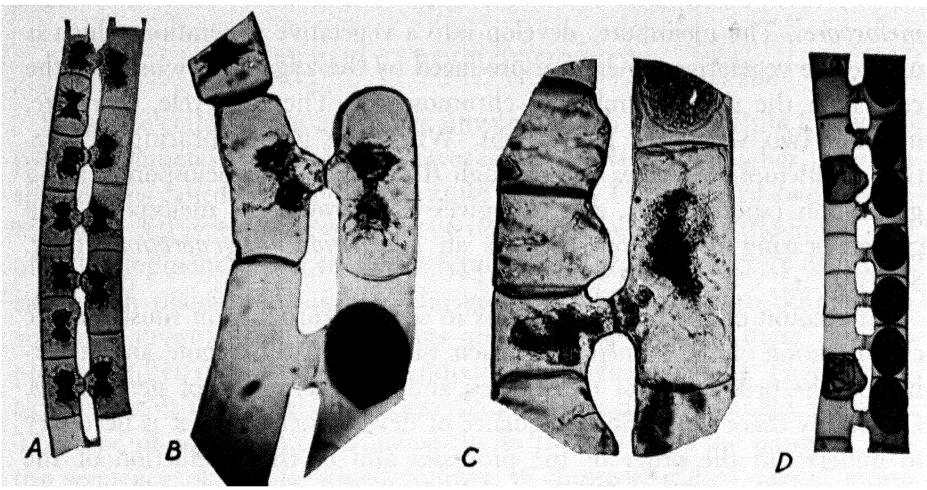


FIG. 8–11. Reproduction in two filamentous algae. *A*, two paired filaments of *Zygnema* showing early stages of conjugation; the protoplasts are distinct, but the conjugation tubes have formed. *B*, the same under greater magnification; a zygote has formed in one cell. *C*, early stage, highly magnified, of conjugation in *Spirogyra*, showing beginning of migration of a gamete on the left. *D*, two filaments of *Spirogyra* after conjugation, showing dark zygotes on the right and empty cells on the left. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

may extend from one growing season to the next—the zygote germinates and gives rise to a new *Spirogyra* filament similar to the parent filament. By the time of germination the zygote nucleus has divided to form two daughter nuclei and these have in turn divided so that four nuclei are present. Three of these four nuclei disintegrate, but the fourth persists and from it are derived the nuclei of the cells of the new filament.

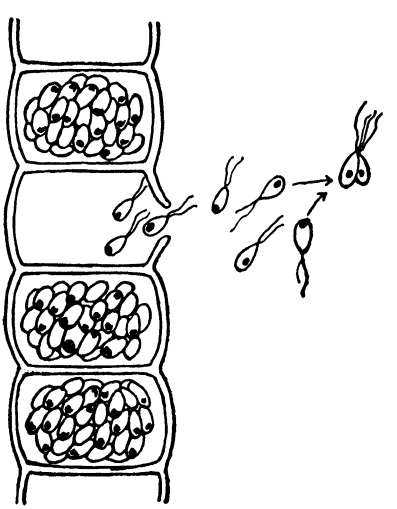


FIG. 8–12. The formation of like gametes in *Ulothrix*.

The formation of zoospores in the green alga *Ulothrix* was described earlier. In other filaments, or sometimes in cells of the same filament, gametes are formed in the same manner as the zoospores (Fig. 8–12). The gametes are frequently smaller than the zoospores because the original vegetative protoplast may have become subdivided by additional divisions into 16, 32, 64, or 128 cells. These

small cells also differ from the zoospores in having two instead of four cilia. They escape and swim about as the zoospores do, but do not develop into new filaments as the spores do. They are gametes and after a time come together and unit in pairs. The conjugation of these similar gametes forms a zygote with four cilia which continues swimming for a time. Eventually the cilia disappear, a wall is formed, and the zygote comes to rest. When the zygote germinates there are formed 4 (sometimes 8 to 16) meiospores each of which may develop into a new filament.

The Formation of Differentiated Gametes

In the fresh-water alga *Oedogonium,* which has vegetative filaments resembling those of *Spirogyra* and *Ulothrix,* the production of gametes is different. There are two kinds of gametes which are quite unlike in size and in other respects. The small ones are male gametes, or *sperms;* the large ones are female gametes, or *eggs.* The sperms are produced singly or in pairs by the protoplasts of special small, disc-shaped cells. They have a collar of cilia, similar to that described from the zoospores of *Oedogonium,* and swim about after escaping from the walls surrounding them. The eggs are developed singly from the protoplast of a single vegetative cell. The egg does not develop cilia but remains within the old cell wall, although free from it. A pore or slit forms in the wall through which a sperm enters to unite with the egg (Fig. 8–13). The union of a sperm with an egg is called *fertilization* and results in a *zygote* or *fertilized egg.* The zygote in *Oedogonium* develops a thick wall and is ultimately set free by the disintegration of the enclosing wall of the former vegetative cell. Germination takes place after a rest period; the wall breaks and the protoplast forms four meiospores, each of which develops into a new filament.

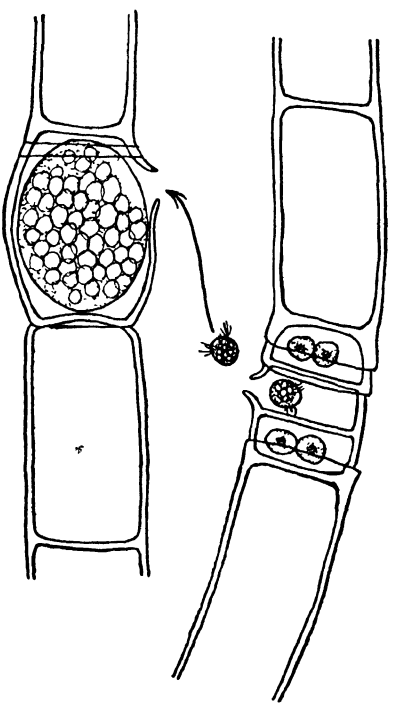


FIG. 8–13. The formation of unlike gametes in *Oedogonium.*

The differences between gametes such as exist in *Oedogonium* are recog-

nized as sexual differences. Here there is an obvious division of labor. The burden of effecting the union is on the small gamete which is active; the burden of providing nourishment for the zygote is on the large gamete, where there is opportunity for food storage. Such a differentiation exists in the gametes of many plants. Apparent structural differences usually are evident in the organs producing the unlike gametes. Sometimes the (individual) plants themselves show sexual differentiation. In some species of *Oedogonium* there are two kinds of filaments, one of them male and the other female, which may differ in size.

It is possible to express the facts in another way by saying that the differentiation is physiological where the gametes are alike, while it is physiological and structural where the gametes are unlike.

In another green alga commonly known as green felt (*Vaucheria*) the sperms and eggs are borne in special cells which were not previously vegetative cells. In this plant sexual differentiation has proceeded to the point where there are special sex organs, but individuals are not sexual since both organs are produced by the same individual (Fig. 8–14).

In some mosses which are more advanced the sex organs are borne by separate individuals. This is the case in the haircap moss (*Polytrichum*). The individuals bearing the sperm-producing organs (*antheridia*) are readily distinguishable from those bearing the egg-producing organs (*archegonia*). The former have rosette-like structures at the tips of the leafy branches which are lacking in the latter (Fig. 8–15). Here is a genuine structural basis for male and female individuals that is comparable in every way to the maleness and femaleness so familiar in the animal world. Animals have developed still further, producing male and female sex cells in different individuals which not only differ in stature and other visible ways, but which may differ also in dispositions and habits.

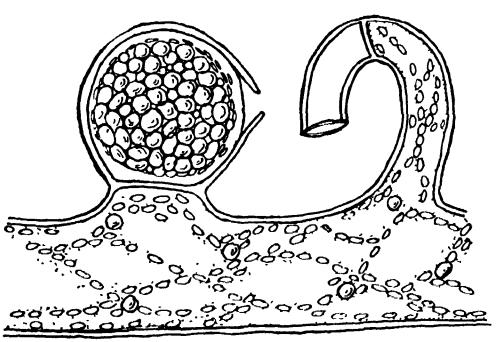


FIG. 8–14. The formation of unlike gametes, sperms and eggs, in special sex organs in the alga known as green felt (*Vaucheria*).

We are tempted to review this discussion of the production of unlike gametes in the words of an eminent botanist, who writes:

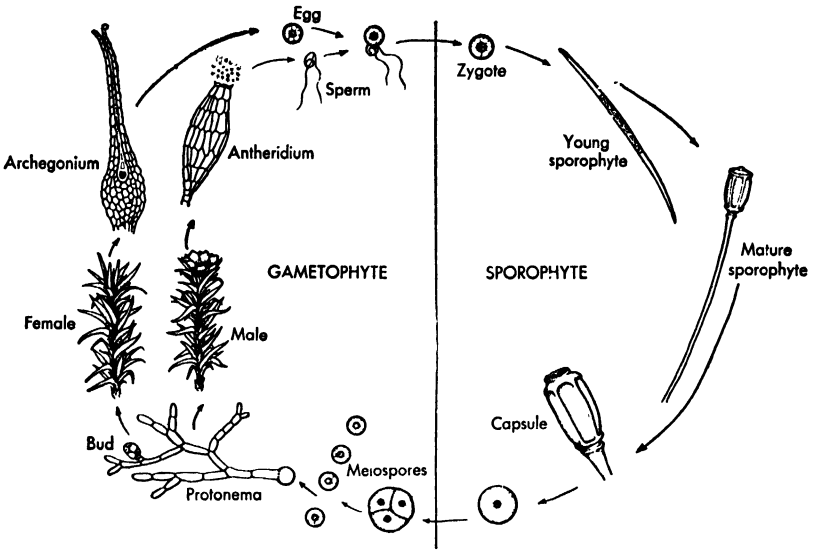


FIG. 8–15. Diagrammatic life cycle of the haircap moss, *Polytrichum*. On the left, note one gametophyte with rosette and the other gametophyte without this structure, the two representing maleness and femaleness, respectively. For further particulars see text and compare Fig. 8–16.

There runs throughout all sexual differentiation the one constant thread of the fusion of the two sex cells, which brings together the parental chromosomes in equal contribution to the constitution of the offspring. It is only the mechanisms subsidiary thereto which vary. These mechanisms originate in a way to imply that the two sexes were originally alike, and the differences between them arose through a division of labor, at first between the sex cells and later between the individuals which produce them, in connection with two subsidiary features of sexual reproduction,—viz. effecting the union of the sex cells, and nourishing (and later protecting) the offspring. Even in the highest plants and animals, sex seems to mean no more than this difference, developed to such a degree as to produce structures, organs, and even individuals, fitted to the respective parts taken by the sex cells. It is indeed possible that other factors are also involved in the result, but if so, they are obscure, while these are obvious.[1]

The Zygote and Its Behavior

The union of the gametes forms a *zygote*. The number of chromosomes in each gamete (sperm or egg) may be represented by n. The numerical value of n varies in different species. The zygote nucleus, therefore, contains $2n$ chromosomes. Sooner or later, through the process known as *meiosis*, the n number of chromosomes is reestablished. The process in-

[1] *A Textbook of Botany for Colleges*, by William F. Ganong, p. 308. Reprinted by permission of The Macmillan Company, publishers. Copyright 1916 by The Macmillan Company.

volves two nuclear divisions, but the chromosomes are divided only once. As a result, four nuclei are formed each of which has the *n* chromosome number.

In the green algae, to which reference has been made, meiosis takes place when the zygote germinates. All the vegetative cells of the filaments in these plants have the *n* number of chromosomes. The gametes, which are transformed vegetative cells, also have the *n* number. In these plants the zygote is the only cell that has the *2n* number of chromosomes.

In liverworts, mosses, ferns, and seed plants (and in many algae and fungi) meiosis does not occur when the zygote germinates. The zygote develops into a vegetative generation and the *2n* number of chromosomes is passed on to all its cells. Sooner or later this *2n* generation brings about a reduction in the number of chromosomes in a comparatively consistent manner. A *spore mother cell* possessing the *2n* number of chromosomes undergoes meiosis thereby forming four daughter cells called *meiospores,* each of which has the *n* number of chromosomes in its nucleus. The process of meiosis, so far as the chromosome number is concerned, is the reverse of gametic union. Nothing similar to meiosis occurs in the cell divisions which bring about vegetative growth.

The *2n* generation originates from the zygote. The spores produced by the *2n* generation give rise to the *n* generation which produced the gametes. In the liverworts, mosses, ferns, and seed plants, and in many algae and fungi there is a reproductive cycle involving the production of two generations alternately. In the algae and fungi there are many variations, but in

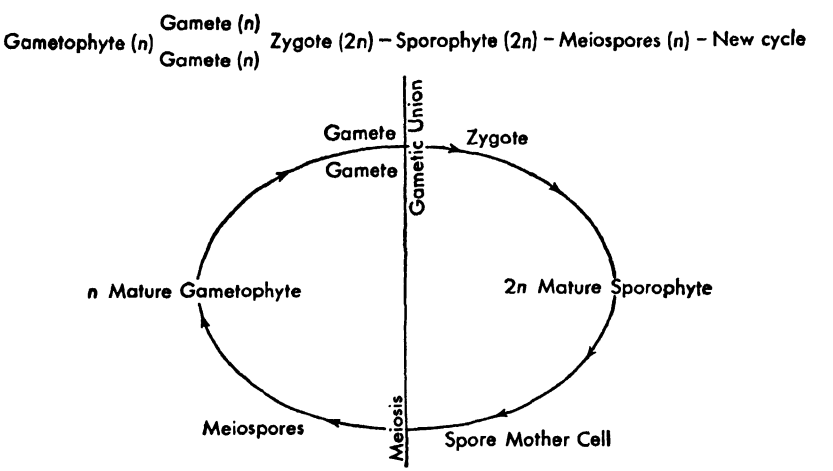


FIG. 8–16. Life-cycle diagrams of plants in which there is an alternation of generations.

the higher plants the pattern of alternation of generations is comparatively uniform. The *n* generation is called the *gametophyte* because it produces gametes. The *2n* generation is known as the *sporophyte* since it produces meiospores, originally called simply *spores*. The two generations together constitute a life cycle which can be expressed diagrammatically as in Fig. 8–16.

LIFE CYCLES IN THE HIGHER PLANTS

An understanding of sexual reproduction in the higher plants can be obtained by visualizing the life cycles with the generalized diagram which presents the sequence of the principal events. With the aid of graphic diagrams the cycles of different plants can be readily compared and their variations understood.

The Liverworts and Mosses

The genus *Riccia* is a simple liverwort (Fig. 8–17). The gametophyte is a small plant body (thallus) growing on boggy ground or floating on the surface of pools or ponds. The sex organs are embedded in a furrow on the upper surface of the thallus. The sperms are small cells that swim by means

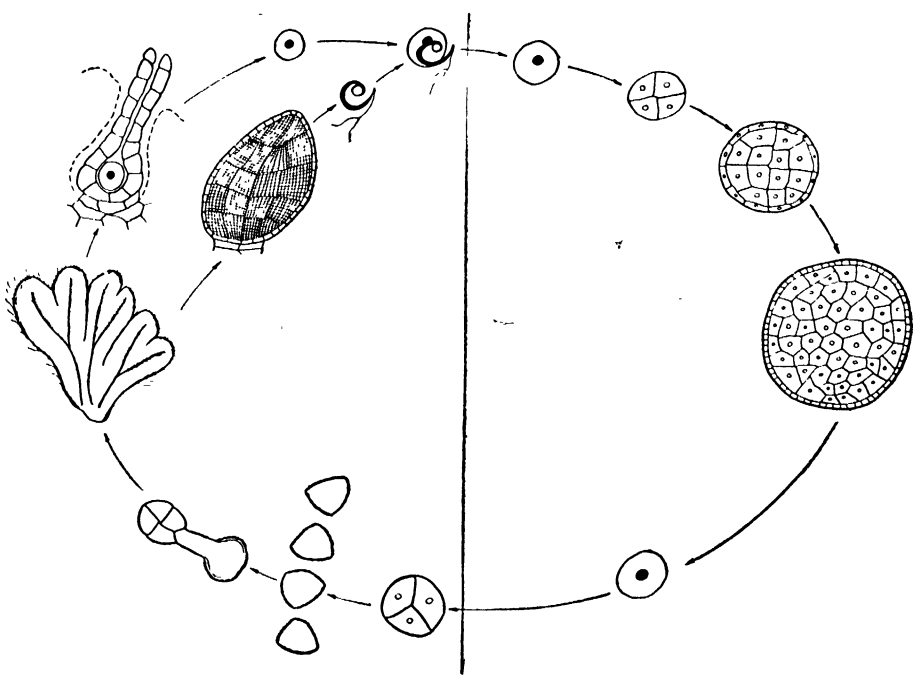


FIG. 8–17. Life-cycle diagram of the liverwort, *Riccia;* see text for explanation.

of two long cilia or flagella. They are borne in large numbers in multicellular bulb-shaped organs called *antheridia.* The eggs are comparatively large inactive cells. They are borne singly in the base (*venter*) of flask-shaped organs called *archegonia.* The egg remains in the venter of the archegonium. Sperms reach the egg through a canal which forms in the neck of the archegonium. The sperms appear to be guided to the egg by substances in the canal. Several may enter and one of them fuses with the egg.

The zygote develops into a sporophyte within the venter of the archegonium where the union of the sperm and egg took place. The sporophyte is a tiny spherical structure which at maturity consists of a mass of meiospores surrounded by a jacket of sterile cells, i.e., cells which do not develop into spores. In its development the internal cells of the globose mass function as spore mother cells and the outermost layer becomes the jacket. The mature sporophyte is in reality only a spore case (*sporangium*) containing meiospores. This sporophyte is a distinct generation but does not carry on an independent vegetative existence. Although capable of some photosynthetic activity it is largely parasitic upon the gametophyte generation. The spores are eventually liberated by the death and decay of the surrounding tissues. Each spore may give rise to a new gametophyte. The same gametophyte may bear both archegonia and antheridia.

In *Marchantia,* another liverwort (Fig. 8–18), both gametophyte and sporophyte are more complex than in *Riccia.* The gametophyte grows in moist locations on rocks or soil. Sex organs are borne on special upright branches. In the common *Marchantia* the male and female branches are borne on separate plants. Male and female gametophytes are indistinguishable except when bearing the reproductive branches. The antheridial branches consist of a stalk and a lobed disc. The archegonial branches are umbrella-like structures. Fertilization is effected by a sperm passing through the neck canal of the archegonium. Water is necessary for the swimming sperms. Fertilization takes place before the stalk of the female branch elongates to any extent.

The zygote, as in *Riccia,* develops within the venter of the archegonium, which enlarges so that the growing sporophyte remains enclosed. The sporophyte is not a simple globoid spore-producing organ as in *Riccia.* A considerable portion of the *Marchantia* sporophyte is devoted to nutritive and spore-distributing functions. It consists of three parts: (1) the *foot,* a vegetative structure attached to the gametophytic thallus and drawing water and food from it in a parasitic manner; (2) the terminal spherical *sporangium* in which meiospores are formed; and (3) the *stalk,* which elongates

and pushes the capsule away from the gametophytic tissue. The meiospores are developed by meiosis from spore mother cells. Intermingled with the spores are long cells with spirally thickened walls called *elaters* which,

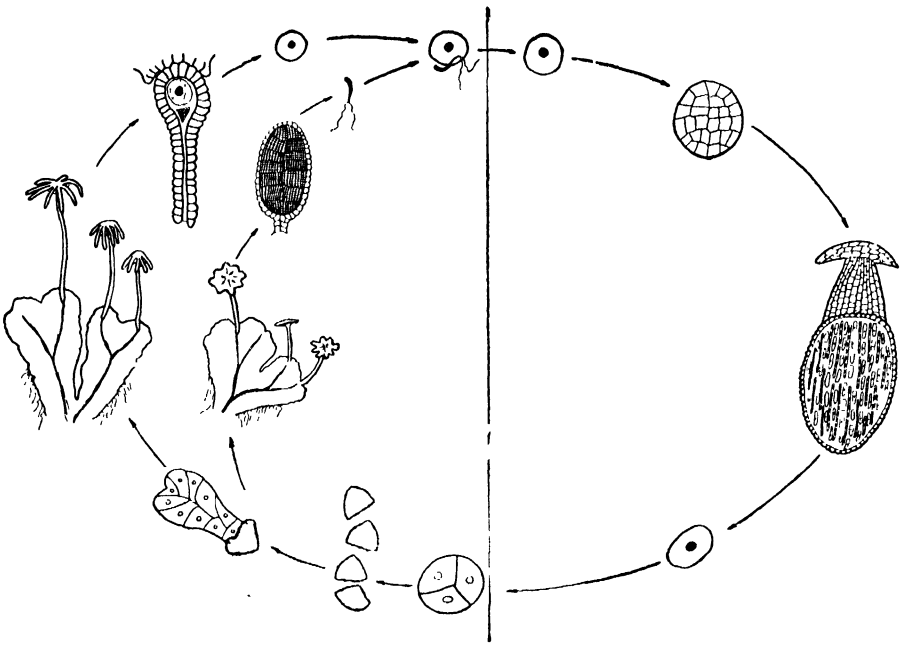


FIG. 8–18. Life-cycle diagram of the liverwort, *Marchantia*, see text for explanation.

through twisting movements as they become alternately moist or dry, aid in the dispersal of the spores. Each spore may give rise to a new gametophyte.

Although the mosses differ from the liverworts in several respects, the two groups have much in common and are closely related. In each group the gametophyte generation is the independent generation and the sporophyte generation is parasitic upon it.

The moss gametophyte begins its development as a branching filament of cells which resembles a green alga. This filament is known as a *protonema.* Groups of compact cells called buds develop on the protonema and these give rise to leafy shoots which are ordinarily called moss plants. The sex organs are borne at the tips of the leafy shoots. In some mosses both male and female organs are borne on the same shoot; in others the antheridia and archegonia are borne on different shoots. In the haircap moss (*Polytrichum*) the male individuals can be recognized by the terminal rosettes which are lacking in the female plants. (See Fig. 8–15.)

Fertilization takes place in the venter of the archegonium as in the liver worts. The zygote begins its development while still within the archegonium. The mature sporophyte is a leafless structure with three parts—a foot, a stalk, and a sporangium or capsule containing meiospores. The sporophyte appears to be growing from the tip of the leafy female gametophyte. Although apparently a continuation of the gametophyte it can be separated readily by a slight pull. The meiospores are developed in groups of four from spore mother cells and each one may develop into a protonema.

The Ferns

Most of the ordinary ferns are land plants. In their adaptation to growing on the land they are in contrast to the algae, which are water plants. Liverworts and mosses are in general land plants, but the ferns are above them in the scale of adaptation to life on the land, i.e., in the terrestrial habit. Capacity to flourish on the land, rather than in the water, is dependent both upon the methods of reproduction and upon the character of their vegetative bodies.

In the liverworts and mosses there is an alternation of reproduction by gametes and by meiospores. The male gametes are swimming sperms and their distribution, upon which the process of fertilization depends, can be carried out only in water. The spores are air-borne and their distribution takes place in the air. From our consideration of reproduction it is evident that this is an incomplete adjustment to terrestrial life. The vegetative generations also are not adapted for efficient water absorption and conduction, and for the prevention of water loss by transpiration.

In the ferns there are the same two alternating types of reproductive units. The sporophyte vegetative generation is what we know as the fern plant. With its roots, stems, leaves, and vascular system the sporophyte is adapted for terrestrial life. The male gametes, as in the mosses, are swimming sperms that require water for their transfer to the eggs. This makes clear the necessity for the gametophyte to live in a moist location and emphasizes the incomplete adjustment of the fern life cycle to terrestrial conditions.

The fern gametophyte is a small, independent, and separate vegetative generation known as a *prothallium* (Fig. 8–19). A fully mature prothallium is a thin, flat, heart-shaped plant varying from an eighth to a third of in inch in diameter. These little plants are so inconspicuous that they are rarely observed in nature. Nevertheless, a prothallium is just as much an

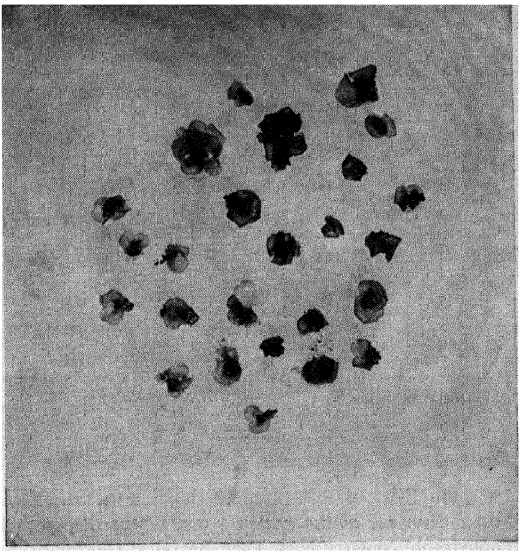


FIG. 8–19. Gametophytes (prothallia) of the spleenwort fern. Actually they grow in clusters but have been separated for the photograph; about natural size. (Photograph by Albert Kligman.)

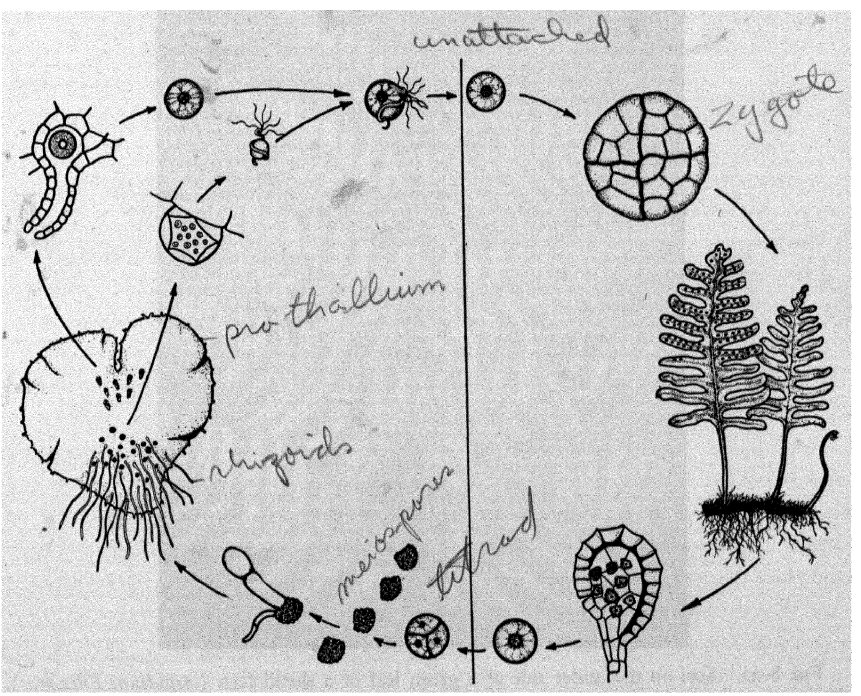


FIG. 8–20. Life-cycle diagram of a fern; see text for explanation.

FIG. 8–21. Young sporophytes of the spinulose shield fern (*Aspidium spinulosum*) becoming established on the surface of the soil in a pot, where the prothallia had developed from the spores. (Photograph, courtesy New York Botanical Garden.)

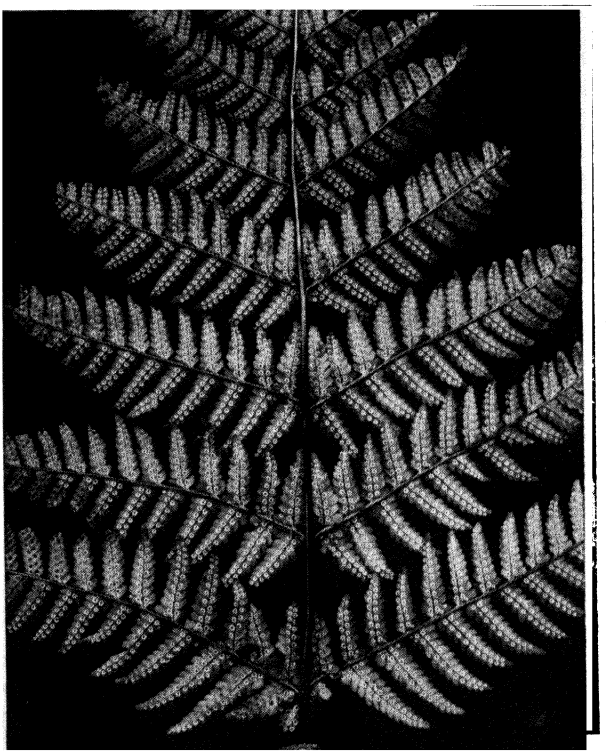


FIG. 8–22. Sori on the under side of a green leaf of a shield fern (*Aspidium Filix-mas*). The sori are nearer the midvein than the margin. (Photograph, courtesy New York Botanical Garden.)

independent plant as is the fern plant. It possesses chlorophyll and absorbs water from the damp ground by special organs of attachment (*rhizoids*). Prothallia usually grow in clusters.

Antheridia and archegonia are borne on the under side of the prothallium (Fig. 8–20). The egg is retained in the venter. Sperms are formed and liberated as in the liverworts, but differ in having numerous flagella instead of only two. They are so small that a film of water is sufficient for their activity. Both kinds of sex organs are produced on the same prothallium; but since they are rarely mature at the same time, the gametes which unite are usually from different plants.

The zygote begins its development within the venter of the archegonium. By successive cell divisions a young sporophyte (*embryo*) is formed. In the early stages four lobes are apparent. One lobe develops into a foot which absorbs food from the prothallium for the growing embryo. Instead of remaining attached, however, as in the liverworts and mosses, the fern embryo soon establishes an independent life (Fig. 8–21). The other three lobes develop into primary root, primary leaf, and stem respectively. Secondary roots and leaves are produced, and slowly a fern plant is developed. The leaves become successively larger until they attain the size and structure of the mature plant. Meiospores are produced in sporangia which are borne on the leaves. In some ferns the sporangia are borne in clusters (*sori*) on the under side of the green leaves (Fig. 8–22); in others the whole or part of a leaf is modified and given up to sporangial production (Fig. 8–23). When the meiospores are mature the sporangium bursts open and the meiospores are discharged. In a suitable damp location a meiospore germinates and develops into a prothallium.

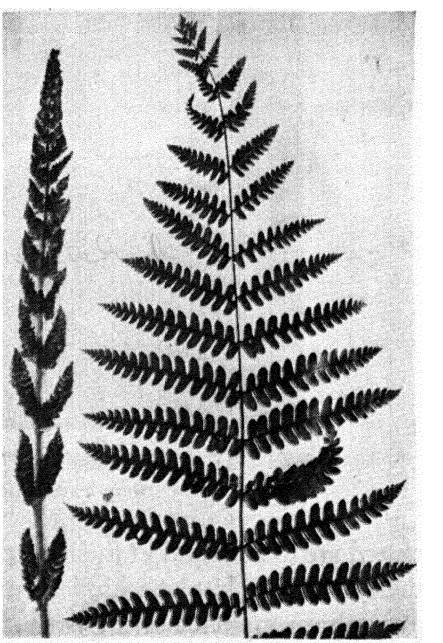


FIG. 8–23. The cinnamon fern (*Osmunda cinnamomea*); fertile frond bearing sporangia on left; sterile blade on right. (Photograph by L. O. Overholts.)

The Club Mosses

The sporophytes of the club mosses are small evergreen plants. Most of them have small scale-like leaves in contrast to the usual large compound leaves of ferns. In many of the club mosses the sporangia are borne in club-shaped *cones*—another characteristic in which they differ from ferns (Fig. 8–24). The gametophytes of the common club moss *Lycopodium* are also unlike the prothallia of the ferns. The sex organs have the general antheridial and archegonial structure, but the small prothallia mostly lack chlorophyll and live saprophytically in the soil.

Still further and important departures from the cycles previously dis-

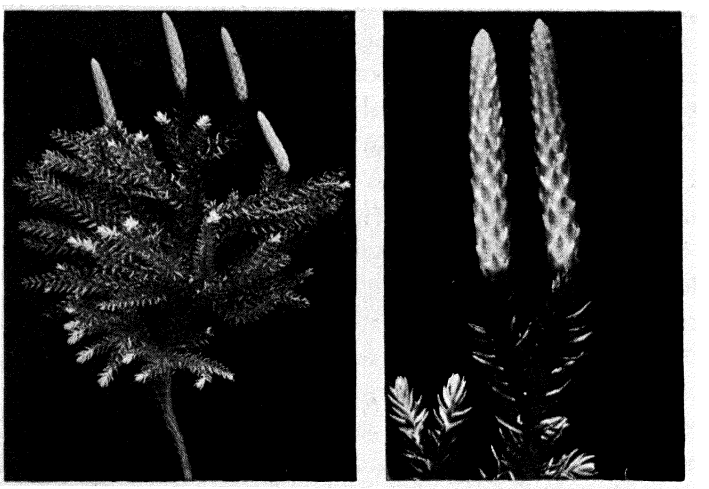


FIG. 8–24. A species of club moss (*Lycopodium*) showing scale-like leaves and club-shaped cones.

cussed are to be found in the little club moss (*Selaginella*). Up to this point there has been but one kind of meiospore, which has produced in most cases a gametophyte bearing both sperms and eggs. In *Selaginella* two kinds of meiospores are formed which differ greatly in appearance (Fig. 8–25). Some sporangia of a cone develop a large number (hundreds) of small meiospores (*microspores*), and other sporangia form a small number (usually four) of larger meiospores (*megaspores*). The production of two kinds of meiospores is known as *heterospory,* in contrast to *homospory* where the meiospores are all alike. The significant fact is that a microspore develops into a male gametophyte, a megaspore into a female gametophyte. Both kinds of gametophytes are extremely small and their development begins before the spores are shed. The male gametophyte is contained within the

microspore wall. The female gametophyte is largely contained within the megaspore wall. Some prothallial tissue bearing archegonia is formed which later becomes exposed by the cracking of the spore wall. The sperms have two cilia and water is necessary to enable them to swim to the archegonia.

The zygote begins germination at once. The embryo consists of a foot, a stem with two leaves, and root. By continued growth the embryo be-

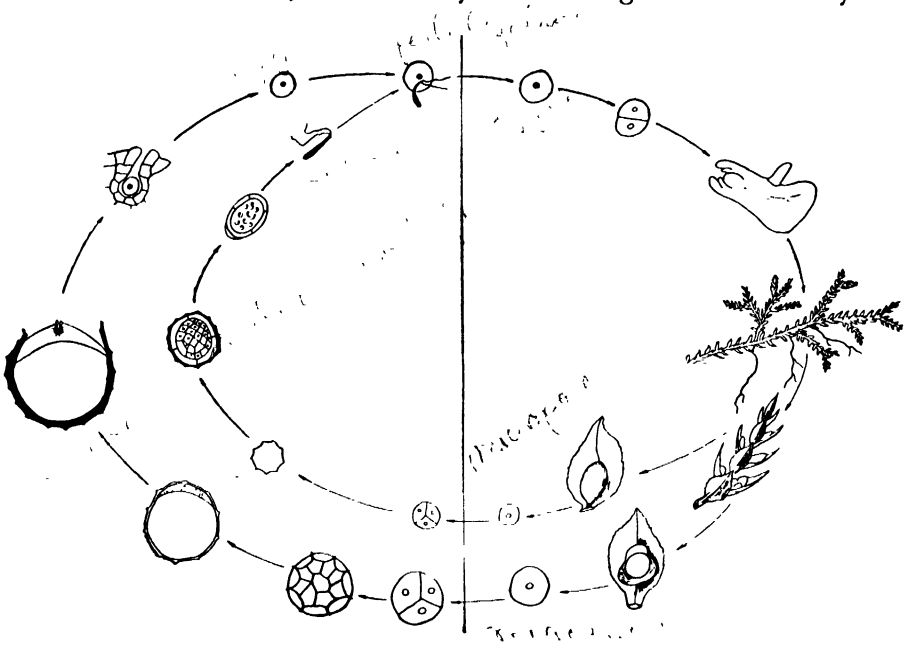


FIG. 8–25. Life-cycle diagram of the little club moss (*Selaginella*); see text for explanation.

comes rooted and independent. In this cycle the gametophyte generations (male and female) are not independent as far as nutrition is concerned. Such growth as they have is dependent upon food stored in the spores. The young sporophyte, in turn, is dependent for its nourishment largely upon food stored in the megaspore by the old sporophyte.

In *Selaginella* the female gametophyte ordinarily is developed under the conditions of a moist location, and water is necessary for the swimming sperms to complete the process of fertilization. *Selaginella* is therefore not perfectly adjusted to land life. It is interesting to consider how certain changes on the reproductive side might bring about a complete adaptation to terrestrial conditions. The retention of the megaspore in the megasporangium would be a necessary step. If it germinated and produced the female gametophyte in this protected position, the danger to the eggs from drying

would be removed. Another necessary step would be the bringing of the microspores to the megasporangium, or to its vicinity, in such a manner that the sperms produced by them might be transferred to the egg without external water. As a result of two such steps the zygote would be within the megasporangium. The development of the embryo of the new sporophyte within the megasporangium would form a seed. These steps occur rarely in *Selaginella;* they are regular phenomena in the reproductive part of the life cycle in the seed plants. Their further consideration is the basis of the next chapter.

The Two Generations Compared

A comparison of the gametophyte and sporophyte generations in the higher groups can be very brief. The gametophyte is the conspicuous and independent individual in the liverworts and mosses, it is independent but inconspicuous in the ferns, and it disappears from view by becoming a dependent internal parasite in the seed plants. The story of the sporophyte is the reverse of this. It is a comparatively inconspicuous dependent parasitic individual in the liverworts and mosses, a conspicuous important individual in the ferns, and the only independent individual in the seed plants.

CHAPTER 9

REPRODUCTION THROUGH FLOWERS

(Pollination, Embryogeny)

Reproduction is the process by which organisms give rise to new organisms of their kind. It has been pointed out that the essential feature of reproduction is the separation of a cell, or cells, capable of initiating new individuals. The production of detachable cells or structures which make possible the formation of new generations of descendants is a matter requiring further consideration. In the preceding chapter it was shown that reproduction is effected in two different ways, vegetatively and sexually; and our previous discussion dealt with the significance and development of these methods of reproduction. We must now be concerned with further characteristics of the sexual process as it occurs in the higher plants, where flowers and seeds are produced. We must give attention to some of the arrangements and devices for effecting the union of sex cells in these plants. We must also consider in some detail the question of how nourishment and protection are afforded the offspring by the parent before and after separation.

The flower is an organ concerned with the development of the structures that bring about fertilization. But it is more than this. After fertilization the floral structures furnish nourishment and protection while the zygote is developing into an embryo (a rudimentary plant). A part of the flower develops into the fruit. Inside of the fruit are the seeds. The embryos in the seeds are in a resting condition, they can be disseminated readily in that form, and they grow into new plants when they are given the proper conditions.

Functionally, then, flowers are associated with meiosis, gamete production, fertilization, embryo development, and seed dispersal. They furnish the means by which two non-moving, separated parents can cooperate in reproduction.

THE STRUCTURE OF FLOWERS

From the point of view of anatomy, the flower is a shortened shoot. We must keep in mind our previous concepts. A shoot is a stem and its leaves. The floral axis is comparable to a stem, and the floral parts are comparable to leaves. Although they differ greatly in character and function, the parts

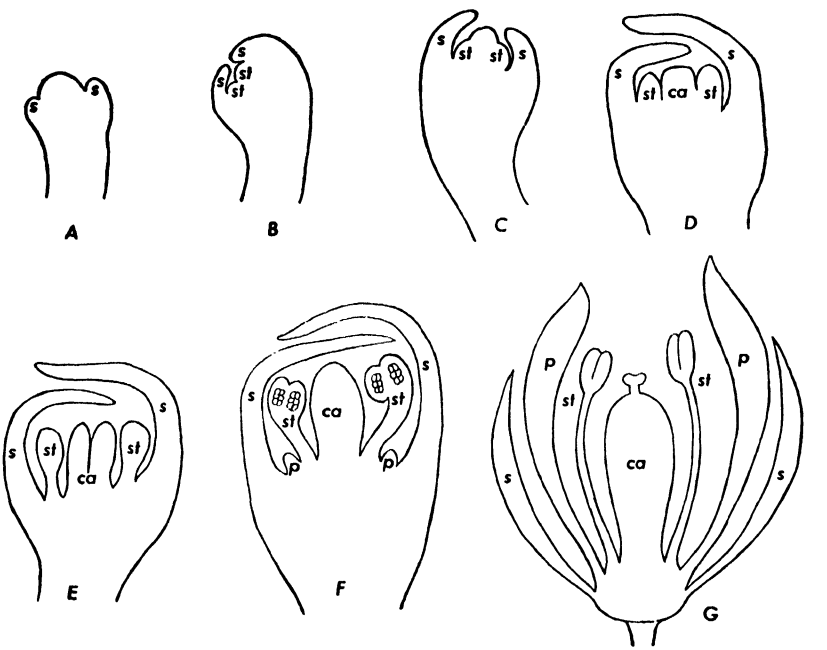


FIG. 9–1. Origin of flower parts in shepherd's-purse (*Capsella*). *s*, sepals; *st*, stamens; *ca*, carpels; *p*, petals. (*A–F* adapted by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

of the flower arise in a manner similar to that described for the origin of foliage leaves on the vegetative cone (Fig. 9–1).

Although flowers differ widely in size, color, and shape and in the number and condition of their parts, it is possible to form a concept of a representative floral plan. In such a conventional flower there are five kinds of structures: the floral axis or *receptacle* and four types of floral leaves, *sepals, petals, stamens,* and *pistils* (Fig. 9–2).

The Sepals and Petals

The *sepals* are the outermost parts. In our conventional flower they form a *whorl* which is termed the *calyx*. Ordinarily the sepals are similar to the

foliage leaves in texture and venation. They are usually green. In the young or bud stages of the flower the sepals envelop and protect the other parts.

Next within are the *petals,* collectively known as the *corolla.* In our generalized flower they also form a whorl. Usually the petals differ markedly from the foliage

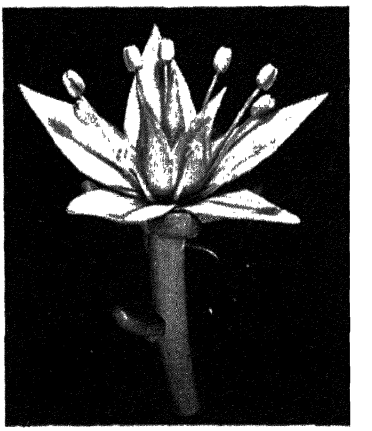


FIG. 9–2. Photograph of a conventionalized flower, modeled after a species of stonecrop (*Sedum*), showing sepals, petals, stamens, and pistils. (Photograph by L. O. Overholts.)

leaves. The beauty of flowers is due, in large part, to the delicate texture and gay colors of the petals. They aid in protecting the stamens and pistils, but another function is the attraction of insects. This is a matter to which we must give attention later. The calyx and corolla do not produce spores. Together they constitute a sterile floral envelope which is called the *perianth.*

The Stamens and Pistils

Next within the perianth are the *stamens* (Fig. 9–3). In our conventional flower there are two whorls of stamens. A single stamen consists of a stalk, or *filament,* supporting a terminal spore-bearing structure called the *anther.* The meiospores which are borne in the anther are *microspores* and the whole stamen is termed a *microsporophyll.* The microspores develop in *microsporangia* (also called *pollen sacs*), of which there are usually four in an anther. By the time the anther is mature the microsporangia coalesce in pairs so that there then appear to be two *locules* or *sacs* rather than four. The microspores when first formed are single cells containing a single nucleus. They go

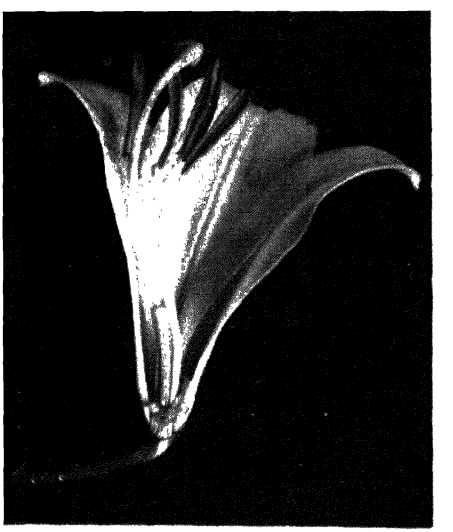


FIG. 9–3. A lily flower with one side removed, showing four stamens with long filaments and ruptured anthers, and a central pistil with ovary, style, and stigma. (Photograph, courtesy New York Botanical Garden.)

through a certain development which results in the formation of a *male gametophyte* (or *microgametophyte*) bearing two sperms. At this stage the structure is commonly called a *pollen grain.* Collectively the pollen grains are often spoken of merely as the *pollen* (from the Latin, meaning fine dust). When the pollen grains are liberated and distributed they carry the developing male gametophytes within them. If the two male gametes, or sperms, have not formed before the shedding of the pollen grain, they will form later in the pollen tube. Thus we may begin to appreciate the role of the pollen in securing a union of the sexes.

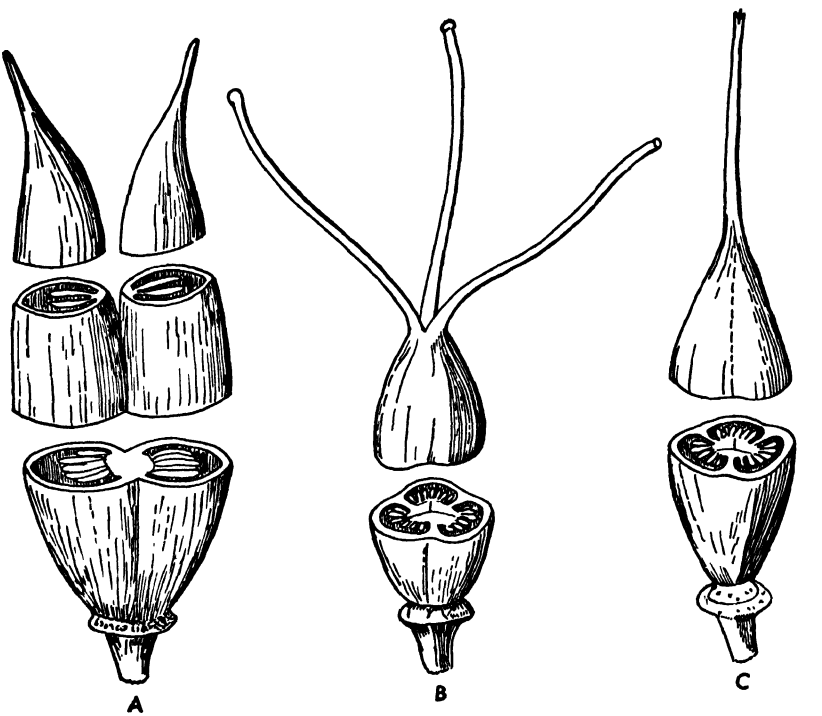


FIG. 9–4. Three types of pistils. *A*, two simple pistils or carpels, united below, free above (saxifrage); *B*, three carpels united to form the ovary, the styles distinct (common St. Johnswort); *C*, carpels and styles united throughout (another St. Johnswort). (After Gray.)

At the center of the flower is the *pistil* (Fig. 9–4). A pistil consists of three parts: *ovary, style,* and *stigma.* The ovary is a bulbous basal portion; the style is a stalk-like extension arising from the ovary; the stigma is a roughened swelling surmounting the style. Pistils may be simple but commonly they are compound. The fact that they consist of several units, called *carpels,* can usually be observed by divisions in the ovary or by branches of the style or stigma. The carpels are spore-bearing. The meiospores borne

here are *megaspores,* hence the carpels are properly called *megasporophylls.* The ovary contains one or more bodies called *ovules* which are the rudiments of the seeds. An ovule consists of a central portion, or *nucellus,* surrounded by one or two coats or *integuments.* Within the nucellus there is produced the *megaspore* which develops into a *female gametophyte* bearing the female sexual cell, the *egg.* In some flowers a single ovule is borne in the ovary, but in other flowers there are several, and in some flowers there are many.

Divergences in Floral Structure

We have described what may be considered a conventional flower—one which we may use as a standard for comparison. Nothing has been said about the number of units in the various parts. It may have three sepals, three petals, two whorls of stamens of three each, and a compound pistil of three united carpels. Trillium flowers are like this. We could as easily select a flower in which the whorls have five members each, i.e., five sepals, five petals, ten stamens (two whorls), and five carpels. Some of the stonecrop, or live-forever flowers, are like this. Or we might find a flower with parts in fours. Evening primroses have this plan. In studying any of these flowers we would find a characteristic arrangement which calls for attention. The members of one whorl normally occur between those of the whorl next outside and

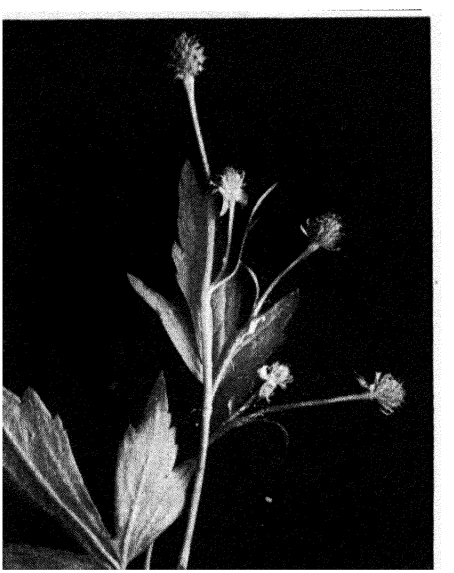


FIG. 9–5. A buttercup with several flowers. In the older ones where sepals, petals, and stamens have dropped, the spiral arrangement of the numerous carpels is evident.

next inside, and are said to alternate with them; i.e., the petals alternate with the sepals, the outer stamens alternate with the petals, and so on. If there is but one whorl of stamens, as may be the case, it is easy to tell whether it represents the outer or inner whorl by determining whether the stamens are alternate with the petals or opposite them (on the same radius).

Floral leaves in whorls, a colored perianth, and the possession of both

stamens and pistils are features characteristic of many flowers, but there are numerous exceptions. It would carry us too far to attempt to present anything like a complete picture of the possible variations, but we must give attention to some of them.

In our conventional flower the sepals, petals, stamens, and carpels are all arranged in whorls. A different situation prevails in some flowers where

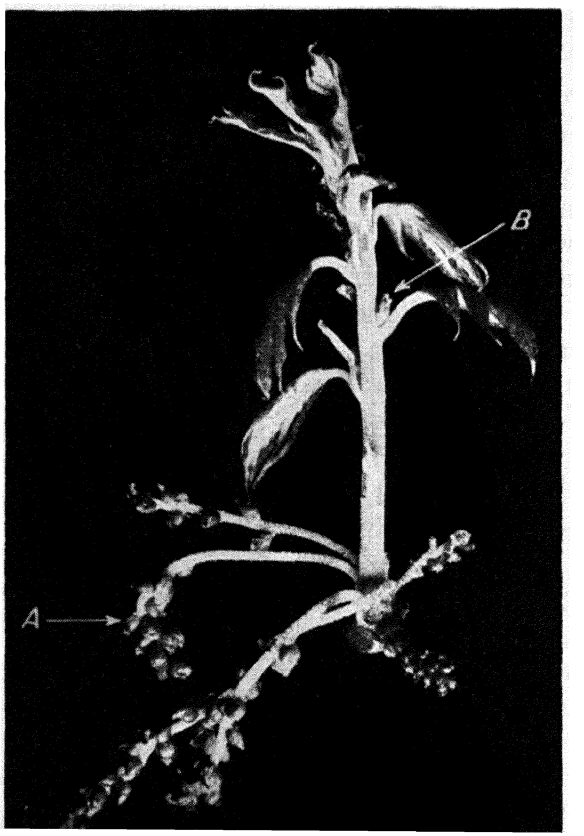


FIG. 9–6. Flowers of an oak. *A*, staminate; *B*, pistillate; both on the same plant (*monoecious*).

there are numerous sporophylls (stamens and carpels) spirally arranged. It will be recalled that foliage leaves are sometimes arranged spirally around the stem. Likewise stamens and carpels may be spirally arranged. In such a case the carpels are not united into a compound pistil but are separately arranged around the cone-shaped terminus of the receptacle. Buttercup flowers are like this (Fig. 9–5). The calyx and corolla form two whorls of five parts each.

We have pointed out that most flowers have both stamens and pistils. Such flowers are said to be *perfect.* Some flowers bear only stamens and are referred to as *staminate;* others have only pistils and are called *pistillate.* When the stamens and pistils occur in separate flowers there are two possible arrangements—both kinds on the same plant (*monoecious*) or the two kinds on separate plants (*dioecious*). Beeches and oaks are monoecious (Fig. 9–6); willows and poplars are dioecious.

Another modification involves the condition of the calyx and corolla. In our conventional flower the sepals and petals are separate units. There are many species in which the sepals are united laterally to form a bell or a tube. Likewise the petals may be fused. Everyone is familiar with the funnel-shaped corolla of the common morning-glory (Fig. 9–7). Sometimes the stamens are more or less united. They may be united by their filaments to form a tube or column as in some legumes, or the filaments may be separate and the anthers united into a tube as in the composites.

Another modification of importance concerns the insertion or attachment of the calyx, corolla, and stamens. In our conventional flower these floral parts are all inserted on the receptacle separately and below the ovary. Such a flower is called *hypogynous*—the ovary is said to be *superior.* In some flowers the bases of the outer floral parts (sepals, petals, and stamens) are united; they grow upward about the ovary and are fused with it. This makes it appear that the ovary is sunken in the receptacle. The calyx, corolla, and stamens seem to arise above the ovary. Such a flower is *epigynous*—

FIG. 9–7. Flower of wild morning-glory, showing funnel-shaped corolla.

the ovary is said to be *inferior.* There is an intermediate condition in which the united bases of the outer floral parts grow upward or outward, forming a disk or cup around the ovary, but do not fuse with it. Such a flower is called *perigynous.* (See Fig. 9–8.)

A modification of importance both biologically and structurally involves the plan or symmetry of the flower. So far we have been considering flowers with *radial symmetry* (Fig. 9–9). Such flowers can be divided into similar

halves by a plane passing through the axis along two or more different radii. Many flowers possess *bilateral symmetry* (Fig. 9–10). They can be

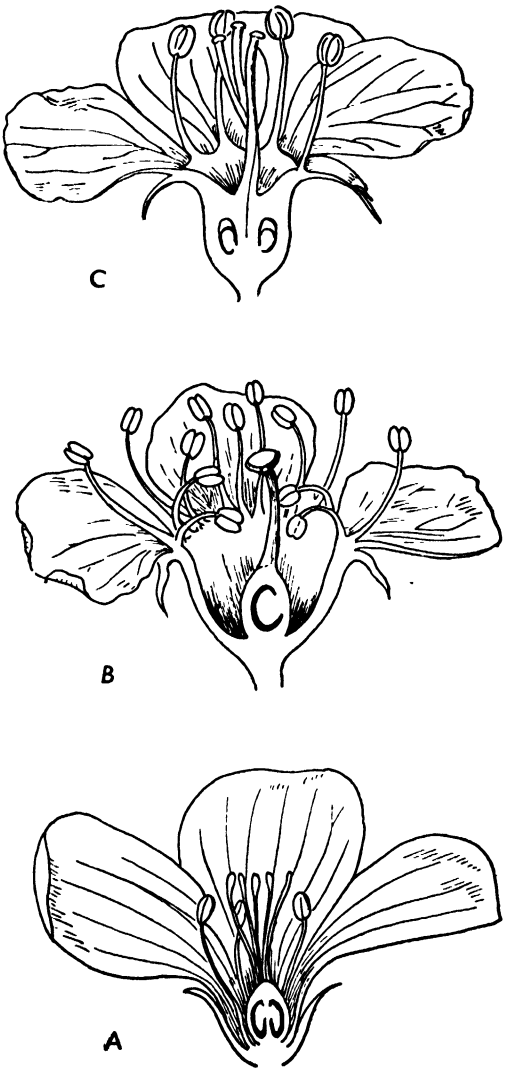


FIG. 9–8. Drawings to show structure of hypogynous (*A*, flax), perigynous (*B*, cherry), and epigynous (*C*, hawthorn) flowers. (After Gray.)

divided into similar halves by only one plane. Flowers of the legume family are sometimes described as *papilionaceous* to indicate their resemblance to a butterfly. Orchids, mints, and figworts are also good examples of plants with bisymmetrical flowers. Sometimes it is the corolla which is particularly

responsible for the bilateral symmetry; sometimes the other floral parts are involved. Spurs, or sacs, may develop from the corolla, as in columbine (Fig. 9–11), or from the calyx, as in the jewelweed.

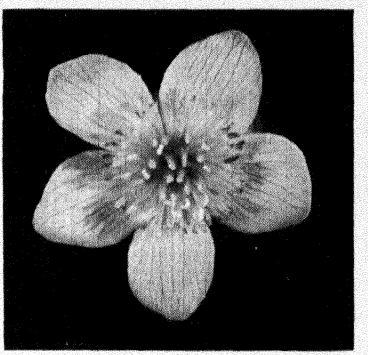


FIG. 9–9. Radial symmetry in a flower of marsh marigold. Note also numerous stamens and carpels.

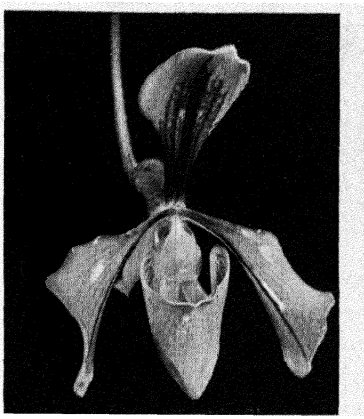


FIG. 9–10. An orchid flower showing bilateral symmetry.

Significance of Floral Variations

Flowers present a great array of characters and variations that are helpful in building up a classification. Flowers have been found to offer very good clues to an understanding of relationships. Long and patient studies of flower structures have enabled botanists to reach conclusions concerning the ways in which some of the floral divergences have come about. They believe that they can interpret certain trends of development. For example, they believe that there has been a trend from the hypogynous toward the epigynous type of flower. Studies of the floral structures commonly used in classification have brought about general agree-

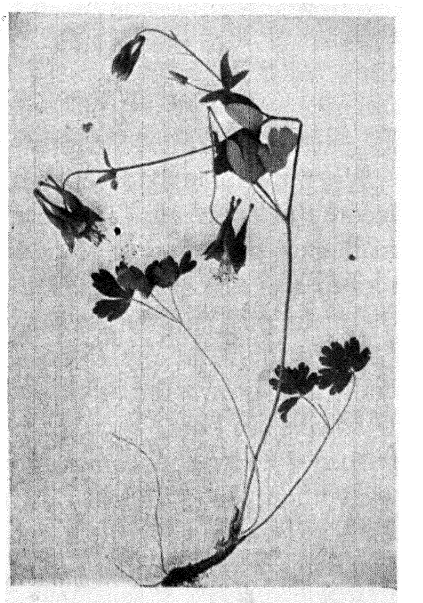


FIG. 9–11. Columbine with flowers having long hollow spurs, produced by the petals, extending backward between the sepals. (Photograph by L. O. Overholts.)

ment that certain characters indicate relatively low positions and others relatively high positions in the scale of classification. The following tabulation illustrates the situation:

Relatively Low or Primitive Development	Relatively High or Derived Development
Numerous or indefinite numbers of parts	Few or definite number of parts
Spiral arrangements	Whorled or cyclic arrangements
Separate or distinct parts	Fused or united parts
Hypogyny	Epigyny
Radial symmetry	Bilateral symmetry
Powdery pollen	Coherent or massed pollen
Small embryo in endosperm	Large embryo in scanty or no endosperm

While some species may possess all low characters and others all high characters it must be understood that all sorts of combinations may exist. Or, in other words, some flowers may stand low with respect to certain characters and high with respect to other characters.

Although it seems to be true that some trends have developed largely without relation to possible advantages, there are other trends in which advantages exist. The role of flower parts in bringing about the union of the sexes may be mentioned as an example of the latter. This is considered under the topic of pollination.

Flower Clusters or Inflorescences

Flowers may occur singly at the tips of branches or in the axils of leaves. Commonly they are borne in groups or clusters on specialized branch systems that differ from the regular vegetative branch systems and are called *inflorescences*. Leaves which subtend the flowers or the branches in an inflorescence are termed *bracts*. The stalk of a flower is a *peduncle*.

When the main axis of a cluster produces a terminal flower which opens before the lateral ones and an end is thus put to further elongation of the main axis, the inflorescence is said to be *determinate*. Such a cluster is described also as a *cyme*. The lateral branches develop more vigorously than the main axis, and the cluster is usually broad and flat-topped.

When the main axis elongates indefinitely, developing new flowers laterally as it grows, the inflorescence is said to be of the *indeterminate* type. If flowers are borne on stalks along such an elongated axis the cluster is termed a *raceme*. A compound raceme is called a *panicle*. If the flowers are without stalks (sessile) on an elongated axis there is a *spike;* a spike with a thickened succulent axis is a *spadix;* a spike which falls off after flowering or fruiting is a *catkin*. When the number of pedicels of approxi-

mately equal length arise from a shortened main axis and spread like the stays of an umbrella, the inflorescence is an *umbel*. Compound umbels occur. Sessile flowers on a very short axis form a *head*. These are some of the more frequent kinds of inflorescences (Fig. 9–12).

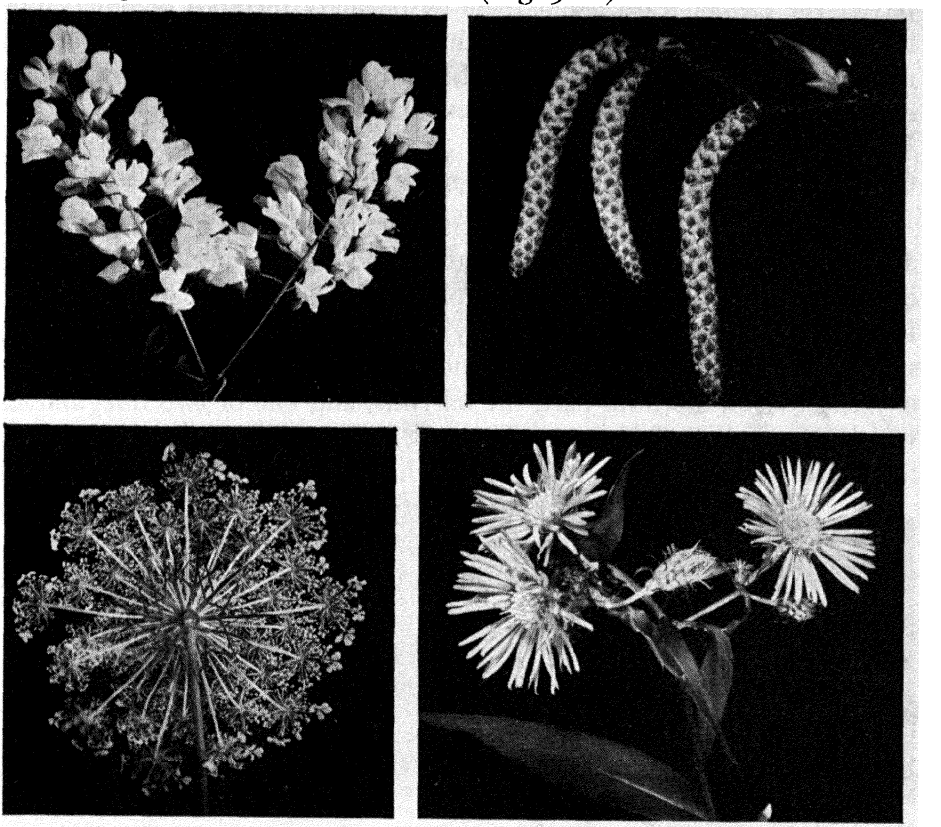


FIG. 9–12. Four types of inflorescences. *A*, racemes in locust; *B*, catkins in beech; *C*, umbel in wild carrot; *D*, heads in aster. (Photographs by L. O. Overholts.)

THE ROLE OF FLOWERS

Much has been said about what flowers are like but not enough has been said about what they do and how they do it. It has been pointed out that they function in meiospore production, gamete production, fertilization, and embryo development. These are important activities and deserve further and fuller attention.

In flowering plants there is a life cycle of two generations, sporophytic and gametophytic, and these alternate one with the other. The sporophytic generation is so called because it produces spores, and the gametophytic

gets its designation because it produces gametes. The plant itself, with shoot, root, and flowers, is sporophytic. Without special study no one can be aware of the existence of the gametophytic parts of the life cycle—we say parts because there are two, a female gametophyte and a male gametophyte. We cannot learn about these by ordinary methods of observation because they are too small to be seen with the unaided eye and, furthermore, they are hidden within the tissues of the sporophyte body where they exist in a parasitic manner.

Ovule Development

The ovule is an extremely important structure and it is necessary that we acquire a full understanding of it and its activities. Ovules occur in closed chambers within the ovary. In a simple pistil there may be but one ovule. In compound pistils several or many may be produced. They arise from special regions of the ovary walls known as *placentae.* An ovule consists of a short stalk, a central part, the *nucellus,* and one or two *integuments* which grow over and about it (Fig. 9–13). The integuments come finally to enclose the nucellus completely, but there is a minute pore at one end called the *micropyle,* where the integuments do not grow together. There are different types of ovules, but in many plants the ovule bends around in such a way that the micropyle comes to lie close to the stalk and so is near the ovary wall.

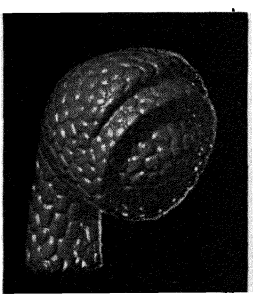


FIG. 9–13. Photograph of a model of a developing ovule, exterior view, showing appearance of the two integuments which form successively and gradually surround the nucellus as the ovule becomes curved; see Fig. 9–14. (Jewell Model. Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

Within the nucellus there appears one cell which is different from the others (Fig. 9–14). It is the *megaspore mother cell.* By two divisions a row of four potential *megaspores* is

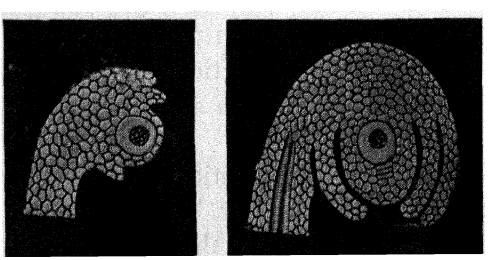


FIG. 9–14. Photograph of two models of a young ovule, showing in one a megaspore mother cell; in the other a row of four potential megaspores of which only the large inner one is functional. (Jewell Models. Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

formed, but actually only the innermost one is functional. The nucleus of the megaspore mother cell contains the same number of chromosomes as each vegetative cell of the shoot and root of the sporophytic plant. In the development of the megaspores the nucleus of the megaspore mother cell undergoes meiosis in which the number of chromosomes is reduced to one-half the number in the nuclei of the cells in the sporophytic generation.

The megaspore is now ready to begin the development of the *female gametophyte* (or *megagametophyte*). This development takes place within the ovule. By this time the megaspore is enlarging and comes to occupy the main part of the nucellus; we would be right if we were to say that it is the important reproductive part. In germination the megaspore nucleus divides and the two daughter nuclei move to opposite ends of the cell. By two more divisions four nuclei are formed at each end. One nucleus from each of these groups moves toward the center; these *polar* nuclei come together and usually unite later to form a *fusion* nucleus ($2n$). This rudimentary growth of eight, or seven, cells is the female gametophyte. The

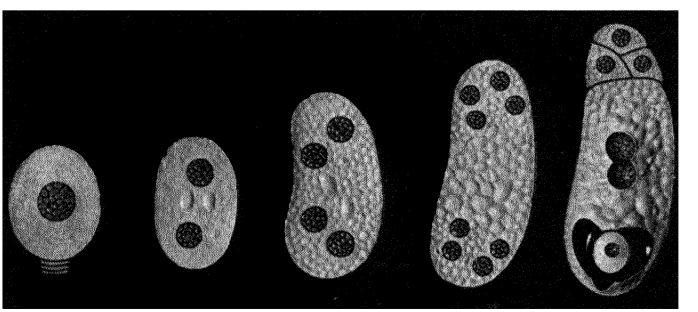


FIG. 9–15. Photographs of models of embryo sac showing development of the female gametophyte; the series begins at the left. See text for further explanation. (Jewell Models. Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

middle cell at the end toward the micropyle is the gamete or *egg cell;* the other two are called *synergids.* The three at the opposite end of the gametophyte are called *antipodals.* (See Fig. 9–15.)

In most descriptions this 7-nucleate sac-like structure within the ovule is designated the *embryo sac.* This is an appropriate term, for it is here that gametic union takes place after the introduction of the sperm, the fertilized egg becomes a *zygote,* and the zygote develops into the *embryo* of the next sporophyte generation. We must now give our attention to how the sperms are produced and how they are brought to the embryo sac.

Pollen Development

It has been explained that pollen grains are germinated microspores and that they are borne within the anthers. How they are borne can be observed best by a cross section of an anther (Fig. 9–16). If the section is made when the anther is young four groups of special cells are observed. Each group is surrounded by a special layer (*tapetum*) which nourishes the developing spores. The *microspores* are produced by mother cells. Each *microspore mother cell* undergoes divisions that produce four cells, each of which functions as a microspore. As described in connection with megaspore production, meiosis takes place. After meiosis each microspore contains one-half the number of chromosomes possessed by its mother cell.

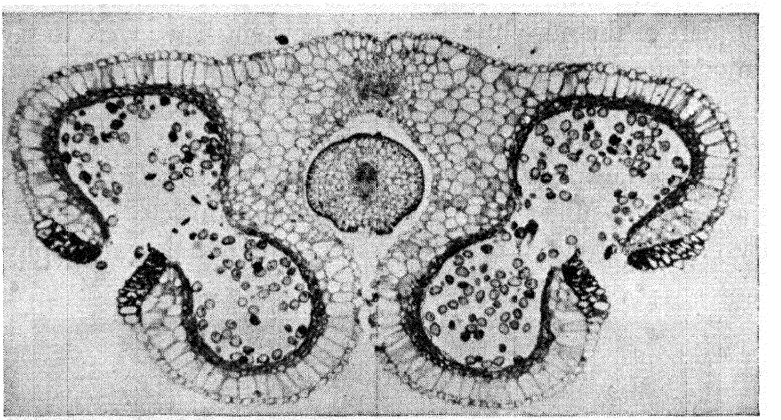


FIG. 9–16. Cross section of an anther of lily, showing cavities fused to form two pollen sacs containing pollen grains; the special cells where the sacs break down are evident; the tapetum has broken down and does not show. (Photograph by D. A. Kribs.)

The microspores are young pollen grains. While they are developing the surrounding tissue disintegrates, especially the tissue between the pair of sporangial cavities on each side, so that at maturity there are two pollen sacs. These sacs break open to shed the pollen in different ways—in some anthers by a terminal pore but in most anthers by a longitudinal slit. The walls of the sacs frequently curve or curl with moisture changes so that the pollen is discharged under dry conditions and protected under moist conditions.

Each young pollen grain has a single nucleus. At the time of shedding this has in most instances divided to form a *tube nucleus* and a *generative nucleus*. The generative nucleus divides to form two *male gametes*. This latter division takes place sometimes before shedding and sometimes later.

This two- or three-nucleate pollen grain is the *male gametophyte* (or *micro-gametophyte*).

No further development occurs until the pollen grain is transferred to the stigma. The transfer of the pollen grains from the anther to the stigma has long been called *pollination*. It is a process so important and so inter-

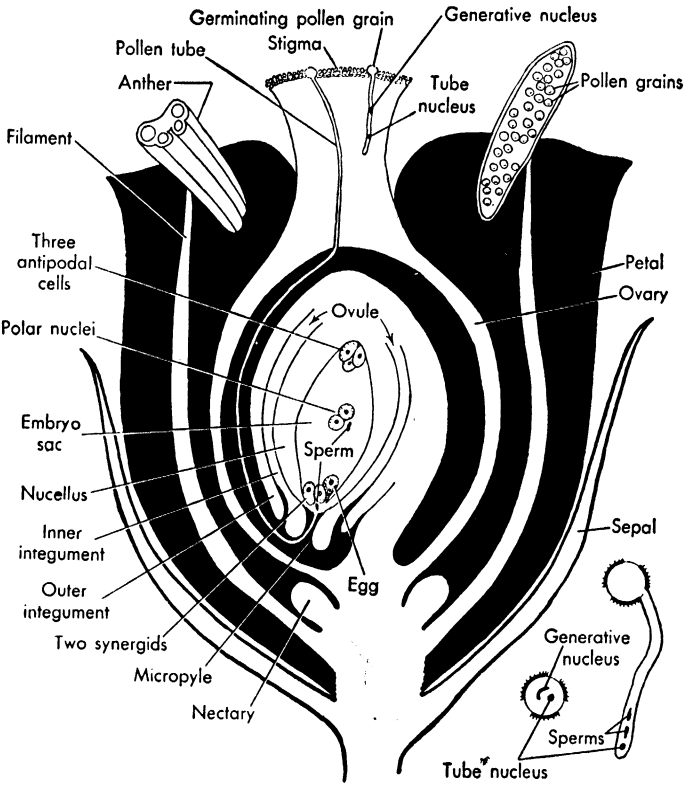


FIG. 9–17. Diagram of a sectional view of a flower to show germination of pollen grains and development of pollen tubes that bring the sperms to the embryo sac.

esting that special attention must be given to it. But pollination bridges only part of the distance between the two gametes. With the pollen grain on the stigma the union of the gametes is still not effected. The union is made possible by a tube which grows out of the pollen grain down the style and through the ovary wall until it reaches the ovule (Fig. 9–17). There are usually thin spots in the wall of the pollen grains and the tube protrudes through one of these spots. The tube grows in a parasitic manner through the tissues of the pistil. The tube nucleus apparently plays a part in this vegetative growth. By the aid of enzymes it dissolves the tissues and uses the

material for its own growth. Through this tube the male gametes pass. The gametes (sperms) have no means of locomotion but are carried by cytoplasmic streaming within the tube. The tube becomes a virtual canal for their passage. The gametes may or may not be organized as cells; i.e., they may be naked nuclei or they may have their own cytoplasm.

Fertilization

The pollen tube enters the ovule, often through the micropyle, and penetrates the embryo sac. The two male gametes move out of the tube into the sac. One of the male nuclei then fuses with the egg nucleus. This fusion of the two gametes is *fertilization* (Fig. 9–18). The result is a *fertilized egg* or zygote. The zygote is a complete cell—nucleus, cytoplasm, and cellulose wall. By divisions it initiates the embryo of a new sporophyte. The fusion of the two gametes has restored the double chromosome number characteristic of the sporophytic generation.

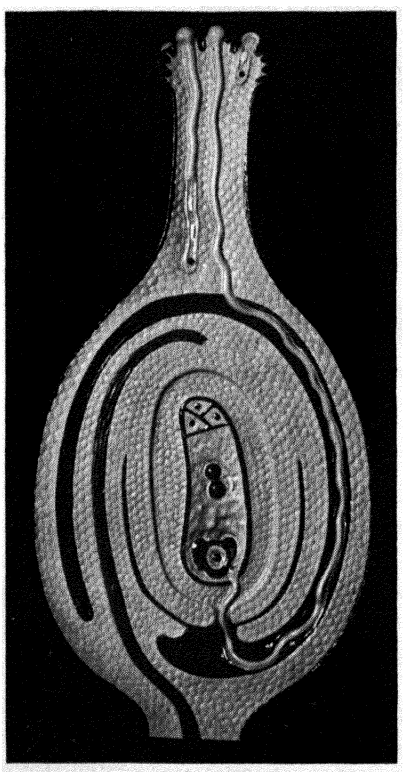


FIG. 9–18. Photograph of a model to show fertilization of the egg to form the zygote, and triple fusion to form the endosperm nucleus. (Jewell Model. Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

This process of fertilization is typical, in principle, of sexual reproduction in both plants and animals. The accessory structures and the conditions vary greatly but the basis is the same. Male and female nuclei, carrying similar contributions of chromatin material, are brought together and organized into a single nucleus. In plants living in the water, such as some of the algae, both gametes are discharged and they swim about. They are attracted to each other and fusion takes place in the water. In lower plants that live on the land, the female gamete is retained in an organ where it is protected from drying out and yet is accessible to the male gamete which requires water in order that it may swim to the place of fertilization. Such plants must be low-growing and confined to wet places where water is present at least some of the

time. But flowering plants live in dry situations. A swimming sperm cannot effect fertilization. The solution is this: Pollen grains containing the male gametes bridge the space from anther to stigma and the pollen tubes carry the male gametes the rest of the way through the tissues to the deeply buried female gametes. The flower parts and the devices for insuring the transfer of the pollen, and comparable sexual parts developed by animals, are accessory, "being merely arrangements to enable the male cell to effect fertilization and the female cell to receive it."

But we are not yet through with the activities within the embryo sac at the time of fertilization. The second male gamete joins the fusion nucleus in the center of the sac and fuses with it. If the two polar nuclei have not yet fused, then the three unite coincidently (triple fusion). In this way there is formed the *endosperm nucleus* ($3n$ chromosomes) which develops into the nutritive tissue for the embryo, called *endosperm.*

The fusing of the second sperm with the fusion nucleus of the embryo sac brings about a condition which is called *double fertilization.* The possible significance of this secondary fusion is uncertain. It has been suggested that the fusion nucleus, which is so closely related to the egg nucleus, attracts the one sperm in the same manner that the egg attracts the other sperm. But this is not an explanation of the significance of the act. It does serve, however, to explain how certain characters of the pollen parent can appear in the ripening seed. For example, if yellow-fruited corn is pollinated in part by pollen from a red-fruited parent, red kernels will develop. The endosperm, like the embryo, is a hybrid. Its hybrid character can be discerned immediately, whereas the hybrid character of the embryo is apparent only when it grows and fruits.

Embryo Development and Seed Formation

After fertilization has been effected, the stigma shows signs of withering. The petals and stamens wither and usually drop off soon afterward. Sometimes this is true also of the sepals. The ovary ripens into the fruit (in some cases other parts of the flower consolidate with it) and the ovules mature into seeds. We must now trace ovule development from the time of fertilization to maturity. There are two activities going on simultaneously —the development of the zygote into the embryo and the development of the triple-fusion nucleus into the endosperm. We should not be unmindful of the fact that this enlargement within the ovule necessitates some growth and change in the integuments which later form the seed coat. The embryo is the new sporophyte. Although it is developed by the intervening gametophyte generations (male and female), we must keep in

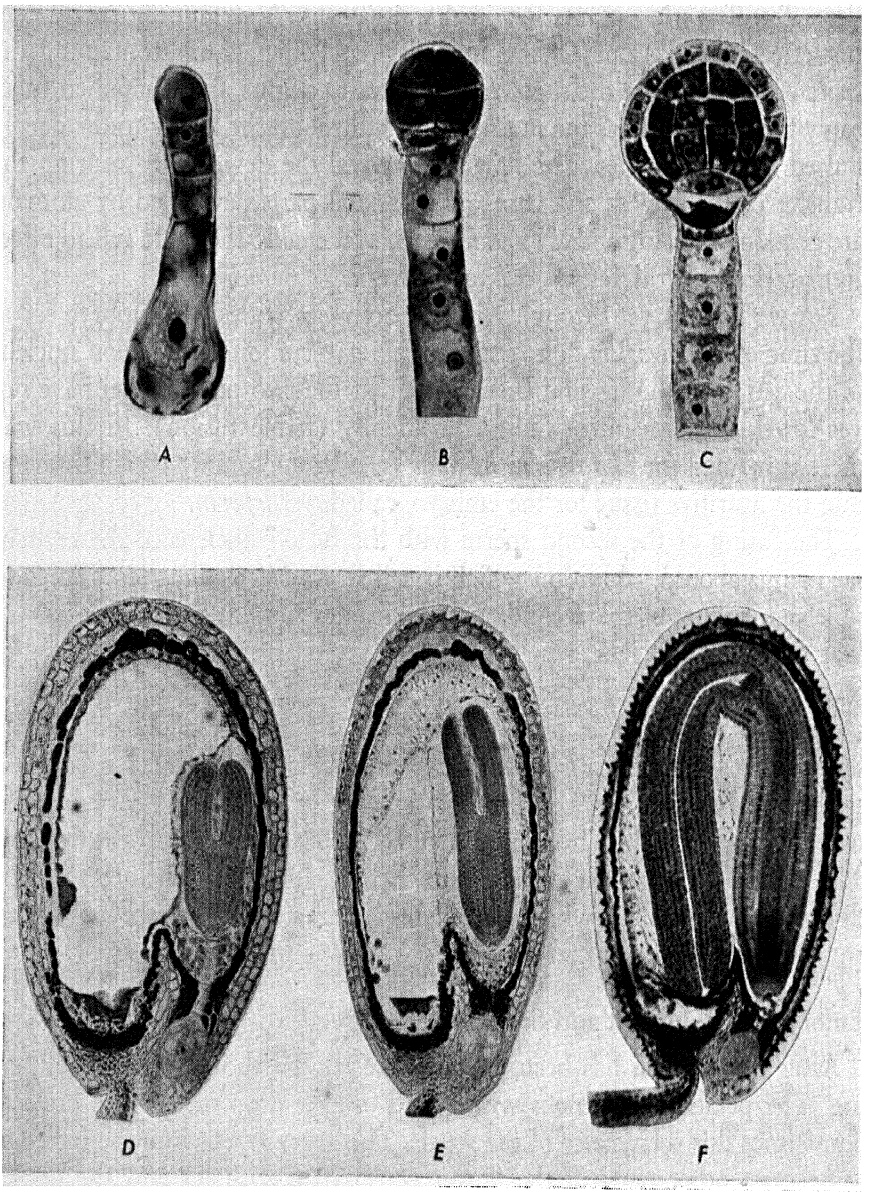


FIG. 9–19. Photomicrographs showing the development of the embryo in shepherd's-purse (*Capsella*). *A*, the zygote has divided transversely and, with subsequent transverse divisions, has formed a filament of four cells (proembryo). *B*, the terminal cell has divided and these cells will form the embryo; the filament of cells below is the suspensor. *C*, later stage showing enlarging embryo. *D*, *E*, *F*, later stages of the growing embryo shown within the ovule; the cotyledons are emerging in *D*, and some endosperm cells are present; a well-developed embryo is shown in *F*, with cotyledons, hypocotyl, and plumule; remains of suspensor with its enlarged basal cell still show in *D*, *E*, and *F*. (Photomicrographs by D. A. Kribs.)

mind that it is protected and sustained by the old sporophyte generation.

The endosperm nucleus divides and further divisions ensue until a large number of nuclei come to lie about the walls of the embryo sac. Walls form about the nuclei and they increase in number to form a considerable mass of endosperm tissue, which surrounds the developing embryo and furnishes nourishment for it.

The development of the zygote is so varied that only a generalized account can be offered. The zygote lies in the embryo sac near the micropyle. Usually the first divisions are transverse and there is built up a row of cells called the *suspensor.* The apical or innermost cell then divides in a longitudinal plane and from these cells and others derived from them by repeated divisions the embryo is formed (Fig. 9–19). For a time the embryo is only a rounded mass of cells. It elongates rapidly and before long it is possible to recognize an axis, which will become the *hypocotyl,* and two outgrowths which are to become the *cotyledons* (the first leaves of the embryo). The hypocotyl and the rudimentary root are called the *radicle.* Between the cotyledons is a rudimentary bud or growing point called the *plumule.* The origin of the parts of the embryo and their final form vary in the different groups of seed plants: dicotyledons have two cotyledons; monocotyledons have a single cotyledon; some gymnosperms have several cotyledons.

The extent to which the embryo develops before it goes into a dormant state varies. Sooner or later the seed ripens and further activity of the embryo ceases. In some species the endosperm is entirely consumed by the embryo in its formation. In other species a considerable amount of endosperm tissue remains at the time of seed maturity. It persists in such cases and nourishes the embyro when it develops into a seedling at the time of germination. Morning-glories, castor beans, and coffee have seeds of this sort. In some seeds the embryo is comparatively small or slender and the endosperm is conspicuous and plentiful.

A seed is a ripened ovule consisting of a dormant embryo that is supplied with reserve food, either inside its own body or in the form of separate endosperm, and surrounded by a protective coat (Fig. 9–20). As there is great variation in flowers there is likewise great variation in seeds—variation in size, shape, color, and texture. Commonly the embryo advances to the stage where it is possible to recognize hypocotyl, plumule, and one or more cotyledons. The hypocotyl is usually more or less stem-like. Sometimes the plumule is merely a growing tip but in other cases it may be developed to the point where partially differentiated leaves are recognizable. All the growth above the attachment of the cotyledons is termed the *epi-*

cotyl. Although cotyledons are genuine leaves they are ordinarily unlike the later leaves. When modified for food storage they may be thick and fleshy. In other seeds they may be thin and blade-like, with recognizable venation. In grains there is but one cotyledon and it is highly modified, functioning merely to absorb food from the endosperm.

The seed coat, or *testa,* is usually thickened and tough; sometimes it is hard and bony. In some seeds the testa is single, but in others it is double. On the surface of the testa we can ordinarily recognize the scar

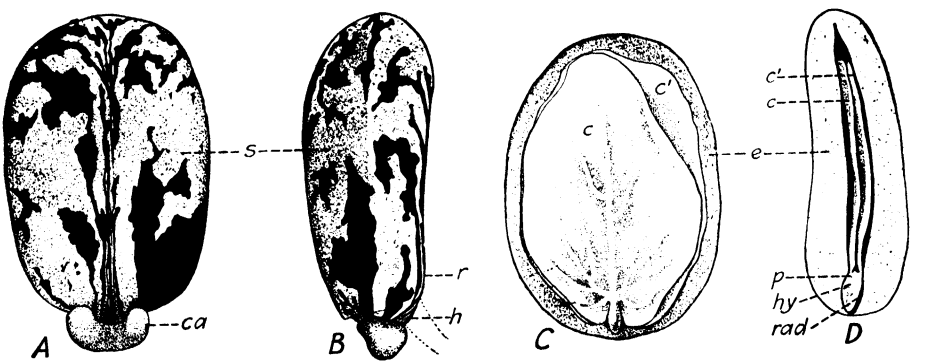


FIG. 9–20. Seed of the castor bean. *A,* surface view; *B,* edgewise view; *C,* interior view, showing two thin cotyledons lying against the endosperm; *D,* interior view cut lengthwise along its narrow axis; *s,* seed coat; *ca,* caruncle; *h,* hilum; *r,* raphe; *c* and *c'*, cotyledons; *e,* endosperm; *p,* plumule; *hy,* hypocotyl; *rad,* radicle. (Drawing by Elsie M. McDougle. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

where the stalk has broken apart from the ovary wall. This is called the *hilum.* We can usually observe the micropyle as a minute pit. In many seeds it is close to the hilum, but its location depends upon the type of ovule from which the seed has developed. In some cases where there is only one ovule in an ovary the seed coats and the ovary walls coalesce in the process of maturing. In such cases the seed is never set free from the ovary; and the product, although commonly called a *seed,* is actually a *fruit.* Grains are one-seeded dry fruits.

Fruits

While everyone is familiar in a general way with fruits it is entirely likely that the ordinary conceptions are not sufficiently broad. It is not adequate to think of fruits only as edible products. We must think of fruits as those structures which have to do with the development of seeds regardless of edibility or aspect. We have talked about the variability of flowers and seeds.

Fruits are as variable. Variations are found in size, shape, color, and texture. Many are merely ripened ovaries. In some instances other parts of the flower are involved and become part of the fruit.

To consider first the simple fruits, i.e., those formed by the ripening of a single ovary, it is customary to divide them into two classes according to

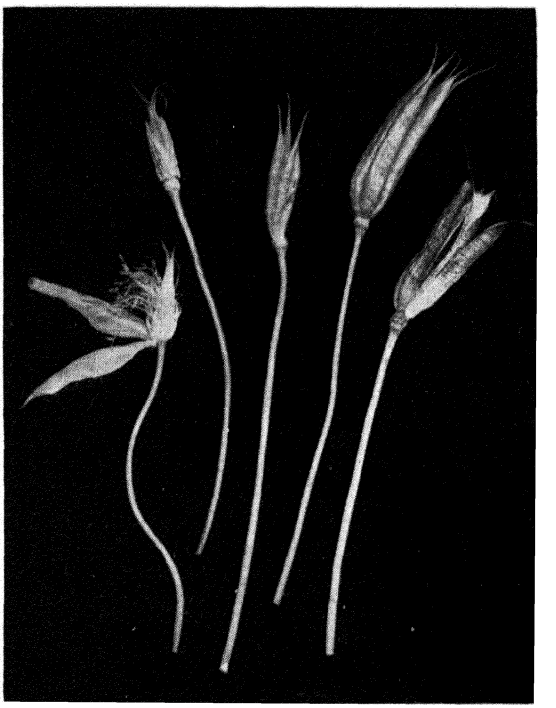


FIG. 9–21. The development and ripening of the carpels of a flower of *Aquilegia* into a head of dry fruits (follicles). (Photograph, courtesy New York Botanical Garden.)

whether they are dry or fleshy. Pods, capsules, nuts, and grains are dry fruits (Fig. 9–21). Berries, drupes, and pomes are fleshy. Dry fruits may break open at maturity (*dehisce*) to discharge the seeds, or they may remain closed. A dry fruit from a simple ovary dehiscing along one line is a *follicle* (larkspur, milkweed); if along two lines it is a *legume* (beans, peas). Any dry dehiscent fruit developing from a compound ovary is a *capsule* (cotton, iris). A one-seeded, dry, indehiscent fruit in which the seed is separable from the ovary wall is an *achene* (buckwheat, any of the composites); if the seed is inseparable such a fruit is a *grain* or *caryopsis* (cereals). A dry indehiscent fruit from a compound ovary, in which the one-seeded carpels separate at maturity, is a *schizocarp* (maple, celery).

A winged indehiscent dry fruit is a *samara* (ash). A dry fruit, either simple or compound, with a hard bony ovary wall is a *nut* (oak, hazelnut).

The principal fleshy fruits from single ovaries are the *berry,* the *pepo,* and the *drupe.* A fruit with a completely fleshy or pulpy ovary wall is a *berry* (grape, tomato). A fruit with an outer fleshy portion and an inner hard or stony part constitutes a *drupe* (cherry, peach). Some inferior ovaries develop a hard outer rind with a fleshy interior portion and are termed *pepo* (watermelon, pumpkin). In some fleshy fruits formed from inferior ovaries the fleshy portion originates from the tissues surrounding the ovary, the ovary wall being papery or cartilagenous. Such is the *pome* (apple, pear). In other fruits there is an aggregation of simple fleshy ovaries which may or may not separate from the receptacle at maturity (raspberries, blackberries). These are known as *aggregate fruits.* Some fruits having much the same appearance but differing in being an aggregation of separate flowers, rather than of separate pistils of a single flower, are called *multiple fruits* (mulberry, pineapple). In other cases there may be an aggregation of dry fruits (achenes) over the surface of an enlarged and fleshy receptacle (strawberry). These are sometimes called *accessory fruits* from the fact that more than the pistil is involved (Fig. 9–22). Generally speaking, fleshy fruits are likely to be found in bright and contrasting colors.

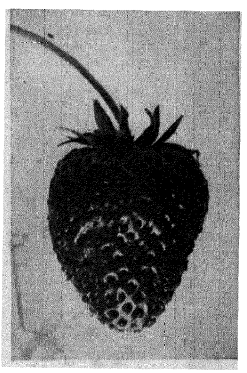


FIG. 9–22. The strawberry, an accessory fleshy fruit; the individual achenes on the surface are evident. (Photograph by L. O. Overholts.)

Pollination

The transfer of the pollen grains from the anther to the stigma is pollination. Except in a few unusual flowers pollination is necessary if fertilization is to be effected. In most flowering plants pollination is essential and it is one of the outstanding activities associated with flowers. There are certain flowers (some of the violets) that never open, the pollen tubes growing directly from the anthers to the ovules.

Pollen grains possess no inherent power of movement or locomotion. They depend upon external motive agencies—the wind and insects are the ones most commonly utilized, but there are others. In order to understand how the accomplishment of pollination is rendered reasonably certain, it is necessary to give attention to many special features of flowers.

There are three types of pollination: (1) *close* or *self*-pollination, involving the anthers and stigma of the same flower; (2) *cross*-pollination, involving two different plants; and (3) *intermediate* pollination, involving two flowers on the same plant. In many species all three forms of pollination are possible and take place. There are many plants in which close pollination is impossible or at least difficult and cross-pollination is facilitated and accomplished. When we become familiar with the arrangements and contrivances of many flowers to insure cross-pollination it is difficult to escape the conclusion that this form must be tremendously important in the process of reproduction. An effective condition which results in cross-pollination is the bearing of staminate and pistillate flowers on separate individuals. We have referred to this condition as *dioecious*. Obviously in such cases two separate parents must be involved. But where the flowers are perfect, close pollination may be rendered unlikely in several ways. One is the maturing of the stamens and pistils at different times. Sometimes the pistils mature first, but more often the stamens mature first and discharge their pollen before the pistils of the same flower are mature. This results in either cross- or intermediate pollination. Another device which tends to bring about cross-pollination is the production of two forms of flowers in which the anthers and stigmas are borne in different positions. Such a condition exists in primroses, flax, and the partridge berry. One form may have long styles and short stamens and the other form the reverse. When a plant bears flowers of only one form, cross-pollination is favored. An insect will carry pollen on the back part of its body from the long stamens of one flower to the stigma on the long style of another flower, and on the front part of its body pollen from the short stamens to the stigma on the short style. Another condition which insures cross-pollination is *self-sterility* or *impotency*. In such cases the pollen from the anthers of a flower do not grow pollen tubes and effect fertilization on the stigma of the same flower. Complete impotence is rare but does exist in the day lily, buckwheat, and some legumes. There are a good many plants in which the pollen from other flowers is more effective than that from the same flower. There are various structural arrangements which make it likely that an insect will touch the stigma upon entering a flower but not upon leaving it. This means that pollination will be effected by pollen brought from another flower but not by that secured in the same flower. The iris is a good example of this arrangement.

Insect pollination is a most fascinating subject. There is evidence that some insects have become adapted to certain flowers and that some flowers have become dependent upon certain insects; we may safely say that here is a marvelous condition of mutual adaptation. Surely everyone has noticed

how insects visit flowers. It seems likely that insects visit them chiefly in search of nectar. This is a sweet liquid secreted in little glands. The glands, or *nectaries,* are variously arranged but always so that insects in visiting the flowers will come in contact with the anthers and stigmas. Since there is more or less correlation between showiness of the perianth or fragrance and the production of nectar, we may say that these features serve as advertisements to attract insects. Sometimes the flowers themselves are inconspicuous but are surrounded by large showy leaves or bracts, as in poinsettias and dogwoods. The effect is the same. Bees are the chief pollinating insects, but butterflies, moths, and beetles play their parts. While it is likely that nectar, revealed by color and odor, serves as the main attraction for insects in the majority of cases, we know that some insects visit flowers to obtain pollen which they use as food for their larvae. In some species of bees there is a structure on the hind legs known as a "pollen basket" which serves to carry the pollen. Most fruit growers recognize the fact that a light crop is likely to set unless large numbers of bees are present in the orchards at blossoming time.

Some flowers have interesting contrivances which assure deposition of pollen on visiting insects. In the barberry and in mountain laurel (Fig. 9–23) the filaments of the stamens bend or spring when touched at a certain

FIG. 9–23. Flower of the mountain laurel (*Kalmia*). The anthers are held in pouches of the corolla but may be released by the touch of insects. Note the opening of the anther sacs by large terminal pores.

place so that the anthers are forcibly moved. The sensitive spot is near the nectar gland; hence it is sure to be touched by a visiting insect. Many flowers especially adapted to pollination by insects have the bilateral type of symmetry. Here the corolla may form a lower lip which serves as a landing place for the insect (Fig. 9–24). The weight of the insect may cause the style and stigma to emerge and pollination is at once effected by pollen

brought from another flower. This is the case in some legumes. The orchids exhibit marvelous adaptations for insect pollination. Some orchids are pollinated only by a particular species of insect; on the other hand, the insect may be dependent upon that orchid for its food. In the moccasin flower, or lady's-slipper, the lower lip of the corolla forms a large sac or pouch. The nectar is inside. A bee can enter through a slit on the upper side. In crawling out it first encounters the stigma, where it deposits pollen which it has brought from another flower, and just as it leaves it brushes against an anther which deposits more pollen on its back to be carried to other flowers. Some flowers remain closed so that the nectaries are not accessible to small crawling insects such as ants which would not effect pollination. The Spanish bayonet, or yucca, is a highly specialized case. The agent of pollination is a small moth (called *Pronuba*). In the process of laying its eggs in the ovules pollination is effected. When the eggs hatch, the larvae feed upon and destroy the ovules in which they develop, but there are always some ovules which are not affected and which develop into seeds. The larvae drop to the ground and become encased in cocoons where they remain until blooming time the next year when they emerge as moths. The development of the fig is equally dependent upon a parasitic wasp.

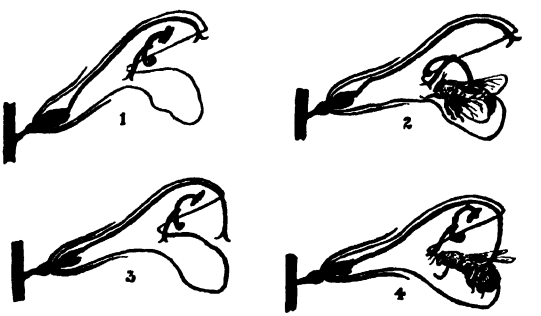


FIG. 9–24. The provision in salvia flowers for insect pollination. The stamens are on a hinged mechanism. When a bee visits flower No. 1 the anthers are brought down upon its back (No. 2). The same insect subsequently visiting flower No. 3 touches the elongated stigmas with its back (No. 4), and cross-pollination is effected.

Insects are not the only kind of animal life that brings about pollination. Many people have seen hummingbirds visiting garden flowers such as nasturtiums, scarlet sage, and trumpet creepers. Large tubular flowers with abundant nectar are particularly suited to pollination by these birds. The birds are especially effective with many species of tropical flowers where they may vie with insects as important pollinating agents. Snails, or slugs, are said to visit certain low-growing tropical flowers and, although destructive because they eat the fleshy parts, they sometimes serve as pollinators.

Although our attention is drawn rather naturally to insect pollination, we must not fail to realize that the simplest and most direct form of pol-

lination is brought about by air currents. This is the method most closely related to spore dispersal in the lower plants such as fungi, mosses, and liverworts, and is evidently the most primitive method. Pollen grains are always small and light and if they are also dry and powdery they are wafted readily by the wind. Wind pollination is common in a good many plants, especially those species that grow in exposed locations or where large numbers of individuals grow close together as is the case with forest trees and grasses. Pollination by the wind is left wholly to chance. The wind is as likely to distribute pollen in one place as another. The method is extravagant as regards the amount of pollen required. In order to insure the transfer of some grains to the stigmas the air must be literally full of pollen; hence in

FIG. 9–25. A generalized grass flower showing versatile exserted anthers which facilitate pollen distribution by the wind, and feathery stigmas which favor pollen reception.

flowers dependent upon wind distribution immense quantities of pollen are produced. In this way the chances that some of it will reach the stigmas are increased. A corn tassel (staminate flower group) is estimated to produce 20 to 50 million pollen grains. This means that if only one out of 40 or 50 thousand grains reaches a stigma there would still be fertilization of all the ovules. In corn the so-called "silks" are the stigmas. In all pollination, one pollen grain must reach the stigma for each ovule. In pines enormous quantities of pollen are produced. Yellow pollen from pine forests sometimes accumulates in such amounts that the term "pollen rain" or "showers of sulphur" is used to describe it.

There are flower features that are especially characteristic of wind-pollinated flowers just as others are characteristic of insect-pollinated flowers. Some features favor the scattering of the pollen by the wind and others favor the reception of the pollen from the wind. When staminate flowers

are borne in pendulous inflorescences (catkins) that swing easily, the pollen is shaken and readily carried away by the wind. This is the situation in the hickories, oaks, birches, poplars, and alders. In many such species the flowers bloom before the leaves unfold in the spring and thus pollen reception by the stigmas is favored. In tropical forests where there are mixtures

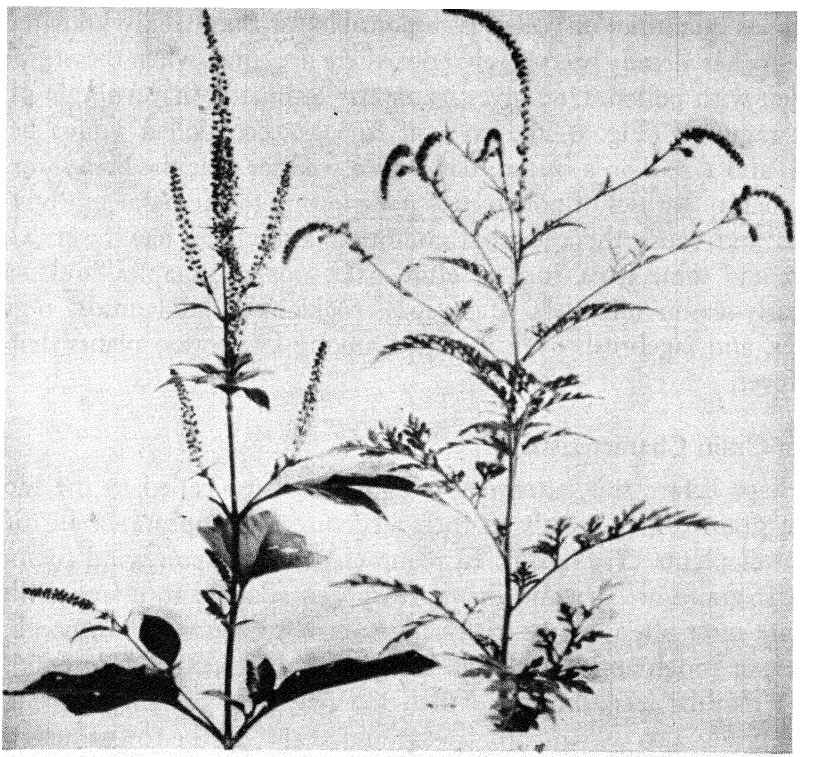


FIG. 9–20. Two species of ragweed which give off great numbers of pollen grains that cause hay fever. The one on the left is the great ragweed; the other is known not only as ragweed but also as Roman wormwood. (Photograph, courtesy New York Botanical Garden.)

of species rather than large associations, the trees are more likely to be insect-pollinated than wind-pollinated. In the grasses the anthers are attached near the middle so that they turn freely on the tip of the filament (*versatile*). This, together with the fact that they are protruded outside the glumes (*exserted*), means that pollen distribution by the wind is facilitated (Fig. 9–25). Grass flowers also have branched or feathery stigmas which favor reception. For the most part grass flowers are borne on inflorescences that are terminal and above the leaves where the wind strikes and shakes them easily. In general, wind-pollinated flowers are inconspicuous, odor-

less, and nectarless. Although wind pollination seems to lack some of the advantages of insect pollination, nevertheless, it is extraordinarily successful. This fact is evidenced by the abundant seeding of many wind-pollinated plants such as grasses, ragweeds, pigweeds, sagebrushes, and most of the forest trees.

The fact that many plants are wind-pollinated and so produce such enormous quantities of pollen is responsible for the malady known as *hay fever*. As has already been pointed out, there are times when the atmosphere is laden with pollen. One investigator has estimated that a single plant of giant ragweed (Fig. 9–26) gave off 8,000,000,000 pollen grains between 8 A.M. and 1 P.M. on a certain day. Little wonder that the breathing of air with such quantities of pollen may be irritating to the nasal mucous membranes and cause the catarrhal condition known as hay fever. Grasses, tulips, and some trees, such as elms, oaks, poplars, maples, and walnuts, are early-season offenders. Ragweeds, cockleburs, goldenrods, pigweeds, thistles, and sagebrushes are included among late-season plants that cause hay fever.

Pollen Grain Characteristics

Perhaps before this, attention should have been called to the fact that pollen grains differ greatly in their structure and appearance in different species of plants (Fig. 9–27). In plants dependent upon wind for pollination the grains are dry and dusty. In species adapted to insect pollination they are most often oily or sticky. The outer surface may be smooth, as in grasses, or rough and spiny, as in composites. Frequently thin spots (germ pores) may be seen through which the pollen tubes will protrude. The pollen grains also vary greatly in size and shape. In the forget-me-not they are minute; in the hollyhock they are comparatively enormous. All four grains produced by a mother cell may be viable, whereas in some groups (as in the sedges) only one out of each four may mature. Usually at maturity they are entirely separate and do not show how they were previously in contact, but in a few cases they remain united in fours (quartets). Sometimes the pollen grains are waxy and cohere in masses (pollinia), as in milkweeds and orchids.

Ordinarily pollen grains have two coats or walls. The outer coat functions to protect the contents from drying out and from mechanical injury. It is provided with grooves, or furrows, so that it is semi-rigid and can accommodate itself to changes in the volume of the contents caused by variations in moisture. In connection with these furrows the germ pores are developed. The spines or net-like ridges are sculpturings of the outer coat.

Pollen grains of closely related species have a tendency to be similar; we might say that the degree of similarity may be an indication of the closeness of relationship. In the pines and some other cone-bearing relatives, the

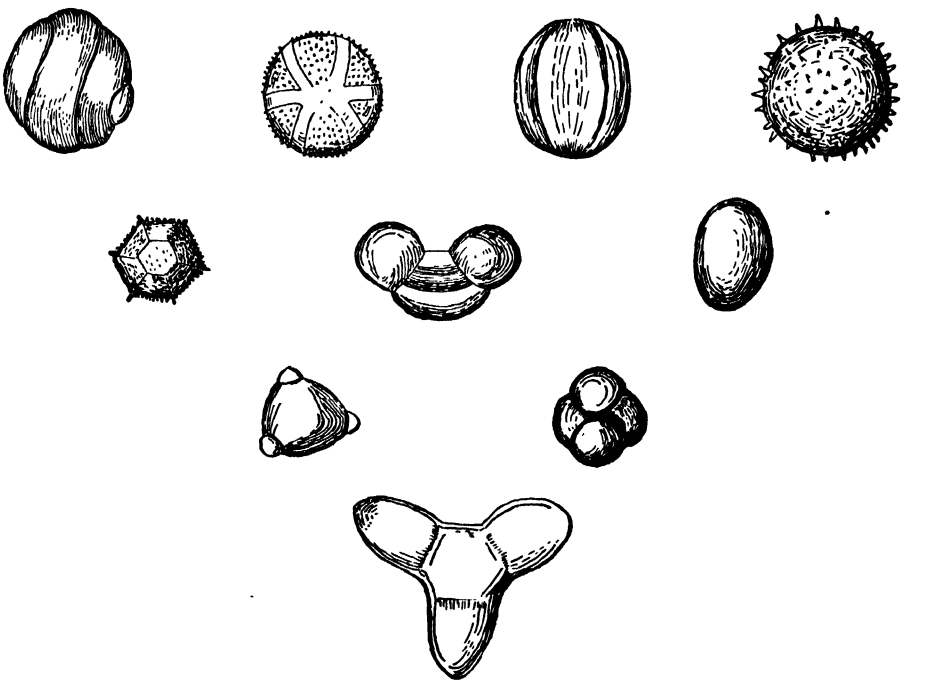


FIG. 9–27. Various kinds of pollen grains. From left to right, beginning at the top: musk plant, spirally grooved; one-seeded cucumber, with bristly points and smooth bands; wild balsam-apple, grooved lengthwise; rose mallow, with prickly points; succory, many-sided; pine, with two bladders; lily, oval and smooth; enchanter's nightshade, with three small lobes; laurel, four grains united; and evening primrose, with three large lobes. (After Gray.)

pollen grains possess two wing-like bladders. These serve to increase their buoyancy and assist in their dispersal by the wind.

There is considerable variation in the length of time that pollen grains remain alive and capable of germination (*viable*). Temperature and moisture are the chief factors which affect the viability of pollen. In corn the pollen grains usually do not remain active for more than a day after shedding. It is reported that the pollen of the date palm will remain viable for several months if kept dry. Apple pollen will remain alive for several months if stored in closed chambers where drying is prevented. Dry pollen withstands extremes of temperature better than moist pollen. The pollen of the apple and the pear will stand temperatures close to freezing, but such temperatures are injurious to the pollen of the peach and the apricot.

In marshes and bogs there accumulates vegetable matter—the remains of the surrounding plants. As time goes on these layers of decomposed remains form what is known as *peat*. Pollen grains do not decompose readily under such conditions and are to be found in a fossil condition in peats and sediments. Since it is possible to determine from what plants these pollen grains came, they furnish us with a means of determining the history of the succession of trees. By applying statistical methods to the frequency of the different pollens, the changes in the forest types from one period to another can be traced.

CHAPTER 10

DISPERSAL AND ESTABLISHMENT OF THE PROGENY

(*Dissemination, Germination, Associations*)

One of the most obvious facts about plants is their fixity or immobility. Some of the microscopic one-celled plants swim, some larger ones float, and a few creep; but most plants remain rooted to a spot. And yet plants invade new areas. Many plants when introduced into a new region spread widely and become an established part of its flora. There is constant *dispersal.* Many of our common plants, especially weeds, have been introduced from some foreign land. This possibility of the development of plants in new territory is brought about chiefly in connection with reproduction. Dispersal in animals is not commonly associated with reproduction, but in plants the two processes are conspicuously associated. If the detachable structures of plants which bring about reproduction were not capable of dispersal the reproductive process would be deprived of much of its significance. Provision for change of location is imperative; if the parents cannot move, the progeny must be able to migrate. Only thus can they find space and conditions in which to develop.

Both spores and seeds are well adapted for dissemination. It has been aptly said, "A seed is a little plant packed for transportation." In the lower plants spores are effective in dispersal. The spores are constantly floating in the air and some of them are likely to come to rest where there are growing conditions. In 1883, all the vegetation on the island of Krakatoa was destroyed by a volcanic eruption. It is reported that algae, fungi, mosses, and liverworts were the first plants to reappear, having been brought by wind-borne spores. Ferns, also distributed by wind-borne spores, developed abundantly in advance of seed plants. An account states that after fifteen years fifty-three species of seed plants had reestablished themselves on the island. It was estimated that more than one-half of these were carried by ocean currents, about one-third by winds, and the remainder by animals. Ten years later there appeared a number of species whose mode of migration was unknown.

DISSEMINATION

In addition to water, wind, and animals, which are the chief means by which plants acquire a change of location, there are several other methods. Man disseminates seeds and plants. Some plants have a way of discharging their spores and seeds so that they are actually forcefully propelled some distance. Gravity, under certain conditions, plays a role. Reproduction through vegetative growth, although a slower process, is effective in the spread of plants. These various processes call for further explanation. Our consideration is chiefly from the point of view of the method by which plants shift their locations. We need not, however, be unmindful of certain advantages. We have spoken of the obvious necessity for the progeny to find space for their development. Perhaps better soil conditions may cause better development. New localities may be freer from insect pests and diseases.

Our discussion will refer most frequently to seeds. In the higher plants seeds are primarily the agents of dissemination. Sometimes it is the fruit which is the medium of seed transportation. We must not overlook what may be regarded as the protective role of seeds. Remembering that a seed has within it a little plant, we are in a position to see how it protects that little plant. A living plant is subject to danger of many kinds. It may die from drought. Seeds are particularly resistant to dryness. Of all plant parts they are the most capable of withstanding dryness of the air and soil. The embryo in a seed remains alive when conditions for the plant itself are so unfavorable that it cannot exist at all. Our annual plants (i.e., those which live for only one growing season) exist through the winter only in the form of seeds. When we think of the many weeds, such as the ragweeds and pigweeds, that die at the end of autumn and reappear in such abundance in the spring, we realize how adequately the seed serves to insure the perpetuity of the species. Of course seeds are exposed to dangers also; one of the greatest is that of being eaten by animals. Their production in great numbers is the chief insurance that some will escape such a fate. In some cases they pass through the digestive tracts of animals unharmed. In other cases the fruits are spiny and thus protected from fruit-eating animals.

Dispersal by Water

The coconut is frequently seen floating in tropical waters and is often cited as one of the most striking examples of waftage by water. The nut is surrounded by the husk of the fruit, which is composed of coarse, tough fibers (Fig. 10–1). It floats well, and probably the wide distribution of the

coconut palm has been aided in this manner. There is some doubt about the resistance of the husk to water. Some observers believe that it protects the nut well, keeping the embryo alive for a considerable time. Others believe that the embryo soon loses its vitality through soaking and that transportation to great distances is unlikely.

The fruit of the bladdernut has large air spaces which cause it to float. There are three separate compartments so that it will float even if one or two compartments are injured. Many seeds and fruits are lighter than water,

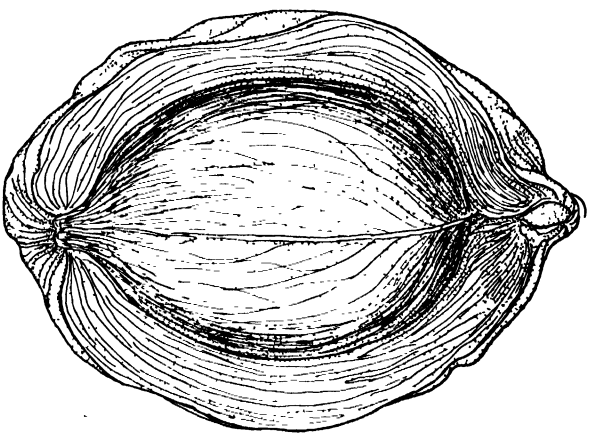


FIG. 10–1. Coconut with part of the husk, which causes it to float, removed.

float readily, and may be carried long distances. This is especially true of plants growing in the water or in swampy places, such as the bur reed and arrowhead. The fruit of the latter has corky margins. The seeds of the milkweed have corky margins. Some sedges that grow in moist places have inflated fruits which serve to buoy them. The spikelets of some grasses, still containing the grains, float in a raft-like manner. Doubtless many seeds not floating by themselves are carried by water in driftwood and debris. Many seeds resist the infiltration of water when immersed and remain viable for a considerable time.

Some living plants are transported by water currents. Many aquatic algae are not anchored. The Sargasso Sea gets its name from large quantities of a floating seaweed called sargassum. Some of the liverworts and their buds (gemmae) float. All owners of water-lily pools are familiar with such floating plants as the duckweed (*Lemna*), *Azolla, Salvinia,* water lettuce (*Pistia*), water fern (*Ceratopteris*), and water hyacinth (*Eichornia*). Some of the watercresses are not firmly attached and are readily shifted from

place to place. Some water plants form detachable buds which float freely. Water currents may carry broken twigs, as of the willows, which easily strike root in new locations.

Water is not as effective as the wind in the dissemination of seeds and plants, but it is nevertheless an agent of much importance. Whether in streams, lakes, or in the oceans, water furnishes a good means of transportation. The splashing of rain plays some part in the distribution of bacteria and the spores of fungi, mosses, and ferns.

Dispersal by Wind

Without doubt wind is the most effective disseminator of seeds and fruits from the standpoint of the number of units carried. One of the requisites for wind distribution is that the body be comparatively light in weight. Or perhaps we should say that there must be a considerable exposure of surface in proportion to the weight. One of the common ways by which this condition is brought about is through extensions which serve as wings or sails (Fig. 10–2). Most people are familiar with the fruits of the maples.

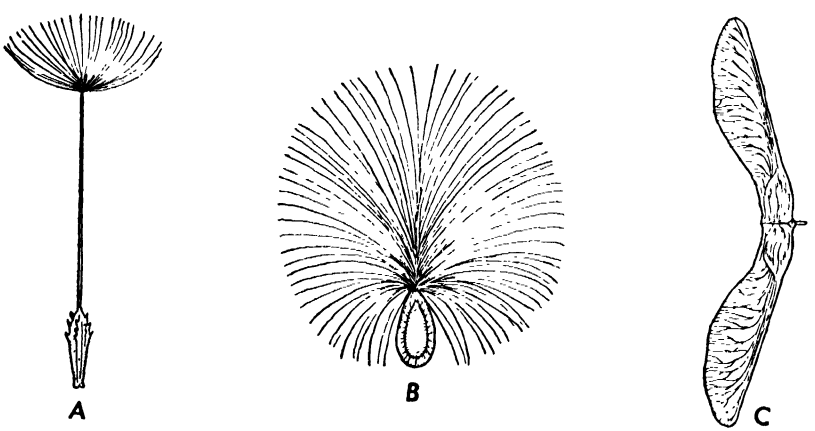


FIG. 10–2. Examples of dissemination by wind through buoyancy. *A*, fruit (achene) of dandelion, with a parachute-like structure; *B*, seed of milkweed, with a growth of soft floss; this seed also has a corky margin which serves to buoy it in water; *C*, winged fruits of maple.

We have already referred to them as *samaras*. The carpels are produced in pairs with a wing growing from the back of each. Ash fruits are also winged, with the seed-bearing portion at one end. In the hop tree and the elm the seed-bearing portion is central with a surrounding marginal wing. Sometimes the seeds are winged. This is the case in the catalpas, the pines, and the spruces. In the linden the fruits, several in a cluster, are attached

to a membranous bract which acts as a sail. Many of the winged fruits and seeds have the wings more or less twisted or are one-sided or otherwise unbalanced so that they fall with a whirling motion. Strong winds may carry them considerable distances. Another construction which results in much surface for the weight involved is that of envelopes around the seeds such as are found in the bladdernut and in some orchids.

Many seeds and fruits float readily in the air because of the presence of hairs or feathery outgrowths. Common structures of this sort are found in the so-called composites. The dandelion is a fine example (Fig. 10–2). The inflorescence is a head with many flowers. Each ovary ripens into a single achene (a one-seeded dry fruit) which is tipped with a silky plume that acts like a parachute. Doubtless everyone will agree that the dandelion has a mode of distribution which is highly effective. The plumes are good lifting devices and the seeds are often transported great distances. Thistles, goldenrods, asters, and many others of the composite family resemble the dandelion. The fireweed, belonging to the evening primrose family, has seeds crowned with a tuft of hairs. The soft floss from milkweed seed (Fig. 10–2) is sought for use in mattresses, aviation suits, life preservers, and soundproof linings. In the cotton grass there is a tuft of hairs encircling the fruit which is considered to represent the perianth. The hairs are not always developed by the same part. So far as dissemination is concerned it makes no difference whether the development takes place from the seed itself, or from the fruit, or from other parts of the flower. In the virgin's bower it is the style with encircling hairs which forms the feathery plume. In general it would seem that the winged mode of dispersal is more common in trees and the plumed mode in herbs.

A different and striking mode of wind dispersal is to be found in a class of plants known as the tumbleweeds. Pigweeds, Russian thistle, and old-witch grass are of this sort. At maturity the whole plant, or portions, become detached and go tumbling about as they are blown by the wind. They may be blown along separately or may become attached together, thus rolling over obstructions more effectively. In any event the progeny are scattered far and wide. Such plants are more common in prairie regions. In some plants the fruit cluster only is broken loose and blown away. Or dry pods may be rolled along by the wind. It must not be overlooked that certain climatic conditions may favor such scattering of fruits and seeds. Snow with a frozen crust offers particularly favorable conditions for the wind distribution of many structures that do not readily fly through the air. Many seeds are found in snowdrifts and move along with the drifting snow.

Dispersal by Animals

Animals are effective distributors of seeds. The ways in which animals bring about dispersal are various. In a number of cases the dispersal is associated with the food habits of the animals. Fleshy fruits in which there is an outer pulpy sweet portion are often sought as food. The fleshy part of the fruit may be eaten and the seeds rejected, or the seeds may be swallowed and pass through the alimentary tract without being harmed. Often the seeds are protected by a thick or stony covering which prevents their digestion. Birds are particularly concerned with the distribution of the seeds of such fleshy fruits as cherries, mulberries, and barberries. Such birds as ravens, robins, blackbirds, and thrushes do not injure the seeds which pass through their digestive systems and they are likely to carry seeds for considerable distances. Fleshy edible fruits are often brightly colored when ripe and this conspicuousness undoubtedly attracts birds and fruit-eating animals, although it is entirely possible that the advantage of showiness may be overestimated. It is not difficult to recall examples of showy fruits. The cherry, holly, and barberry are red; the huckleberry, blueberry, and red cedar are blue; the blackberry and blackhaw are black; the snowberry and mistletoe are white; hawthorns are usually yellow or red but some are blue or black. Nuts are sought by squirrels and if eaten are destroyed. Sometimes, however, the squirrel plants them and may not retrieve all of them; if one now and then escapes, distribution is effected. Birds also scatter nuts. Beechnuts and acorns are scattered by bluejays and woodpeckers.

An entirely different way in which animals distribute fruits and seeds is by transporting them on their bodies. Fruits or seeds may cling to the animal

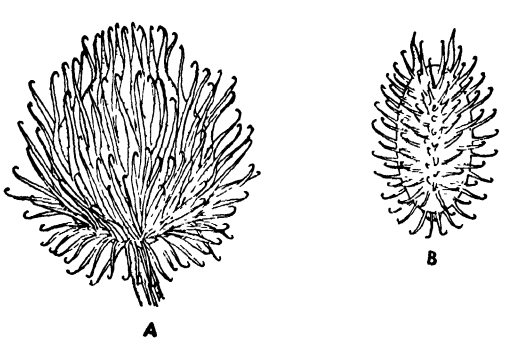


FIG. 10–3. Fruits with hooked appendages which become fastened to the fur of animals, or to the clothing of man, and are thus dispersed; *A*, burdock (*Arctium*); *B*, cocklebur, *Xanthium*.

by means of hooked appendages or because they are sticky. The cocklebur, the burdock, the beggar-ticks, and the bur grasses have hooks or barbs by which they cling to the fur of passing animals or the clothing of man (Fig. 10–3). The fruit of the unicorn plant has two stout hooks which catch readily in the tails of horses or the fleece of sheep. There are many others.

The fruits and seeds that cling because of stickiness are less numerous. Mistletoe berries cling to the feet or feathers of birds and in this way become attached to trees. The twinflower has fruits which are sticky because of glands that secrete an adhesive substance. Seeds of flax, peppergrass, and plantain become sticky when wet. Seeds of swamp plants are often distributed by wading birds, such as herons, through the mud that adheres to their feet. Seeds in mud may be carried by water animals, such as the muskrat, or even by land animals. Distribution of this kind is accidental but effective. Some plants have more than one possibility of dispersal. We have referred to the burdock as being carried by animals. It is the flower head which is provided with hooks, and in addition each little fruit (achene) is provided with a pappus for wind dispersal. Ants distribute some kinds of small seeds, especially those that may have an oily outgrowth (called *caruncle*) which serves as food for the ants.

Dispersal by Man

We must not overlook the importance of man in the dispersal and distribution of plants. On the one hand he may carry burs on his clothing as animals do in their hair or fur. Who has not some time or other picked from his clothing the clinging fruits of cocklebur, beggar-ticks, tick trefoil, stickseed, hound's-tongue, Spanish needles, or enchanter's nightshade? On the other hand, man has distributed plants both intentionally and unintentionally through his agricultural operations. He buys and sells seeds and introduces them from one part of the world to another. He exterminates plants in an area and substitutes other plants of his choice. Many weed seeds have been distributed with farm and garden seeds. In order to prevent weed distribution in this manner many states have passed pure seed laws that make it unlawful to offer for sale farm seeds containing weed seeds. Man may be an unwilling agent in distributing plants; nevertheless, in many incidental ways he has been an effective agent. Muenscher in his book on weeds (1935) states that at least 300 out of 500 weeds of the northern United States have been introduced.

In the packing of nursery stock or in other kinds of packing and ballast weed seeds are distributed. Seeds are taken from place to place in baled hay and straw. As such materials are hauled and shipped the distribution proceeds. Threshing machines may scatter weeds from farm to farm. Along roadsides and particularly along railroad tracks one often sees plants which have been transported by man. It is possible for man to do much toward the prevention of weed distribution. We have mentioned the laws which make it illegal to market farm seeds that contain weed seeds.

Many states maintain seed-testing laboratories. Some states have laws which require landowners to prevent seed distribution by cutting plants before the seeds are produced. Such laws have been directed especially against the Canada thistle. Whether or not there are laws, much can be done by good cultural practices which prevent weeds from going to seed and being distributed in various ways.

So far we have referred to weeds that have been introduced incidentally by man's activities chiefly as impurities in commercial seeds or as interlopers in materials being transported. Our story would not be complete if we did not refer to the fact that many plants now considered weeds were originally introduced by man as useful plants. They have escaped from cultivation and in many cases have become plentiful and noxious. A long list could be presented, but we shall mention only a few. Moneywort, cypress spurge, bouncing Bet were introduced as ornamentals; tansy, poison hemlock, and celandine as drug plants; chicory and wild parsnip as vegetables. All these have escaped and have become weeds in some parts of the United States.

Dispersal by Projection

There are some cases in which the plant itself throws or ejects its seeds from the fruit in a more or less violent manner. It is true that dispersal by such means covers only short distances and that as a method it is relatively ineffective. Yet it may aid in spreading smaller plants and hence must not be overlooked. There are various ways in which the projection is accomplished. In some legumes such as the wistaria, the lupine, and the vetch, the two halves of the pods twist apart suddenly as they dry out and this torsion expels the seeds in an effective manner (Fig. 10–4). When the seeds are at the proper stage of ripeness any sudden tapping may cause them to burst. In the wild geranium the mechanism is different. The seed capsule splits and coils upward under tension so that it expels the seeds with real force. In the witch hazel the fruits open at the apex and the sides press against the hard smooth seeds so that they are shot out for several yards.

Quite different from the forces developed by the elasticity of drying tissues are the forces developed by cells which are gorged with sap and hence have great internal pressures (turgescence). Under certain conditions such pressures may eject seeds effectively. In the squirting cucumber the tension is great enough to force out the seeds together with some of the internal fruit tissues. In jewelweed the pods burst suddenly when touched. This fact is responsible for another common name, touch-me-not, and also for the scientific name, *Impatiens*. In one of the mistletoes the fruits explode at

maturity. In this case the seeds are sticky and cling to the leaves or bark, but in many of the plants where propulsion takes place the seeds are smooth, round, and comparatively heavy. In the poppies, the evening primroses, the pinks, the bluebells, and the figworts the seeds lie in open capsules borne on long elastic stalks. When these stalks are blown over by the wind or pushed by animals they recoil with a jerky movement sufficient to throw out the seeds. Gravitation may aid in dissemination by causing seeds to roll down cliffs and hills. Some seeds after being ejected may continue on their way by rebounding from leaves, stems, and other objects.

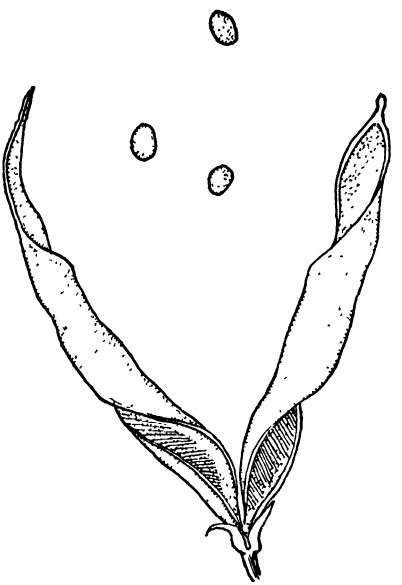


FIG. 10–4. A dry pod of a legume bursting and scattering the seeds. (After Beal.)

Many of the fungi are known to discharge their spores with considerable force so that they are carried far enough to be caught up by air currents. Some of the cup fungi when jarred discharge clouds of spores which can be readily seen. A little fungus known as *Pilobolus* discharges the whole sporangium with sufficient force to propel it a distance of several feet. The sporangia of many ferns discharge the spores so forcibly that the stalk may be broken and the sporangium itself left in a torn condition.

Change of Location Through Growth

In our discussion of vegetative propagation it was pointed out that some of the lower plants, fungi, mosses, and liverworts spread radially from an original center (Fig. 10–5). Portions of this vegetative growth may eventually become isolated. It is a relatively slow process, but such extensions through growth do result in new plants arising in new, even if not distant, locations. Higher plants may send their modified stems or roots underground, and new plants, known as *suckers,* may arise some distance from the parent plant. Some plants accomplish the same end through the rooting of the tips of stems above ground. We have referred to the rooting of strawberry runners. Raspberry canes root at the tips in a similar manner. The walking fern is another example. The reclining branches of one of the

viburnums often take root. Because they remain attached for a time and effectively trip the unsuspecting hiker, such shrubs are given the common name hobblebush or witch hobble. By this means of rooting they do "straggle along." There are some plants which live over winter as an underground stem and send up new shoots from the tip each season. As the older part dies and the rhizome grows onward, the plant actually moves along

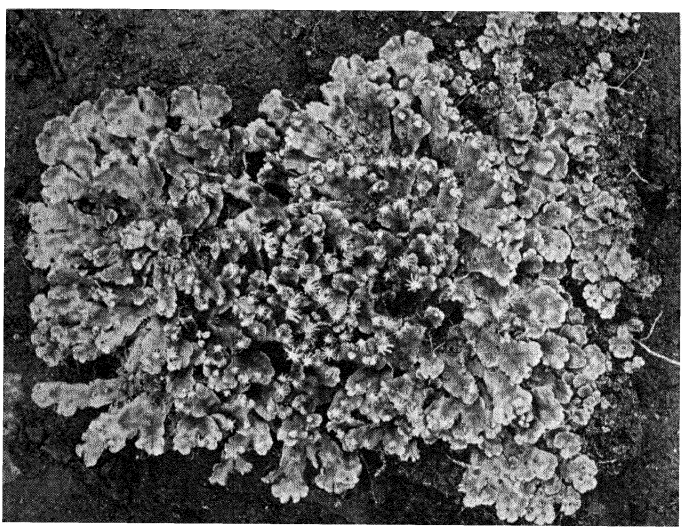


FIG. 10–5. A liverwort spreading in all directions through vegetative growth.

from season to season. In the tropics there are plants growing upon the trees (epiphytes) which gradually change their positions on the tree branches in a similar way. The point may be made that some of these peculiarities of vegetative growth do not serve to disseminate plants in a widespread manner, but it is true, nevertheless, that such methods may be responsible for results of real importance.

Review of the Various Means of Dispersal

As the discussion of the agencies by which plants spread from place to place has proceeded, doubtless the resemblance of this problem to that of pollination has been evident. The two processes do have much in common. Bodies which have no independent means of locomotion must secure a change of location through some outside agency. Wind, water, and various forms of animal life distribute pollen. They also distribute fruits and

seeds. It is hoped that the similarity of the problems and the partial identity of the methods of solution will not bring about any confusion between these two processes—pollination, the transfer of pollen from anther to stigma, and plant migration, the change of location of plants—which are so different in significance.

Wind is without doubt the most effective disseminating agent from the point of view of numbers. Many sorts of seeds are scattered far and wide by the wind. The scattering is indiscriminate and wasteful because the seeds are as likely to be deposited in unfavorable as in favorable places. Animals may not carry as many seeds and may not carry them as far but they are likely to drop them in favorable places. Water is more likely to transport seeds for long distances. Not only does water distribute the seeds of plants growing in the water, but heavy rains, floods, and temporary streams are important transporters of land plants. Migration through extension by growth will impress everyone as relatively slow. Perhaps even some of the other methods will give the same impression, for we as human beings are accustomed to rapid modes of travel. But we must keep in mind that even these imperceptible movements produce results of consequence through the geological ages. Finally we must agree that mankind has greatly modified the natural distribution of plants. Human activities have been the means of distributing both useful plants and weeds. Man is often the instrumentality for transporting seeds across natural barriers such as oceans and mountains. After the plants have become established, wind, water, animals, and other agencies aid their spread locally.

GERMINATION

Our study of seeds has revealed the presence of a young plant within the seed. We have just given consideration to the ways by which seeds are dispersed. For the establishment of a new plant two necessary conditions must be fulfilled. The first condition is that the embryo in the seed shall remain dormant and yet retain its vitality during dispersal. The second is that the embryo must break this period of dormancy later and emerge as a seedling (this is known as *germination*) when in a favorable location. The compactness of the tissues of the embryo and the small amount of water contained by them help to make the seed resistant to drying and to extremes of temperature. The firmness of the coat protects it from mechanical injury. Germination is facilitated or retarded both by seed characters and by external conditions.

The Time of Germination

Some kinds of seeds are capable of germination at maturity if provided with suitable conditions. Seeds of willows will grow as soon as shed and will die if they do not have an early opportunity for growth. Seeds of the sensitive plant will germinate when ripe but will retain their viability for years; one report says that they have been known to remain alive for sixty years. Many seeds require a certain period of dormancy. It has been observed that seeds of the same species vary in the time of germination. Sometimes the seeds of a given crop may germinate over a period of several years. In the common cocklebur there are two seeds in each fruit. It has been observed that one of these seeds germinates the first spring and that ordinarily the other one does not germinate until the second spring. It is believed that the delayed germination of the one seed is due to the greater impermeability of its coat. There are other seeds which germinate better the second year than the first year. The seeds of some conifers will not germinate for several years. It is not likely that many seeds will remain alive for more than three or four years after ripening. The variations in the length of the period of dormancy may be due to a lack of maturity of some of the internal tissues or to the retarding of the passage of oxygen by the enveloping seed coat. There are a few plants in which the embryo never passes into a dormant state but continues to grow while still in the fruit. Such plants are said to be *viviparous* and strictly speaking they do not develop seeds but seedlings instead. The mangrove is a good example. The embryo protrudes from the fruit while it is still attached to the tree. The radicle is the heaviest part of the seedling and when it falls from the parent tree it is in the right position—root downward and plumule upward.

Favorable Conditions for Germination

The external conditions favoring the growth of the embryo are an adequate supply of water and oxygen, and a suitable temperature. All three of these conditions are necessary. Dry seeds will not grow even though the temperature is suitable and oxygen is present. Oxygen is necessary for the chemical changes in the food supply and as the source of the energy for growth. Temperature affects the absorption of both water and the oxygen. Germinating seeds evolve heat. This can be demonstrated by placing them in a vacuum bottle and inserting a thermometer through the stopper. There are a few kinds of seeds which require light for germination, some which germinate better in light than in darkness, and a number which are adversely affected by light; but most seeds germinate equally well in light or

in darkness. The seeds of some parasites will not germinate unless they are in contact with their host. Some seeds do not germinate in nature unless a fungus is present. This is true of certain orchids, although it has been found that suitable chemical solutions may take the place of the fungus.

When fixed in the soil the seeds of most plants are in a favorable location for growth. Seedsmen instruct the gardener to regulate the depth of planting according to the size of the seeds. It is not uncommon to find on a seed packet instructions to barely cover the seed from view if they are small, or to cover them to a depth of not more than one-fourth inch, and so on. There is no such regulation of planting in nature. Without doubt many small seeds may be covered too deep for proper germination. On the other hand if seeds are not planted deep enough they may not be supplied with sufficient water. Some seeds and fruits have mucilaginous coats which serve to fix them to the soil and also to absorb moisture which aids in germination. Quince, flax, mustard, and plantain have seeds of this sort. The coats of many seeds are ridged or furrowed or they are covered with bristles or hairs and thus the seeds are firmly anchored in the soil, a condition which is important for germination. A few seeds are furnished with self-planting mechanisms. The fruit of porcupine grass has a long pointed appendage or *awn* which is twisted below. The base of the fruit is sharp. As the tissues of the awn absorb water and then lose it by evaporation, the awn twists and untwists. This spiral movement serves to work the one-seeded fruit into the soil. There are hairs on the fruit which hold it in place as it penetrates the soil. Similar fruits are found in some other grasses and in the stork's-bill, a member of the geranium family.

Emergence of the Seedling

The first noticeable evidence of the germination of a seed is the bursting of the seed coat and the protrusion of the root tip. Absorption of water causes the embryo, or both the embryo and endosperm, to swell with sufficient force to rupture the seed coat. Most seeds have a tendency to lie so that the root is pointing downward. No matter what the position of the embryo may be, the root tip turns downward into the soil and root hairs soon develop. The primary root soon produces lateral branches and the seedling is firmly anchored.

In some plants the cotyledons remain in the seed and the plumule develops into a shoot which pushes its way through the overlying soil (Fig. 10–6). As soon as it is above ground green leaves appear. This is the type of development in the cereals, peas, scarlet runner beans, broad beans, and oaks. In other plants the cotyledons emerge from the seed, turn green, and

function as the first leaves of the young plant. Usually they wither and drop off when their supply of reserve food has been exhausted. In some cases the hypocotyl elongates, forming a curve or arch, while the cotyledons are still in the seed. This hypocotyl arch is the first growth to appear above the ground. The cotyledons are thus pulled rather than pushed through the soil. Once through the soil the bent hypocotyl straightens and

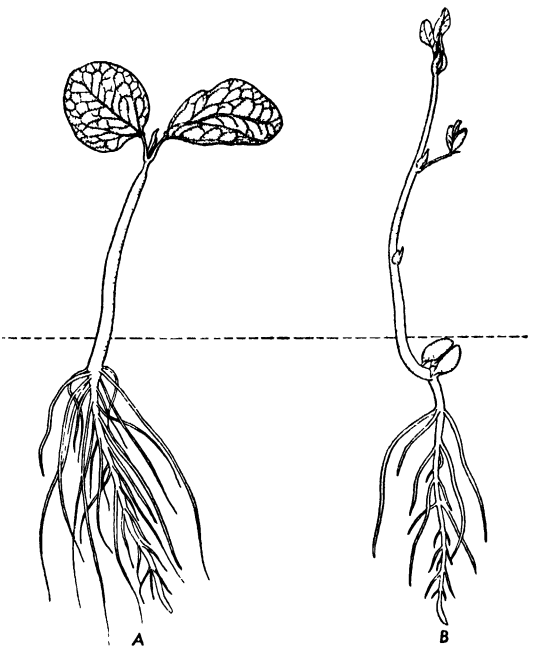


FIG. 10–6. Types of germination. *A*, the cotyledons are raised above the soil by the elongating hypocotyl (castor bean); *B*, the cotyledons remain within the seed, the hypocotyl does not elongate, growth is from the plumule (pea).

the cotyledons come to occupy the position of the first leaves of the young plant. Castor beans, navy beans, lima beans, and pumpkins illustrate this form of seedling development (Fig. 10–7). Frequently the tips of the cotyledons adhere and in this way protect the plumule until it is above the ground.

In this manner the embryo becomes the seedling. While the little plant is emerging from the seed coat and establishing itself, it is not making its own living; it is living on food stored for it by the parent plant. The total dry weight of a young seedling is not as great as that of the original seed. This is due to the fact that so much of the food has been used in respiration to supply energy for the rapid growth. But when the seedling begins to ab-

sorb water from the soil and to carry on photosynthesis in the new shoot, life is begun as a separate and independent individual. Its further growth and development are accomplished through its own activity.

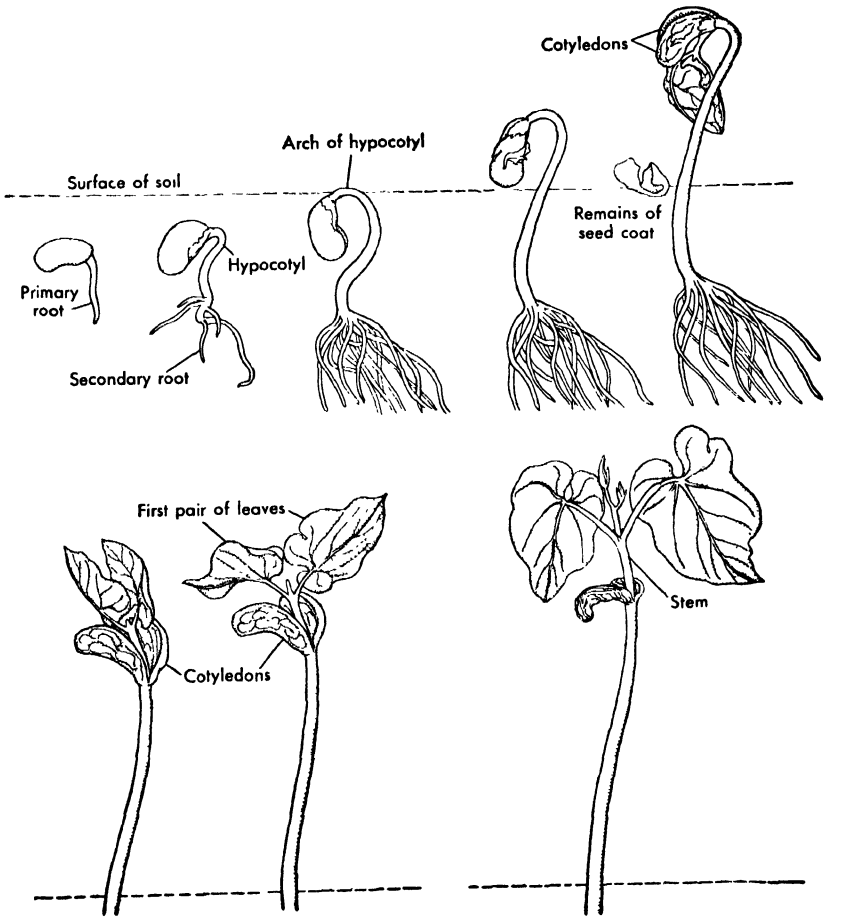


FIG. 10–7. Germination of a bean seed and early stages in the development of a new plant.

PLANT ASSOCIATIONS

When we observe the landscape we usually do not see individual plants but masses of them. When we speak of the forest, or the meadow, or the prairie, we are recognizing that plants are associated in groups. In recent years much study has been given to the relation between plants and their environment. Only superficial observation is necessary to learn that certain

plants grow in ponds, others in swamps, others in forests. Water lilies, pondweeds, and duckweeds grow together in a pond; cattails, rushes, and sedges grow together in swamps; maples, beeches, and ferns grow together in a forest. Different terms have been used—in fact, a good many terms have been used to designate associated groups of plants in nature. One definition is, "A group of plants in its entirety occurring in a common habitat is known as a *plant association.*" Another is, "A mass of vegetation which gives a distinctive aspect to a country, such as a pine forest, or a natural meadow, is called a *formation;* any group of plants commonly occurring together therein is called an *association;* while the word society is somewhat loosely used for any kind of vegetation group." We find also the statement that minor groups within societies are called communities. The general study of organisms in relation to environment is called *ecology.* In general it is a field science. The phase of ecology which deals with the distribution of plants as affected by soil and climate has been called physiographic ecology. It might be called the ecology of vegetation.

We have learned that plants migrate through the dispersal of their spores or seeds. We have found that they become established under favorable conditions. A species tends to expand into any suitable unoccupied region whether or not individuals of other species are already growing in the territory. The spreading continues until a check occurs. Such occupation of a new habitat may be called *invasion.* Successful invasions eventually cause one association or formation to replace another. In other words, there is a *succession* of associations over a period of time. As human beings, we see the world for such a limited time that the things in it may seem to be in a relatively static state. But we know that the world and all things on it have been ever changing. The fossil records in the rocks tell us of a procession of floras from age to age. Investigators are convinced that ancient plants, possessing efficient means of dispersal, migrated in their day from their original home and colonized great areas. Time passed, checking factors operated, even land and water changed places, competitors arose, and the distribution of plants varied. At any given time the range in space for a species or for a group of species may be increasing and for another group may be decreasing.

Doubtless it is generally realized that there are characteristic belts of vegetation as we pass from the arctic latitudes to the tropics (Fig. 10–8). Similarly we pass through well-marked zones of vegetation up and down the slopes of a tropical mountain. The distribution of plants is correlated with climate. We must not conclude that the correlation is simple and direct, because many factors (light intensity, length of day, temperature,

FIG. 10–8. Principal vegetation patterns of North America. (From Transeau, Sampson, and Tiffany, *Textbook of Botany*. Copyright 1940 by Harper & Brothers.)

growing season, rainfall, etc.) are involved and our knowledge of some of them is uncertain and incomplete. Some workers not only speak of life zones but recognize what they call life *realms* in different parts of the world. Accordingly, the northern latitudes of both hemispheres are the Holarctic realms, and South America, Africa, and southern Asia are Neotropical, Ethiopian, and Oriental realms respectively. Australia is set aside as a distinct realm. It should be borne in mind that much of what has been said about the distinctiveness of plants in the various zones, regions, and realms is equally true of animals. And again we must remind ourselves that man is often the cause of the shifting of both land and animal populations. In any event, whatever the causes and whatever the results, we cannot escape the fact that the living world is a shifting world—organisms are always on the move.

Classification of Plant Associations

A simple and widely used classification of plant associations is based on water relations and provides three main divisions: *hydrophytes, xerophytes,* and *mesophytes.* Such a classification is inexact but convenient. *Hydrophytes,* or hydrophytic associations, grow in water or wet places and have soft, usually finely divided bodies (Fig. 10–9). Most algae belong in this group, but also included are some mosses, liverworts, ferns, and flowering plants. *Xerophytes,* or xerophytic associations, grow in dry situations where there is a deficiency of rainfall or a diminished supply of available water (Fig. 10–10). The most extreme types are found in deserts. Reference has already been made (Chapter 5) to some of the characters of xerophytic plants. The members are chiefly flowering plants but include others, such as some lichens. *Mesophytes,* or mesophytic associations, are plants growing in places with medium amounts of moisture (Fig. 10–11). Here the plant body may be small or large, herbaceous or woody. The majority of the species are flowering plants, but many ferns and mosses are included. A common expression of the mesophytic association is the forest with its canopy of trees, undergrowth of shrubs, and carpet of herbs.

Such a classification has its imperfections and disadvantages. It puts together societies that are entirely unrelated in origin and it separates others that are closely related. It is inexact because definite boundaries of demarcation cannot be drawn between the three groups. But as a classification it has its advantages and is widely used. The three large divisions are subdivided into many groups of subdivisions. A detailed classification is impossible in a brief presentation, but it is important that the general principles involved be understood.

FIG. 10–9. A hydrophytic association. (Photo by L. O. Overholts.)

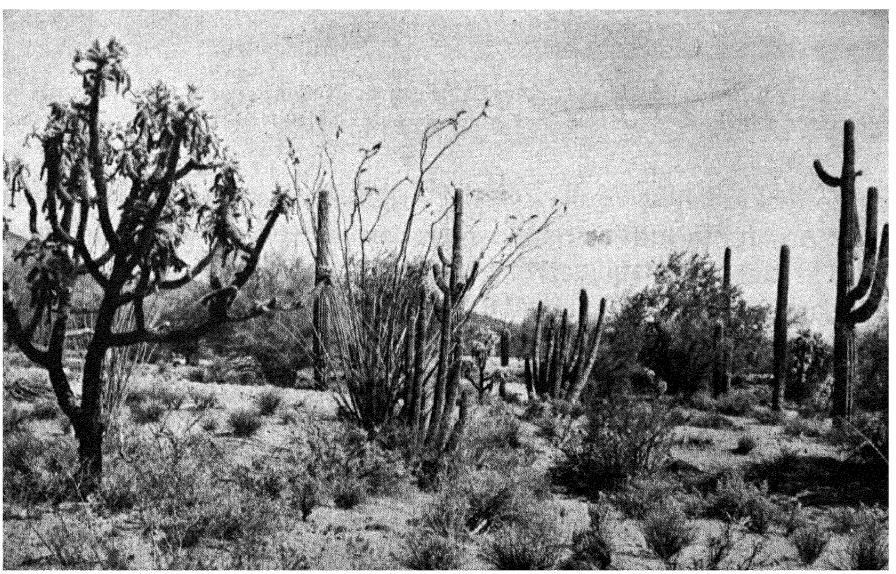


FIG. 10–10. A xerophytic association in Sonoran Desert, Arizona. The ocotillo, palo-verde, bur-sage, desert ironwood, and various cacti are shown. (Photo by National Park Service.)

We have referred to the fact that one type of association may follow another type or that there is a natural succession of types. This in turn is due to changes in the physiographic and topographic development of the earth's surface resulting from the processes of erosion and deposition. Uplands

FIG. 10–11. A mesophytic association in Allegheny National Forest, Pennsylvania. The photograph shows trees, shrubs, and ground cover. (Photo by U. S. Forest Service.)

may be rocky, sandy, or clayey. The original vegetation would be xerophytic. A pond in such a region would have, in the beginning, an aquatic flora. Through denudation and humus accumulation, the upland flora tends to become more and more mesophytic until it finally forms what is known as the ultimate plant association, that is, a deciduous mesophytic forest. During this development the pond is becoming gradually filled with deposited materials, both humus and soil, so that its aquatic vegetation is replaced by a swamp vegetation; and this in turn may be eventually replaced through further accumulation by a mesophytic forest association. Or, if the climate is too dry, the final association may be xerophytic rather than mesophytic. Considerations based upon the principles of succession are necessary in the analysis of vegetation. There is a sequence of succession of plant associations which is coupled with an order of topographic develop-

ments in the ever-changing landscape. Thus it is evident that we must relate plant associations not only to water but also to soil. It is plain that hydrophytic and xerophytic areas are being restricted and that the final stage is mesophytic. "The succession of plant associations," writes a plant

FIG. 10–12. Subalpine spruce-fir forest in Colorado; Engelmann's spruce and alpine fir. (Photo by L. O. Overholts.)

ecologist, "is now a well-established law in biology and should be recognized in all modern field studies. As the habitat factors change, the associations change, and these changes follow orderly sequences that may be detected by appropriate methods of investigation."[1]

Ecologists frequently designate an association by the principal species, or they may include also the secondary species. For example, we find references to spruce-fir and beech-hemlock associations, etc. (Figs. 10–12, 10–13, 10–14). The importance of the role which a species plays in an association is largely dependent upon the number of individuals. Although the term competition is in more or less disrepute it serves well to express certain facts. If we use the term we must say that there is competition between individuals and also between species. At first the conflict is one for space only,

[1] Sampson, *Ohio Journal of Science*, 27:303, 1927.

but later there is competition for light and finally for soil nutrients. The result is dependent upon the rapidity of germination of the seeds and upon the vigor of the seedlings. Of course young plants require less space than

FIG. 10–13. Beech-hemlock association in Allegheny National Forest, Pennsylvania. (Photo by U. S. Forest Service.)

older ones. One investigation reveals that a fifty-year-old pine requires 2 square meters; at one hundred and twenty-five years, 11 square meters; and at one hundred and fifty years, 15 square meters. Therefore, the num-

ber of fully developed individuals that can find space in a given area is definitely limited. According to another report, only one of 2000 young beeches can come to maturity. More than a million ten-year-old plants were found on one hectare (2.47 acres); 4460 in a fifty-year-old pure stand in the same area; and only 509 in a one-hundred-year-old stand. There is a progressive intensity of competition which is very real.

FIG. 10–14. Maple-beech-cherry-hemlock association. (Photo by U. S. Forest Service.)

We cannot close our account of plant associations without at least brief reference to the fact that some plants are dependent in certain ways upon other plants for their distribution. There are the *epiphytes,* which require the support of other plants (Fig. 10–15). They may be independent with respect to food and water (*perchers*), dependent for water (*water parasites*), or dependent for both (real *parasites*). Members of all genealogical groups are found in these classes of epiphytes. Then there are *climbers,* chiefly flowering plants, independent physiologically but with weak bodies. *Trailers* sprawl on the ground and become part of the carpet flora. And finally there are *saprophytes,* which lack chlorophyll and take their food from dead organisms. Here belong many of the fungi. The presence of organic remains is a limiting, though not the only limiting, factor in their distribution. Much is yet to be learned regarding the factors that determine the distribution of saprophytes and parasites. They are by no means

always present in all locations where their food supply is present. There are many parasitic fungi which are not coextensive in distribution with their host plants.

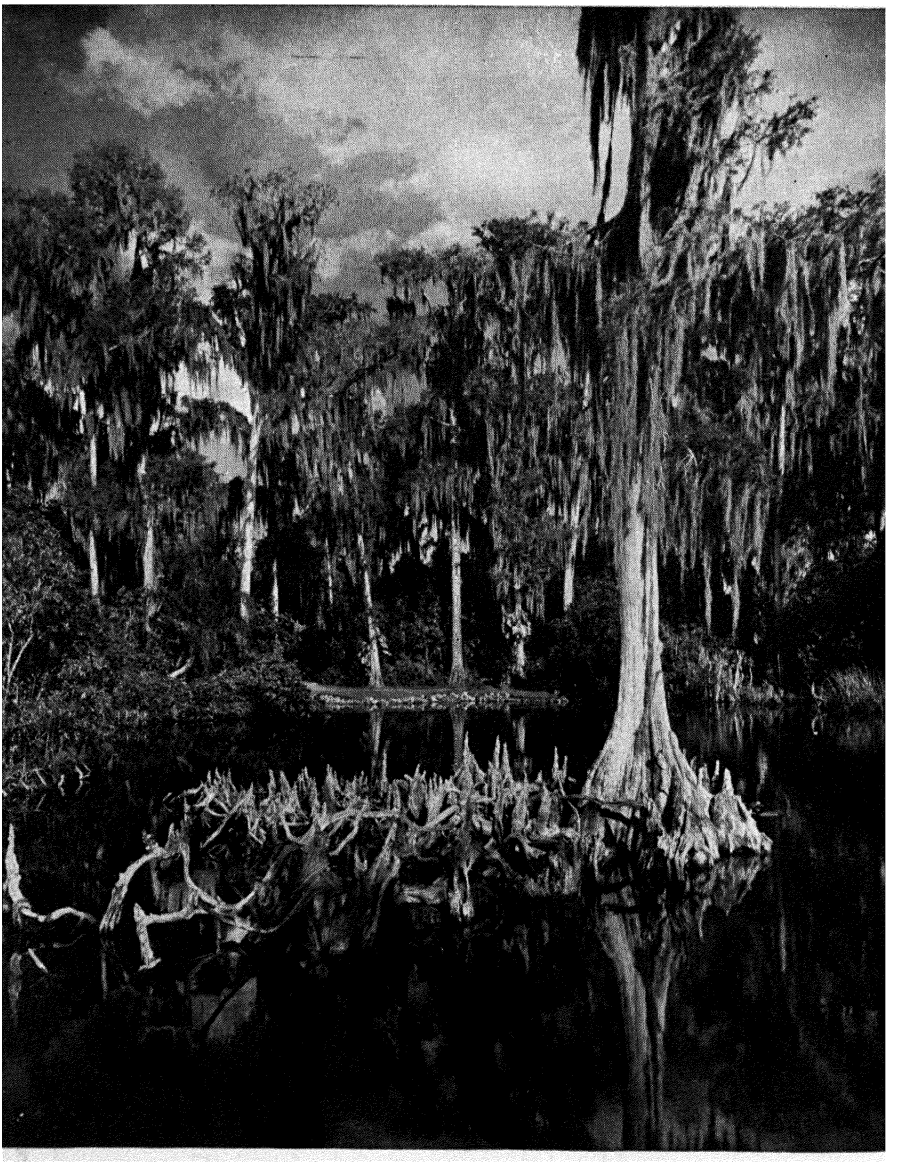


FIG. 10–15. Spanish moss, hanging in festoons from the branches of trees, is an epiphyte. Of interest in this picture are the "knees," developed on the roots of the bald cypress and projecting above the water. (See Supplement, p. 405). (Courtesy, Florida Cypress Gardens, Winter Haven.)

CHAPTER 11

THE CONTINUITY FROM PARENT TO OFFSPRING

(*Cell Division, Heredity*)

Similarities between children and parents are expected. There is an equally widespread belief that the young of animals will have many resemblances to their parents. When we think of plants perhaps our ideas are a little less definite and we may not use the words "young" and "parents," but most surely there is a strong expectation that newly established plants will resemble the stock from which they were propagated. This tendency for offspring to resemble the parents is such a well-established fact as not to require proof. It does, however, require an explanation of how it is brought about. The transmission of characters from parent to offspring is known as *heredity*. It is perfectly proper to say that the potentialities of certain characters, capacities, and peculiarities are *inherited* from parents or ancestors. The qualities which are transmitted, or rather the capacity to develop them anew, constitutes an *inheritance*.

It is obvious that no offspring inherits from the parent a duplication of all the parent characters. While fundamental similarity is the rule it is generally well known that individual differences exist. Deviations from parental type or form are known in biology as *variations*. It may sound strange to say that variations may be inherited. By this time we are familiar with the foundations of sexual reproduction. Where that kind of reproduction prevails, every individual has two parents. Here we may properly speak of *biparental inheritance*. An individual may inherit some characters from one parent and some from the other, or variations may appear as a result of the combination of characters from the two sources. It is also true that a parent may transmit characters possessed in a latent but not evident condition.

It is hoped that no one will be confused by the two statements that seem to be contradictory, namely, that the parents transmit tendencies causing their offspring to be *like* themselves, and at the same time tendencies causing them to be *unlike* themselves. It has been most aptly said that "liv-

ing beings do not exhibit unity and diversity, but unity in diversity." Inheritance and variation are not two separate processes but two imperfect views of the same process.

Mankind has long been interested in the problem of descent—both descent *without* change and descent *with* change. The Greek and Roman naturalists (Aristotle, Plato, Pliny) developed certain philosophies relating to heredity and evolution. Ever since their time there have been theories that the numerous and diverse forms of living beings have arisen from preexistent simpler kinds by a long process of modification or descent with change. The evidences and interpretations of such a theory of descent constitute the doctrine of *evolution;* to be more exact, we should say *organic evolution.*

But investigators have not been satisfied with observations dealing with the resemblances and differences evident in organisms which are related by descent. Experimental studies have been undertaken to aid in interpreting the facts of heredity and to discover the ways and means of the development of racial characters through evolution. The study of these problems constitutes one of the newer branches of modern biology known as *genetics.* The application of the principles of genetics to the development of improved races of plants has resulted in placing *plant breeding* on a scientific basis.

In his great book *The Cell in Development and Heredity,* E. B. Wilson writes, "Long ago it became evident that the key to every biological problem must finally be sought in the cell; for every living organism is, or at sometime has been, a cell." [1] Lester W. Sharp, referring to the habit of interpreting a large organism in terms of its cell units, warns that we cannot emphasize too strongly the importance of interpreting cell behavior in terms of the complete organism. The theories of heredity and evolution have been advanced by the study of cells. A knowledge of cell division has contributed greatly to a solution of these problems. In the chapter dealing with the formation of new individuals we pointed out that cell division is the basis of growth and of reproduction. A new individual begins as a single cell. Its body may ultimately be composed of an infinite number of cells. The new cells arise by division. When this many-celled individual reproduces, it forms germ cells or spores by division. When a cell divides into two cells, the daughter cells derive from the original cell not only their living matter (protoplasm) but also their inheritance. To quote Wilson again, "Upon cell division, therefore, depends not alone heredity but the

[1] From E. B. Wilson, *The Cell in Development and Heredity.* By permission of The Macmillan Company, publishers. Copyright 1925 by The Macmillan Company.

very continuity of life." [2] Cell division is so closely associated with the transmission of hereditary characters that an understanding of the process is imperative.

CELL DIVISION

We must have clearly in mind that a meristem cell, such as is found in the higher plants, consists of *cytoplasm* which contains a *nucleus* and is surrounded by a *wall*. When division is completed, the nucleus has divided into two new nuclei and a wall has been developed between them so that the cytoplasm is divided usually into two substantially equal parts. There are cases in the lower plants where nuclear division is not followed by cell division. This results in multinucleate cells. At this time we are concerned with the usual process where the division of both nucleus and cell body is completed.

Mitosis

The process by which the chromosome group of a nucleus doubles in number and then separates into two similar groups which reconstitute the two new (daughter) nuclei is called mitosis. Strictly speaking, the term *mitosis* refers only to the division of the nucleus, but it has become common practice to apply it to the whole process of *cell division*.

Most of our knowledge of the mechanism of mitosis has been gained from microscopic preparations which have been killed, sectioned, mounted on glass slides, and very carefully stained. By using two or even three stains the details of structure can be brought out so that they can be studied. In the growth zone of root tips the cells are actively dividing and these are favorite sources of material for cell division studies. Onion root tips have been widely used. In the hyacinth the nuclei are larger and offer some advantages. The root tips of May apple and *Tradescantia* have also been investigated, as well as many others.

Within the past few years considerable headway has been made by studying the procedure of division in living cells. Animal cells growing in culture solutions have been used. The changes going on have been studied under the microscope. It is significant that the results of these observations check very closely with the deductions made from the older method.

In the description of a typical plant cell, reference was made to the nucleus and attention was called to its importance in the activities of the cell. We said that there is a nuclear membrane surrounding the nuclear

[2] *Ibid.*, p. 278.

sap, the reticulum, and the nucleoli. In prepared slides of the vegetative condition the reticulum is the most noticeable feature of the nucleus. The vegetative condition is a state wherein the cell is inactive so far as division is concerned, although the processes of nutrition and respiration are being carried on. This state is sometimes called the *resting stage;* this is an unfortunate designation since it implies complete inactivity of all cell functions. The term "metabolic stage" might well replace "resting stage."

When a cell is preparing to divide, changes occur that transform the reticulum of the nucleus into compact separate bodies called *chromosomes.* In the metabolic condition chromosomes are not identifiable as individuals. The methods commonly used in preparing microscopic slides make them not only visible but conspicuous in the mitotic stages. The chromosomes are commonly rod-shaped, but there is considerable variation in form and size. In the early phases of mitosis each chromosome appears to be split into two equal longitudinal halves. One half of each split chromosome passes to one daughter nucleus and the other half to the other daughter nucleus. In this way the chromosomal material of the original nucleus is divided quantitatively and qualitatively between the two new nuclei. Mitosis is the mechanism by which the organization of a nucleus is reproduced in each of the two daughter nuclei. It will be readily comprehended that the process maintains a constant number of chromosomes throughout all the vegetative cells of the plant body. In the nucleus of the body cells of all higher plants (and animals as well) there is a definite number of pairs of chromosomes. The number of pairs varies for the different species but is usually the same for the individuals of the same species. Each germ cell (sperm or egg), when fusing to form the zygote, contributes the same number of chromosomes, and each chromosome in one germ cell is identical in form (except in the special case of *X* and *Y* chromosomes which are involved in sex determination) with a chromosome in the other germ cell (i.e., homologous). This explains why zygotes and all the body cells arising from them possess a definite number of pairs of chromosomes. For example, in cultivated cotton there are 26 pairs; in corn, 10 pairs; in the beet, 9 pairs; in wheat, 8 pairs; in hemp, 10 pairs; in the onion, 8 pairs; in the balsam fir, 16 pairs.

It is possible to recognize the following typical succession of stages or phases in mitosis. (The accompanying figures showing somatic cell division in hyacinth root tips should be studied in connection with this account.)

1. *Prophase.* The initial phase of mitosis is called the *prophase* (Fig. 11–1). In this phase the reticulum of the metabolic condition is transformed

into its constituent chromosomes. At first the chromosomes are thread-like and crooked. At a very early stage of the prophase, the chromosomes appear to be longitudinally double. As they become thicker and shorter, the fact that they are split into two equal longitudinal halves becomes more obvious. Toward the end of the prophase the nuclear membrane

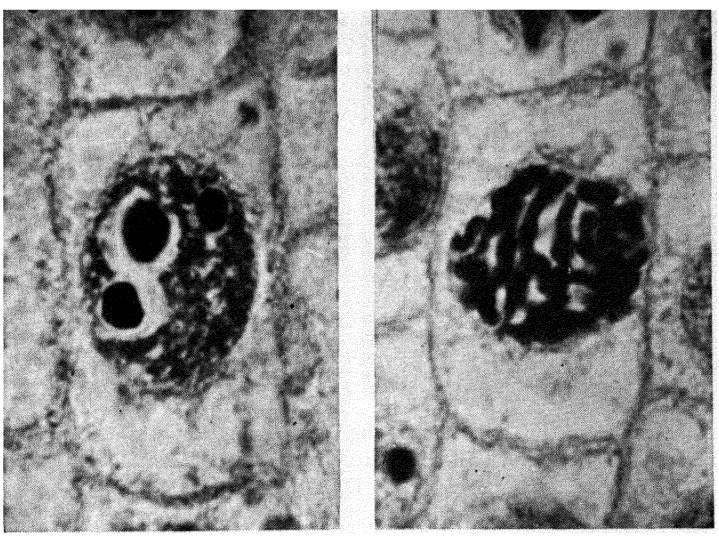


FIG. 11–1. Prophase in cell on the right, developed from the reticulum of the metabolic condition of cell on the left. (Photomicrographs by D. A. Kribs.)

and the nucleoli gradually disappear. In the region which the chromosomes occupy there develops a series of filaments or "fibers" in the form of a bipolar spindle. In animal cells filaments are present which radiate in all directions from the poles of the spindle, threading their way through the cytoplasm. These are known as *astral rays*. They do not occur in the higher plants.

2. *Metaphase.* In the *metaphase* the chromosomes lie in the equatorial region of the spindle (Fig. 11–2). If the chromosomes are short they may lie in a well-developed equatorial plane; if they are long a portion of each one may stretch away from the equatorial plane. Some fibers are attached to the longitudinal halves of the chromosomes. The attached fibers extend toward the poles of the spindle from the places of attachment.
3. *Anaphase.* Following the metaphase the two halves of each chromosome begin to move away from each other (Fig. 11–3). This separation

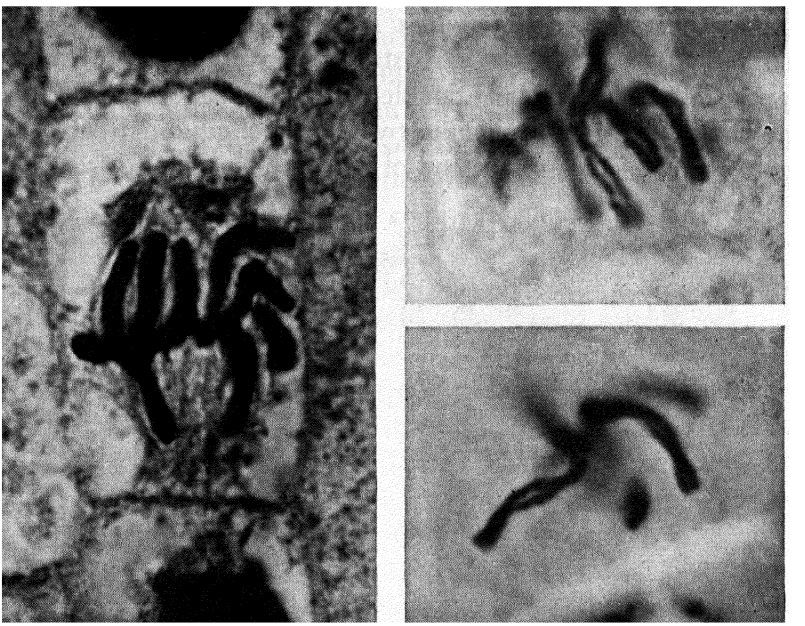


FIG. 11–2. Metaphase, the spindle showing. On the right the longitudinal halves of a chromosome are clearly evident. (These are from root cells of *Vicia Faba* in preparations furnished by H. A. Wahl; photomicrographs by D. A. Kribs.)

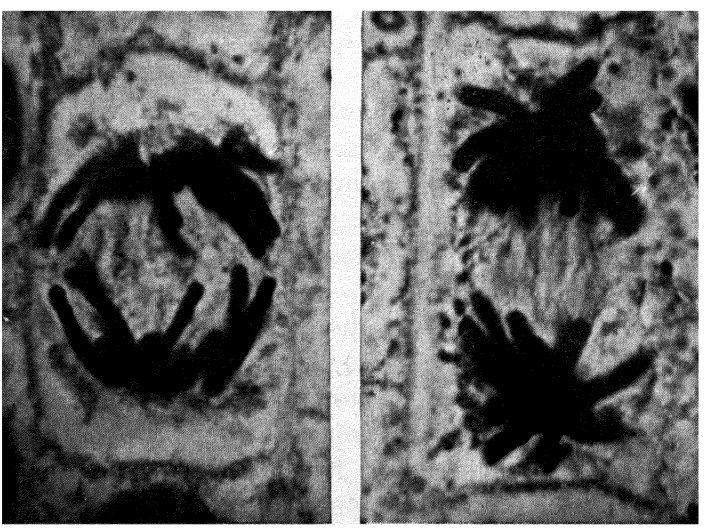


FIG. 11–3. Anaphase, in which the chromosome groups separate and pass toward the opposite poles. On the right the spindle through which the two groups have passed can be seen. (Photomicrographs by D. A. Kribs.)

gives rise to two sister groups of chromosomes which pass to the opposite poles of the spindle. The act of separating, once it has begun, proceeds rapidly. The daughter chromosomes move apart as if they were being dragged toward the poles by the traction of the attached fibers. The anaphase is a period of real activity, in contrast to the stability of the metaphase. In the final anaphase the two groups of chromosomes are fully separated and lie at the poles of the spindle.

4. *Telophase.* Each group of chromosomes now reorganizes into a metabolic nucleus. This reconstruction is known as the *telophase* (Fig. 11–4).

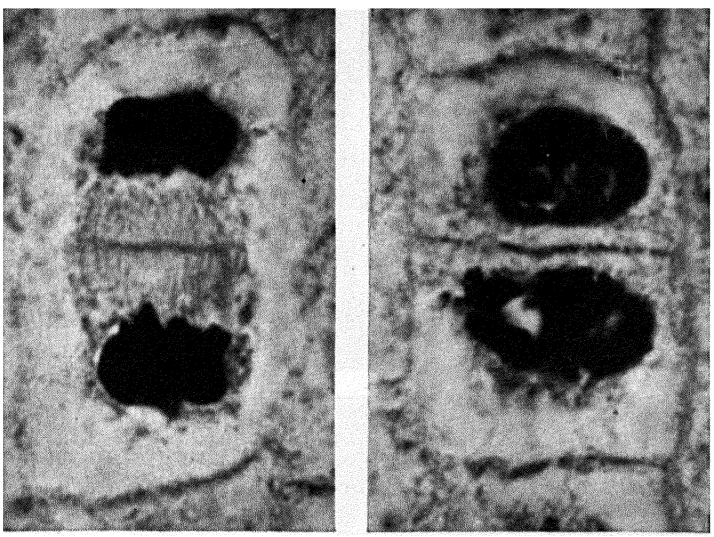


FIG. 11–4. Early and late telophase. Further explanation in text. (Photomicrographs by D. A. Kribs.)

The changes involved are in many respects the reverse of those described for the prophase. Nuclear membranes and nucleoli appear, the chromosomes become transformed into a reticulum, and there are two daughter nuclei each appearing precisely as the original nucleus did before division began.

Cell division is completed when a new partition wall is formed between the two nuclei. Wall formation follows nuclear division closely and is intimately associated with it. In the meristems of the higher plants the first evidence of a new wall is a delicate membrane (cell plate) which appears in the equatorial region of the spindle. The spindle seems to give rise to the cell plate through thickenings on the fibers. The new wall is soon completed and there are two cells, each

with its own nucleus, which have been formed by the division of the original cell. During the time of division the dividing cell usually enlarges only slightly, but soon after division is completed each of the daughter cells increases in size until it equals the size of the original cell.

General Consideration of the Division Process

The processes of mitosis and cell division have been described as they ordinarily take place in the young tissues of the higher plants. In animals, cell division takes place throughout the extent of the body. In the higher plants the dividing of cells occurs in localized regions (*meristems*). Meristems are found at the apices and as cambiums of roots and stems. The apical meristems make possible the extension in length, or elongation, and the cambiums make possible the increase in thickness. The capacity for division is lost by the main bulk of the cells of the plant body but persists in the meristems. Since cell enlargement follows after division, it is clear that a great amount of new protoplasm is being formed in the meristem regions. There is a constant movement of soluble foods from leaves or storage organs to the growing regions.

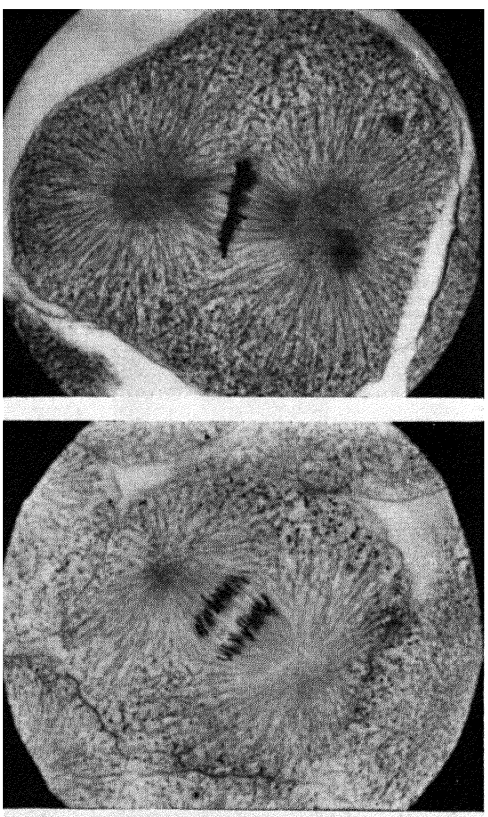


FIG. 11–5. Division in animal (whitefish) cells showing polar asters. The combination of the asters and the spindle constitutes an amphiaster. The upper figure is a metaphase (equatorial plate stage), the lower an anaphase (separation of the daughter groups of chromosomes). (Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

Nuclear division in animal cells is very similar to the process that has been described (Fig. 11–5). One of the most frequent differences in animal cell division is the presence of polar *asters* which contain a central body called a *centrosome*. The combination of the asters and spindle is called an

amphiaster. Centrosomes and asters are lacking in the higher plant cells. On that account dividing plant cells are said to have an *anastral* figure, as contrasted with the *amphiastral* type in animal cells. Another usual difference in cell division in animal and plant is found in connection with the process of cytoplasmic division or cleavage of the cell body. We have described *cell plate* formation as it occurs in the higher plants. An entirely different mode of cell division occurs in the higher animals. It is known as furrowing or *constriction.* A cleavage furrow, or constriction, begins from the sides of the dividing cell and advances toward the center of the cell, eventually cutting the original cell apart in a plane approximately at right angles to the spindle axis. The divisions in plants and animals agree remarkably in essentials. In both, each chromosome splits into two exactly equal longitudinal halves, one of which goes to each daughter cell. All the evidence points to an equal division of the chromatin, both quantitatively and qualitatively.

Most accounts of nuclear division emphasize the appearance and importance of the structures known as chromosomes. Every effort should be made to keep the whole situation clearly in mind. Chromosomes are not ordinarily recognizable except in dividing cells. When cells are not dividing the chromatin appears to form a network or reticulum. Whether the chromosomes retain their individuality in the non-dividing condition is difficult to verify, but it is not difficult to prove that there reappears at the time of division a group of chromosomes identical in number and shape with the group which went into the non-dividing nucleus. Godwin in a recent book summarizes a discussion of chromosome persistence with this statement: "Though fourteen chromosomes may emerge from the resting nucleus at one nuclear division as fourteen went in after the preceding division, and though the shapes are the same, there is no actual proof of chromosome individuality during the resting state, though all the circumstantial evidence points toward it."

Earlier in this chapter it was stated "that the key to every biological problem must finally be sought in the cell." There seems to be no doubt that the nucleus dominates the metabolic activities of the cell and that it is also the mechanism for the transmission of hereditary characters. With these concepts in mind it is easy to comprehend the importance of nuclear division. By cell divisions a fertilized egg grows into a plant with all its vegetative parts. Small portions of vegetative parts—from stems, leaves, or roots—can grow into complete new plants with all of their organs. Every vegetative cell must have in it the potentialities of a whole plant which must be passed along from cell to cell. When a vegetative cell divides, it must

divide its potentialities equally between the two daughter cells. Present-day geneticists believe that heredity is controlled by units called *genes.* The genes are material bodies, or minute organized units of material, arranged in a linear series along the chromosomes. There is strong evidence that each chromosome contains several to many (possibly several hundred) different genes and that the genes control the development of the characters. It is believed that each gene is different from every other gene but that they do not act independently. With the genes arranged along the length of the chromosomes it is clear how the longitudinal splitting of the chromosome provides for the division of the genes also. Thus we see that the genes of one-half of the chromosomes will correspond exactly with those of the other half. We should keep in mind that mitosis is a process for dividing the genes equally between the daughter cells. The chromosomes are the mechanism which makes possible this division and separation of genes. It is common practice to say that a gene is responsible for a certain character, but it is doubtless true that "there is always more than one gene affecting a visible character, and that every gene has more than one effect."

Every vegetative or body cell (also called somatic cell) of a plant or animal has the same nuclear make-up or constitution as every other body cell. Each cell contains a nucleus with genes descendent from those that were in the original zygote (the fertilized egg) from which the organism developed. When a cell divides there are chromosomes in the mitotic figure which appear identical with those that were in the zygote and it is believed that they are the descendants of those original chromosomes.

This account of mitosis presents the main outlines of the formation and behavior of the chromosomes during the division of vegetative or body cells in the process of growth. We come now to a consideration of the situation in connection with the process preparatory to sexual reproduction.

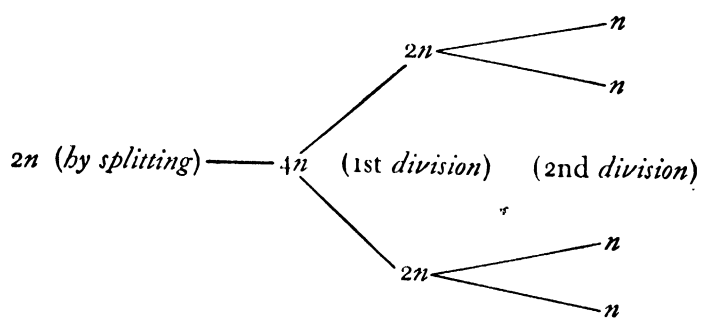
Meiosis

In sexual reproduction there is a fusion of gametes to form a zygote. In the higher plants the gametes are unlike in size and activity. No matter how different the gametes may appear, their nuclei contain similar contributions of chromatin material. It is obvious that the zygote nucleus, organized by the union of the nuclei of two gametes, is in effect a double nucleus. If we speak in terms of chromosomes, we must say that the sperm and the egg each have a complement of chromosomes and that these two complements are alike in form and number. The number of chromosomes in the gametes may be represented as *n;* the actual number varies in different species. It is obvious that the number of chromosomes in the

zygote is $2n$. It would also be proper to say that the zygote nucleus has as many *pairs* of chromosomes as each gamete nucleus had chromosomes; or we might say that fertilization doubles the number of chromosomes.

Since fertilization results in doubling the chromosome number it follows that there must be somewhere in the life cycle a process which is the reverse of fertilization. These quantitative changes in number of chromosomes are interesting in themselves, but they are also of importance in the transmission of characters from generation to generation. Appreciation of the significance of the process can be grasped only through an understanding of the way in which the reduction in chromosome number is brought about and of the effect it may have on the capacities of the nuclei that are formed.

The change from the $2n$ chromosome number to the n number is brought about by two successive nuclear divisions in the course of which there is one chromosome division but two separations. As a result of this entire process, which constitutes *meiosis,* four nuclei are formed, each of which has the n chromosome number. The numerical change can be explained in this manner: each of the chromosomes in the $2n$ nucleus splits, thereby producing a $4n$ condition; one division forms two $2n$ groups and another division forms four n groups. It is possible to express this by the accompanying diagram.



Actually the process is not quite so simple as it might seem to be from such a description. The fact should be stressed that the $2n$ nucleus which initiates meiosis has *pairs* of chromosomes. In preparation for meiosis (prophase of the first nuclear division) the chromosomes associate intimately in pairs, but they do not fuse. The mates of a pair are of the same kind, i.e., carry corresponding genes, and are said to be *homologous.* Very soon each member of a pair divides by splitting so that the homologous pair is converted into a group of four members called *tetrads.* The four members of each tetrad are distributed in two successive nuclear divisions

to the four nuclei (*quartet*) formed at the close of meiosis. Each of the four nuclei contains one complement of chromosomes composed of members from one or both of the two complements which were present in the original double (*2n*) nucleus that initiated meiosis. (Each kind of chromosome is present in duplicate in the *2n* nucleus.) The four nuclei are quantitatively alike; whether they are qualitatively alike or unlike depends upon the amount of difference between the homologous chromosomes of the two complements in the original nucleus. There may be chromosomal interactions in which two of the four chromosomes in one tetrad exchange corresponding portions. This is called *crossing over* and the evidence indicates that it commonly occurs. This complicates meiosis, but the phenomenon must be recognized. The whole process of meiosis must be understood because it affords the basis of the genetic phenomena to be discussed later in this chapter.

In most plants the cells initiating meiosis are spore mother cells, each of which produces four meiospores. In animals the meiotic divisions are generally part of the process of the formation of gametes. The result in the male animal is the production of four sperms, as compared with one functional egg and three functionless polar bodies produced in the female. The process, nevertheless, is fundamentally the same in the two sexes.

In the chapter on reproduction we called attention to the phenomenon of *alternation of generations.* This alternation is characteristic of mosses, liverworts, ferns, and seed plants and occurs in some of the lower plants. The two generations are (1) the *sporophyte,* which produces *meiospores,* and (2) the *gametophyte,* which produces *gametes.* We may review briefly the life cycle in ferns. The fern plant is a sporophyte and bears spores in the brown spots on the lower sides of the leaves. The spores do not grow into new fern plants but into small heart-shaped bodies which are gametophytes. These in turn bear gametes (sperms and eggs) in specialized organs on their under sides. In this case meiosis occurs at the time of production of the spores and not at the time of production of the gametes. This means that all the vegetative cells of the fern plant, the sporophyte, have the double sets of chromosomes (or *2n* condition). The spores are formed by the meiotic divisions of a *spore mother cell.* This results in the characteristic production of *four* spores each with a single set of chromosomes (or *n* condition). When the spores germinate they produce the gametophyte generation. All the cells of this body (*thallus* or *prothallium*) have single sets of chromosomes (*n* condition). When sperms and eggs are produced there are no meiotic divisions because the cells producing them are already haploid (*n*) in the constitution of their nuclei. Fertilization brings

together the paternal and maternal sets of chromosomes in the zygote and this condition is maintained throughout the sporophyte body. There are great differences between the two generations externally, and there are significant nuclear differences in their cells (Fig. 8–20).

In the seed plants the sporophyte generation is the familiar plant with leaves, roots, and stems (Fig. 11–6). It is possible to work with seed plants

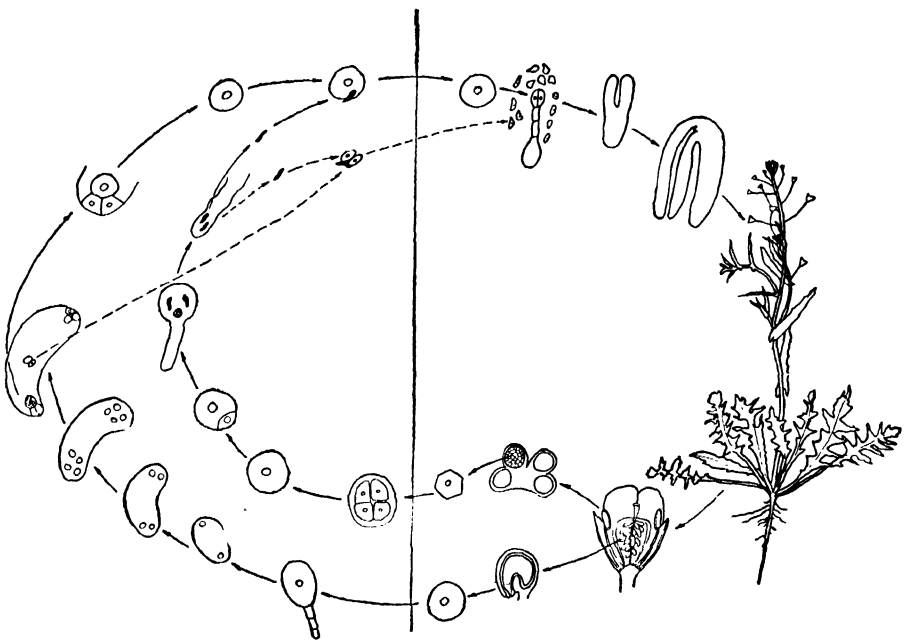


FIG. 11–6. Life cycle of a seed plant showing alternation of the sporophyte generation (right) and the gametophyte generation (left). Further explanation in text.

in a practical way without realizing that there are such things as gametophyte generations. Gametophytes are parasitic and buried within the tissues of the sporophyte. Although so small that they can be observed only in microscopic preparations, they are none the less real. Immature pollen grains are microspores produced in fours by meiosis. Megaspores are similarly produced, but only one of the four potential spores is functional. Microspores and megaspores give rise to simple, few-celled gametophytes (male and female respectively). In all groups of plants where sporophytes and gametophytes occur, the spore mother cells produced by the sporophyte initiate meiosis. In some of the algae where there is no alternation of generations the zygote behaves as a spore mother cell.

With our knowledge of fertilization on the one hand, and of meiosis

on the other, we should be prepared to consider and understand heredity. We are aware that the chromosomes are the bearers of the hereditary units or genes. We know that homologous groups of chromosomes are brought together in fertilization. We know that homologous chromosomes separate one from the other subsequently during meiosis, and that the four spores may have nuclei alike or unlike depending upon the amount of difference between homologous chromosomes. With all these matters in mind we are ready to consider some of the genetic phenomena for which they provide an explanation. We should have no difficulty in appreciating that the two parents contribute equally in the transmission of hereditary characters, that fertilization makes possible new combinations of characters, and that different assortments of paternal and maternal characters are possible in the reproductive cells of the offspring.

HEREDITY

We began this chapter by calling attention to the fact that the offspring of both plants and animals have a tendency to resemble their parents. The study of the manner in which internal, or genetic, factors are transmitted from generation to generation is the science of heredity. Doubtless most people have heard something about *Mendel's laws.* These laws deal with the ways in which genetic factors are transmitted. We should become familiar with them.

FIG. 11–7. Gregor Mendel, whose researches in the fundamental laws of heredity became the foundation for modern plant and animal breeding. (Photograph, courtesy G. H. Shull.)

Gregor Mendel (Fig. 11–7) was an Austrian monk. He carried on his experiments in the monastery garden at Brünn over three-quarters of a century ago. We now realize that Mendel's work was of great importance and that he made some wonderful discoveries. It is a curious fact that the announcement of his discoveries aroused neither acclamation nor animosity. They simply met with little or no interest or comment. This is not the fate of most discoveries of such great magnitude. For a third of a century scientific workers seemed not to be

aware of what Mendel had done. Then, at the beginning of the present century (1900), three investigators independently rediscovered what Mendel had enunciated so many years before (1865). Mendel, however, receives the credit on every hand for his epoch-making work. Everywhere that heredity is studied the name of Mendel enters prominently into the considerations.

Mendel performed an elaborate series of experiments (Fig. 11–8) in which he cross-fertilized varieties of peas (*Pisum sativum*). We might properly say that he carried on experimental hybridizing. As a result he discovered certain facts which he attempted to rationalize. He found that when certain hybrids were bred to each other, an original character of one of the grandparents reappeared in some of the offspring and the contrasting character of the other grandparent in others. Moreover, he showed that the distribution of certain characters which entered into the hybrid separated again, and that half of the germ cells contained one character only, and

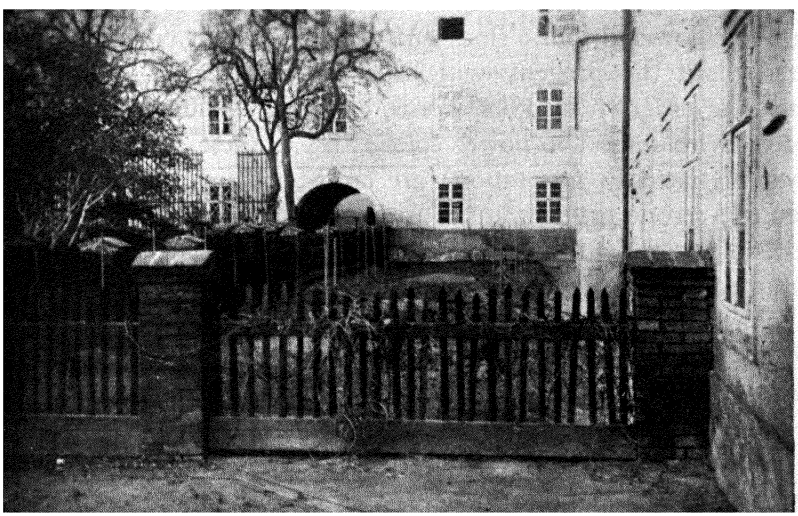


FIG. 11–8. The small monastery garden at Brünn, Austria (afterward Brno, Czechoslovakia), where Mendel carried on his experiments in the breeding of peas. (Photograph by G. H. Shull.)

the other half the other character. It was many years later before there was found a mechanism in the production of germ cells which was capable of carrying out Mendel's postulation of two kinds of germ cells.

We have explained the mechanism in our account of meiosis. Now we shall proceed to give some examples to make clearer Mendel's principles and interpretations. In this account we shall not follow the order in which

our knowledge of heredity actually developed. In other words, historically certain facts were discovered and to explain them the existence of a mechanism had to be assumed. Now we reverse the situation by becoming familiar with a mechanism first and then finding out how it works to produce certain results. Doubtless it is immaterial which way the approach is made. In any event we must be able to harmonize mechanism and results, or results and mechanism—the order is not important. Neither is it important that we use only Mendel's examples or present them in the order used by him.

Some writers refer to Mendel's law in the singular number. It is then designated as the *law of alternate inheritance.* Other writers use the plural and refer first to a *law of segregation* of characters and second to a *law of independent assortment* of characters. Some writers also refer to a *law of dominance.* Thus we see that it is possible to refer to Mendel's laws.

Law of Segregation

If a white-flowered four-o'clock (*Mirabilis jalapa*) is crossed with a red-flowered plant the progeny will have uniformly pink or rose-colored flowers. The progeny, in other words, exhibit a blending of the parental characters with respect to flower color. Now if these pink hybrids (commonly designated F_1 generation) are cross-fertilized, or interbred, there is obtained a second generation (F_2) in which the flowers are not uniformly colored. In this F_2 generation we find three colors—the white and red of the grandparents, and the pink of the parents. Not only are there these three colors, but the individuals occur in definite proportions—25 per cent white, 50 per cent pink, 25 per cent red, i.e., in a ratio of 1 : 2 : 1.

Further breeding shows that the white-flowered group produces only white-flowered progeny and that this is true for all their descendants. The same situation is found in the red-flowered group. The pink-flowered plants (the 50 per cent) is found to split up again just as the pink-flowered group did in the previous generation, and to yield white, pink, and red in the ratio 1 : 2 : 1. (See Fig. 11–9.)

These results are explainable by assuming that the germ cells of the pink-flowered hybrid plants are themselves not of a hybrid nature, but that the factors which condition flower color are segregated and that there are *two kinds of germ cells formed by the hybrids.* Biologists are very sure that this explanation is correct.

It works out this way. In the germ cells of the white-flowered parent there is a gene in one of the chromosomes which is the hereditary factor for white flowers. Similarly there is a gene for red flowers in an homologous

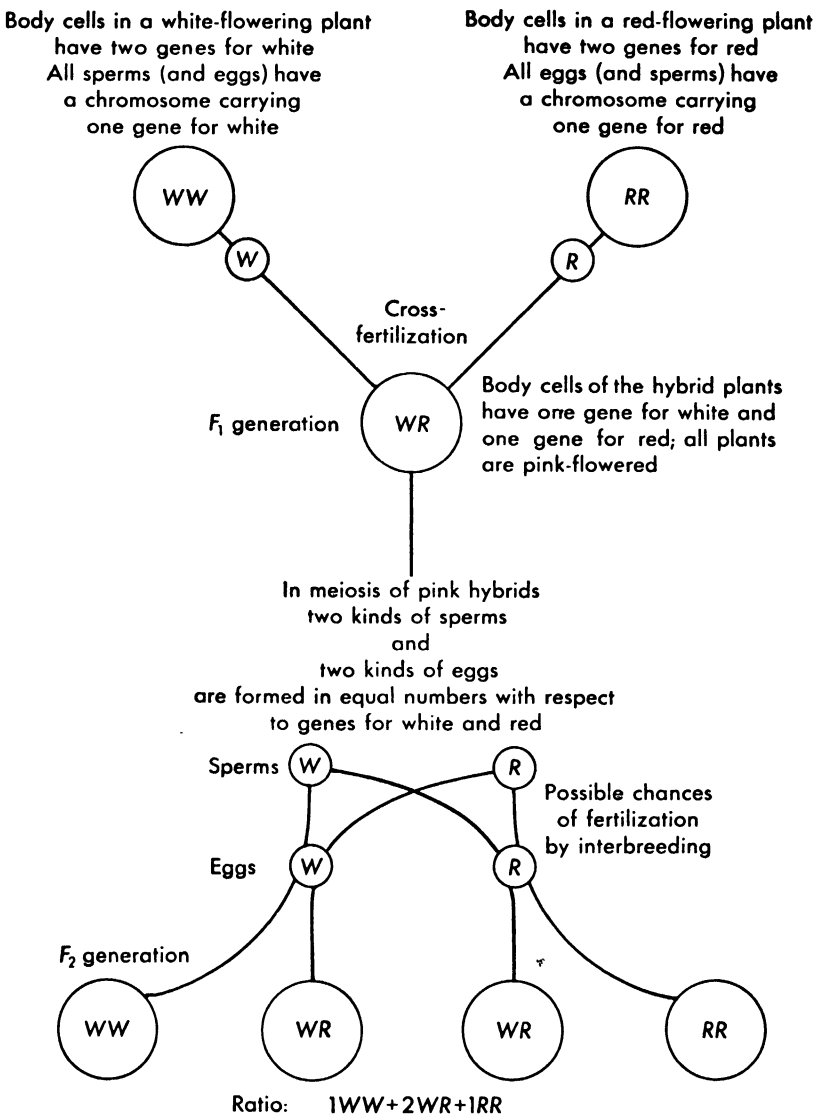
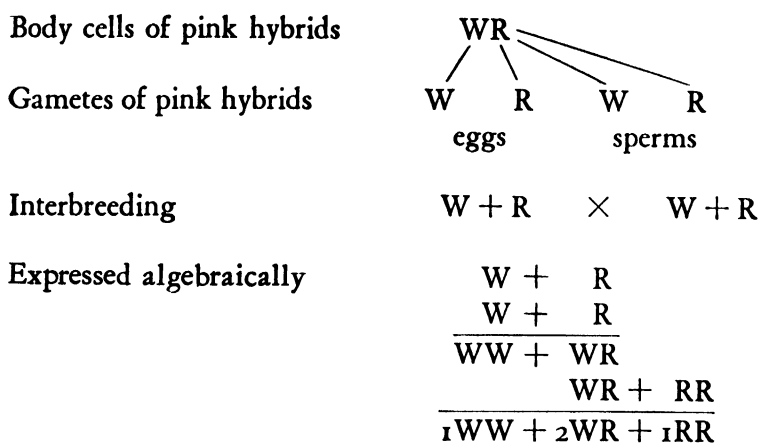


FIG. 11–9. A diagrammatic representation of the relation of factors of flower color in the four-o'clock.

chromosome of the germ cells of the red-flowering parent. In the hybrid every body cell contains factors for both characters which were brought together in the zygote. Two such factors forming a contrasting pair are called *alleles;* the adjective form of this term is *allelic*. The allelic genes are located in the same relative positions on homologous chromosomes, i.e., chromosomes of a pair. In meiosis the chromosomes carrying allelic genes

separate so that one gamete receives the gene for whiteness and the other the gene for redness. This separation, or segregation, of allelic genes is the crux of Mendel's first law, for in this way these two contrasting factors pass into separate gametes. Thus not only are there two kinds of gametes, but these gametes are present in exactly equal numbers.

Let us indicate the factor for whiteness by the letter W and that for redness by the letter R. Then we may say that half of the gametes of the hybrids may be represented by W and the other half by R. When the hybrids are inbred the mathematical chances are that W will meet R twice as often as W meets W or R meets R. This means that the combination WR will prevail twice as often as WW or RR. The result is 1WW + 2WR + 1RR. In the body cells of the WW combination the flowers are white; where WR exists the flowers are pink; and where RR occurs the flowers are red. Thus we have the 1 : 2 : 1 ratio. We may represent the possible combinations as in the accompanying diagram.



Dominance of One Gene

It is a well-established fact that the characters in which the parents differ do not always blend in the hybrids. In the case of the four-o'clocks the characters did blend to produce pink flowers. In many instances, perhaps more usually, the hybrids completely resemble either one parent or the other. Where the hybrids show outwardly the character of one parent that character is said to be *dominant.* The contrasted character is present in an undeveloped or latent condition and is said to be *recessive.* Mendel found that when flowers of a tall race of peas were pollinated from the flowers of a dwarf race, the hybrid offspring (F_1) were all like the tall parent, and not intermediate in form. The character of tallness of one parent is *dominant,*

and the contrasted character of the other parent that does not appear in the F_1 generation is *recessive*. When these F_1 hybrids are inbred the individuals of the F_2 generation occur in the proportions 75 per cent tall and 25 per cent dwarf, i.e., in the ratio of 3 : 1. But this is not all the discovery. Mendel found that the 25 per cent dwarfs when inbred always produced dwarfs and nothing else. On the other hand, of those that show the dominant character, tallness, in the F_2 generation, not all breed true. Only a third of these tall individuals are pure and give rise exclusively to dominants. If we indicate tallness by the capital letter T and dwarfness by the small letter d we may present the matter in this way: All hybrids have a body cell constitution of Td. It must be kept in mind that although the dwarfness character is present, it does not show outwardly. One-half of the gametes may be represented by T and the other half by d. As in the case of the four-o'clocks the chances are that, on the average, T will meet d twice as often as T meets T or d meets d. The end result will actually be the same as in the four-o'clocks, 1TT + 2Td + 1dd, although it will not appear to be the same because here TT and Td will look alike.

Other cases might be cited. The laws apply to animals as well as to plants. If a gray mouse is crossed with a white albino mouse the hybrids are all gray like the one parent. When these gray hybrids are inbred they produce offspring in the proportion of 3 gray to 1 white. Inbreeding these white individuals gives only white, and this remains true for all their descendants. Inbreeding the gray individuals reveals the fact that one-third of them are pure and produce only gray descendants. The other two-thirds of the gray individuals are hybrids and in turn produce both white and gray mice, and so on.

It is impossible to predict which of two contrasting characters will be dominant in any cross; this is a question that can be answered only by experiment. In black and white guinea pigs it has been found that black is dominant. In two kinds of stinging nettles (species of *Urtica*), one with serrate leaves and the other with entire leaves, the serrate character is dominant. In black and white Andalusian fowls there is a blending, and in the first generation (F_1) all the offspring are blue. In the second generation (F_2) the offspring are of three colors: 25 per cent black, 50 per cent blue, and 25 per cent white. This condition of blending, just described in the Andalusian fowls and previously described in the four-o'clocks, is sometimes referred to as *incomplete dominance*. Such cases are now known to be numerous. Segregation of the genes in meiosis takes place just as in the instances of complete dominance.

In all the experiments in hybridizing it must be kept in mind that the

ratios 1 : 2 : 1 or 3 : 1 hold true only when large numbers of individuals are considered. Even with fairly large numbers the ratio may not be exact in every set of experiments. In one of his experiments with peas Mendel obtained 1084 plants of which 784 were tall and 277 were dwarfs. This is an approximation of 3 : 1.

There are two more terms with which we should be familiar—*homozygous* and *heterozygous*. In an individual which is pure bred for any given character (i.e., not a hybrid), the body or vegetative cells will have a pair of genes which are alike and the individual is said to be *homozygous* for that character. Thus in white four-o'clocks we represented the body cells as WW, and the red ones as RR. But the first generation (pink) hybrids had vegetative cells with a pair of contrasted genes. We represented the condition as WR. Such individuals are said to be *heterozygous*.

Backcrosses

In our description of the experiments with the four-o'clocks there are two possibilities which we did not consider. We accounted for the mating of red with red, which gives 100 per cent red; white with white, which gives 100 per cent white; white with red, which gives 100 per cent pink; and pink with pink, which gives the proportion of 25 per cent white, 50 per cent pink, and 25 per cent red. We should inquire what happens when the pink hybrids (WR) are mated with pure whites (WW) or pure reds (RR). Such matings between heterozygous (hybrid) and homozygous (pure) individuals are known as *backcrosses*. Even a brief consideration will show that the offspring must be of two sorts—one-half like one parent and one-half like the other. The heterozygous individuals have two kinds of gametes in equal numbers, whereas the homozygous ones have but one kind. Only two kinds of zygotes can be formed and the chances are that they will be formed in equal numbers.

Law of Independent Assortment

The examples we have so far presented concern only a single pair of contrasting characters; these are cases of *monohybridism*. The question may well be raised as to what will happen when the parents differ in two pairs of characters. Such cases are termed *dihybridism*. Mendel worked out several such instances and thereby established a second principle or law of heredity. The different characters are independently transmitted and assorted in the descendants; hence the *law of independent assortment*. Of course, the separate pairs of characters each obey the original law of segregation but they are transmitted entirely independently of each other.

A tall yellow-seeded pea was crossed with a dwarf green-seeded one. The yellow and green colors are in the cotyledons of the seeds. As before, tallness was dominant and dwarfness recessive. The experiment revealed that yellow was dominant over green. In the F_1 generation all the plants exhibited the combination of the two dominant characters and were tall and yellow.

The interesting test came in the F_2 generation as a result of the inbreeding of the F_1 hybrids. There appeared not only the original tall yellows and dwarf greens but two new combinations, namely, tall greens and dwarf yellows. In all, there were four distinguishable combinations. Examination of the results showed that talls and dwarfs appeared in the usual ratio of 3 : 1 and that yellows and greens were in the same ratio. If 16 plants were considered there were 12 talls and 4 dwarfs, also 12 yellows and 4 greens—definitely 3 : 1 ratios. Among the 12 talls, however, yellows and greens showed up in a ratio of 3 : 1; and of the 4 dwarfs, 3 were yellow and 1 green. Thus it will be seen that out of 16 plants there were 9 with combinations of both dominants; two groups of 3, each showing the dominant character of one pair and the recessive of the other; and one plant possessing both recessive characters. These were the proportions that were obtained by early workers and the experiments have been confirmed many times. We can write the ratio for these two pairs of characters as 9 tall yellow : 3 tall green : 3 dwarf yellow : 1 dwarf green.

We are not yet through with the *dihybrid* case. From the ratio just given it is evident that there appear to be only four classes. Both further experiments and studies made from the point of view of meiosis reveal the fact that in these *four* classes we are dealing with *nine* types of individuals. To individuals of the same actual hereditary composition the term *genotype* is applied; to individuals which look alike because the differences are masked by dominance, but which do not have the same hereditary constitution, the term *phenotype* is applied. In dihybrid crosses there are *nine* genotypes but only four *phenotypes.*

We must consider the gene constitution of the gametes and the possible mating of the gametes. This we can do best with symbols and a diagram. In the dihybrid peas which we have considered there are *four* kinds of gametes in equal numbers. Each of the four kinds of eggs may be met by any of the same four kinds of sperms.

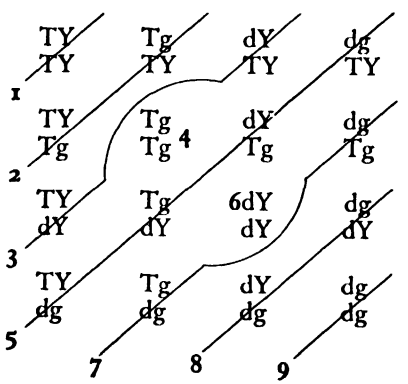
It will be obvious that the situation becomes more complicated if three contrasted characters are involved. In such a trihybrid crossing there are 27 genotypes, in which 8 phenotypes are evident. As the number of characters increases, the results are complex and difficult to analyze. Experi-

Body cells of tall yellow hybrids — $\frac{TY}{dg}$

Gametes of hybrids { four kinds of eggs — TY Tg dY dg
four kinds of sperms — TY Tg dY dg

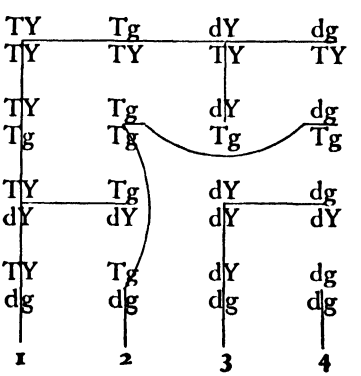
Possible matings

	TY	Tg	dY	dg
TY	TY TY	Tg TY	dY TY	dg TY
Tg	TY Tg	Tg Tg	dY Tg	dg Tg
dY	TY dY	Tg dY	dY dY	dg dY
dg	TY dg	Tg dg	dY dg	dg dg



Nine possible combinations or genotypes

1. TYTY
2. TYTg
3. TYdY
4. TgTg
5. TYdg
6. dYdY
7. Tgdg
8. dYdg
9. dgdg



Four visible combinations or phenotypes

1. At least one T and one Y = tall yellow (9)
2. At least one T and two g = tall green (3)
3. Two d and at least one Y = dwarf yellow (3)
4. Two d and two g = dwarf green (1)

ments indicate that each specific character follows the law or segregation. If four pairs of characters are involved, there are 81 hybrid combinations. If 10 pairs are involved, the number of possible combinations is more than a million.

Linkage

In our discussion of independent assortment of genes it should be understood that such a free assortment as described takes place only when the genes are located on different pairs of chromosomes. If characters are carried by genes on the same chromosome they are said to be *linked.* In such cases the characters carried by these genes do not separate but are inherited together. In the language of the geneticist, "All the genes on a pair of homologous chromosomes collectively form a linkage group."

The case of peas with smooth cotyledons and tendril-tipped leaves contrasted with wrinkled cotyledons and leaves not tendril-tipped is interesting. The dihybrid ratio, 9 : 3 : 3 : 1, does not occur because the genes for the smooth cotyledons and tendrils are apparently in the same chromosome and the contrasting characters are in the homologous chromosome. It is reported that the linkage is not perfect, however. *Crossing over* is the name given to certain deviations from the principle of linkage.

Genes

In this account considerable emphasis has been placed on the physical basis of heredity. Modern genetic studies have given us much information about genes and chromosomes. The actual composition of genes is not known, but it is generally accepted that they are located not only on particular chromosomes but at definite places on the chromosome. Apparently they constitute only a small part of the mass of chromosomal material. Genes play an important role in the evolution of organisms through their alterations or mutations. Further discussion of genes is presented in the next chapter.

CHAPTER 12

THE IMPROVEMENT OF PLANTS BY MAN

(*Plant Breeding*)

Centuries before Gregor Mendel performed his famous breeding experiments with garden peas, men the world over had recognized that certain individuals in a given population were superior or more desirable than others, and that this same superiority or desirability was passed on to their progeny with considerable regularity. By the time of the Crusades, the Arabs by selective breeding had developed the Arabian horse, which gave superior performance under the desert heat.

The earliest attainments in breeding were in the animal kingdom. Doubtless this was due to the early recognition that reproduction in animals was a sexual act involving two distinct individuals. All man had to do was select the parents, isolate them, and await the progeny. The fact that a sex mechanism existed in plants was not demonstrated until 1694, when Camerarius proved by experiment that the anthers of a flower were male elements containing male reproductive cells. Many workers in various countries confirmed this work. Governor Logan of Pennsylvania was one. In 1739 he demonstrated the function of the anthers and also established the importance of the stigma and style in the fertilization of corn.

With this knowledge of the sex mechanism in flowers, plant breeders were able to control the parentage and for the first time plant improvement could be planned. Previously selection from the population nature had provided was the only avenue of approach to better crops. By 1766 accounts began to appear of crossing and hybridization induced by the hand of man. There followed descriptions of the appearance of the first generation, hybrid vigor, and insect pollination.

The great Dutch hybridist, Gärtner, published in 1849 an extensive work summarizing the results of some thousands of crosses involving over 600 species from which were obtained some 250 hybrids. He noticed that hybrids in some cases resembled one or the other parent in whole or in

part, whereas in other cases the offspring were intermediate. In the same year that Mendel published his findings (1866), Wichura observed that reciprocal crosses gave like results and concluded that the pollen and the egg have an equal influence on the progeny arising from fertilization. The facts relating to the fusion of the nuclei of the male and female sex cells were not understood, however, until the work of Strasburger appeared in 1884.

Although the recognition of maleness in the anthers gave impetus to explorations in plant improvement by breeding methods, it was the work of Mendel which furnished the science with the strong measure of exactness which had hitherto been lacking. Mendel published his classic results in 1866. His work did not, however, come to the attention of scientists until it was rediscovered in 1900. Shortly after that, an Englishman by the name of Bateson introduced the word "genetics" to cover "the study of heredity and variation among related organisms." Soon a wide interest developed in this field. In 1934 a *Bibliography of Plant Genetics* assembled by the library of the United States Department of Agriculture listed more than 10,000 publications. This represented the first third of a century of "the application of Mendel's laws to the problems of heredity."

Mendelism today is a working tool of the breeder. Through it the synthesis of new plants has been largely removed from the realm of chance into that of mathematical expectancy and predictability. The demonstration of the fact that crossing makes possible new true-breeding plants which combine desirable characters of two parents has made crossing of basic importance to the plant breeder in search of "better crops."

The term "better" crop has broad connotations. Consider the tomato, for example. It is used as a food or condiment. It appears in soups and salads. It is canned as a vegetable or served as a drink. It is an important ingredient of catsup. Tomatoes are grown in every state in the Union. They are shipped from California to Boston, from Florida to Chicago. They are raised in the short summers of Maine and in the short winters of the South. They are cultivated under glass. A dozen fungous diseases and many insect pests attack them. What is a "better" tomato?

For the housewife a better tomato may be red or salmon pink, depending on her preference. To be stuffed it must have large seed cavities; to be sliced it should have smaller seed cavities. For canning it must maintain its shape after cooking; for juice it should disintegrate. The farmer in temperate regions requires a tomato that matures before frost. In addition, it must be disease-resistant and high yielding. The market gardener wants

an early tomato that enables him to capitalize on the "between season" market. The greenhouse grower demands a variety that ripens well in the cloudy winter days and is resistant to *Cladosporium* leaf mold. It is de-

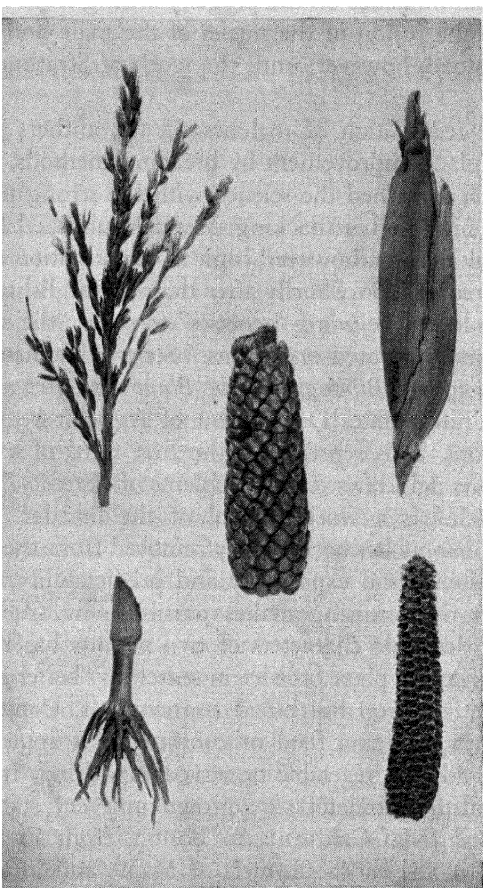


FIG. 12–1. Early pre-Columbian corn excavated near Arica, Chile. Except for the spiral arrangement of the kernels on the ear, all parts have a familiar appearance. Corn was cultivated centuries ago over large areas of North, Central, and South America. (Photograph from American Museum of Natural History, New York.)

sirable, too, that the variety produce fruit over a long season to insure a regular supply. The southern growers in California, Texas, and Florida demand a good shipper, a fruit that looks well after several days en route. It is no small task for the breeder to meet all these demands. Nevertheless,

breeders are "custom-building" plants with remarkable regularity. A few of the accomplishments of plant breeders have been selected for presentation here.

SOME RESULTS FROM PLANT BREEDING

Corn

The word "corn" is used in America to designate the typical American cereal otherwise known as "maize." Corn is often said to be the backbone of American agriculture. "Of all things that are characteristic of America, corn is perhaps the most characteristic." In the United States it exceeds in production and value the combined crops of the other cereals.

There has been much speculation about the origin of the corn plant (Fig. 12–1). No wild forms of corn have been found. It is certain that corn is one of the oldest of all cultivated plants (Fig. 12–2). The possibility of

FIG. 12–2. Representation of corn in ornamentation of pottery of ancient Peruvian Indian tribes is proof of its age as a cultivated plant, and of the superstitious reverence with which the plant was regarded in prehistoric times. (Photograph, courtesy of the Museum of the American Indian, Heye Foundation.)

improving corn through cultural practices and breeding has been in the minds of growers since colonial days. It is reported that the Pilgrims in 1623 "began to thinke how they might raise as much corne as they could, and obtaine a beter crope than they had done. . . ."

The earliest attempts in corn improvement involved a method known as *mass selection.* The process consists in collecting seed from certain selected individual plants in the main crop. Since the ears of corn are large and can be handled individually it is relatively easy to carry on mass selection. There can be no doubt that the practice does result in a gradual improvement. Continual selection of a type of plant or of ear gradually builds up a variety, but long periods of time are required to obtain results.

The newest and most remarkable achievements in corn improvement have been developed through the application of genetic principles to prac-

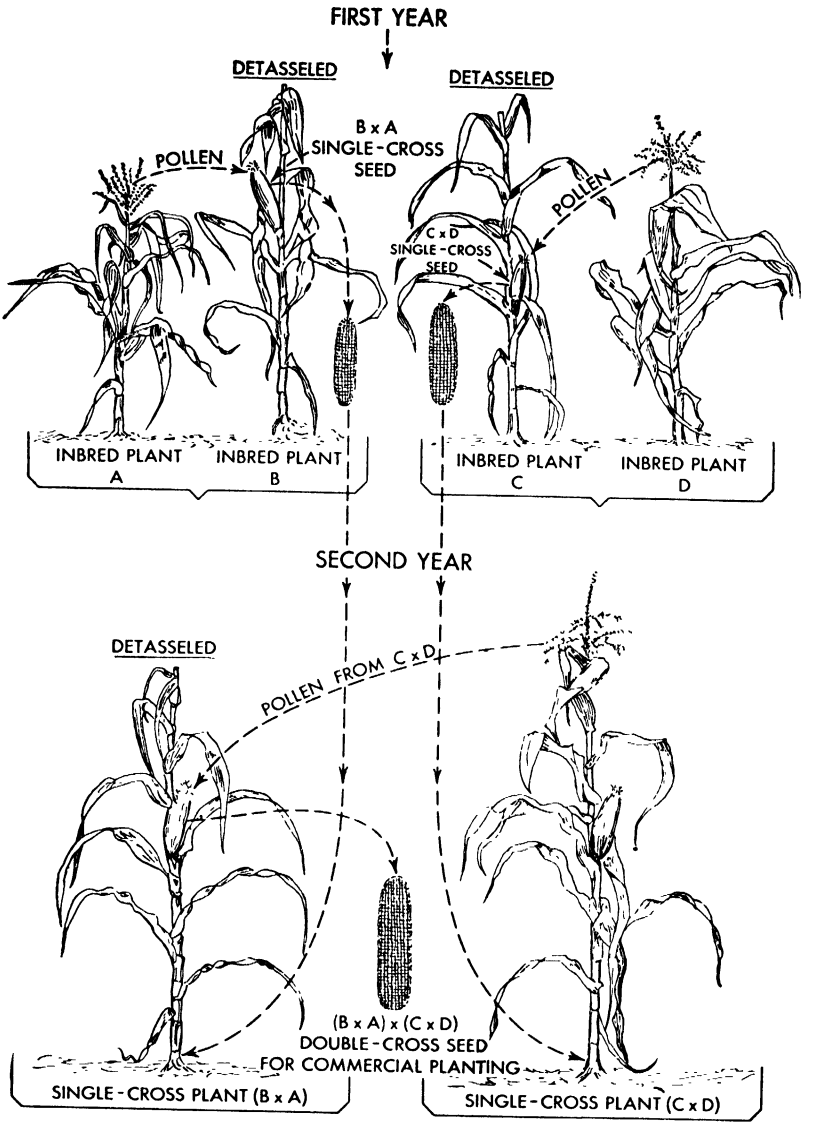


FIG. 12–3. Diagram of method of crossing inbred plants and the resulting single crosses to produce double-cross hybrid seed. (*Yearbook of Agriculture, 1937.*)

tical breeding. The result is "hybrid corn" (Fig. 12–3). According to the *1936 Yearbook* of the United States Department of Agriculture, hybrid corn "is an outstanding example, perhaps the most outstanding example, of the influence of theoretical scientific research in revolutionizing the production practices of an agricultural crop." Although a comparatively

new development, "the hybrids already developed have established their superiority in productiveness and in resistance to wind, disease, and other unfavorable conditions." In 1939 Iowa planted three-fourths of the total acreage to hybrid corn; Indiana, Illinois, and Ohio used the hybrids on about three-fifths of their acreage. Hybrid seed costs twice as much as ordinary seed, but the increased yields more than justify the expense.

"Hybrid corn" seed is the F_1 generation hybrid between two, three, or four strains of corn. Such seed is used for the production of a crop of corn. The corn from this crop, although splendid in appearance, cannot be used for seed for another generation without a loss in yield. The hybrids must be produced anew for every crop.

The strains which are used for crossing to produce the hybrid are developed through *selfing*. Selfing means self-pollination. It consists in pollinating the silks of a plant with pollen from the tassels of the same plant. This necessitates some method of controlling pollination. This can be accomplished by bagging the ears and tassels and pollinating by hand. Self-pollination develops inbred lines or strains and is properly called *inbreeding*. The purpose of inbreeding is to produce lines that will breed true for the characters they possess. When selfing by hand is continued for several generations the inbred lines become highly uniform and will breed true for most of the characters. When two inbred lines are crossed, the F_1 or first-generation plants are all alike, for each individual inherits a full set of genes from each parent and it expresses the dominant characters of both of them. Although the inbred parents were lacking in vigor, the F_1 hybrids are often unusually vigorous in size and productiveness. This is what is known as *hybrid vigor*. The crossing of inbred parents on a commercial scale is accomplished by planting them in alternate blocks in an isolated field and removing the tassels from one kind before the pollen is mature. One pollen row will pollinate two to four detasseled rows. The seed picked from the detasseled rows is the hybrid seed. Actually, commercial hybrid corn is usually a cross between two F_1 hybrids. The researches of G. H. Schull at the Carnegie Institution Station on Long Island, and of E. M. East at the Connecticut Agricultural Experiment Station, which were begun in 1905, laid the foundation for the development of hybrid corn.

By this time the uninitiated reader may have been led to believe that corn breeding is a finished piece of work. Much has been achieved but much remains to be done. What has been accomplished in the corn belt must be recreated in other areas. The reason for this lies in the knowledge that factors express themselves favorably or unfavorably in response to

certain environmental conditions. A very desirable hybrid in Iowa may be an inferior one in Pennsylvania because of differences in the environment. Environmental conditions may vary even within the areas of states. Minnesota, for example, recognizes three environmental areas in its corn-breeding program, and specific hybrids are recommended for use in the different areas.

Not every crop lends itself to the methods employed in producing hybrid corn. Many plants are naturally self-pollinated and in the course of reproduction through the ages already exist in a pure (*homozygous*) condition. Some plants produce only a few seeds—a condition prohibiting the manipulation employed with corn. Other crops such as sugar cane are propagated asexually by cuttings, a method of reproduction which impedes the rapid distribution of superior plants. Nevertheless, plant breeders have succeeded in overcoming various difficulties and practically every major crop today is an improvement over that of thirty years ago.

Wheat

It is impossible to overemphasize the importance of wheat to mankind. The fact that it has been one of the chief foods of man is the basis for the striking statement that "much of the energy for the work done by man has for generations been furnished by wheat." Wheat was in cultivation at the beginning of recorded history. Without doubt we can say that it played an important role in developing civilization. It could be grown, stored, and prepared for use by a comparatively few individuals, "thereby releasing human energy for pursuits other than constantly hunting a food supply." Such a major food plant is naturally grown extensively throughout the world. The total wheat acreage of the world amounts to 300 million acres. The six largest producers in order of acreage are the United States, China, Russia, India, Canada, and Argentina. The United States and Canada together account for more than one-fourth of the world production.

It is probable that the major improvements in the wheat plant have come about by the slow processes of nature operating through the ages. There are reasons for believing that it must have been a fine product in the hands of the most primitive peoples. Nevertheless, man has done much to improve wheat in yield, quality, tolerance to unfavorable climatic conditions, and resistance to diseases.

There are many varieties of wheat. The varieties possess different combinations of such characters as color and texture of kernel, awnedness, early or late maturity, and inheritance of disease reactions. In the United States at least 275 standard varieties are recognized. These varieties have been

grouped under five commercial classes, which are grown in the following general regions:

1. Hard red spring varieties—North Central states.
2. Hard red winter varieties—South Central states.
3. Soft red winter varieties—Eastern states.
4. White varieties—Western states.
5. Durum varieties—North Central states, chiefly Minnesota and the Dakotas.

The varieties of wheat in the United States have originated through introduction, selection, and hybridization. The variety that made possible the hard spring wheat industry of the North Central states came originally from Poland. In its migration to the United States it came through Germany, Scotland, and Canada. A grower by the name of David Fife, of Ontario, Canada, had obtained a sample of winter wheat from Scotland. A single plant proved to be spring wheat. Fife saved the seeds from this plant and from them developed a variety which he named Red Fife. Another Canadian, C. E. Saunders, used Red Fife as one of the parents in breeding experiments and developed a variety known as Marquis, which became world-famous. It produced high yields and its qualities were excellent for milling and bread making. For twenty years Marquis remained the "King of wheats." Although there are now several newer improved varieties which are better yielders and more resistant to diseases, the development of Marquis still stands out as a great achievement in wheat-breeding history.

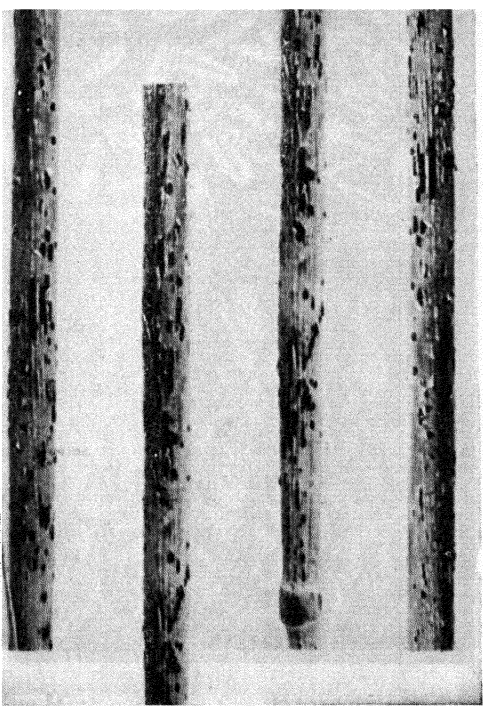


FIG. 12–4. Rust as it appears on wheat stems.

In the hard winter wheat region, the South Central states, several varieties were introduced from Russia. From one of these, Crimean, there was developed by selection an outstanding strain which was named

Kanred. Durum wheat was also introduced from Russia. The durum wheats are hard and are used for macaroni. Some of the durum varieties are rust-resistant. In a cross between Marquis and Iumillo (durum) a hard red spring variety, Marquillo, was obtained which inherited the rust resistance of the durum parent. A more recent introduction is a double cross (Marquis X Iumillo) X (Kanred X Marquis). It will be recognized that this variety is a combination of hard spring, hard winter, and durum varieties. It is known as Thatcher and is one of the most promising newer varieties. It is resistant to many strains of stem rust, and has the spring habit and high quality of Marquis.

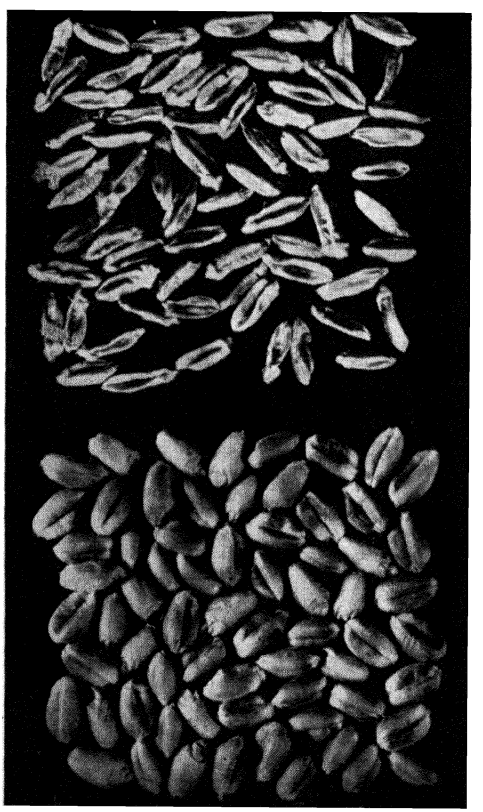


FIG. 12–5. Plump and rust-shriveled wheat kernels.

New varieties of wheat are continually being developed by public and private agencies. Breeders in state agricultural experiment stations and in the United States Department of Agriculture test new varieties and are able to recommend the best varieties for any state or locality. New varieties must be better than old varieties —not merely just as good—if they are to replace them. Much has been accomplished in wheat improvement, but, with financial support by the government and with administrative interest, still greater results may be expected. It is likely that future progress will be dependent upon genetic research. Such research leads to an understanding of the principles of heredity and will make possible more effective breeding operations.

The importance of disease resistance cannot be overemphasized (Figs. 12–4, 12–5). Stem rust is one of the most serious diseases against which resistance or immunity is necessary. It has been discovered that the rust fungus, as well as the wheat, exists in many varieties or forms. The forms of

the rust fungus hybridize on the barberry, which is its alternate host. In this manner new forms of the fungus originate. It is evident that plant breeders must take into account this possibility of the development of new hybrid forms of the fungus. A variety of wheat may be resistant to certain forms of the rust but not to others. In other words, man breeds resistant wheat and nature breeds more virulent rust fungi. This fact makes it necessary for breeders to understand as much as possible about the factors which create resistance or near-immunity in wheat varieties. It also emphasizes the desirability of eradicating the barberry which is nature's breeding ground for the rust.

Cotton

The northern states of the Mississippi valley constitute the corn belt; the southern states of that great valley and those to the east of it are no less

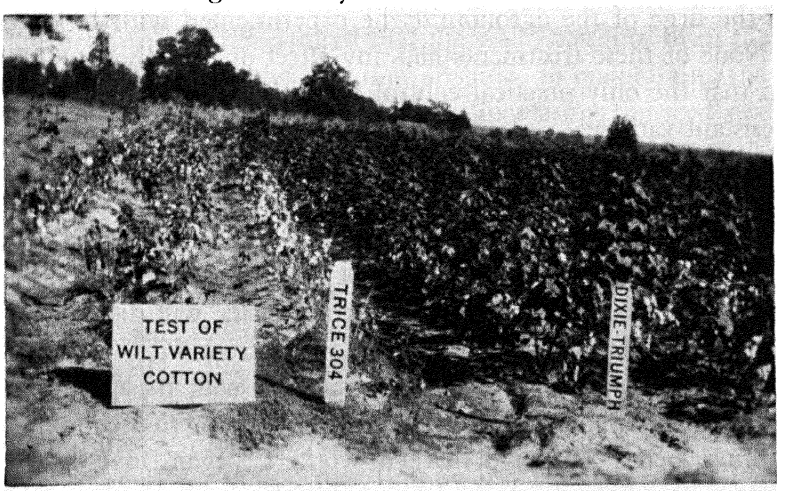


FIG. 12–6. Comparison of wilt-susceptible and wilt-resistant varieties of cotton; Dixie-Triumph (wilt 0.69 per cent) at right and Trice 304 (wilt 33 per cent) at left. (Photograph, courtesy V. H. Young. From *Bulletin No. 234,* Arkansas Agricultural Experiment Station.)

known as the cotton belt. The economic history of the South is synonymous with the economics of cotton. Yet in 1900 there were large areas of the Southeast that could not safely be planted to cotton. This was due to cotton wilt (Fig. 12–6), a disease caused by the fungus *Fusarium vasinfectum,* which invades the water-conducting tissues of the plant and inhibits the normal transfer of water. Cotton plants may succumb at any stage in their growth. The fungus lives from year to year in the soil and once established in a field remains there as a constant threat to cotton plants. The more

frequently cotton is planted in an area the more severe becomes the disease, because of the rapid multiplication of the fungus. Crop rotation helps to diminish the fungous infestation in the soil, but the cotton belt is a pronounced one-crop area.

In 1895 the cotton growers grew alarmed at the spread of the cotton wilt disease and appealed to the United States Department of Agriculture for aid. Scientists at first did little more than investigate the nature of the disease and urge farmers to select wilt-resistant individuals. Some promising results were obtained, but the planters were disappointed with the progress. Congress was persuaded to make an appropriation to study and devise control measures. In 1899 W. A. Orton, a pathologist, began his monumental work with this disease.

Orton urged planters to continue to select disease-resistant plants but he realized it would be a slow process. His pathological training urged him to seek a speedier remedy. He tried seed and soil treatments with fungicides; under the urge of the agronomists he experimented with fertilizers and lime. None of these treatments had any effect on the disease. Orton concluded that the only practical control of this disease was the breeding of wilt-resistant varieties.

With the problem clearly defined, Orton devoted his energies to the discovery of wilt-resistant cotton. Cotton is naturally self-pollinated, but 5 to 20 per cent natural crossing may occur, depending on the season. This natural crossing made breeding difficult since the progeny of individual plants proved to be variable in their reaction to the wilt disease. However, in 1905 the wilt-resistant variety, Dillon, was introduced.

Although Dillon was extremely resistant to wilt, its agronomic characters were so disappointing that planters were willing to use it only so long as nothing better appeared. Other workers began investigations. In Alabama a stray hybrid appeared—probably the result of a natural cross—which showed not only remarkable resistance but very desirable agronomic characters as well. This new hybrid was named Dixie.

The hybrid nature of Dixie precipitated a diligent search for new and better cotton in the progeny of carefully considered crosses. The superlative resistance of Dillon to the wilt disease was not forgotten, and Dillon was one parent of many hybrids. Out of this work Dixie-Triumph was developed. It proved a most popular and satisfactory variety. Others were named too—Cook, Toole, Georgia, Webber, Foster, and one designated as Cook 307–6. This latter variety seems peculiarly adapted to Alabama conditions. Truly its genes respond most favorably in a specific environment.

The *Yearbook* of the United States Department of Agriculture for 1936 states, "As a result of the breeders' work cotton can now be grown without danger from the wilt hazard in every section of the south."

One of the plant breeders' greatest difficulties is to maintain a source of pure-line seed of a superior variety once it is produced. Cotton seed is no exception. A cotton fiber is an elongated epidermal hair on the seed coat. The epidermal hairs persist on the seed coat and are separated from it by a machine known as the saw gin. The gin is so constructed that seeds lodge in it and may remain there for a considerable length of time. In other words, the gin may harbor at any one time seeds of many different bales of cotton. In the gin the seed of several varieties of cotton may become mixed together. Seed stocks are thus contaminated.

To avoid this contamination many states have adopted "the one-variety-community plan." As the name suggests, only one variety is grown in a community. For seed purposes this community has all its cotton ginned at one time. Prior to its use in a community the gin is cleaned of all foreign seed. The growers are thus assured that the seed emerging from the gin is their own pure variety. In this way they are aided in maintaining the purity of superior strains and at the same time in increasing the seed stock very rapidly at a minimum cost. Another engagement is thus being won on the battlefront of plant improvement.

Flax

The fight against cotton wilt in the South was not the only battle of its day in the war against plant enemies. On the northern frontier an equally important campaign was conducted against flax wilt, which was so serious that it threatened the flax industry. The enemy was another species of soil-inhabiting fungus, *Fusarium lini*. The tactics of this belligerent were similar to those of the cotton wilt fungus, i.e., invasion of the land, continued decimation of its population, and finally complete suppression. The refugee flax was driven from one area of virgin soil to another until the crop was virtually eliminated. That was in 1900.

Botanists often refer to flax in relation to the linen industry since the sclerenchyma fibers are spun into linen thread. The invention of the cotton gin in 1792 ruined the flax fiber industry in America, but flax growing is important for the production of seed. The United States produces from one-tenth to one-sixth of the flax seed of the world. Flax seed is crushed for linseed oil, which is important in the paint and varnish industry. The oil content of flax seed varies from 33 to 42 per cent in the medium-height large seeded flax which is grown for the oil content. Linseed oil may sell

for as much as 10 cents a pound, and the crushed seed known as linseed meal for 1½ cents per pound. Linseed meal is used as a supplementary feed for livestock. Five hundred pounds of seed per acre is considered a very good yield.

H. L. Bolley, of the North Dakota Experiment Station, heard of Orton's work in selecting wilt-resistant cotton. Bolley had just discovered that the

FIG. 12–7. *A*, young plants of non-resistant flax dying in flax-sick soil; *B*, two plants beginning to wilt when about five or six inches tall; *C*, two resistant plants about the same age as those in *B*. (After Bolley. From *Press Bulletin No. 46*, North Dakota Agricultural Experiment Station.)

fungus causing flax wilt was also a species of *Fusarium*. It seemed reasonable that the procedure which had been successful with cotton was worthy of a trial with flax. Accordingly he began growing flax on flax-sick soil. His associates in agronomy had already assured him that the trouble was not due to lack of soil fertility. He did not need to waste time with fertilizers; his sole aim was a wilt-resistant flax.

Bolley did not limit himself to his own locality. He visited flax-sick fields far and wide seeking surviving plants and collecting their seed. The results were often disappointing. The progeny were not always resistant even though flax is a self-pollinated plant. Possibly the parents were heterozygous for resistance. But this was 1900 and Mendel's paper was just being rediscovered after thirty-five years. Bolley at that time probably knew little of heterozygosity as Mendel explained it. Perhaps there were different types or strains of the flax wilt organism. The possibility ap-

parently never occurred to him, or if it did he dismissed it. Scientists did not become aware of strains or biological races until 1914. Bolley merely kept on trying. The linseed crushers encouraged him. They sent him seed from all parts of the world to plant on his flax-sick soil. So many plants had died that only the fittest could survive. Again and again he planted seed. Occasionally a survivor came to light. Finally, the efforts were successful and a wilt-resistant flax was available (Fig. 12–7). But, like Dillon cotton, many of these plants were poor yielders. The search had to be continued; selection for other characters was necessary. Other stations began researches and made their contributions. Eventually satisfactory wilt-resistant flaxes were found and today there is not much need for worry about flax wilt.

The story of cotton wilt and flax wilt would not be complete without a final statement. Orton and Bolley were the first men in the history of agriculture to submit plants to an epidemic of disease in order to obtain selections resistant to a disease. Survival of the fittest became their motto. Today it is basic in all plant breeding for disease resistance.

Marigolds and Nasturtiums

Several hot dry seasons in succession during the early nineteen-thirties created a demand among garden lovers in the middle-western states for a dependable hot-weather flower. Seedsmen began to be conscious that some easily grown heat-loving flower might be popularized provided it were sufficiently attractive. A seedsman by the name of David Burpee thought of the marigold as a possibility. It needed, however, certain improvements. One objectionable characteristic was its late-blooming habit and another was the strong odor which many people regarded as disagreeable. If early and odorless varieties could be developed the marigold might become popular, since it flourished under hot dry conditions. The development of early varieties was not a matter to worry about, but the development of odorless ones presented real difficulties.

In the course of many generations there was a possibility that the genes controlling odor in the marigold might have been altered or lost. Such changes are known as mutations. Burpee thought it worth while to find out whether such mutations were not already in existence. It was his plan to collect marigold seeds from as many places as possible and to test the progeny with the hope that some odorless plants might be found. In the first test 642 collections from Europe, Africa, Asia, Australia, and America were available. All the plants proved to have the usual odor.

Then a missionary in China wrote that he knew of a marigold there

which had odorless foliage. After some delay, negotiations were made and a half ounce of seed finally arrived. Most of the plants had tiny unattractive blossoms, but the foliage was odorless. One plant was late in blooming. Finally its flower buds burst and revealed the finest golden-orange blossoms

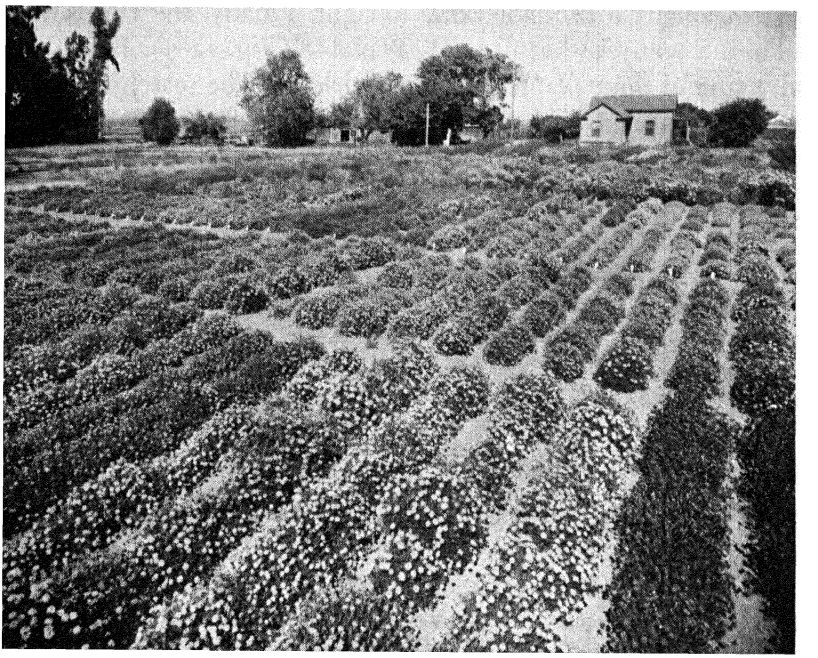


FIG. 12–8. A partial view of Burpee's trial garden devoted to marigolds. (Photograph, courtesy W. Atlee Burpee Company.)

in the trial gardens. This success gave seedsman Burpee sufficient encouragement to cause him to carry his search further. Since the type of mutation for which he was looking was found in the seed from China, perhaps a similar mutation might be found elsewhere. There were 554,000 marigold plants in his trial gardens (Fig. 12–8). When the smelling of so many plants was proposed it is said that the employees spoke freely of the seedsman's insanity. One young college graduate threatened to leave. He did not do so, however, and according to reports it was he who found some plants in the garden that did not have the usual strong odor. In fact, there was a whole row of them that had been reared from a single outstanding plant selected the year before. Since it was not one of the 642 special cultures, no one had taken occasion to smell it. By using the odorless plants in crosses with other marigolds, hybridizers were able to build

a stock of odorless plants, varying in the color range of the flowers and with other desirable qualities such as early blooming. Odorless varieties have not entirely replaced the old-fashioned strong scented forms, for some people like the old-fashioned ones.

Commercial plant breeders have a monopoly on their new introductions for one year only. After that their competitors are able to sell the same product. Competition has been responsible for some remarkable results in plant breeding. The development of sweet-scented double nasturtiums in various colors makes an interesting story (Fig. 12–9).

The first sweet-scented double nasturtium to be introduced came in one color only. It was highly desirable that fragrance and doubleness in

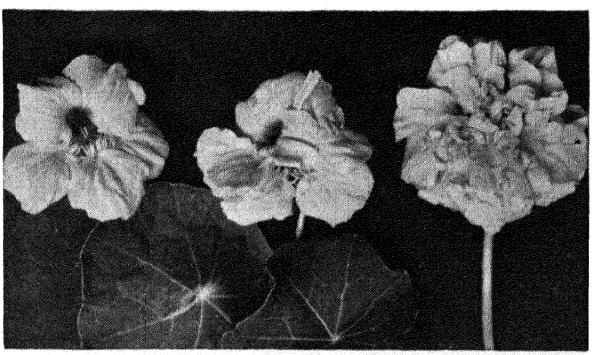


FIG. 12–9. Comparison of different forms of nasturtium, single, double, and super-double. (Photograph, courtesy W. Atlee Burpee Company.)

nasturtium flowers should be combined with a variety of colors. When a single was crossed with a double, all the hybrids were single. In the F_2 generation it was found that 78 plants were single and 27 were double. Since this was nearly a perfect 3 : 1 ratio, the situation was simple, and thus it was possible to have colors represented in the double-scented type in the next generation. To obtain three generations would call for a three-season program. (Reference is again made to Burpee's work to show how a program ordinarily calling for three years was condensed into one year.)

One summer Burpee hired 200 women to hand-pollinate nasturtium flowers. In one month 40,000 flowers were manipulated. By August the seeds began to ripen. The seeds, which germinate soon after maturity, were planted in greenhouses and by November the second generation produced seed. By May the seed crop from the third generation in the greenhouses would be ready for the market. These new fragrant double flowers in many

colors would be extremely valuable and it was desirable to have a larger crop than could be grown in the greenhouses. A fertile mind thought of attempting to grow the third generation outdoors where growing conditions were favorable between November and May. Seeds were shipped by air express to Argentina, Puerto Rico, Florida, and California. The experiment was not entirely successful. In Puerto Rico the plants grew vigorously but did not set seed. In the Imperial Valley in California there was a cold spell followed by a heat wave, and the crop perished. The crops in the greenhouses and in Argentina and Florida were favorable. Not as many seeds were available for May delivery as had been promised, but the feasibility of condensing a three-year program into one year was demonstrated.

PROBLEMS AND POSSIBILITIES IN PLANT BREEDING

In a single chapter on plant breeding a great deal must be omitted. Nothing has been said of the fruit or vegetable crops, the forage crops, soybeans, sugar cane, sugar beets, potatoes, tobacco, forest trees, and ornamental trees and shrubs. Much progress has been made with all of these. And by no means is all the plant improvement carried on by governmental and commercial workers. Many people engage in plant breeding as a hobby and to them the world owes its gratitude. Large numbers of our newer varieties of ornamental plants have originated in the back yards of amateurs. Many farmers have selected superior plants from the varieties they had under cultivation and have increased them for local introduction.

Another interesting feature of plant breeding is the problem of permanency. The plant breeder's work is never done. Situations and demands of the world are ever changing. In the words of Ganong, the art of plant breeding "is long, and the life of man is short, and fancies change, and things that are profitable vary; wherefore improvement has been spasmodic, and along most devious courses. . . . The potentialities of improvement, indeed, have a vast burden of practical troubles to carry; and it is this which makes its progress so halting and laborious."

Prohibition, for example, changed the course of barley breeding; repeal of the Eighteenth Amendment changed it again by once more focusing attention on the brewing qualities of this grain. The popularity of vitamins sent plant breeders into chemical laboratories for vitamin analyses of their products. The automobile industry made such demands on rubber that breeders began a systematic search for high-yielding rubber trees. It is interesting to note the great influence which the plastic industry exerted on soybean breeding. A change in government resulting in a corresponding

change in tariff and trade relationships may alter the whole breeding program for such crops as sugar cane or citrus. What problems the future will bring, the plant breeder can only guess.

The advent of the intercontinental airplane brings added possibilities of the introduction of foreign pests and diseases. New diseases appear and the search for resistant plants begins. Many expeditions to foreign countries have been financed by the federal government. Plant disease situations change continually because crops and diseases and conditions change. "Only by elucidating principles and accumulating wisdom through research," writes E. C. Stakman, "can we foresee possible future developments and prepare to meet them. . . . We hear much about preparedness. Preparedness is essential in plant protection, but we had better prepare for the future before it arrives instead of after it is present or past. And preparedness must be based on research." Stakman deplores the fact that many people seem to have a child-like faith that science can perform miracles. Quite aptly he points out that "miracles of science" may be a good figure of speech, but that most scientific miracles are the result of long and laborious search and research.

FIG. 12–10. Comparison between tetraploid (above) and diploid (below) marigolds. The diploid variety is known under the trade name Guinea Gold. The doubling of the chromosome number is the result of colchicine treatment. (Photograph, courtesy W. Atlee Burpee Company.)

A discussion of plant improvement would be incomplete indeed if some reference were not made to unusual or new procedures in plant breeding. Our accounts of improvement gave examples of "close" crosses between strains, varieties, or most closely related species. Experiments with "wide" crosses between unlike species and even between genera offer a great deal of interest. Through such work there is the possibility of producing plants

quite different from any now existing. For example, some headway has been made crossing sugar cane and sorghum. The possibility of a new plant with more sugar content than sorghum and more hardiness than sugar cane is alluring. Much further exploration is necessary. A beginning has been made in crossing wheat (*Triticum*) with various other genera such as rye (*Secale*), wheat grass (*Agropyron*), and goat grass (*Aegiliops*). Such wide crosses are usually sterile, and literally thousands of hybrids must be grown to find one that will reproduce. The work is difficult and often discouraging, but enough has already been done to indicate that such efforts might revolutionize agricultural practices.

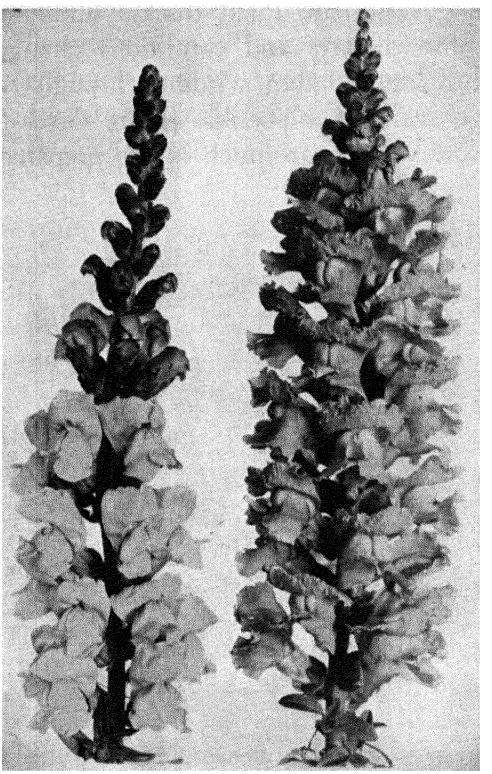


FIG. 12–11. Comparison between diploid (left) and tetraploid (right) snapdragons. In the latter the flowers are larger, many are beautifully ruffled, and the stems are stronger. Tetraploidy was induced by the use of colchicine. (Photograph, courtesy W. Atlee Burpee Company.)

As this chapter is being written the newspapers are carrying such headlines as "New Plants and Animals May Be Spawned by Science" and "Use of Chemicals Expected to Revolutionize Breeding Possibilities in Future." These are not merely wild popular assertions—they have a real experimental basis. We may refer briefly to the use of one substance known as colchicine (Figs. 12–10, 12–11). It is an alkaloid drug prepared from crocus (*Colchicum*) plants. In a scientific magazine it was recently stated, "The use of the chemical colchicine as a means of chromosome doubling [*polyploidy*] has opened a large reservoir of possibilities in plant breeding work. The fact that any numerical change in chromosome number fundamentally entails a mutation which may be expressed in a number of characters of the experimental plant indicates the significance of the above statement." A. F. Blakeslee, of the Cold Spring Harbor Station of

the Carnegie Institution, a prominent investigator of the use of colchicine, says, "We now no longer have to wait ages for the chance hybridization between species and the later rare spontaneous doubling of their chromosomes in order to secure such superior varieties [referring to wheat, oats, timothy, tobacco, and cotton]. We can now make them up to order."

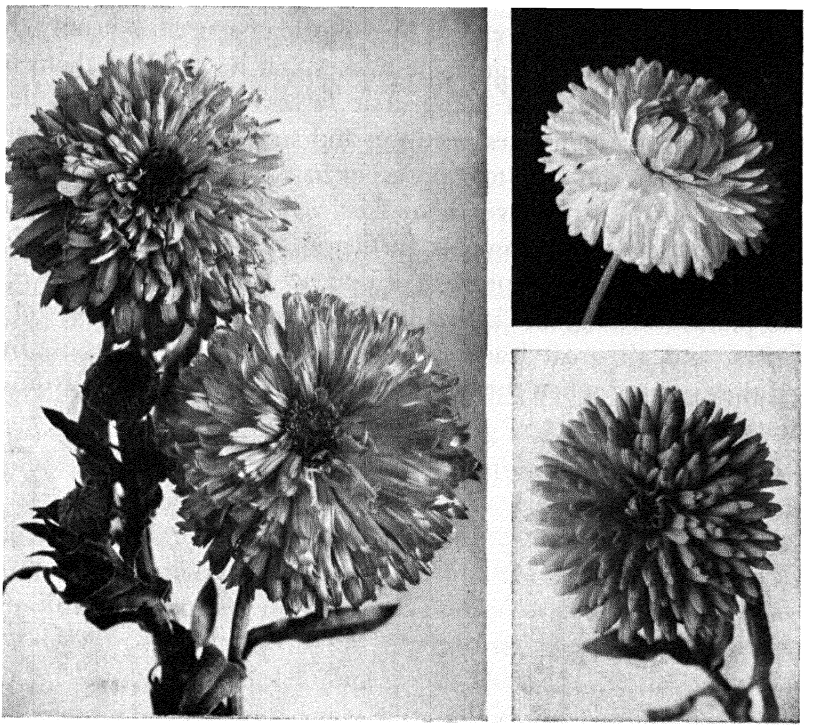


FIG. 12–12. Two new varieties of calendulas known under the names Glowing Gold (above) and Orange Fluffy originated by X-ray treatment of the seeds of the two varieties Sunshine and Radio. (Photograph, courtesy W. Atlee Burpee Company.)

Other well-known scientists agree that artificial induction of chromosome doubling opens immense possibilities. One major effect upon colchicine-treated plants involves change of size; another, change in the shape of parts such as leaves and fruits. In this brief presentation it is impossible to describe fully the technique of colchicine application. The colchicine may be applied in an aqueous solution, in glycerin and water, in glycerin and alcohol, in an agar solution, and in lanolin paste. Seeds, seedlings, growing tips, or expanding buds may be treated. It seems obvious that the colchicine must diffuse into the cells from the surface applications in order to produce its effects. Without presenting further details we may conclude

that the results already obtained indicate that further progress in the realm of plant breeding through artificial stimulation of polyploidy is to be expected. Treatment of seeds by X-rays may also induce marked changes in the progeny (Fig. 12–12).

The following remarks of Ganong in his book, *The Living Plant,* are extremely pertinent in conclusion: "It is evident that in his improvement of plants, man never creates, except by a figure of speech, but only directs. He cannot compel plants to go as he wishes, but he can lead them in any direction they are capable of going. The forces of improvement lie deep inside of the plants themselves, seething and smoldering ready for an outbreak; all that man can do is to suppress or bank them in places where they are doing no good, and give them free vent where they can produce beneficient results." He comments further that "the method of effecting desired results through the guidance of internal forces is not, however, confined to plant breeding, but is that by which all great organizers of large enterprises, and all great leaders of men, effect their successes. By this method they succeed when those who try to force improvement from without meet only with failure." [1]

[1] Reprinted by permission of Henry Holt & Company, Inc.

CHAPTER 13

THE DEVELOPMENT OF THE VARIOUS KINDS OF PLANTS

(*Evolution*)

Nothing can be more obvious than the variable nature of the living beings inhabiting the earth. On every hand we encounter different kinds of animals and different kinds of plants. Our common experiences cause us to think not only of fishes, insects, birds, seaweeds, ferns, flowers, and many other groups, but of many diverse kinds of fishes and flowers. Some naturalists have devoted their attention to describing and classifying living things and from their work we find that there have been described about 800,000 kinds of animals and 350,000 kinds of plants. Natural scientists have long used the term species to refer to a certain kind of organism. A species is a group of individuals alike in essential features of form and structure, although differing in minor details of proportion or color.

How does it come about that there are so many species of organisms in the world? "Upon every developing mind, whether infantile or consciously philosophic, there presses at times the question of the origin of things." The early naturalists believed in "the existence of the universe substantially unchanged during an infinite past." How they supposed that the different species sprang into existence is not clear, but it is certain that they considered the origin of each species to be independent of the origins of all other species. This philosophy, that each kind of organism is fixed and immutable, that one species is not related to another, may be referred to as the doctrine of special creation.

The doctrine of special creation must always have been beset with difficulties. We find thinkers saying that "this philosophy of things is not only incapable of being really grasped by the highest effort of the intellect, but it is incessantly contradicted by experience; it has never gained any real acceptance from the simplest common sense, much less any confirmation from science." As opposed to this theory of permanence we have the alternative theory of change, or the doctrine of evolution. The doctrine of evolu-

tion as it applies to biology overthrows the belief in the immutability of species and concludes that the modern forms of life have been derived from the earlier forms by changes and modifications through the operation of natural laws.

The idea that higher organisms evolved from lower ones by a process of descent with modification was held by some of the Greek philosophers. Ever since their day there have been exponents of the theory of organic evolution. However, the progress of the theory through the ages was slight. What we recognize today as the theory of evolution in the living world is essentially modern. The work of Charles Darwin in the middle of the last century presented so much scientific evidence regarding the doctrine of descent with modification that this doctrine became recognized as a fundamental axiom of biology.

In our books today we find authors saying that the principle of evolution is as well established as the law of gravitation and that "the evolutionary interpretation of nature is accepted today by all scientists of recognized standing." It is universally agreed that the establishment of the principle of evolution has had a profound influence on human thought and has contributed much to man's conception of himself in particular and of the world in general.

In presenting such an emphatic picture of the recognition of the principle of evolution among biologists it would be unfair to leave the impression that there have been no controversies. But the biological controversies have been concerned not with the question whether evolution has been going on but rather with the explanations of how it has proceeded. At this point it is well to call attention to the fact that the "Darwinian theory" was in reality not so much a proof of evolution as an interpretation of its procedure. The full title of Darwin's great book—*The Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life*—fairly well sums up his explanation of the method of the evolutionary process. In the generation just before his, Buffon, Erasmus Darwin, Lamarck, and others had argued in favor of evolution, but their solutions of the various problems did not attract many supporters. It remained for Charles Darwin (Fig. 13-1) to present the doctrine of descent with change, and to interpret and apply it in such a way as to inaugurate a new epoch in biology and philosophy. This fact was emphasized by the great biologist Huxley, in the following statement: "Whatever be the ultimate verdict of posterity upon this or that opinion which Mr. Darwin has propounded; whatever adumbrations or anticipations of his doctrine may

be found in the writings of his predecessors; the broad fact remains that, since the publication of *The Origin of Species* the fundamental conceptions and the aims of students of living Nature have been completely changed." Accordingly, we give much credit to Darwin for bringing about a conception of an evolutional world as opposed to a static world.

All known living organisms have been derived from other similar living organisms without change, or from other unlike organisms with change. The higher organisms have been evolved from the lower. The simpler organisms have given rise to the more complex ones. These views are supported by many facts. Their acceptance may make it necessary for us to alter some of our previous concepts. Without doubt, most of us think of animals and plants as two great and sharply distinct groups. But if the higher forms have come from the lower, then the two groups cannot be so readily separated. The characters which are so distinctive of higher animals and plants must have appeared somewhere

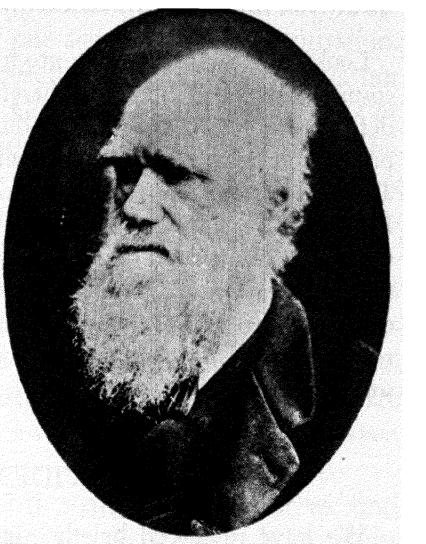


FIG. 13–1. Charles Darwin.

along the line in the course of development, and must be wanting in the lower forms. It is fair to ask if some simple organisms are not now still in existence which have neither animal-like nor plant-like characters and which might be like those which formed the starting point for both developments. The answer is in the affirmative.

The basic differences by which we separate plants from animals are concerned with structural differences of the cells and the manner of obtaining food. We have previously pointed out that firm cell walls and chloroplasts are definitely plant characters. Those organisms which, in their descent, have continued these characters are plants. They have the capacity of producing their food from constituents of the air, water, and soil. Another distinctly plant characteristic is the unlimited development of the individual body through growing points. We like the concept that plants and animals represent "two kinds of organisms, each of which has developed a pattern of living successful in its own way."

If we are to trace plants and animals back to a common ancestry we may raise the question whether we must not push back still further and seek the origin of living substances. Man has given thought to this problem and many theories have been developed. We believe with the animal biologist, Woodruff, that "we may more profitably turn to a consideration of the present manifestations of life, and dismiss the insolvable problem of the origin of life on the Earth. . . ." [1] Like Woodruff we are inclined to quote the following from Huxley:

> Looking back through the prodigious vista of the past, I find no record of the commencement of life, and, therefore, I am devoid of any means of forming a definite conclusion as to the conditions of its appearance. . . . But expectation is permissible where belief is not: and if it were given to me to look beyond the abyss of geologically recorded time to the still more remote period when the Earth was passing through physical and chemical conditions, which it can no more see again than a man can recall his infancy, I should expect to be a witness of the evolution of living protoplasm from not living matter. . . . That is the expectation to which analogical reasoning leads me; but I beg you once more to recollect that I have no right to call my opinion anything but an act of philosophical faith.

SOME EVIDENCES OF EVOLUTION

We have reviewed briefly man's attempts to explain how the world of today comes to be occupied by so many kinds of living things, commonly known as animals and plants. Reference has been made to the theory of special creation, which postulates that each of the multitudinous forms came into being as the result of an act of special creation in its present condition and without previous developmental history. We have concluded that this theory must be rejected as untenable. On the other hand, science accepts a theory of organic development involving changes in the course of descent. This means that the present-day forms are the modified descendants of earlier forms; that in some way different forms have arisen, and have in turn given rise to still other forms. Although science accepts the principle of evolution as a fact there is no agreement as to the causative and guiding factors. "To believe in organic evolution, however, is one thing, and to explain it is a very different thing." It will be well at this time to examine some of the evidence which may be offered in support of the theory of evolution.

[1] *Animal Biology*, by L. L. Woodruff, 2nd ed. Reprinted by permission of The Macmillan Company, publishers. Copyright 1938 by The Macmillan Company.

Structural Similarities

Frequently when we see people that look much alike we suspect relationship. Sometimes when two persons are practically identical we conclude without further evidence that they are twins. When not so near alike but with strong resemblances we may be sure that they are brothers, sisters, parents and children, and so on. What is it that indicates to us such certainty in blood relationships? Most surely it is similarity in form and structure. A little reflection will convince us of our acceptance of this situation. Cousins resemble cousins, grandchildren resemble grandparents. It is not accidental. Most everyone would say that these similarities exist because of relationships. We might say that similarities in structure indicate common origins, but this expression would not be commonly used. To press this reasoning further it is logical that the greater the similarity the more intimate the relationship, and the less the similarity the more remote the relationship. More similarities are expected between brothers and sisters than between cousins, more between children and parents than between grandchildren and grandparents. It may be said that this is true because the relationships are more intimate or more distant or because the origins are closer or more remote. Definitely we are aware that similarities between people do exist because of common origin.

We must be prepared to accept similarity in structure, wherever we find it, as an indication of origins. Common origins in people, animals, or plants are responsible for similarities and, conversely, similarities suggest common origins. But we must go beyond individuals. We have already explained how similar individuals are regarded as constituting a group known as a species. Thus we speak of the white oak as one species, the red oak as another, and the live oak as still another. If we were at all familiar with oak trees we would identify individual trees as belonging to one of these species. In a like manner we talk about pines, recognizing the white pine, the Scotch pine, and the long-leaf pine as different species. Who has not heard the familiar question, "What kind of tree is this?" Perhaps the answer "It is an oak" or "It is a pine" may satisfy; but more often than not we hear, "Yes, I know it is an oak, but what kind of an oak?" The questioner, whether he knows it or not, means "What *species* of oak?"

Surely it is a natural tendency to think of trees not only as individuals but as groups of individuals. All the white oak trees that we know we class together as a species. And so we may know not only three species of oaks —namely, white, red, and live—but many others. There are in the northeastern United States at least twenty species of oaks. Botanists use Latin

names; under their system the white oak is designated as *Quercus alba,* the red oak as *Quercus rubra,* and the live oak as *Quercus virginiana.* The first name designates the oaks as a group; the second applies to the species.

By this time it must be plain that there are groups of groups. This may sound strange at first, but in reality it is not strange at all. We need more terms to make our expression sound better and to aid us in clear thinking. A species is a group of individuals—that is group number one. But when

FIG. 13–2. Leaves and acorns of white, red, and live oaks showing how they are alike and yet how they are different.

we talk about oaks we are recognizing that we are dealing with a group of species. The same is true for the pines; we might cite examples indefinitely. The group of species is a *genus* (plural *genera*). The number of species that may form a genus varies. Occasionally there is a case where a species has no others similar to it and there is only one species in the genus. But as a rule there are several species—sometimes scores—in a cluster or genus. White oaks, red oaks, and live oaks are much alike (Fig. 13–2). They are much more like each other than any of them is like a pine. The conclusion is inevitable that the assemblage of species into genera on the ground of similarity cannot be accidental. If the species in a genus are similar because their origins are associated in some way, this constitutes evidence in support of the principle of evolution.

But our grouping does not end with species and genera. We find that genera are subject to group arrangements. Who would not recognize that peas and beans have much in common? They belong to separate genera, but certainly the two genera are closely associated. There are numerous other genera with similar flowers and seed pods. Among these may be men-

tioned clovers, lupines, vetches, trefoils, and wild beans. Such an association of genera constitutes a *family*.

In like manner we find families associated in larger groups called *orders*. If we draw our examples this time from the animal world we find dogs, wolves, foxes, and jackals in one family; civets and mongooses in another; bears in another; and so on. All these animals have sharp teeth and are flesh-eating, and their toes have claws. In these respects they differ from sheep, deer, pigs, and horses, which have flat teeth adapted to a vegetable diet, and which possess hoofs. Accordingly the flesh eaters with claws form one order (*Carnivora*) and the vegetable eaters with hoofs form another order (*Ungulata*). Gnawing animals such as rats, mice, and beavers form another order (*Rodentia*).

Carnivora, Ungulata, and Rodentia differ in many respects but they agree in other ways such as the possession of a hairy skin and the fact that they suckle their young. In these two latter ways they differ from birds, which have feathers and hatch their young from eggs. And so the various orders of quadrupeds form a higher group called a *class* (*Mammalia*), whereas birds form a different class (*Aves*). The scaly lizards, snakes, and turtles form another class (*Reptilia*); the scaleless frogs, toads, and salamanders make up a class (*Amphibia*); and the finned fishes form a class (*Pisces*).

Although differing in many characters, mammals, birds, reptiles, amphibians, and fishes possess in common red blood and an internal skeleton, and never have more than two pairs of limbs. Thus they differ from insects, crabs, and scorpions, which have colorless blood, an external skeleton, and numerous limbs. These differences are greater than class differences and so the backboned animals form a larger group or *phylum* (*Chordata*), whereas the insects and their relatives form another phylum (*Arthropoda*). There are several other phyla.

The fact to be kept in mind about all this is that the animal kingdom, and the plant kingdom also, is composed of groups within groups. The important point is this: Such a grouping within groups would not be likely to occur if each group had an independent origin. Even people who formerly professed not to believe in evolution accepted the idea that the different individuals of a species had a common ancestry, but thought that the progenitor of each species was totally unconnected with that of every other. The principle of evolution leads to the belief that the species of a genus have a common ancestry. Accordingly, we conclude that the genera of one family have a common origin, and this origin must be different from the origin of the genera of another family; and that the families of an order,

the orders of a class, and the classes of a phylum have common origins. The possibility of classifying so many forms of living things in obviously related groups has led to such expressions as "order in diversity." A hundred years ago workers thought it a most remarkable circumstance that all the varied plants and animals could be arranged in groups having a subordi-

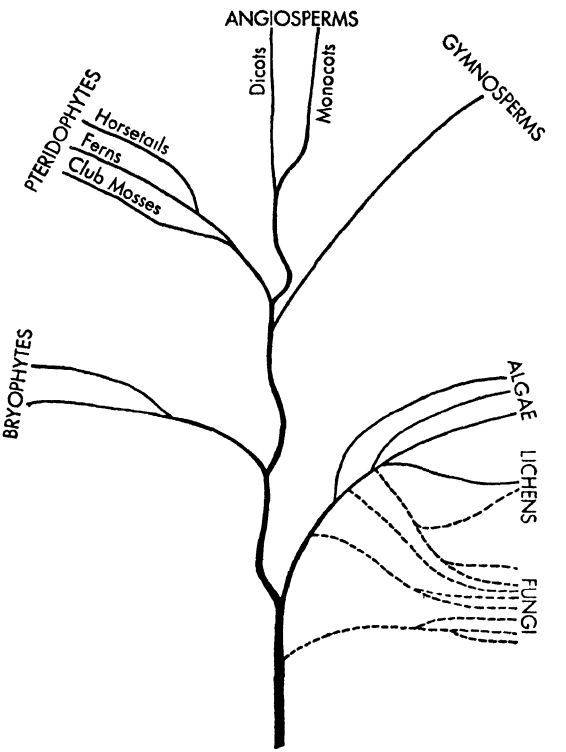


FIG. 13-3. Showing how the relationships of kinds of plants may be represented by a tree. (After Ganong.) Some botanists believe that the relationships in the plant kingdom can be illustrated better by a tree surrounded by several shrubs. (See Fig. 14-8.)

nation one to the other. The doctrine of evolution does not detract from the remarkableness of the situation but explains why it is so.

It is possible to represent the relationship between the kinds of plants (or animals) by a tree, the branches of which diverge and keep on diverging. There is an advantage in using a tree-like diagram (Fig. 13-3). In such a diagram our present-day forms are at the tips of the branches. Two branch tips close together are thus regarded as closely related, not because one has given rise to the other but because they are connected at the fork of a branch.

Evidence from Domestication

Man has not created new species of plants or animals. Yet we know that by selection and breeding he has brought about many changes. Anyone who has attended a chrysanthemum exhibit must have been impressed with

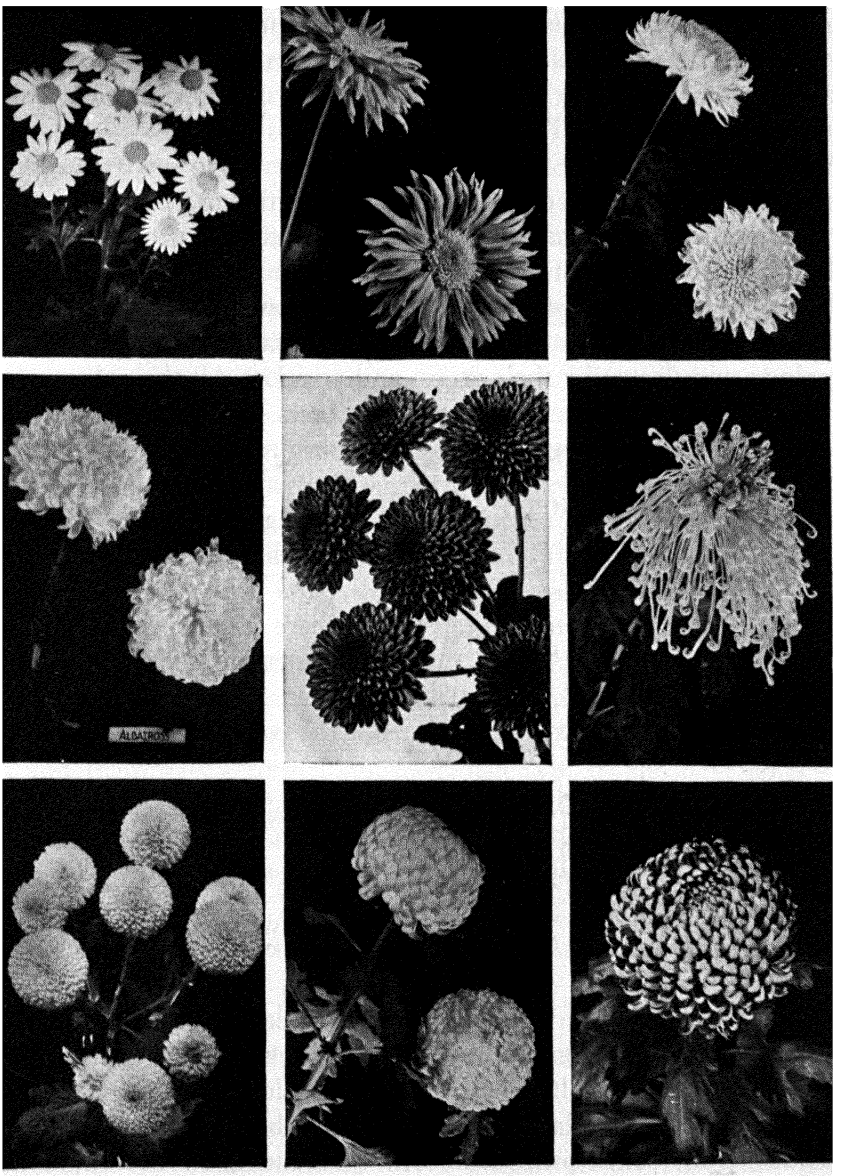


FIG. 13-4. Different types of chrysanthemums all having the same origin. (Photographs, courtesy Ira D. Yoder.)

the numerous types—"the prim little pompon, the star-like anemone, the stiffly-correct reflex, the shaggy Japanese, and a number of others"—all differentiated from the same origin (Fig. 13–4). Our cultivated fruits and vegetables, our domesticated animals all bear witness to the fact that plants and animals have changed and are changing under the hand of man. Is it not logical that they have changed in the past under the influence of what we may call nature? "The breeding of animals and plants under domestication through the years has really been a vast series of laboratory experiments in evolution."

Morphological Evidence

In earlier chapters we discussed the typical higher plant body with its parts—root, leaf, and stem—and showed that special structures such as tendrils and thorns represent modifications of the regular structures. If a tendril is borne in the axil of a leaf it is homologous with a stem. If a thorn has a bud in its axil it is homologous with a leaf. Bracts and scales show homology with leaves by their origin and position. All these diverse structures which can be traced to origins from simpler preexistent structures are evidences of changes that have taken place. In the specialization of these parts for particular functions there is often such an amount of structural alteration that they bear little or no resemblance to corresponding unmodified

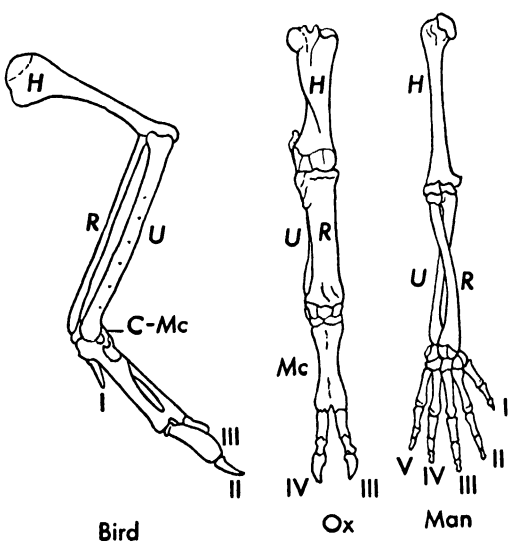


FIG. 13–5. Vertebrate fore limbs showing homologous skeletal structures. Bird, left wing; ox, right foreleg; man, right arm. *C*, carpels; *H*, humerus; *Mc*, metacarpals; *R*, radius; *U*, ulna; *I–V*, digits. (Redrawn from Woodruff.)

parts. Good examples of "similarity in dissimilarity" may be found also in animals. The forelegs of mammals, the wings of birds, and the arms of man are all built on the same basic plan (Fig. 13–5). They are interpreted as signs of relationship and lead to the conclusion that all have descended from some primitive form that furnished the fundamental plan.

Evidences from Individual Development

Our discussion of sexual reproduction has made clear the fact that each individual begins its existence as a single cell known as a zygote. By cell division a multicellular condition is built up, and there is a series of stages during which greater structural complexity is gradually developed. Attention has been called to the fact that there are primitive organisms which exist permanently as single cells. There are also somewhat higher organisms which are multicellular but which do not develop much structural complexity even in their adult condition. There are series of organisms of greater and greater complexity in the scale of plant life until finally there are the higher forms with roots, leaves, and stems. The zygote is comparable to the primitive unicellular forms. The stages in development from zygote to adult represent in a general way the various kinds of plants in the scale from the simple to the complex. The development of an individual is known as *ontogeny*. The development of the scale of plants from simple to complex in evolution is known as *phylogeny*. The situation is tersely summed up in the expression "*Ontogeny* repeats *phylogeny*." The hypothesis that the *individual* in its growth and development passes through stages similar to those passed through by the *race* in its development and evolution is known as the *theory of recapitulation*. The parallelisms between individual and racial development are often striking even though only approximate.

Better examples of the repetition of phylogeny in ontogeny are to be found among animals than among plants. A comparative study of the embryos from different classes of animals yields most convincing evidence. Fishes have a two-chambered heart, amphibians a three-chambered, and birds and mammals a four-chambered structure. In the development of the embryos of birds and mammals the heart passes through a sequence from a two-chambered to a four-chambered condition. Adult fishes have gills. In the embryonic stages of birds and mammals gill slits are developed (Fig. 13-6). In the development of the excretory and reproductive systems and in the brain of the embryos of mammals the same evidence of former stages pertains. It is generally agreed by zoologists that "one cannot avoid the fact that the organs of higher animals during development pass through stages which correspond with the larval or adult condition of similar organs in lower forms."

We are not without examples of recapitulation in plants, but to appreciate them fully requires a considerable familiarity with the various groups of plants and their anatomy. Moss spores upon germination produce a fila-

mental stage (*protonema*) which is very definitely like the adult condition of some algae. Fern spores upon germination also produce a short filament suggestive of algal ancestry. Young plants sometimes produce leaves unlike those developed later by the adult plants. In some of the cone-bearing

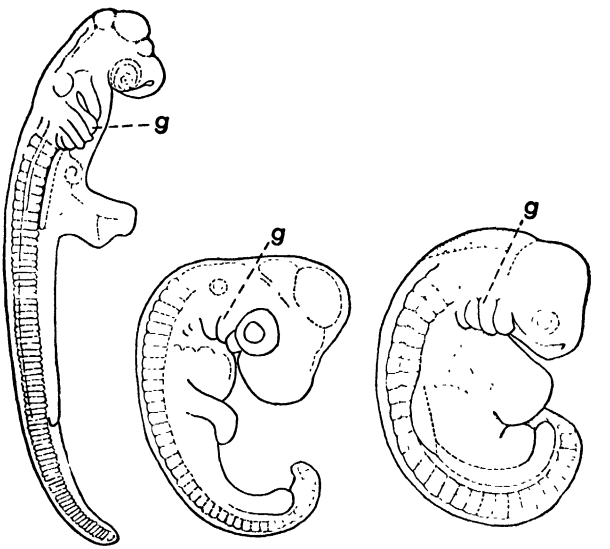


FIG. 13–6. Embryos of fish, bird, and man (left to right) in corresponding stages of development; *g*, gill slits. (Redrawn from Woodruff.)

trees the juvenile form of leaves is similar to the form believed to be ancestral. Recapitulation is sometimes evident in stem anatomy through changes from the seedling to the mature form which simulate the differences existing between primitive and advanced racial types.

Evidences from Physiology

The evidences of kinship discussed thus far are based on structural similarities. There are also physiological evidences based on chemical similarities. We refer to properties revealed by serological tests. In a later chapter reference is made more specifically to the method. On the basis of such tests it is possible to determine the degrees of similarity in the types of blood in animals and of proteins in plants. At this point we need say only that the physiological evidences are in agreement with the structural evidences. It is significant indeed that chemical reactions so thoroughly support evolutionary conclusions that have been reached on other grounds.

Evidences from Distribution

Darwin went on a long voyage on the ship *Beagle*. This enabled him to study the distribution of plants and animals in many islands and several continents. On this subject he afterwards wrote, "In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants can be wholly accounted for by the climatal and other physical conditions." He pointed out that the land areas of the western hemisphere and those of the eastern hemisphere each have similar diversified conditions—humid districts, arid deserts, lofty mountains, grassy plains, forests, marshes, lakes, and great rivers, in a variety of temperatures. He was struck by the fact that there was hardly a climate or condition in the one hemisphere that was not paralleled in the other. And yet as a result of his observations he concluded, "Notwithstanding this general parallelism in the conditions of the Old and New Worlds, how widely different are their living productions!"

If the climatic conditions of Australia, Africa, and South America are similar but the kinds of plants and animals are different, it is evident that climatic differences cannot account for distribution. The facts show that most species are limited in their range to certain restricted regions. On the continents similar but distinct species frequently are found in adjacent regions. Natural barriers such as mountains, deserts, or lakes may prevent them from intermingling. In the oceanic islands, which are distant from other land, a large percentage of the species are not found elsewhere. Statistics show that 83 to 85 per cent of the plants of the Hawaiian Islands do not occur anywhere else in the world; that 40 per cent of the plants and 96 per cent of the animals of the Galápagos Islands are restricted to those islands. There are about 250 species of birds in Madagascar, half of which are not known elsewhere. Three-fourths of the plants of New Zealand are peculiar to that island. Not all islands are so distinctive. The British Isles are very similar to Europe in their fauna and flora. In this case it is believed that the geological separation is comparatively more recent.

The facts of distribution fit well with the theory of evolution and not at all with the theory of special creation. If species have "originated somewhere within, or not far distant from, their present ranges" we can understand the geographic distribution as we find it. Of course, some species migrate widely over a long period of time and some have become cosmopolitan, but this does not at all invalidate the generalization that "most species are now mostly around or near their starting points." The likeli-

FIG. 13–7. Impressions of fern-like leaves are common fossils of the carboniferous age. Many of these were seed plants, but true ferns existed at the same time.

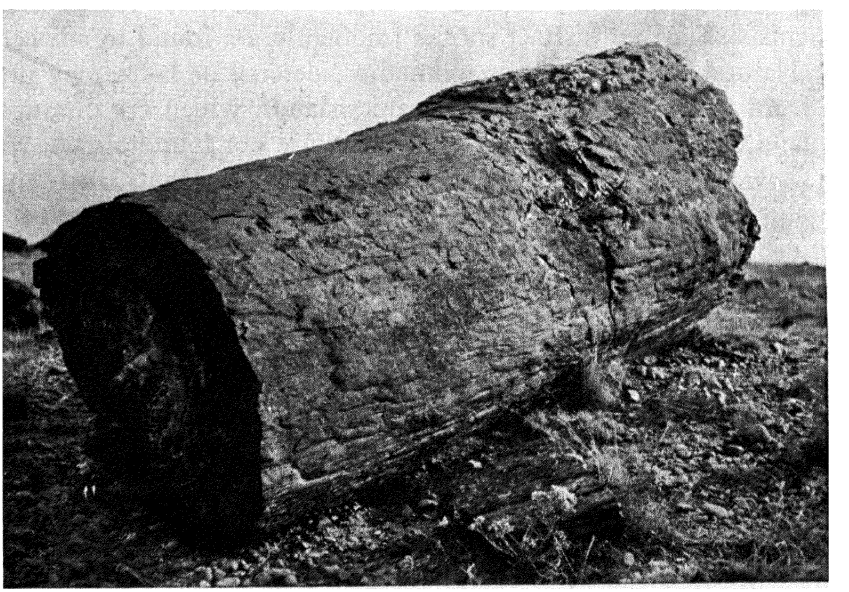


FIG. 13–8. Petrified trunk of a tree. Both the outer surface and the sectional end view show typical structural features. (Photograph, courtesy of William Nelson.)

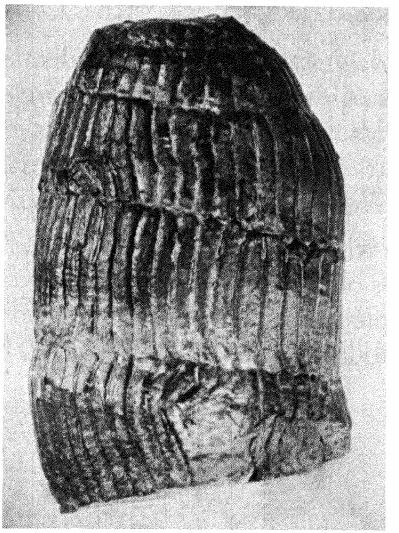


FIG. 13–9. Fragment of a jointed stem from the carboniferous coal measures that has many of the characters of our present-day horsetails (*Equisetum*). These old plants are supposed to "have had the stature and something of the habit of large Bamboos." This specimen is three inches in diameter.

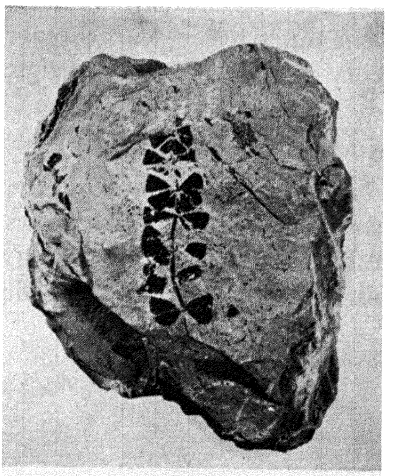


FIG. 13–10. A herbaceous plant (*Sphenophyllum*) in which the shoot was jointed and ridged as in the modern horsetails; the leaves were in whorls. It flourished in the carboniferous period, dying out in the Mesozoic era.

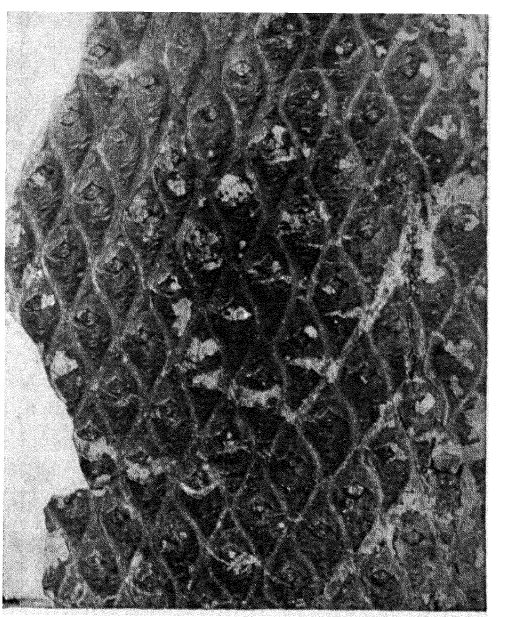


FIG. 13–11. The diamond-shaped pattern on the bark of this carboniferous tree (*Lepidodendron*) is formed by leaf scars. This Lycopod, known only as a fossil, belonged to the same group which includes our present-day herbaceous club mosses and ground pines.

hood that organisms have arisen in widely separated places and at different times fits in with the peculiarities of distribution and supports the theory of the evolutionary origin of species.

Evidences from Fossils

There is a history of life on the earth in what may be called the geological record. Animal and plant bodies, or parts of them, have been preserved in the form of fossils by the relatively simple process of burial under conditions retarding or preventing decomposition (Figs. 13–7 to 13–11). These

FIG. 13–12. A carboniferous landscape of 275 to 225 million years ago (a restoration). There can be no doubt that the vegetation was luxurious. There were trees more than 100 feet in height which are represented in our present-day flora by the small club mosses; fern-like plants bearing seeds, not represented today, and true ferns were the most abundant plants. It was at this time that extensive deposits of coal were formed. (Photograph, American Museum of Natural History.)

fossils are found embedded in the rocks. Some animals and plants which have soft bodies do not fossilize easily. Bones of animals and woody parts of plants on the other hand are often well preserved. Fossils may preserve the external form only, as casts or impressions, or they may preserve both the external form and the internal structure, as petrifactions. Coal is a

compression of masses of plant material. Although the fossil record is incomplete it nevertheless constitutes a very significant proof of what has been going on in the living world.

A study of fossils makes two facts stand out clearly. First it is clear that the living forms of one age were different from those of another age. Our present-day forms are not identical with those of past ages (Figs. 13–12 and 13–13). This means that changes have occurred and thus we have evidences of evolution. In the second place the geologists know how to identify the rocks in chronological order. The periods of succession have been arbitrarily

FIG. 13–13. A landscape as it is thought to have appeared 35 to 20 million years ago (Tertiary period). The broad-leaved trees and grasses give it an essentially modern aspect. (Photograph, American Museum of Natural History.)

arranged as in the accompanying table. Studies of the fossil remains indicate progressive changes through the ages. The study of fossils reveals something of the history and development of existing groups and also introduces us to many extinct types. Not only is the sequence of the appearance of the groups of animals and plants significant, but the intervals of time separating their appearance are equally significant. In this pageant of life, even though incomplete, we have extremely convincing evidence of evolution.

Table Showing Some of the Divisions of Geological Time, and Types of Plant Life

Geological	Periods	Plant Life	Millions of Years
	Present day		
Cenozoic	Quaternary	Angiosperms dominant	1½
	Tertiary		70
Mesozoic	Cretaceous Jurassic Triassic	Gymnosperms dominant	180
Paleozoic	Carboniferous		225
	Devonian		350
	Silurian	Seed ferns; ferns and lycopods abundant	370
	Ordovician		
	Cambrian	Algae only	
	Pre-Cambrian		

PHYSICAL BASIS OF EVOLUTION

For the past three-quarters of a century men of science have not always been in agreement regarding the mechanisms of evolution. A quarter of a century ago a textbook said that the fact of evolution was one thing, that the method whereby it had come about was another, and that the explanation of its method had been "for a half a century the foremost problem of philosophical biology."

It may sound odd to say that the theories relative to evolution have passed through an evolution, but it is literally true. We have had the theories of the transmission of acquired characters, of natural selection, and of mutation, sponsored in turn by Lamarck, Darwin, and De Vries. Actually none of these theories explained how changes were brought about.

According to the "acquired character" theory, changes occurring in individuals in their adjustments to their environment are transmitted in

some way to the next generation; hence a certain character might be intensified from generation to generation. It was proposed that the body cells which had become changed somehow registered these changes in the germ cells. This theory had its difficulties. There were many who believed that changes in the germ cells would produce changes in the body cells, but they did not think the reverse could be true.

The "natural selection" theory in reality explained not the origin of the changes but rather how changes were guided and developed. It assumed that changes were occurring freely and constantly in some spontaneous fashion. If these changes were of a sort which better fitted an organism to live in competition with other organisms, such an organism survived and the less fortunate ones perished. Since nature was the selector of what was successful the term natural selection was an apt one. This theory did not explain how or why changes occurred in the germ cells but assumed that their mechanisms were in a continual state of unstable equilibrium and were thus constantly producing new or varied characters in greater or lesser degrees of intensity. These changes were then, so to speak, offered to nature for acceptance or rejection. When the theory of natural selection was proposed many workers doubted whether the "determiners" of heredity were in such a constant unstable state of being. Some thought them void of all variability. Others argued that there were evidences of an inherent instability even though they could not understand the material basis.

Then came the "mutation theory" of Hugo De Vries, which was in a way a modification of Darwin's explanation of evolution. This theory maintains that changes are not slow and gradual but sudden and occasional. Accordingly they may occur in one jump from parent to offspring. The theory assumes that there may be long periods of stability in transmission, punctuated by the interpolation of sudden and spontaneous changes. This would not affect natural selection which would still operate to determine whether changes would survive or perish. The contribution of this theory was that changes were intermittent and pronounced as opposed to being constant and gradual. Much evidence was offered in support of the theory, but the material basis for operation was still not clear.

The Mechanism of Evolution

We know it to be a fact that characters are preserved from one generation to another. We expect the offspring to be like the parents. The biological term for the transmission of characters is heredity. We are familiar with germ cells, nuclei, chromosomes, and genes. Through these

structures we have the physical basis of heredity and through these same structures we have the physical basis of evolution. If the genes function so as to bring about stability in reproduction we call that heredity. If they function so as to bring about modification we call that evolution. The modifications or changes in a species are due to changes which are introduced in some manner into the hereditary mechanism. The mechanism which is responsible for heredity is also responsible for evolution. Perhaps we might use a homely comparison. We are all familiar with what is called the transmission in an automobile. It is a mechanism that is involved in making the car move. The car can move either forward or backward. It can move forward at different speeds. Whatever the movement and regardless of the direction, it is the same mechanism that is responsible. What happens to the car is dependent, however, not only upon this mechanism but upon its relations to other parts of the propelling mechanism. And so we may understand that the genes are a transmitting mechanism, that they are able to behave in different ways, and that what they do depends upon their relations to other parts of the genetic mechanism.

The main features of heredity are traceable to the genes, which are minute bodies located along the chromosomes. They must be very numerous. It is believed that several genes are involved in one character as, for example, the eye color of an insect. If this is the case a great number must be necessary to control the development of the total characters of the whole insect body. The gene composition of the fruit fly (*Drosophila*) has been studied by many workers and is understood better here than in any other living organism. The estimates of the number of genes for this little insect vary from 3000 to 5000. We can well believe that the number must be greater for more complex beings.

Genes are capable of dividing and producing other genes like themselves. This is evident when we remind ourselves that organisms develop from a single cell, the zygote when sexual reproduction is involved. Every cell of the adult body has a nucleus with chromosomes and genes just like the originals in the zygote. This means that throughout the many cell divisions the genes have been dividing to make possible so many identical nuclei. In these body cells the kinds of chromosomes are ordinarily present in homologous pairs. In meiosis, when germ cells are formed, the pairs of chromosomes separate so that the chromosomes are present in the germ cells singly. In meiosis before separation, the homologous chromosomes are brought together in a parallel manner so that the homologous genes are at the same level. At this time it is possible for genes to pass from one homologous chromosome to the other. This exchange is called "crossing

over." If all the genes in each pair of homologous chromosomes are exactly alike, then crossing over does not change the chromosome pattern. If some of the genes are not exactly alike, then as a result of this interchange, or trading, each chromosome will be slightly different from what it was before. This possibility of crossing over makes new associations of genes and these new associations are passed along through the germ cells to the next generation. Thus we see that when germ cells are formed there is an opportunity for genes to dissociate from their former associates, and when fusion takes place there is an opportunity for them to join new associates. Here we have a situation of significance in the process of evolution.

Mutations

Without doubt the rearrangement and recombination of genes is a source of variability and must be considered of primary importance in evolution. Also of great importance are changes in the constitution of the genes. Such changes are called "gene mutations." They must be chemical or physiological in nature. They cannot be detected in the genes themselves but only by some new character transmitted by the mechanism of heredity and appearing in the offspring. If a plant or an animal exhibits a character which is unlike any known among its ancestors and is not even a recombination of ancestral characters, and if this new character is passed along to succeeding generations, a mutation is known to have occurred.

Such sudden changes do occur and, having occurred, are preserved by heredity. In the fruit fly literally hundreds of mutations have been observed. They affect eye color, body color, spines on the body, and structure of the legs, antennae, and internal organs. Rats, mice, and guinea pigs have undergone mutations especially with regard to eye color and color and length of hair. Many crop plants, such as corn and other cereals, and garden plants, such as sweet peas, snapdragons, and morning-glories, have shown numbers of modifications which must be classed as mutations.

When the matter of mutations is being discussed most people naturally think of visible changes in form and color. We must not overlook the fact that physiological changes may also occur. In plants such mutations may affect rate of growth, reaction to soil fertility, or resistance to disease. The existence of such variations might easily be overlooked by ordinary observations and yet their importance may be of greater influence than is true of many of the visible variations.

It is known that mutations may be brought about through chromosome changes which may involve the number or arrangement and position of

chromosomes but without specific gene mutations. Sometimes chromosomes are broken and unusual situations are known to follow. In laboratory experiments certain genes have been killed by X-ray treatments and changes have been induced by this artificial method. The results are suggestive of what may happen if for any reason certain genes are absent.

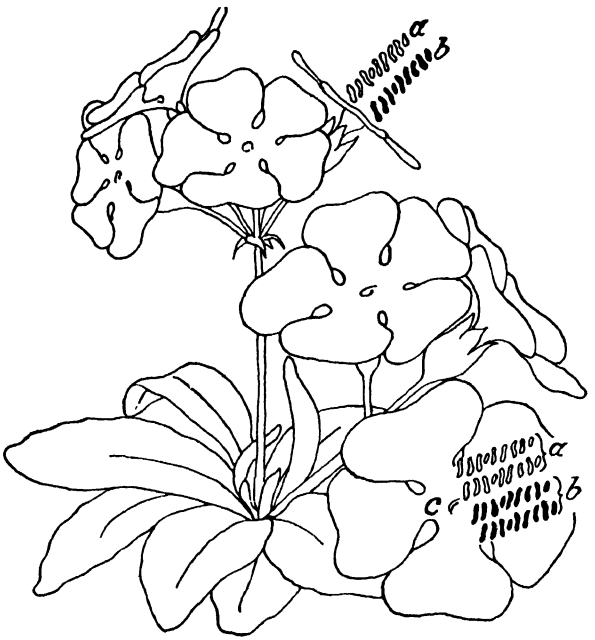


FIG. 13–14. Diagrammatic drawing showing the effect of the doubling of the chromosome number in a species hybrid. The plant is a cross between (*a*) the Arabian primrose (*Primula verticillata*) and (*b*) the buttercup primrose (*P. floribunda*). It has 18 chromosomes like each of its parents (the chromosomes are represented near one of the upper flowers). Suddenly it produced the lower branch with larger flowers, and this was found to have 36 chromosomes (represented on one of the petals). Whereas the hybrid itself was sterile and set no seed, the new branch with 36 chromosomes was fertile and set seed. This fertile side branch was the progenitor (*c*) of the well-known Kew primrose (*P. kewensis*). (Drawing and description from *The Yearbook of Agriculture, 1937.*)

Numerous well-known cases involve changes in chromosome numbers. One of the best known of such aberrations is the doubling of the chromosome number (Fig. 13–14). The doubling may occur at the first division of the fertilized egg. It is supposed that the chromosomes divide without a corresponding cell division. The result would be a cell with twice the ordinary number of chromosomes, and this may then be maintained. Such a case has appeared in the evening primrose. The ordinary species is known by the botanical name *Oenothera Lamarkiana* and has 14 chromosomes.

The altered form has been named *Oenothera gigas* and has 28 chromosomes. The latter is, in general, larger in size. Leaves, buds, fruits, and habit of growth are all affected. A case of chromosome doubling is known also in the Jimson weed (*Datura*). Increase in size is again one of the chief changes. Plants have been produced with one and one-half of the usual number of chromosomes by crossing normal plants with those having twice the normal number. Another type of variation occurs when only one additional chromosome is present. The Jimson weed ordinarily has 24 chromosomes, i.e., 12 pairs. A series of plants have been investigated in which 25 chromosomes are present. This means that 11 of the pairs are as usual, but in place of the 12th pair there are three of one kind. Variations in growth habit and in shape and character of the leaves and fruits are the result.

Causes of Mutations

Thus far we have said much about the way in which mutations occur but not much about why they occur. We have said that recombination of genes, alteration of genes, and aberration in chromosomes occur and that when they occur both visible and invisible modifications may be the result. We must keep constantly in mind that once a modification is started it may persist through the hereditary mechanism just as tenaciously as the original character preceding it persisted. It is now logical to inquire into the reasons for the recombination and alteration of genes and the aberration of chromosomes. Is it possible to discover what conditions or agencies tend to bring about or favor such changes and alterations?

The earlier workers believed that environmental agencies were responsible for initiating modifications. More than a hundred years ago the famous biologist Lamarck advocated a theory of acquired characters. The gist of his theory is summed up in these principles: (1) Important and sustained changes in environment produce change in needs; (2) change in needs demands new habits or functions; (3) changed functions bring about changed structures; (4) such changes are transmitted from parents to offspring. Lamarck's principles made an appeal because they seemed to explain the fitness of organisms to their surroundings. Some naturalists after Lamarck believed that surroundings could produce changes by direct action and not merely indirectly through changed physiological processes. Darwin knew that some variations were transmitted and that some were not, but he was more interested in the guidance of variations than in their origins.

The problem of the modification of the genes has, in recent years, been attacked by the experimental method. In animals the attempts have in-

volved temperature, substances in the blood, and radiation. The latter has also been used in experiments with plants. Many alterations which have been termed mutations have been caused artificially by X-rays and radium emanations. There is much doubt whether radiation can be regarded as a cause of mutation in nature. It seems fair to sum up the whole situation by saying that the causes of natural mutations are considerably in doubt.

GUIDANCE OF THE PROCESS OF EVOLUTION

Our conclusions thus far are in three parts: (1) that evolution has been going on; (2) that there is a mechanism which can account for the evolutionary changes; and (3) that much remains to be done before we can understand the causal agents of these changes. We next need to consider the guidance or direction of the evolutionary process. We find that certain forms, species, and groups are now in existence. We know that other forms have been in existence but have disappeared. We might imagine forms which never have existed. Why is it that evolution has given us what we find and not something else? There must be natural factors or forces which have put their "stamp of approval" upon some changes and not upon others. We must try to gain a conception of the theories offered in the solution of these problems.

Natural Selection

It is fitting that we should examine further the theory of natural selection which was so strongly advocated by Darwin as being responsible for guiding the course of evolution. Darwin was impressed by the fact that man had, through the ages, found differences in plants and animals and that through his selections he had increased and preserved these differences. Darwin did not believe that man either originated new varieties or prevented their occurrence. He believed that variations were constantly occurring in nature and that forces were at work there to preserve the changes which were beneficial and to destroy those which were injurious. His own words were: "This preservation of favorable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest." In justification of his phraseology he wrote, "Several writers have misapprehended or objected to the term Natural Selection. Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its condition of life." In using the expression Darwin was criticized for personifying or

deifying nature. On that point he said, "It is difficult to avoid personifying the word Nature; but I mean by Nature, only the aggregate action and product of many natural laws, and by laws the sequence of events as ascertained by us. With a little familiarity such superficial objections will be forgotten."

Darwin took variations for granted. He did not know how they were brought about, but it is evident that he thought they occurred "according to the laws of chance, in all directions about a central type or norm." He was impressed by the fact that individuals of a species are seldom exactly alike. New characters were supposed to build up gradually from minute variations. At that time nothing was known about marked and sudden changes such as are now called mutations.

Overproduction and a struggle for existence loomed large in the natural selection hypothesis. It is easy to see that reproduction does not proceed in an uncontrolled manner. If it did the world would soon be covered by the progeny of a single pair. Linnaeus calculated that if an annual plant produced only two seeds, and their seedlings the next year produced two, and so on, in twenty years the progeny would amount to a million plants. It is hard to imagine any annual plant producing only two seeds. Many such plants produce seeds by the thousands. Darwin estimated that a pair of elephants having a life span of one hundred years would bring forth six young. If these lived and reproduced accordingly there would be nineteen million descendants in the course of 750 years. A single codfish produces eggs by the million.

Darwin was impressed with the struggle for existence which he assumed inevitably follows "from the high rate at which all organic beings tend to increase." The struggle may be for room, for food, or against enemies, and may involve individuals of the same or different species. In the case of plants it may be a matter of destruction of seeds or seedlings. According to the Darwinian theory, superior fitness in meeting conditions of the environment and the competition of other living things would be rewarded by survival. In other words, there is a natural selection of the fittest. These in their turn perpetuate the traits or characters which made them successful. As time goes on, the succeeding generations should have larger proportions of individuals possessing the advantageous characters. Continued long enough, this would mean that eventually all survivors would be of the fittest type.

The doctrine of natural selection has had its difficulties. It was not universally accepted when proposed. Criticisms have been advanced from time to time. Darwin himself seemed to have felt that one of the most seri-

ous objections was that intercrossing would tend to swamp individual variations. The question has been raised as to the "actuality of the struggle for existence" in the sense of competition among individuals of the same species. It is not denied that there are enormous losses of life, but it is possible that the manner of destruction is such that selection may be operative only infrequently. There are numerous instances where structures have developed far beyond the point of usefulness—even to the point of becoming cumbersome and detrimental. Some people have inquired why such characters have survived if "usefulness" is a criterion of survival.

Some recent writers believe in the general doctrine of natural selection. They think that this theory is assuming a more important role than it did in the early part of this century, but they point out that it is coming to be considerably modified from the form in which Darwin originally presented it. Shull in his book on evolution (1936) is particularly vigorous in pointing out that the struggle for existence does not need to occur in the form of competition. He believes that there are other ways of insuring the permanence of a type besides killing off its competitors. He supports the thesis that the leaving of many descendants is the criterion of success. Shull concludes: "In general it can be said that while the natural selection theory has not come through its crossfire of criticism unscathed, it still is not disabled. While there are things in living nature which it does not explain, it gives every indication of validity in a considerable field of evolutionary phenomena."

Internal Guidance or Orthogenesis

Some workers have not been satisfied with a theory of random variations guided in their development by external factors in nature. It should not come as a surprise to find a theory holding that evolution is determined from within—that there is some internal directing force within living organisms which causes them to vary along predetermined lines. Such a theory is known as *orthogenesis*. Literally the term means straight-line evolution. It is better described as internally directed progressive evolution. Such a theory might account for the development of characters which do not seem to be advantageous, i.e., do not adapt the being to its environment. Much of the evidence comes from fossils and is concerned with the characters of such organs as the horns, teeth, and feet of various mammals. The evolution of the horse is cited as the best evidence for orthogenesis. All the known fossil forms of the horse fit into a series which show a progression from the earliest horse ancestor down to the modern horse.

At least some of the proponents of the orthogenetic theory thought there

was a relation between changes or modifications and the environment. They proposed that the external conditions stimulated the changes and that internal conditions guided them. So far as guidance is concerned, orthogenesis and natural selection are in opposition.

CONCLUSIONS

Evolution is today without doubt the generally accepted theory for accounting for the infinite and variable kinds of living beings in the world. To be more exact, we should say organic evolution. The theory of evolution is as essential to biological science as the theory of gravitation is to physical science. It is necessary to think in broad terms and to consider both animals and plants in order to obtain adequate conceptions. Evolution and heredity work through the same mechanism. Darwin's theory of natural selection still holds a strong place in accounting for the guidance of evolution. The variations upon which natural selection operates are now thought to be chiefly of the type known as mutations. Mutations are sudden variations brought about through changes and aberrations of the genes and chromosomes. Experimental genetics has thrown much light on these matters. Biologists believe that they have a fair concept of the methods by which variations are transmitted and directed, but there is much uncertainty as to the means through which the variations are inaugurated in nature. The theory of organic evolution has disturbed some people unduly. This should not be so. To the theory must go credit for its inestimable influence not only on all departments of natural history, but also on the origin of man and his history, on psychology, and on the social theories which have a bearing on our future progress.

CHAPTER 14

THE PURPOSE AND METHOD OF CLASSIFICATION

(*Taxonomy*)

Ancient man had a practical need for a knowledge of the forms of plant life around him. By trial and observation he found that there were some plants which were useful, some which were useless, and others which were harmful. There was a necessity for knowing how to select the plants that could be used for food, medicine, shelter, implements, and weapons, and how to avoid those that were useless, poisonous, and noxious. Classification naturally arose from the need of "distinguishing between plants that ministered to man's wants and those which did not." Primitive man orally handed down information so that his descendants could profit from his knowledge of plants. Although this information was crude and scientifically unorganized, we owe an incalculable debt to this early simple kind of plant study.

Botany is a classic science and classification is its oldest and most fundamental branch. As time passed, man's knowledge of plants increased; and with the mastery of printing, names and descriptions were recorded. The early literature of natural history reveals a recognition of the fact that plants could be placed in groups, and in groups within groups. The early efforts may have lacked accuracy and fullness, but their purpose and spirit remain unchanged today. By continued observation and increased perception of likenesses and differences the groups became more and more clearly separated and classification naturally developed. "A large part of our thinking about living things is bound up with some system of classification." It is a natural tendency of logical minds to form groups, successively to make distinctions, to point out similarities, and then to assemble the things that are alike. "It applies to everything from chemical elements to college fraternities."

NOMENCLATURE

Biological science, which seeks to organize the vast and varied facts or phenomena presented by and peculiar to the living world, cannot make satisfactory progress without a comprehensive system of applying names to plants and animals. Identifying plants and animals correctly is a necessity if we desire to study and understand them. Both scientific and common names are encountered. The whole matter of systematic naming is called *nomenclature.* Some of the principles of nomenclature, both scientific and common, have been presented, but a fuller consideration of some of the problems is essential. Naming, describing, and classifying are intimately related to one another and to many other phases of biological study and research.

The Naming of Plants

Individuals which differ among themselves only in minor details constitute a species; groups of species which resemble one another more or less closely form a genus. A name is provided both for the species and for the genus. The name is thus double, consisting of a *generic* and a *specific* part, and is said to be a *binomial.* The binomial system of naming plants was established by the Swedish biologist, Linnaeus (Fig. 14–1), in 1753 and has been followed ever since. The generic name is always written first. In order that plant names may be uniform in all languages, it is necessary that they be formed from words which are universally understood. Derivation of scientific names from Latin has proved satisfactory. When taken from other languages, Latin terminations are usually given the name.

Both generic and specific names are more acceptable if they are in some way descriptive of the plants to which they belong. For example, the generic or group name of the clovers is *Trifolium,* a Latin word referring to the *three leaflets.* The name of white clover is *Trifolium repens;* the specific part, *repens,* means creeping and refers to the habit of the stems. Specific names may also be place names, referring to localities where plants were first found or where they are known to be especially abundant. The name of the common red cedar is *Juniperus virginiana.* This tree was first known to botanists from Virginia. Of course, it is also common in many other states, but according to the rules the name must be retained even though it afterwards proves to be somewhat inappropriate. A specific name may be made up from the name of the person who discovered a species or was instrumental in calling attention to it. For example, one of the wild

asters is named *Aster Tradescantii* in honor of Tradescant, gardener to Charles the First of England.

Generic names may also be personal. The genus name of American laurel is *Kalmia,* dedicated to Peter Kalm, a pupil of Linnaeus, who trav-

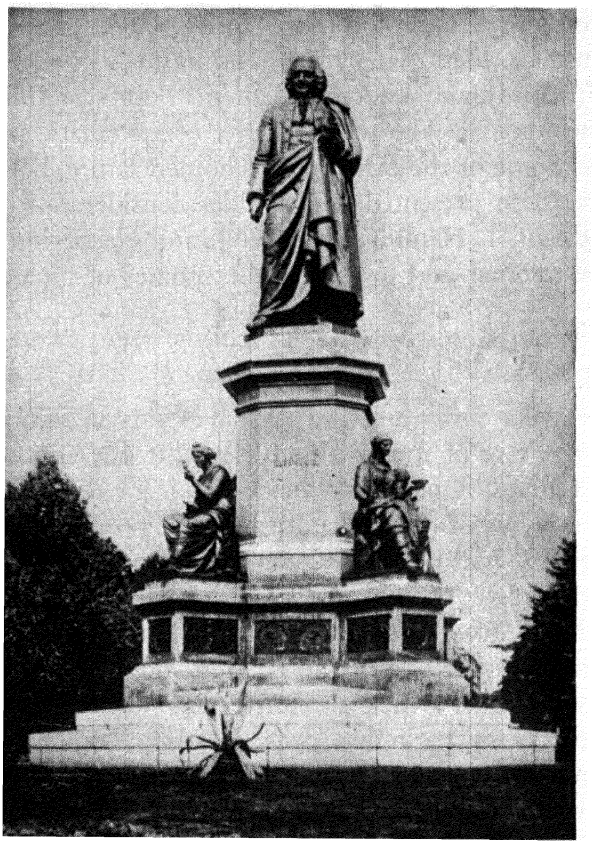


FIG. 14-1. Monument to Linnaeus in Stockholm. At the base of the pedestal are figures representing Botany, Zoology, Mineralogy, and Medicine. (Photograph, courtesy New York Botanical Garden.)

eled in America. One species of *Kalmia* is named *latifolia* because the leaves are broad; another, *angustifolia* because the leaves are narrow; and a third, *hirsuta* because the leaves and branches are hairy. The common yarrow or milfoil is named *Achillea Millefolium.* The story is that Achilles used the leaves to staunch the wounds of his soldiers, and since he is supposed to have discovered its virtues it was named for him. The leaves are finely divided and give the impression of being numerous; hence the specific

name *Millefolium,* which means a "thousand leaves." The ironweed has the genus name *Vernonia* for William Vernon, an early English botanist. The star thistle is named *Centaurea* because of a poetical association with Chiron, the *Centaur.* The basis of this particular association, however, has no really satisfactory explanation.

For the most part genera are named with old Greek or Latin names. *Chrysanthemum* is an old Greek name for "golden flower." *Rhamnus,* the genus name of the buckthorn, is the ancient Greek name for the plant. *Ulmus* (elm), *Ilex* (holly), and *Curcurbita* (gourd, squash, pumpkin) are old Latin names. The name of the trailing arbutus is *Epigaea repens.* The genus name comes from two Greek words meaning *upon* and *earth,* evidently referring to the trailing growth. The specific name *repens* also means creeping, so the habit of growth is doubly emphasized. It must be admitted that some names are of uncertain derivation.

To make the matter of the plant's designation still more definite the name of the person who proposed the name of the plant may be included after the binomial. If the person's name is long and he has named many plants, an abbreviation is used. Thus the complete form for white clover is *Trifolium repens* L., the capital L standing for Linnaeus. Such a name as that of our famous American botanist, Gray, would be written in full. For example, one of the gentians has the name *Gentiana flavida* Gray. In practice the author's names are frequently omitted and some advocate their elimination, but there are many circumstances when their citation lends accuracy. If there are two men's names and one of them is in parenthesis, the parenthetical one indicates the man who proposed the specific name but placed the species in another genus, and the other name designates the man who is responsible for the change. The name of the American mountain ash is usually written *Pyrus americana* (Marsh.) DC. A man by the name of Marshall described the species in another genus, and de Candolle transferred it to the genus *Pyrus.* The genus used by Marshall was *Sorbus* and the original form of the name as proposed by him was *Sorbus americana* Marsh.

Many plants are known by their common names. A useful purpose is served by common names, but it must be obvious that science could not proceed without a more exact method. Common names are useful in our everyday contacts with plants in the field, forest, or garden, but they are loosely applied and, of course, the names used in one language are not known in another. Combined with modifying adjectives, the word moss is used for widely separated and wholly unrelated plants. Sea moss is ap-

plied to algae; common moss belongs to the moss group—we might say that this is the correct usage—club moss is one of the fern allies; and Spanish moss is a seed plant. The name lily is applied to no less than 30 genera other than the true genus *Lilium,* for which it should be reserved. The coconut is known in many lands whose inhabitants speak a multitude of languages. It is said that it has more than 200 common names. Coffee is also known and used by many peoples, but only about ten names are used for coffee. It is interesting that the names used in English, Arabic, French, Dutch, Italian, Spanish, Russian, and Chinese all apparently come from one root.

Still more confusing than the use of many names for one plant is the application of the same name to different plants. As people have moved about they have applied old names to wholly different new plants because the new plants have some resemblance to the old familiar ones. Laurel has been applied to almost any broad-leaved woody plant with evergreen leaves. Our so-called mountain laurel belongs to the heath family and not to the laurel family. The latter includes aromatics such as cinnamon and camphor. Cedar and pine are used as names for almost any evergreen coniferous plant. Pine should be reserved for the genus *Pinus,* which has its needles in bundles, but it is commonly applied to several different genera. Mushroom is applied to many different kinds of fleshy fungi. Toadstool is also indiscriminately used. Usage implies that mushrooms are edible and that toadstools are poisonous, but these are properties that cannot be determined by appearance.

Sometimes we use the botanical names as common names. Most people use the names chrysanthemum, hydrangea, acacia, and aster. They are the scientific names of these genera. We use the name geranium commonly, but curiously enough we apply it not to the real genus *Geranium* but to a genus properly known as *Pelargonium.* It is not clear how this confusion came about. Sometimes the common name is the scientific name anglicized and may differ only slightly in form. Thus we say rose for *Rosa,* amaranth for *Amaranthus,* lily for *Lilium,* and thyme for *Thymus.* Some common names are merely translations of the botanical form. Such are horsetail for *Equisetum* and sunflower for *Helianthus.*

This brief account is sufficient to demonstrate the importance that is attached to the naming of plants. Not only is it of practical value in botanical classification but it is of interest to see the implications of history, legend, biography, and linguistic compounds which unite in the formation of plant names.

The Problem of Naming New Species

Botanical names of plants must be published in a journal or book in order to be established. When a name is proposed it must be accompanied by a description. The International Rules of Botanical Nomenclature (further reference is made to these later in the chapter) require that the descrip-

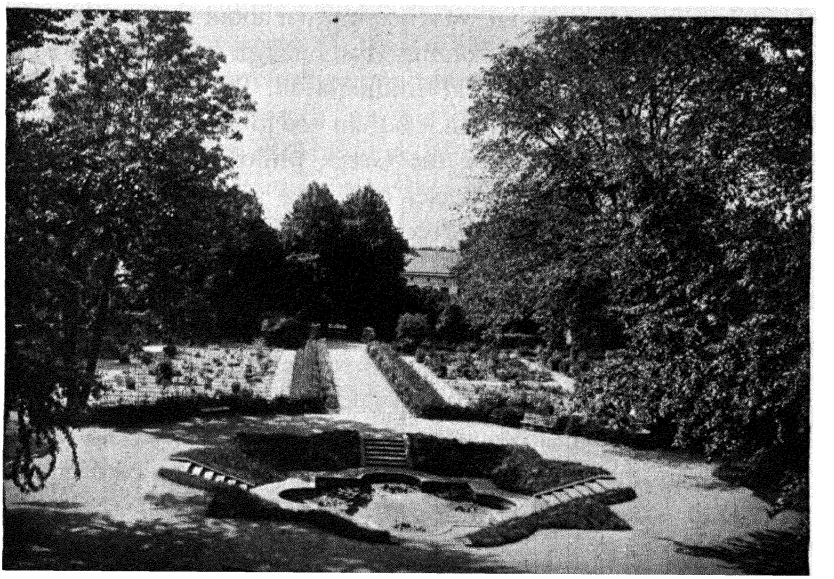


FIG. 14–2. Old Botanic Garden, Upsala, Sweden, as it appeared in 1925. The garden was a hundred years old even when Linnaeus became its director. As near as possible it has been maintained in the condition it was when he was in charge, even to the same kinds of plants.

tion be written in Latin, the nearest approach to an international language. A summary of the principal characteristics is essential to make possible the identification of the particular plant to which the name belongs. Identification is materially aided by the inclusion of illustrations. If we look at botanical journals, we find frequent mention of *new species*. Linnaeus described and named many species of plants (Fig. 14–2). Other botanists of his time and immediately after him found plants not included in his publications. It was natural that they should claim that they had new species. And from that time to this, botanists have been discovering and naming additional species. The expression *new species* does not mean that the author thinks the species has just come into existence, but that it has not been described previously anywhere in botanical literature, and hence is "new" in that sense. It means new to botanical science. It has been esti-

mated that new species of ferns and flowering plants were named and described at the rate of 4800 per year during the twenty-five-year period from 1910 to 1935.

A brief review of the development of our knowledge of the plant life of the world reveals some interesting figures. In 1910 Charles E. Bessey, of the University of Nebraska, published a paper in *Science* [1] in which he brought together in compact form what was then known about the number of kinds (species) of plants with which botanists had enough acquaintance to permit their systematic arrangement and enumeration. Bessey's account showed that the number had jumped from less than 500 to 210,000 in the 2200 years since the days of Theophrastus, the Greek philosopher. It is frequently stated that there are 250,000 species of living plants now known. This figure is doubtless far too low; recent surveys indicate that 350,000 is a better estimate.

We are indebted to Bessey for the following statistics as indicative of the progress through the years:

Dioscorides, 1900 years ago	600 species
Bauhin, 260 (now 290) years ago	5,266
Linnaeus, in 1780	8,551
de Candolle, in 1819	30,000
Lindley, in 1845	80,000
Duchartre, in 1885	125,000
Saccardo, in 1894	174,000
Bessey, in 1910	209,680

Bessey's estimate of the distribution of names to the various groups in 1910 was as follows:

Algae	15,460
Fungi	63,700
Mossworts	16,600
Ferns and allies	3,420
Seed plants	110,500
Total	209,680

Formulation of International Rules of Botanical Nomenclature

We have given credit to Linnaeus for organizing and elaborating the binomial system of naming plants about the middle of the eighteenth century. Linnaeus was a great naturalist with interests in both botany and zoology. It is difficult to distinguish between his contributions to these two sciences. He was as influential in the naming of animals as he was in the naming of plants. Prior to his time there was great confusion in applying names to either group. No plan had been adopted for securing uniformity

[1] *Science*, **32**:669, 1910.

in naming either plants or animals. A systematic method for cataloguing plant and animal life was needed. Linnaeus helped to supply this need for scientific nomenclature. Without detracting from the credit due him, however, it is fair to say that he did not actually invent the binomial nomenclature. There were anticipations of such a system before his day.

Perhaps the naturalists at the time of Linnaeus, and for some time thereafter, thought that a simple plan of providing binomial Latin names was sufficient to insure satisfactory progress in natural history. For a while there were relatively few workers publishing names and it was not difficult for them to be familiar with all previous names. But the number of workers increased. Men in different countries began proposing names. The number of publications increased. It became more and more difficult for a worker to be sure that he had consulted all previous publications. Thus the same species might have different names applied to it by different workers. Obviously such a situation could lead only to confusion and error.

Different practices and customs developed in different countries regarding the manner of forming and establishing names and of designating the various groups or associations which constitute the plant kingdom. Eventually it became evident that botanical science could not make satisfactory progress without a more comprehensive system for naming plants. It was clear that international rules were needed to govern the application of names to plants. Different languages could be used in the different countries without confusion, but confusion arose when plants had different names in different countries. However, it was easier to recognize the problem than to solve it. All of us know the difficulties in securing unanimity of action on matters calling for international consideration. When we think of the history of wars between nations and how the peoples of the world have been unable to get together on such matters as trade relations, armaments, and territorial rights, it is little wonder that scientists have had difficulties in the standardization of plant names.

Obviously a universal system could be worked out only through the agency of international meetings. Looking forward to this end, several international botanical congresses were held. The first real progress was made at the International Botanical Congress which met in Paris in 1867. Two subsequent congresses, one at Genoa in 1892 and one at Madison (Wisconsin) in 1893, did not contribute much. Notable advances were made in 1905 at a congress in Vienna, for a code designated as the *International Rules of Botanical Nomenclature* was adopted at that meeting (Fig. 14-3). These rules applied only to seed plants and ferns. They were amended or extended at Brussels in 1910 to cover the lower plants. Several matters were

reserved for a congress scheduled for London in 1915, but this congress did not convene. It was planned to hold a congress every five years. No attempt was made to have a meeting in 1920. A congress was held in Ithaca (New York) in 1926, but no legislation dealing with nomenclature was passed.

RÈGLES INTERNATIONALES
DE LA
NOMENCLATURE BOTANIQUE
ADOPTÉES PAR LE
CONGRÈS INTERNATIONAL DE BOTANIQUE DE VIENNE 1905
DEUXIÈME ÉDITION MISE AU POINT D'APRÈS LES
DÉCISIONS DU CONGRÈS INTERNATIONAL DE
BOTANIQUE DE BRUXELLES 1910
PUBLIÉE AU NOM DE LA COMMISSION DE RÉDACTION DU CONGRÈS.
PAR
JOHN BRIQUET
RAPPORTEUR GÉNÉRAL

INTERNATIONAL RULES
OF BOTANICAL NOMENCLATURE
ADOPTED BY THE INTERNATIONAL BOTANICAL CONGRESSES
OF VIENNA 1905 AND BRUSSELS 1910

INTERNATIONALE REGELN
DER BOTANISCHEN NOMENCLATUR
ANGENOMMEN VON DEN INTERNATIONALEN BOTANISCHEN KONGRESSEN
ZU WIEN 1905 UND BRÜSSEL 1910

JENA
VERLAG VON GUSTAV FISCHER
1912

FIG. 14-3. Title page of *International Rules of Botanical Nomenclature* adopted at Vienna, 1905, and Brussels, 1910; published in 1912; the pages are 7½″ × 10½″.

No further headway was made until the congress at Cambridge in 1930. A congress at Amsterdam in 1935 is to be credited with further progress. It is needless to add that an international congress to have been held in 1940 in Stockholm was impossible and that no plans for 1945 were possible. The Stockholm Congress will convene in 1950.

The International Rules as adopted in Vienna, and amended in Brussels, did not recognize a "type method" of applying names. The type method maintains that a species is a group of individuals similar to the *type speci-*

men which the author has in hand when he names a species. Similarly a genus is a group of species allied to a designated "type species." According to the other method, a species is a group of individuals having a given combination of characters; a genus, similarly, is a group of species having a given combination of characters. With the type method we name *plants;* with the other method we name our *conception of plants.* There is a real difference. The acceptance of the type method at the Cambridge Congress in 1930 was a revision of the International Rules which was received with favor by many botanists.

The botanists from the various countries of the world who met in the several international congresses had many problems to take under consideration. They had to recognize the fact that the regulations which they passed could not be imposed with authority. They could hope to achieve success only by having their rules "simple and founded on considerations clear and forcible enough for everyone to comprehend and be disposed to accept."

One of the first articles of the International Rules deals with the principle of *priority.* Attention has been called to the fact that different names have been applied through the years to the same species of plant. Likewise different names may have been applied to such groups as genera, families, and orders. According to the rules, each natural group of plants can bear only one *valid* designation. If more than one name is in existence, the *oldest* name must be the valid one; later names are known as *synonyms.* It has been estimated that the total number of binomial names published up to 1935 for ferns and seed plants was 687,000. Since this number is about three times the number of actual species in these groups it is obvious how many established names must fall as synonyms.

It may happen that the oldest, or prior, name of a plant is not the one which has been used most widely. A strict application of the rule of priority in such cases means that the name in common use must be regarded as a synonym and that another name must be used because it is older. The necessity of discarding a familiar name and becoming accustomed to an unfamiliar one is objectionable to many people. It is desirable to avoid changes in names as far as possible, but changes cannot be entirely avoided if the rules of nomenclature are to be retroactive. A provision to conserve a limited number of familiar generic names, even though they may not be the oldest names in existence, overcomes some of the difficulties arising from objections to changes in names.

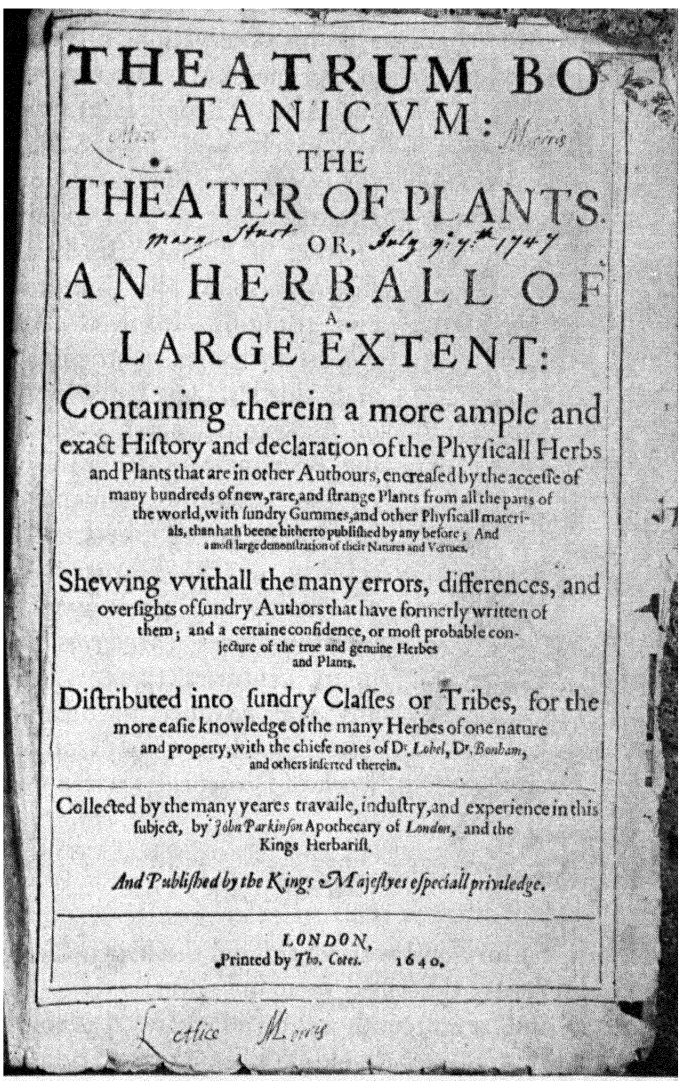
There are those who believe that the procedures embodied in the systems of nomenclature proposed thus far leave too much to expediency and

personal preference and do not rest sufficiently upon fundamental principles. It has been pointed out that "there is no guarantee—if, indeed, there is any hope—that the system which may be adopted today will be accepted by the next generation." For that matter, we do not know that anything man devises will continue. We should not, however, look upon this or any other problem in such a futile manner. There are difficulties, to be sure; but they are not insurmountable.

FIG. 14-4. Frontispiece of Parkinson's Herbal of 1640.

CLASSIFICATION

The arrangement of plants in groups, and the further arrangement of the groups in relation to one another, is called *classification*. From the fact that arrangements are made according to a system, this phase of botanical study has been called *systematic botany*. The studies dealing with the principles of classification, and involving names and descriptions of plants,



THEATRUM BO
TANICVM:
THE
THEATER OF PLANTS.
OR,
AN HERBALL OF
A
LARGE EXTENT:

Containing therein a more ample and exact Hiſtory and declaration of the Phyſicall Herbs and Plants that are in other Authours, encreaſed by the acceſſe of many hundreds of new, rare, and ſtrange Plants from all the parts of the world, with ſundry Gummes, and other Phyſicall materials, than hath beene hitherto publiſhed by any before; And a moſt large demonſtration of their Natures and Vertues.

Shewing vvithall the many errors, differences, and overſights of ſundry Authors that have formerly written of them; and a certaine confidence, or moſt probable conjecture of the true and genuine Herbes and Plants.

Diſtributed into ſundry Claſſes or Tribes, for the more eaſie knowledge of the many Herbes of one nature and property, with the chiefe notes of Dr. *Lobel*, Dr. *Bonham*, and others inſerted therein.

Collected by the many yeares travaile, induſtry, and experience in this ſubject, by *John Parkinſon* Apothecary of *London*, and the Kings Herbariſt.

And Publiſhed by the Kings Majeſtyes eſpeciall priviledge.

LONDON,
Printed by *Tho. Cotes*. 1640.

FIG. 14–5. Title page of the Parkinson Herbal. Names have been inscribed by some of the owners of this copy; the margins of the page are worn with age; the pages are 8¾" × 13½".

comprise a division of botanical science called *taxonomy*. Taxonomic botany includes much more than furnishing the scientific names of plants. It brings together knowledge of structure, development, reproduction, and distribution, to provide a resulting classification that will indicate the interrelationships of the plants that make up the earth's vegetation.

Early Contributions to Classification

Aristotle, of ancient Greece, is known as the "Father of Natural History." "The genuinely scientific character of his observations of biological facts" have been recognized by many modern biologists. His favorite pupil and successor, Theophrastus, worked more extensively with plants and considered their organs, structure, relations, and environment; he has been called the "Father of Botany." In his writings "he discusses some four hundred fifty species, ranging from truffles and seaweeds to pines, domesticated grasses, and thistles." A considerable number of his genus names were latinized by the Romans and are part of our present-day scientific nomenclature. Dioscorides, a Greek physician of the first century of the Christian era, named 600 plants in a great work on medicinal substances (*Materia Medica*). For many centuries there is no record of any real advance in botanical science. After the development of printing, the work of Dioscorides was published at the

FIG. 14–6. Photograph of a drawing of the common foxglove as it appears in Parkinson's Herbal.

end of the fifteenth century and was considered the best book about plants because he had excellently described so many species.

In the sixteenth and seventeenth centuries there appeared numerous illustrated books known as *herbals* (Figs. 14–4, 14–5). These publications are interesting from both botanical and artistic points of view. Several of the authors were German botanists; others were Swiss, English, Flemish,

and French. The earlier herbals were concerned primarily with medical botany, their chief object being to depict the "virtues" of plants; and they "undertook to make easy and sure the identification of remedies by publishing new and lifelike engravings of medicinal plants, executed from actual specimens" (Figs. 14–6, 14–7). Some were more extensive, including plants of all kinds, and placed more emphasis upon descriptions and less upon illustrations. An outstanding contribution was a descriptive treatise,

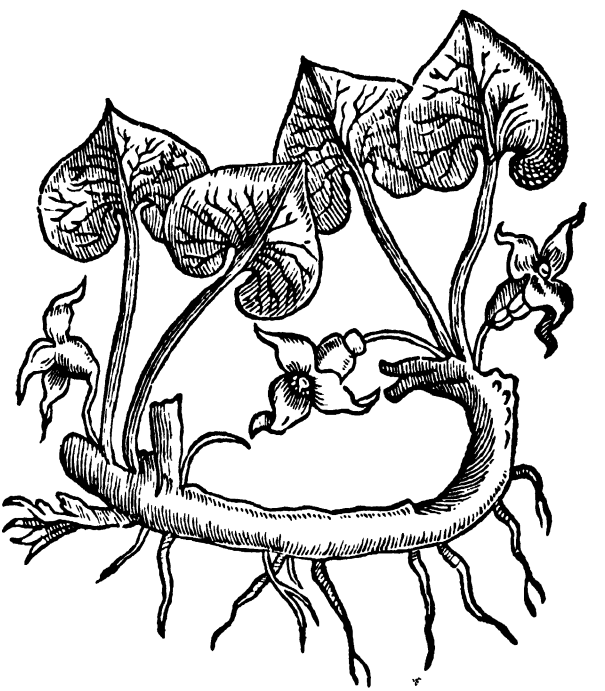


FIG. 14–7. Another reproduction of a drawing from Parkinson, an American plant called by him *Asarum Americanum*, later named *Asarum canadense* by Linnaeus. It is now commonly called wild or Indian ginger, although the name asarabacca is also in use. The drawing is an excellent likeness.

Pinax Theatri Botanici, by the Swiss botanist Caspar Bauhin, which presented a systematic arrangement of 6000 species. These various publications reflect slow but none the less continuous advances in classification.

Later Contributions to Classification

Reference has been made to the part played by the Swedish biologist Linnaeus in establishing the acceptable system of binomial nomenclature. Linnaeus was also a systematic biologist and was influential in the field of

classification. In 1735 he introduced a system of classifying plants which immediately became popular with many botanists. It was a workable arrangement, grouping the plants in such a manner that it was readily usable for their identification. Linnaeus and others of his day recognized the desirability of a natural classification, in which arrangements would be made according to relationships. So long, however, as it was believed

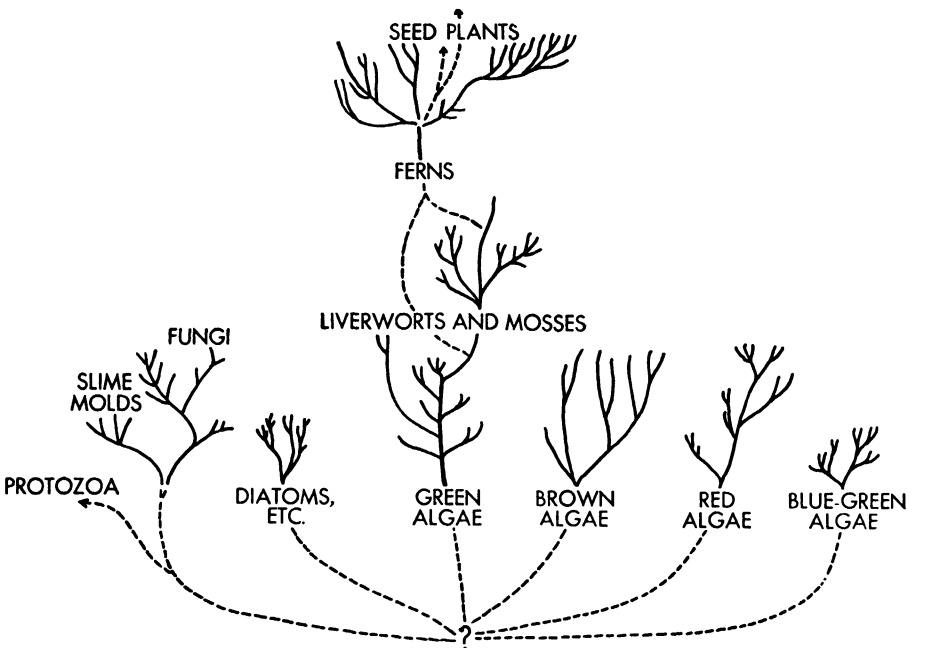


FIG. 14–8. Diagram suggesting interrelationships of the divisions of the plant kingdom. (Adapted by permission from Cryptogamic Botany, Volume I, by G. M. Smith. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

that each species had an independent origin, the arrangement of a system expressive of relationship was impossible. The theory of evolution first provided a true basis for the assembling of all living organisms in natural groups. With the exposition of the concept of evolution by Darwin in the middle of the nineteenth century, schemes of classification were afforded new significance. It was then possible to talk of closely related groups, or distantly related groups, with real meaning. Descent explained similarities and, conversely, similarities suggested descent. From a thorough knowledge of structure it was possible to infer developments and to trace probable relations between one form and another (Fig. 14–8). A natural system based on ancestral development (phylogeny) as revealed by essential innate

characteristics, as opposed to an artificial system based on superficial characteristics, has since been the goal of taxonomy. Such a goal is difficult to attain, as it is impossible to determine, directly and definitely, the phylogenetic origin of all plants. Phylogenetic connections may be derived only indirectly by the comparison and interpretation of structures and behavior. The difficulties in deriving interpretations which are indisputable account for the fact that there are many botanists "who still feel that a natural system is not wholly within our grasp." It is generally agreed that the aim is "both legitimate and essentially justified" and that "active imperfections" are much better than "deferred perfection."

Reference was made earlier to the various classificatory groups—species, genus, family, and class. These groups are generally recognized by both zoologists and botanists. In zoological classifications classes are grouped in a larger assemblage called a *phylum,* and finally the various phyla constitute the animal kingdom. In botanical classifications the larger group above the class is usually designated as a *division.* Although the mutual relationships of the divisions (or phyla) may be imperfectly understood, any scheme of natural classification aims to place only plants of undoubted relationship within a division.

Extra groups may be interpolated and designated by the prefix *sub,* making it possible to have suborders, subfamilies, etc. This makes a plan of classification more elastic. The International Rules of Botanical Nomenclature sanction the following ranks:

Vegetable Kingdom
Division [Phylum]
Subdivision
Class
Subclass
Order
Suborder
Family
Subfamily
Tribe
Subtribe
Genus
Subgenus
Section
Subsection
Species
Individual

Although we speak of the species as the elementary group, we find it variously subdivided under different designations. A subspecies may be based on variations of color, proportion, or habitat, all of which are of a minor nature and yet are rather definite and uniform. Varieties, races, and forms are also subdivisions of a species.

According to the system of plant classification widely used in recent years, four major divisions are recognized, as follows:

I. *Thallophyta* (Slime molds, bacteria, diatoms, algae, and fungi)
II. *Bryophyta* (Liverworts and mosses)
III. *Pteridophyta* (Ferns, horsetails, club mosses)
IV. *Spermatophyta* (Seed plants)

Many botanists feel that it is no longer possible to retain this "time-honored" system. They point out that it does not represent the later sound developments in plant relationships. Several newer systems have been proposed. Some of these have been progressive in the treatment of the lower plants but conservative as far as the vascular plants are concerned; others are just the reverse as regards the adoption of progressive and conservative points of view. In the accompanying table, one of the newer systems which reflects recent developments in all the groups is presented in a manner to

THE PLANT KINGDOM

	Divisions	Phyla
Algae	Thallophyta	Euglenophyta Cyanophyta Chlorophyta Chrysophyta Phaeophyta Rhodophyta Pyrrophyta
Fungi		Schizophyta Myxomycophyta Eumycophyta
Liverworts and Mosses	Bryophyta	Bryophyta
		Tracheophyta *Subphyla*
Club Mosses Horsetails	Pteridophyta	Lycopsida Sphenopsida
		Pteropsida *Classes*
Ferns		Filicinae
Seed Plants	Spermatophyta	Gymnospermae Angiospermae

facilitate comparison with the four-division system. It will be noted that the lower plants—algae, fungi, liverworts and mosses—account for 11 phyla, and that the great groups of vascular plants—club mosses, ferns, and seed plants—are included in one phylum. This is indicative of closer relationships between the vascular groups than between the non-vascular groups. It is interesting to note a parallel situation in the animal kingdom. The lower forms of animals—protozoans, sponges, jellyfishes, worms, starfishes, insects, and mollusks—make up 13 phyla, while the fishes, amphibians, reptiles, birds, and mammals are assembled in one phylum. It will be evident that universal agreement in classification is difficult to attain. In order to reflect new conceptions of relationships and development, classifications must undergo constant adjustments. The system of the future must be a synthesis of many views; it must be subject to revision as new knowledge demands, and yet for practical purposes it must possess reasonable stability.

Other Points of View on Classification

In a comparatively recent paper [2] Herbert F. Copeland has summed up evidence and presented argument "to the effect that organisms can be arranged, naturally, and more conveniently than in the past, in four kingdoms" as follows:

Kingdom 1. Monera (Bacteria and Blue-green Algae)
Kingdom 2. Protista (Protozoa, Diatoms, Red and Brown Algae, Slime Molds, and Fungi)
Kingdom 3. Plantae (Green Algae, Liverworts and Mosses, Ferns and Allies, Seed Plants)
Kingdom 4. Animalia (Metazoa, i.e., multicellular or higher animals).

To those who have been accustomed to thinking that all living organisms must be either plants or animals the recognition of two new groups as kingdoms may seem revolutionary. It is true, however, that the line between lower plants and lower animals has been a difficult one to draw. It must be admitted that there are difficulties in placing together in the Kingdom Protista organisms which previously were in two different kingdoms. Nevertheless, the proposal has advantages.

It is entirely probable that the classification of the future will have a physiological background. In the words of Seifriz, we need "a physiological verification of the validity of purely morphological criteria of relationships." Much headway toward such a goal has already been made

[2] *Quarterly Review of Biology*, 13:383–420, 1938.

by the German botanist Mez and his associates. They have studied plant relationships by serological methods. These studies determine the nature of the proteins. Their theory holds that closely related plants have proteins which are chemically similar. The procedure is this: The plant protein, or *antigen,* is injected into the body of an animal, and an *antibody* is formed which is studied by a precipitation reaction. By comparing the intensity of the precipitation reactions between such antibodies and plant proteins the closeness of the relationships of the proteins is indicated.

We are indebted to William Seifriz for the following fine summary which appears in his book, *The Physiology of Plants:*

> Using such methods, Mez has constructed a family tree which corroborates almost fully the older classification based on taxonomic (morphological) characters. Where differences in results by the two methods exist, the correct relationship is just as likely to be shown by the newer serological reactions as by the older anatomical evidence. It is of great significance to the field of evolution and phylogenetic relationship that a purely chemical basis of classification should so well support a purely anatomical one. Relationships between plants established by serological methods hold well for families but not so well for genera and not at all for species. This is due simply to lack of delicacy in the technique; species differences in proteins must, of course, also exist.[3]

Descriptions of Plants

To make botanical names of service, there must be available somewhere exact descriptions of the plants. Descriptions of plants are to be found usually in one or the other of two kinds of publications: (1) *monographs,* treatises devoted to special plant groups; or (2) *floras,* treatments dealing with the plant life of some special regions. Publications of the floral type far outnumber the monographic works and also exceed them in bulk. The monographs are technical in character and are used chiefly by those making special studies or investigations; the floras are often more popular and are arranged with the idea of making possible the identification of plants by the general worker. The monographs contain complete descriptions and the full situation as to names is presented. In other words, if more than one name exists, a complete list of synonyms, with citations of places of publication and dates, is included. Detailed studies of plant groups are of fundamental importance to both science and industry. In the floras, the descriptions are usually brief and synonymy is often incomplete. Tables designated as *analytical keys,* which present comparative arrangements of conspicuous distinguishing characters of members of a group, usually form part of both monographs and floras. These keys furnish a basis for analyz-

[3] Reprinted by permission of the author and of the publishers, John Wiley & Sons, Inc.

ing characters, and for tracing the identity of a specimen in hand to its ultimate position.

The basis of an analytical key is an arrangement with a series of contrasting characters in outline form. The ideal arrangement is what is known as a *dichotomous* plan. This means that only two choices are offered at a time. As the successive choices are made, the possibilities are narrowed until finally the end of the branch, so to speak, is reached. To aid in making this clear, an example is offered in the form of a key to the species of the genus *Trifolium*. This is adapted from *Gray's Manual*.[4] It is to be understood that this would be preceded by two other keys, one to the Families, and the other to the Genera. By using the first key the family, Leguminosae, would be located, and the second key would lead to the genus, *Trifolium*. The following key should then make possible the determination of the species:

Flowers sessile in dense heads
- Calyx-teeth soft-silky, longer than the corolla . . . . 1. *T. arvense*
- Calyx-teeth ciliate, villous, or glabrous, shorter than the corolla
  - Heads cylindrical; corolla scarlet to deep red 2. *T. incarnatum*
  - Heads globose or ovoid; corolla magenta or purple (rarely white)
    - Calyx soft-hairy . . 3. *T. pratense*
    - Calyx nearly glabrous . . . 4. *T. medium*

Flowers pedicellate in looser heads
- Corolla white, roseate, or purple
  - Calyx-teeth bristle-tipped
    - Calyx villous or hispid
      - Leaflets narrowly oblong . . . . . 5. *T. virginicum*
      - Leaflets obovate . . . . . 6. *T. reflexum*
    - Calyx essentially glabrous
      - Stoloniferous
        - Flowers 1–1.3 cm. long, corolla red 7. *T. stoloniferum*
        - Flowers 6–9 mm. long, corolla white or pink 8. *T. repens*
      - Not stoloniferous . . 9. *T. hybridum*
  - Calyx-teeth lanceolate, herbaceous . . 10. *T. carolinianum*
- Corolla yellow
  - Corolla striate and furrowed in age
    - Leaflets all sessile . . . . . 11. *T. agrarium*
    - Terminal leaflet stalked . . . . . 12. *T. procumbens*
  - Corolla not at all striate in age . . . 13. *T. dubium*

[4] *Gray's Manual*, American Book Company, 7th ed., pp. 508–509. Copyright 1908 by The President and Fellows of Harvard University.

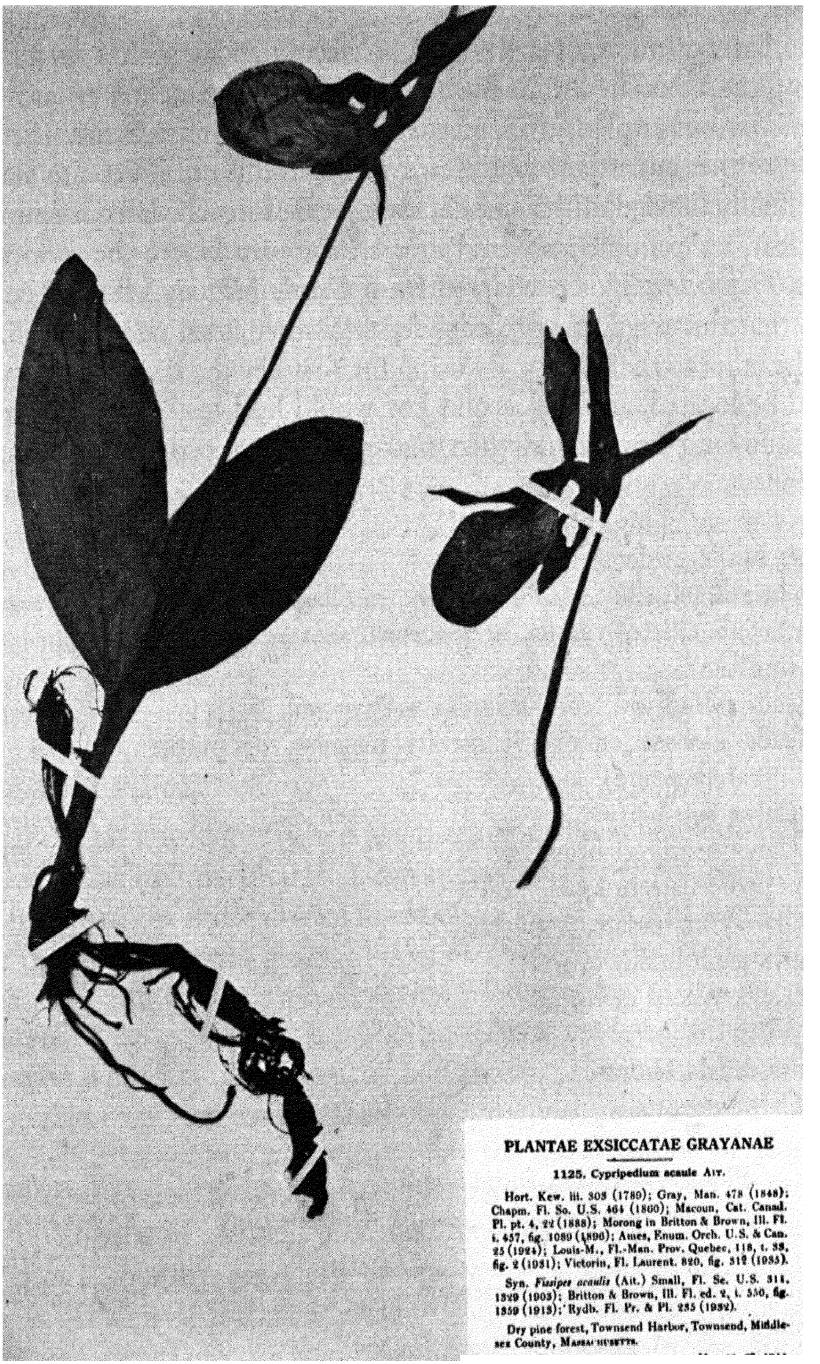


FIG. 14–9. Showing arrangement of a flowering plant glued to an herbarium sheet 11½″ × 16½″.

Collections of Plants

We have stressed the importance of having good descriptions of plants in order that names may be applied with accuracy. No matter how carefully descriptions are prepared, it is difficult to make them completely satisfactory. The best description may leave many things unsaid. Attention has

FIG. 14–10. In preparation for a botanical collecting trip. In the panniers borne by the burro are plant presses, and protruding is a large metal collecting case (vasculum), with lid opening on the side. The vasculum keeps the plants fresh until they can be placed in the press.

been called to the use of drawings and photographs to supplement descriptions. These aids are most helpful, but even they may fall short of conveying all that is desired.

About the middle of the sixteenth century, botanists came to the realization that their studies would be materially advanced if they preserved for future reference the actual specimens which they described. This would make possible the comparison of new and old specimens. Fortunately it was found that many kinds of plants could be preserved in a dried condition. Flowering plants, ferns, mosses, liverworts, many fungi, and some algae may be thus preserved. It has long been the custom to press them as flat as possible and then mount them on sheets of heavy paper (11½ by 16½ inches is the standard size). They can be fastened to the paper by glue or by gummed strips of cloth, or both (Fig. 14–9). Small plants can be pressed and dried entire; large plants must be represented by selected portions—shoots, flowers, and fruits. Leaves bearing parasitic fungi are placed in special envelopes which are mounted on herbarium sheets. Specimens must be accompanied by such data as the place and date of collection

and the collector's name. A collection of pressed and mounted plants is called an *herbarium*. If such specimens are properly stored and precautions are taken to prevent insect depredations, they will keep indefinitely.

Herbarium making has come to be an important feature in botanical science. Herbaria are to be found in all the civilized countries of the world —in museums, botanical gardens, governmental agencies, universities, and colleges. Many individuals collect and preserve plants as a hobby, and systematic botany has been enriched by the contributions of many enthusiastic private investigators who have had no institutional support. Whether in the hands of institutions or individuals, the value of the herbarium as a working tool cannot be overemphasized. The herbarium of the Royal Botanical Gardens in Kew, England, has a collection of 3,000,000 specimens; the United States National Herbarium in the Smithsonian Institution at Washington contains more than 1,500,000 specimens of flowering plants and ferns. Such large collections as these, and many similar ones, have been accumulated largely through expeditions sent by the institutions to make explorations and collect plants. Botanical explorers and collectors deserve much credit for the part they have played in making known the flora of the world (Fig. 14–10).

SUPPLEMENT

THE PLANT KINGDOM

(The Great Groups of Plants)

THE ALGAE

Algae are distinctly water plants. They flourish in both fresh and salt water. They are to be found in ponds, lakes, and streams, even in hot springs. They make up such vegetation as is found in the ocean. They grow on the north side of trees, on snow and ice, and in the soil. Some of them live in the digestive tracts of animals. To say that they grow in many diversified habitats seems to be stating the facts too conservatively. Some algae grow in an association with certain fungi in such a manner that the two components appear to be a single plant. Such combinations are known as lichens. It is interesting that some lichens survive in locations, such as bare rocks and arctic regions, where other plants are practically non-existent, although others thrive best where there is abundant moisture.

In size algae have a wide range. Many of them are unicellular and microscopic. Tiffany states that 200,000 of the smallest ones could lie on your thumbnail at one time. Some of the giant kelps of the Pacific Ocean attain a length of 100 or 150 feet. According to some early writers they grew to greater lengths, but those accounts were much exaggerated.

In the matter of color the algae are also extremely variable. This fact is recognized by the common names of the various groups. On this basis four classes are well known—blue-greens, greens, browns, and reds. Not so well known are the yellow-greens and the golden-browns. But this is not all. The color may vary in the same individual at different stages of growth. An alga may be bright green when vegetating, and yellowish or brownish during reproduction. All the groups, regardless of color, contain chlorophyll. The chlorophyll, however, may be so masked by the other pigments that it cannot be seen at all.

The range of variation in the shape of the vegetative body is as great in the algae as in any group in the plant kingdom. They may be unicellular, colonial, or multicellular. The unicellular species may be either free-swimming (motile) or motionless. The single cells may be spherical,

cylindrical, ellipsoid, clavate, spiral, wedge-shaped, or triangular. It would be difficult indeed to list all the various shapes.

The unicellular algae often form definite groups or colonies. The cells in a colony are not as intimately associated as in a multicellular plant. There are both free-swimming colonies and attached colonies. The motionless colonies may be either aquatic or terrestrial. Some of the colonies are filamentous, i.e., cylindrical cells joined end to end. Some are made up of few loosely associated cells forming flat plates or star-shaped discs. Others consist of many very uniform meshes. In some kinds the cells are embedded in a jelly-like matrix. The walls of the cells, whether in unicellular or colonial species, may be smooth or they may exhibit a great variety of ornamentation.

Many of the smaller multicellular species are simple chains of cells forming filamentous or hair-like bodies. All the cells may be practically identical in form, except the lowermost one, which serves for attachment and is called a *holdfast*. Some of the larger marine algae have branching holdfasts, leafy stalks, and bladder-like floats, which superficially resemble roots, stems, leaves, and fruits of the higher plants.

In the words of Lewis H. Tiffany, "Such are the citizens of the algal kingdom; their number is legion; their abodes are many; their patterns are varied; they are largely our friends. We may name all of them, in spite of their dissimilarities, *Algae*."[1]

The Blue-Green Algae (Cyanophyceae or Cyanophyta)

The blue-green algae are to be found in a variety of locations. They flourish in ponds, streams, and reservoirs. They form slimy masses or coatings on the soil. They are likely to occur in any damp place where there is decaying organic matter. A few of them grow within the outflow of hot springs where the temperature is as high as 75° C. (167° F.). Some of them are inhabitants of the ocean, chiefly in the zone between low and high tide. The fresh-water forms occur in abundance only during the warmer part of the year.

The blue-green algae are mostly unicellular but they are commonly associated in colonies. Cell division goes on without separation so that groups of cells are produced. When joined in rows, a thread or filament is the result (*Anabaena, Oscillatoria*). Sometimes the filaments branch so that they are in effect multicellular organisms (*Rivularia*). Some of the colonies are plate-like (*Microcystis*). The outer portion of the walls surrounding

[1] *Algae: The Grass of Many Waters*, p. 12.

the protoplasts is gelatinous and of considerable thickness. This means that the colored protoplasts are surrounded by gelatinous envelopes. Sometimes the sheaths around the individual cells coalesce so that they appear embedded in a jelly-like mass. The filamentous colonies may also be surrounded by a gelatinous sheath. The gelatinous sheath may be conspicuous or it may be so colorless and watery as not to be noticeable.

The protoplasts of these algae lack definite nuclei with nuclear membranes. Their pigments are distributed throughout the outer portions of the protoplasts. They contain chlorophyll and in addition other pigments. They are by no means limited to blue and green pigments, as the common name would indicate. They may be orange, yellow, rose, purple, brown, or violet. Some are even red. It sounds strange to say that the Red Sea gets its name because of a red alga which belongs to the blue-green group, but this is the case.

The blue-green algae reproduce only by asexual methods. They do not produce any swimming spores (zoospores). They are evidently ancient and primitive forms of life. There are approximately 1400 species belonging to about 150 genera.

The Green Algae (Chlorophyceae or Chlorophyta)

The majority of the green algae are fresh-water plants and grow submerged in the water. Some are to be found on moist soil, on damp rocks, or on the bark of trees. Pond scums and green felt are common names for aquatic and terrestrial green algae respectively. Some of the species are marine. Sea lettuce is a common name for a marine green alga.

The green algae are unicellular or multicellular. A common, motionless unicellular species is to be found on the bark of the shady side of trees (*Protococcus*). There are several unicellular swimming species (*Chlamydomonas, Sphaerella*). Swimming is accomplished by cilia or flagella, usually two in number and of equal length. Like the blue-greens these algae are frequently colonial. The colonies may be simple or complex and are made up of aggregates of motionless or motile individuals. *Scenedesmus* has 2 or 4 motionless cells in a row. *Pediastrum* has 8 or 16 cells arranged in a flat plate. *Hydrodictyon,* the water net, has an indefinite number of cells arranged in a geometrical fashion to form the meshes of a net. There are numerous genera of colonial nature made up of individual cells of the *Chlamydomonas* type. Such colonies vary from simple colonies of 4, 8, 16, 32, 64, or 128 cells up to the interesting genus *Volvox,* whose cells are said to range in number from 500 to as many as 40,000. *Volvox* has the form of a hollow sphere. The desmids are interesting fresh-water

species in which the bodies, although diverse in form, usually consist of two similar halves joined by an isthmus.

Some of the species which are of unusual biological interest are filamentous. Of such a nature are *Ulothrix, Oedogonium,* and *Vaucheria* (green felt). The body of *Vaucheria* is unicellular but multinucleate, a condition known as *coenocytic.* We have referred to these genera in the chapter on reproduction.

The student of biology who wishes to learn something of the evolution of reproductive processes will find a study of the green algae most illuminating. He finds that here reproduction may be asexual or sexual. In these plants it is possible to see how sexual reproduction, involving a union of *gametes,* may have arisen from a purely asexual method involving only *spores.* It is possible to discover not only how sex may have become established but also how it persisted and differentiated. In the genus *Ulothrix* transformed vegetative cells produce one or more flagellated cells (*zoospores*) which reproduce the plants asexually. When many flagellated cells are produced in an identical manner, these cells fuse in pairs and function as *gametes.* It is thus seen that sex arose not through the production of *new bodies* but through a *new behavior* of *existing bodies.* In *Ulothrix* the flagellated gametes are of equal size and the condition is said to be *isogamous.* In other species, such as *Pandorina* or *Codium,* one gamete (the *male*) is smaller and the other larger (the *female*). This condition is described as *anisogamous.* In others, such as *Oedogonium* and *Vaucheria,* a small motile male gamete (*sperm*) unites with a large motionless female gamete (*egg*). This is a condition of *heterogamy* or *oogamy.* Several series in the green algae are illustrative of this evolution from isogamy to oogamy.

The green algae contain chlorophyll and carotenoids in about the same proportions found in the higher or vascular plants. The pigments are contained in definite plastids, *chloroplasts.* The majority of the species store starch as a reserve food. Starch frequently accumulates about rounded bodies in the chloroplasts, which are called *pyrenoids.*

Biologists are convinced that organic evolution is an established fact. This means that the higher organisms have come into being through changes in lower organisms. Just how the lower organisms have given rise to the higher ones is not always clear. Nor is it always clear just which forms may or may not have evolved anything higher than themselves. Botanists believe that we must look for the origin of our higher land plants in certain algal-like ancestors. There is general agreement among botanists that it is the group of green algae which has given rise to the mosses and liverworts, to the ferns, and to the seed plants. The organization of their

bodies, their morphological and physiological features, and their reproductive structures all lead to this conclusion. The other groups of algae have made a certain amount of progress but are not believed to have evolved anything higher than an algal-like plant. With this in mind, we cannot fail to recognize the unusual place which the green algae occupy in biological studies. The other algae are interesting for what they *are;* the green algae are interesting for what they *are* and for their *relationships.* There are nearly 6000 species belonging to approximately 350 genera. (See Figs. 1–1*C,* 3–8*A,* 3–9, 8–7, 8–9, 8–11 to 8–14.)

The Brown Algae (Phaeophyceae or Phaeophyta)

The brown algae are, with rare exceptions, seaweeds and occur chiefly in the colder waters of the arctic and temperate zones. The gulf weed *Sargassum,* of the Sargasso Sea, is a floating warm-water plant. A large number of species grow attached to rocks in tidewater areas. Without doubt the most widely distributed and best-known brown seaweed is the rockweed, or bladder wrack (*Fucus*). Everyone who has been along the seashore in arctic or temperate regions has seen the great masses of rockweed which are uncovered at ebb tide. It has coarse, branching, ribbon-like strands with air bladders. Another form in the littoral zone is known as devil's apron (*Laminaria*). It is attached to stones by a branching holdfast and has a tough leathery blade. Other well-known brown seaweeds are the large kelps of the Pacific Ocean. These grow in deeper water below the littoral zone. The bladder kelp, called also sea-otter's-cabbage (*Nereocystis*), forms extensive beds from southern California to the Aleutian Islands. It grows in water up to 100 feet deep and may attain a length of 150 feet. The giant kelp (*Macrocystis*) has about the same range as the bladder kelp. The stipes of some of the kelps show annual layers of growth which indicate that they may live for several years. The bladder kelp is an annual.

The brown algae reproduce both asexually and sexually. An alternation of generations is known to occur. In *Laminaria* sporangia occurring in patches on the blade produce meiospores. The meiospores grow into small filamentous male and female gametophytes. The zygote resulting from the union of the sperm and egg grows into a *Laminaria* sporophyte. In other species the gametophyte and sporophyte generations may appear to be practically identical in form.

The Sargasso Sea is an area in the North Atlantic Ocean which has great masses of floating plants of a brown alga belonging to the genus *Sargassum.* The plant body has a stem-like axis bearing globose air sacs

and leaf-like organs. This alga is known only in the free-floating condition and is noteworthy because it propagates in such great quantities.

The brown color of these algae is due to a pigment unique to them. It masks the regular chlorophyll which is also present. The bodies (*thalli*) are always multicellular. It is estimated that there are 900 species divided among 190 genera. (See Fig. 3–10.)

The Red Algae (Rhodophyceae or Rhodophyta)

The red algae are largely marine species. They occur chiefly in the warmer waters of the temperate and tropical seas. A small minority of the species is to be found in the polar seas. Perhaps fifty species grow in fresh-water habitats.

The red algae are frequently referred to as the sea mosses. Some of the rose-red, delicate-foliaged species (*Dasya*) do have a resemblance to the mosses. Some have flattened ribbon-like bodies (*Deleseria*), others have a branching filament-like form (*Ceramium, Nemalion*). Irish moss (*Chondrus*) and the dulse (*Rhodymenia*) are well-known forms. These two are so dark a red that they are almost purplish. The so-called corallines (*Lithothamnium, Corallina*) are genera of red algae which become encrusted with lime. They aid in building up coral reefs and are often mistaken for corals.

Reproduction in the group is both vegetative and sexual. In neither method are swimming reproductive cells formed. This seems strange for plants living in the water. The sexual method is very complex in most of the species. The zygote develops into a fruiting body (*cystocarp*) which bears spores. The specializations and modifications are many.

With one or two exceptions the red algae are multicellular. Compared with the brown algae they are small. Many of them do not reach a height of more than three or four inches, although some of the Pacific coast forms attain a height of three feet. They are normally attached and do not live long if detached. Some species grow only near the surface but in clear water; other species may be found abundantly as deep as 200 or 300 feet. They have been reported from depths up to 600 feet. They contain chlorophyll, and in addition a red pigment and a blue pigment. Variations in the amounts of the red and blue pigments produce the delicacy and diversity of tints which make these plants so beautiful. It is estimated that there are 2500 species belonging to 400 genera. (See Fig. Introd.–2.)

The Diatoms (Diatomaceae or Bacillariophyceae)

An account of the algae without reference to the interesting microscopic forms familiarly known as the diatoms would indeed be incomplete. They

are widely distributed in salt and fresh waters and on damp soil. Most people have heard the term *plankton,* which is applied to the free-floating organisms in oceans, lakes, and rivers. While plankton may include a variety of lower plants and animals, diatoms are usually present in great numbers. According to Tiffany, river planktons show a preponderance of diatoms. He estimates the ratio of diatoms, blue-greens, and other forms to be 10 : 1 : ½. In the ocean both the floating and the non-floating diatoms are important as the basic food of marine animal life. The diatoms are so numerous in the sea "that their total weight has been estimated to be more than that of all vegetation on land." Slimy brown coatings on sticks and stones and on the bottom of ponds and sluggish streams are largely masses of diatoms.

The diatoms are unicellular bodies. They may be oval, ellipsoid, boat-shaped, circular, or curved. They may be solitary, free, or attached, or they may be associated in ribbons or chains. The most interesting feature about them is the fact that each cell is enclosed in two valves which fit together like the two parts of a pill box; i.e., one overlaps the other. The valves contain a flinty or glass-like material which is not laid down as a smooth sheet. Their surfaces appear sculptured with lines or markings, as a result of thin places in the wall. Diatoms are very interesting objects to study under a good microscope because of the ornamentation of the valves.

The siliceous portions of the valves are practically indestructible, and as they are cast off in reproduction or death they accumulate on the bottoms of ponds and in the ocean. In this way vast deposits of siliceous or diatomaceous earth have formed. The fossil beds are known in many places in the world and some of them are extensive. One in California covers several square miles and is several hundred feet in depth.

Multiplication by asexual reproduction (cell division) often takes place at a rapid rate. As the cell divides, each daughter cell forms a new half cell wall. The old half wall remains as the outer valve and the new half wall is the inner one. This generally results in two daughter cells of slightly different size, and in some forms the progeny gradually decrease in size. As many as 5000 species belong to about 170 genera. (See Fig. 3–8*D*.)

Economic Importance of the Algae

There are several different ways in which algae affect the welfare of mankind. Foul odors and bad tastes may occur in water reservoirs where certain kinds of algae are abundant. Fortunately they can be killed by traces of copper compounds which are not detrimental in the water. It is believed that the contamination is due to the decomposition of the organic matter accumulating from the algae rather than to their activity.

There are some algae which grow upon the leaves of higher plants and produce injurious effects. In the tropics and subtropics such plants as citrus, tea, and magnolia are sometimes seriously injured. Defoliation can be prevented by spraying.

We have referred to algae as the chief primary foods for water-inhabiting animals. In this indirect way the algae are of great importance to man. It is probably not a well-appreciated fact that algae are a source of food also for man. Their widest use for this purpose is in China, Japan, and Hawaii. In the Orient they are actually cultivated on a commercial basis. They are also eaten in Europe, South America, and the United States. The Irish moss (*Chondrus crispus*) is used in blancmange. In the Orient it is used in jellies, soups, and sauces. The commercial product known as agar is a gelatinous substance made from several different kinds of seaweeds. It is indispensable as a medium for the laboratory culture of bacteria and fungi. It is also used as a sizing material, in clarifying liquors, and as a laxative.

The larger seaweeds, especially the kelps, have been used to some extent as fertilizers. Such practices are known to have been carried on in many parts of the world. Some of the iodine of commerce comes from seaweeds. Reference has been made previously to the use of diatomaceous earth in polishing substances and in the manufacture of certain explosives. In recent years fine diatomaceous earth has been used as the base of cleaners for automobiles with lacquer finishes; an extensive industrial use is in the filtration of liquids, particularly in sugar refineries.

THE FUNGI

The fungi are organisms which stand low in the scale of life. They are distinguished from the higher plants and from the algae by the lack of photosynthetic pigments. They cannot synthesize food from carbon dioxide, water, and the mineral substances of the soil. In the language of science, fungi are *parasites,* deriving nourishment from other living organisms, plant or animal; or *saprophytes,* subsisting on dead organic matter. Some fungi are strict parasites, some strict saprophytes; some are parasitic at one phase of development and saprophytic at another; and some exist either parasitically or saprophytically.

Most fungi have a vegetative body called a *mycelium,* which forms reproductive bodies after it has reached a certain stage of development. Usually only a part of the plant body becomes reproductive, the remainder continuing in the vegetative state.

The mycelium generally consists of innumerable slender whitish threads

known as *hyphae.* In the case of parasites these ramify through the tissues of the plant attacked, which is known as the *host.* In the case of saprophytes these hyphae radiate in all directions through the decaying materials and may be widely scattered. The mycelium is usually hidden and the reproductive structures are the only evident portions of the fungous plant. *Rusts,* forming reddish, yellowish, or blackish spots upon various plants; *smuts,* converting the heads of grains into black masses; *mushrooms,* fleshy umbrella-like growths; and *brackets,* well described by the name, are the spore-producing portions of vegetative mycelia (plural of mycelium) which ramify profusely through leaves and stems, the humus of the soil, and tree trunks. The thread-like structure of the mycelium persists in the fruiting bodies, the hypha being the unit of structure for the entire fungus. A mushroom is made up of a collection of more or less parallel hyphae which are compacted and interwoven. Some primitive fungi have a simple unicellular vegetative body, not a mycelium, which becomes entirely transformed into reproductive bodies.

In size the fungi vary from microscopic cells up to bodies several inches in diameter. Brackets sometimes reach a diameter of two feet. Other large forms belong to the group popularly known as puffballs because of the fact that most of them, when mature, puff forth their spores in clouds on the slightest agitation. These frequently attain a size equal to large pumpkins.

In color the fungi are never of the chlorophyll shade of green because their chief characteristic is a lack of that substance. Perhaps the more typical color is white, although various shades of gray and brown are not uncommon. The spore-forming portions may be brilliantly colored in yellows, reds, and purples.

In reproduction the fungi are characterized by multiplicity and diversity. Usually the spores are so small that a single one cannot be seen by the unaided eye, but many of them together form a dust-like, readily visible mass. The cap of a mushroom or toadstool placed right side up on paper will make a spore print after a few hours that shows the arrangement of the gills or lamellae. Most of the fungi have attained some form of sexual reproduction. Spores known as "resting" spores, which are thick walled and resistant to dryness, excessive temperatures, or other unfavorable conditions, are produced in many species. In this way they are carried over long periods which may be unfavorable for their vegetative growth.

Fungi are to be found in every conceivable place where there is organic matter and moderate heat and moisture. Their capacity for using most any kind of living or dead organic matter as food, coupled with numerous and

resistant spores for reproduction, makes the fungi ubiquitous and irrepressible. Decaying fruit and vegetables, oily bones, musty shoes, dead woody stems, stumps, logs, and all living portions of plants from root to fruit may be expected to harbor fungi.

Estimates of the number of fungi vary widely. Many of the published names are doubtless synonyms. Some workers believe that about 75,000 species, belonging to 3500 genera, are now known, while others think these figures are much too high. It is likely that there are many undescribed species.

The Alga-Like Fungi (Phycomycetes)

Some of the alga-like fungi are saprophytic and some are parasitic. Among the saprophytes are several of the molds. Here belongs the black, or bread, mold (*Rhizopus*). There are a number of aquatic molds which grow saprophytically upon the bodies of dead fish or insects, or parasitically upon aquatic animals, commonly young fish (order *Saprolegniales*). A number of species are the causes of well-known diseases of cultivated plants such as the downy mildew of grape (*Plasmopara viticola*), the late blight of potatoes (*Phytophthora infestans*), the white rust of crucifers (*Albugo candida*), and the damping-off of various seedlings (*Pythium de-Baryanum*). Some of the species are parasitic on insects, occasionally resulting in their destruction in large numbers. The fly fungus (*Empusa muscae*) is a familiar example. Of this species Underwood writes, "It is a common thing in autumn to see flies with white swollen bodies hanging dead on walls and windows with a white radiant halo about them. These are the victims of the fly fungus."

The Phycomycetes are commonly called the alga-like fungi because of the similarity of some of them to certain algae. There are resemblances both in the vegetative bodies and in the reproductive structures. The body of some of these fungi consists of a single cell parasitic within one cell of the host. Most of the genera, however, have a well-developed hyphal structure that is multinucleate but not multicellular. In the algae this condition was called coenocytic. The same term can be applied here.

Reproduction is both vegetative and sexual. The vegetative spores are produced usually at the tips of hyphal branches and may be either swimming (zoospores) or wind-blown (conidia) in nature. Sexual reproduction is common in the higher forms and may be either isogamous or heterogamous. In the black molds the gametes are equal in size, or nearly so, multinucleate, and motionless. They are brought together by the growth

of the hyphae. In other forms such as the water molds and some of the parasites, the gametes are sometimes unequal in size and are produced in well-developed sex organs, antheridia and oogonia. Fertilization is often effected by a tube grown from the antheridium through the oogonial wall. The zygote formed by the union of the two gametes usually develops a heavy wall and undergoes a period of rest. Upon germination the zygote may form zoospores or may develop a hyphal growth resulting in a mycelium.

The group is made up of about 1500 species belonging to 200 or more genera.

The Spore-Sac Fungi (Ascomycetes)

In habit, size, and structure the spore-sac fungi are extremely variable. For the most part they are inconspicuous, but there are numerous exceptions. Yeasts (*Saccharomyces*) are unicellular saprophytes that commonly grow in sugary solutions. Morels, sometimes called "sponge mushrooms" (*Morchella*), have a fleshy edible fruiting body sometimes several inches in height. Some of the other saprophytic species have sizable fruiting bodies of a woody texture. Many of them are terrestrial; a few are subterranean like the truffles (order *Tuberales*). A large number of species are parasitic and are responsible for some well-known diseases of cultivated plants. Here may be mentioned peach leaf curl (*Exoascus deformans*), plum pockets (*Exoascus Pruni*), brown rot of stone fruits (*Sclerotinia fructigena*), ergot of rye (*Claviceps purpurea*), black knot of plums and cherries (*Plowrightia morbosa*), black rot of grapes (*Guignardia Bidwellii*), apple scab (*Venturia pomi*), a canker of woody plants (*Nectria cinnabarina*), and the various powdery mildews (family *Erysiphaceae*).

Whether the species are parasitic or saprophytic, the vegetative body is made up of a mass of interwoven hyphae, or mycelium. Of course the unicellular yeasts are an exception. The hyphae are divided into cells by transverse walls. In some forms the mycelium is seen as a cobwebby mass but in most it is concealed or buried and the fruiting body is the only part of the plant to be seen.

The majority of the species of Ascomycetes reproduce by more than one type of spores. The vegetative spores are non-motile. The production of spores by the cutting off of cells, singly or in chains, from the free terminal portions of hyphae is common. Such spores are called *conidia,* and the multiplication of the individuals generally occurs in this manner during the growing season. At the end of the season, or under special conditions,

a typical form of sporangium known as the *ascus* is produced. The ascus is a membranous sac usually bearing at maturity eight *ascospores*. It is this spore-bearing structure which is responsible for both the scientific and the common names of this group of fungi. Production of asci (plural of ascus) is dependent upon sexual reproduction, or at least is associated with the formation of sex organs. From this reproductive center a hyphal development takes place which results in a fruiting body bearing the asci. In the higher forms the ascus-bearing fructification (*ascocarp*) is usually a well-defined structure. In the powdery mildews the ascocarp is a small spherical body enclosing the asci; in the cup fungi (order *Pezizales*) it is cup-shaped or disc-like and is lined with a layer of parallel asci; in the peach leaf curl the asci are borne on the leaf surfaces without a well-developed fruiting structure.

It is estimated that there are 25,000 species of ascomycetes belonging to 1500 genera. (See Figs. 3–8*B*, 8–9.)

The Rusts and Smuts (Lower Basidiomycetes)

The rusts are small, mostly microscopic fungi, parasitic in the tissues of ferns and seed plants. They are liable to occur anywhere that these hosts are present. The mycelium is always wholly buried within the host tissues, but the spores are borne in more or less definite groups called *sori* (rarely singly) that are covered, at least at first, by overlying host tissue and set free either by rupture or by weathering. Although the spores are microscopic in size they are usually evident, or even conspicuous, when aggregated into sori. The sori may occur upon any part of the host above ground but they are found most commonly upon the leaves. Presence of rust may be indicated by yellowish or discolored spots on the leaf blades, by swellings and galls on the petioles or stems, or by fasciations of the branches known as witches' brooms.

In consistency the sori may be powdery, compact and firm, or gelatinous. In shape and size there is great variation. Often they are rounded or oval and about 0.2 to 1 mm. across; some are cup-shaped, 0.1 to 0.4 mm. in diameter; others project as cylindrical, filiform, columnar, or wedge-shaped masses varying in length from 2 or 3 up to 10 or 20 mm.

Rusts attack plants in all sorts of physical and climatic conditions from the seashore to the summits of the highest mountains, and from the tropics to the polar regions. There is scarcely a family of flowering plants in which some of the members are not parasitized by these fungi. Rusts are to be found in the fields on wheat, oats, and other cereals; in the orchards on apples, pears, and quinces; in gardens on asparagus and beans; in orna-

mental plantings on roses, hawthorns, and cedars; in greenhouses on carnations and chrysanthemums; in forests on pines, spruces, firs, oaks, and willows; in low places and swamps on sedges and crowfoots; in deserts on sagebrush and greasewood; in wild and waste places everywhere on grasses, sunflowers, asters, goldenrods, dandelions, and hundreds of other herbs and weeds.

The rusts are remarkable fungi because of the number of spore forms that may occur in a life cycle. It is common for a species to have as many as four different kinds of primary spores. By this we mean that these spore forms are so unlike in structure and appearance that there is nothing about them to suggest that they are related and belong together in the life cycle of one plant. They occur in a regular succession. But that is not all. The one of these spore forms which ends the succession (*teliospore*), so to speak, produces upon germination a secondary form of spore (*basidiospore*). Some rusts produce only the teliospore type of primary spore form. There are others that are intermediate between those that produce one form and those that produce four forms.

The rusts are further remarkable because of a peculiar change of hosts which takes place in some of the species. The carrying out of the life history on two separate and distinct host plants is called *heteroecism,* and the species which do this are said to be *heteroecious.* Long ago, 200 years or more, farmers in various parts of the world believed that the prevalence of wheat rust was influenced by the presence of barberry bushes. For a considerable time scientists thought that this contention was a superstition, but about 80 years ago a botanist by the name of deBary proved that the farmers were right.

Wheat rust (*Puccinia graminis*) first appears on the wheat stems as reddish rusty sori. This stage is known as the summer spore stage (*uredo*), and the summer spores (*uredospores*) carry infection from one wheat plant to another during the growing season. Later in the season blackish sori replace the red ones. The black sori contain dark, thick-walled, two-celled spores. These are *teliospores.* They are called winter spores because they remain alive over winter. In the spring they germinate, not with a germ tube, but with a short four-celled structure called a *basidium,* which bears four *basidiospores.* It is because of this structure that rusts are classed as Basidiomycetes. The basidiospore is not capable of infecting wheat but when it falls on barberry leaves it produces an infection there. Two spore forms occur on the barberry. One form essential in sexual reproduction is contained in flask-shaped sori (*pycnia*) on the upper sides of the barberry leaves; the other form is borne in cup-like sori clustered in groups on the

under side of the barberry leaves. These sori are commonly known as cluster cups (*aecia*) and their spores (*aeciospores*) are able to infect wheat but not the barberry.

Thus the wheat rust has a well-defined alternation of hosts—wheat to barberry. The eradication of the barberry would seem to be an obvious way of checking the spread of the rust. This procedure is more or less effective, but the situation is complicated by the possibility of the summer spores (*uredospores*) living over the winter and starting the rust again in the spring. It must be remembered that they can pass from wheat to wheat.

In addition to the heteroecious wheat rust there are many other heteroecious species, as has been proved by carefully controlled experiments. The white-pine blister rust (*Cronartium ribicola*) has species of gooseberries and currants as alternate hosts. The common apple rust (*Gymnosporangium Juniperi-virginianae*) jumps to the red cedar. There are several other rusts which alternate between members of the apple family and the red cedar. Practically all grass and sedge rusts, of which there are scores of species, are heteroecious. But not all rusts are of this sort. The sunflower rust produces all four stages on that host and in contrast is said to be *autoecious*. The rusts of roses and brambles are autoecious. The hollyhock rust (*Puccinia malvacearum*) is an example of a rust which produces only teliospores. In our limited space only a few species can be mentioned. It is estimated that there are as many as 5000 species belonging to 125 genera.

The spores of the rusts vary greatly in shape and size, color and thickness of the walls, and surface markings. The teliospores as a rule show greater variation than the other types of spores. The teliospores may be free or united in bundles, or compacted laterally into cushion-like or columnar masses. They may be one- to several-celled, and in those that are free the stalk (pedicel) that bears them may vary also in shape, size, and color. Rust spores are disseminated chiefly by the wind.

The smuts are also minute parasitic fungi. Like the rusts they possess a delicate vegetative body, the mycelium, which grows within the tissues of the host. The species that have cereals and grasses as hosts are best known, but there are some species which occur on other kinds of plants such as anemone, onion, speedwell, ragweed, and arrowhead.

The smuts reproduce by spores that are often borne in external masses which are conspicuous. Most people have seen the large smutty swellings which occur on the ears and stalks and in the tassels of corn. Farmers are only too familiar with smutty masses of blackish powder in flowering heads of wheat, oats, or barley, where the grain should be. These smutty masses are composed of spores. The smuts produce only two types of spores, those

that make up the smut dust and a secondary form (sporidia) that develops when these spores germinate.

In oat smut the spore masses are mature at harvest time. The spores are distributed by the wind and in the process of threshing. Many spores may cling to the outside of healthy grains and pass the winter there. When such grains are planted and germinate, the smut spores also germinate. Some of the hyphae grow into the grain sprout and there begin their parasitic growth. As the oat plant grows upward the smut mycelium grows upward within it. When the oat produces flowers the smut hyphae grow into the young ovules, consume them, and produce spore masses in their place. A smut with such a life history can be controlled by treating the seeds before planting with formaldehyde, which kills the smut spores without harming the embryo of the seed. Some smuts have a different life history. Loose smut of wheat distributes its spores when the wheat heads are in bloom. The spores germinate at once and penetrate the developing wheat grain. When the wheat grain is mature there is a bit of smut mycelium within it. Such a grain will grow into a wheat plant, but the smut masses will form instead of grains of wheat. This smut cannot be controlled by the formaldehyde treatment. A hot-water treatment is successful because the embryo will withstand a temperature which kills the internal mycelium.

It is estimated that there are 700 species belonging to about 34 genera. (See Figs. 1–13, 7–8, 7–9, 7–18.)

Mushrooms, Puffballs, and Bracket Fungi (Higher Basidiomycetes)

Most people are familiar with at least some of the forms which are included here. When these fungi are fleshy and umbrella-shaped they are commonly called mushrooms; if they are similar in form but poisonous they are called toadstools (family *Agaricaceae*). Puffballs (order *Lycoperdales*) when young are fleshy and white, but when old are brownish and filled with dry spores which may puff forth like smoke. Bracket fungi (family *Polyporaceae*), or shelf fungi, are usually tougher and more woody in texture and may be seen growing on tree trunks or fallen logs in the forest. Mushrooms and puffballs are mostly terrestrial and are common on lawns, in pastures, and on the floor of forests. In contrast to the rusts and smuts, which are parasitic, the higher basidiomycetes are largely saprophytic. The bracket fungi are important because they bring about timber decay. Other lesser known higher basidiomycetes include gelatinous fungi (order *Tremellales*), prickly fungi (family *Hydnaceae*), stinkhorns (order *Phallales*), earth stars (genus *Geaster*), and bird's-nest fungi (order *Nidulariales*).

The higher basidiomycetes generally produce only one form of spore,

the *basidiospore*. These are produced externally in fours on basidia (rarely in twos). Here the basidia do not form when a spore germinates, as in the rusts and smuts, but are part of the fruiting structure. In mushrooms and toadstools the basidia are borne on radiating plates (*gills*) on the under side of the cap (*pileus*). In bracket fungi the basidia line the inside of minute tubes or pores. From the presence of the many pores one genus of these fungi has been given the name *Polyporus,* and from that comes the family name *Polyporaceae*. In the puffballs the basidia form the lining of closed cavities within the body.

In all these fungi spores are produced in tremendous quantities. Most of them perish. Those that are successful in living and germinating grow into a mycelium. After vegetating, the mycelium eventually produces a fruiting body (*sporophore*) which in turn produces spores.

In the gill fungi (family *Agaricaceae*) the basidia are exposed long before the spores are mature. It is interesting that the spores are shot off violently at maturity. In the classification of the *Agaricaceae* the color of the spores is an important character. There are white, pink, brown, purple, and black series. Other characters of importance are the mode of attachment of the gills, the presence or absence of a ring on the stalk, and the consistency of the sporophore.

It is estimated that there may be 17,000 species belonging to approximately 500 genera. (See Figs. Introd.–2, 1–12, 2–6.)

The Fungi Imperfecti

There are some kinds of fungi which are not known to produce zygotes, ascospores, or basidiospores. Whether such stages are really lacking in their life histories, or whether they are just undiscovered, is not known. These fungi cannot be referred to the Phycomycetes, Ascomycetes, or Basidiomycetes. Such imperfectly known fungi are included in a miscellaneous group known as the Fungi Imperfecti. At present there are about 24,000 species belonging to 1200 genera included in this group.

Economic Importance of Fungi

Because of the fact that fungi have remained as scavengers and parasites, they are of great economic importance to man. They may be beneficial, dangerous, or neutral to his world. In securing their food they may do both good and evil.

Forests would soon be clogged by the accumulation of fallen trees, stumps, and underbrush if it were not for the rotting of these woody materials by the action of fungi. Decomposition of the organic substances clears the

forest and adds to the fertility of the soil. Other fungi are known to live in the soil and to produce changes beneficial to the higher plants. The organic part of rich soil known as *humus* is filled with fungi. We have previously referred to the associations between certain soil fungi and the roots of some plants known as *mycorrhiza.* The relations are thought to be mutually advantageous. On the other hand timber decays may be very injurious and productive of great losses. Thus we see that wood-decaying organisms may be either beneficial or detrimental to man's interests.

From the earliest times we find records of man's interest in fleshy fungi as a possible source of food. Wild mushrooms, puffballs, and morels are gathered and used as food to a limited extent. It is safe to say that only the cultivated mushrooms are of much economic importance as food for man. Attempts have been made to cultivate many different edible fungi. In Europe and America success has been attained only with the common field mushroom, *Psalliota campestris.* This species has been cultivated for at least two centuries and probably much longer.

The success of the commercial production of mushrooms depends to a great extent upon the conditions provided. An insulated house or a cave with a fairly uniform temperature, not higher than 65° or lower than 50°, will serve. A somewhat moist atmosphere is required, and ventilation is necessary but should provide for only gradual evaporation. The mushrooms are grown in beds of composted horse manure which must be at just the proper stage of decomposition. The mushroom mycelium used to inoculate the beds is known as *spawn.* Great advances have been made in recent years in the preparation of the spawn. It can be prepared from spores, and in one of the newer methods it is grown on cooked grains (wheat or rye). The grains overgrown with the mycelium are then introduced into the compost beds. A proper place and good spawn, coupled with careful management, should insure success.

Yeasts are fungi that serve such well-known purposes in the baking and beverage industries as to need no further comment. Molds are purposely cultivated in some kinds of cheese for the sake of the flavors which they impart. The green streaks in Roquefort cheese are due to the growth of a green mold. It is a relative of the green mold in Roquefort cheese called *Penicillium notatum* that yields the drug penicillin, which has proved so effective in the treatment of wounds, blood poisoning, and other bacterial diseases.

As a rule molds are intruders in food products and it is desirable to keep them out. The molds are often classed in two groups: the black or bread molds (*Rhizopus*), and the blue or green molds (*Penicillium* and *Asper-*

gillus). Some species of *Aspergillus* develop with black, yellow, or reddish colors. The black molds are common on bread and cake or on any starchy materials. Decaying sweet potatoes and fruits, such as raspberries and blackberries, usually show black mold. Blue or green molds are the common household enemies of preserves and jellies but they grow also on bread and starchy materials. Butter packages and tubs are often attacked in storage by these molds if the house is not kept in a sanitary, well-ventilated condition. Many ripe fruits are attacked by green molds, especially on injured or bruised places. These forms get their common name from the bluish-green color of the moldiness produced by their growth.

It is as agents of disease in plants that fungi assume their greatest economic importance. Spotted, curled, or discolored leaves; unevenly developed or decayed fruits; blighted or wilted twigs or stems, are familiar sights in gardens, fields, and forests. These conditions are often due to the growth of parasitic fungi. There are many different sorts of fungous parasites each producing its more or less particular effects. It follows that the diseases differ in nature and that the common names vary accordingly, since they are applied with reference both to the parasite and to its effect on the host plant. The extreme minuteness of the parts of parasitic fungi causing diseases often makes the use of the microscope necessary in their detection and description. The spores which are the usual means of spreading the fungi have characteristic shapes, sizes, colors, and surface markings. They may be carried from plant to plant by various agencies such as the wind or insects. They may live over from year to year in the soil. Some parasitic fungi pass from plants of one sort to plants of an entirely different sort.

Man's struggle against the fungi which cause plant diseases may have several aspects. He may attempt to exclude the fungi by quarantines, to eliminate them by eradication, to prevent their attacks by spraying, or to render them innocuous by using resistant plants. The existence of man and animals is so dependent upon plants that the work of the plant pathologist, whose main interest is the prevention of plant diseases, becomes a matter of paramount importance.

THE LICHENS

Some reference must be made here to the group known as lichens. A lichen is a combination of two plants, a fungus and an alga, that are associated in such a manner that they appear to be a single plant. Lichens are to be found particularly on the bark of trees and on rocks. They bring

about a disintegration of the rock beneath them. Some thrive best under moist conditions. Others withstand dryness and cold temperatures. The so-called reindeer moss of the arctic tundra is a lichen. There are as many as 15,000 species belonging to some 400 genera.

THE SLIME MOLDS

Our account would be incomplete without some reference to the slime molds (myxomycophyta, myxomycetes or mycetozoa). They lack chlorophyll and reproduce by spores. The vegetative body is a naked mass of protoplasm called a *plasmodium*. A plasmodium moves about with a creeping motion usually in dark places, among rubbish, or in rotting logs. When the fruiting stage is reached the plasmodium usually creeps into an exposed position and becomes transformed into sporangia. The process of spore formation may take place so rapidly as to be completed in a single night. There are more than 400 species belonging to about 70 genera.

THE LIVERWORTS

The liverworts are chiefly land plants of moist and shady habitats; a few are aquatic. They grow on the ground, on rocks, on logs and tree trunks. There is a considerable diversity in external form. Most of them are creepers, but some raise themselves as upright leafy forms. Whether the vegetative body is a flat ribbon-like thallus or a leafy thallus, all of them are fundamentally alike in that there is a decided difference in structure between the upper and lower surfaces; i.e., they are dorsiventrally differentiated. In this respect they differ from the mosses, which have radial symmetry. The vegetative body, except when aquatic, develops on the under side simple filaments called *rhizoids* which serve the double purpose of anchorage and absorption. Internally the cells are differentiated into various tissues in some forms, but a real conducting or vascular system is not present in any of the forms.

The life cycle consists of a well-marked alternation of generations. The "liverwort plant" is the gametophytic generation. The zygote resulting from the fusion of the gametes grows into a sporophyte. The spores produced by the sporophyte germinate and develop into a gametophyte. The gametophyte has green tissue and is nutritionally independent. The group includes about 8800 species divided among 180 genera. The following discussion refers only to a few genera but presents the main characteristics of the class.

The Thallose Liverworts

Our account may well begin with the genus *Riccia.* The species of this genus are found in swamps and bogs. Some of them float on shallow ponds and continue growth on the muddy bottom when the water level lowers. The gametophyte is a small, prostrate, dichotomously branched body. The branches typically cling together in a rosette-like manner. A single branch may be linear or wedge-shaped. The upper surface is covered with a simple epidermal layer. The lower surface bears rhizoids and thin scales. Internally there is considerable differentiation of tissues. Each branch has a noticeable median longitudinal furrow on the upper side.

The best-known and most widely distributed thallose liverwort is a species of the genus *Marchantia* known as *Marchantia polymorpha.* It grows on the surfaces of rocks and on the earth in damp ravines and along small shaded streams. The gametophytic thallus is a dichotomously branched prostrate body with dorsiventral symmetry. The upper surface frequently bears cup-like structures (cupules) containing numerous flat buds (gemmae), which become detached and grow into new plants in a purely vegetative manner. Vegetative multiplication may also occur by the breaking apart of the thallus. The lower surface bears scales and rhizoids. Internally the thallus is divided into two regions. In the lower region the cells are compact and have few chloroplasts. The upper region is divided into air chambers which have branched filaments of cells arising from the floor of the chamber; these cells contain many chloroplasts. This chambered structure causes the upper surface to appear divided into small rhomboidal or polygonal areas. Each chamber opens above with a conspicuous central pore which serves for gaseous exchange in photosynthesis and respiration.

The archegonia and antheridia in *Marchantia* are borne on special branches which arise in an upright manner. Archegonia and antheridia are produced on separate plants. Male and female plants are indistinguishable except when bearing the reproductive branches (gametophores). The archegonial gametophore is umbrella-like, and the antheridial gametophore is disc-like.

One of the thallose liverworts of scientific interest is the genus *Anthoceros.* These forms are referred to as horned liverworts because of the shape of the sporophytes which develop on the upper surface of the gametophytic thallus. The thallus is simple and shows no internal differentiation of tissues. The cells of the thallus usually contain one large chloroplast instead of several small ones as in other Bryophytes. Both antheridia and arche-

gonia occur on the same plant; they cannot be seen without special preparation because they are hidden within the thallus. The sporophyte shows several interesting features. It consists of a foot and a capsule. The lower portion of the capsule continues to grow and thus the structure increases in length with the older part above and the new part below. The central part of the elongated structure is sterile and is called the columella. The spores are borne in a cylindrical region around the columella. Up and down in the cylindrical region are alternating bands of spores and sterile cells. The suggestion has been made that such an alternating arrangement of sterile tissue and spores around a central columella might be the basis of the origin and evolution of the leaves, sporangia, and stems of the sporophytes of the higher plants. The outer tissues of the sporophyte possess chlorophyll, and stomata are present in the epidermis. (See Figs. Introd.–3, 3–11, 8–6, 8–17, 8–18, 10–5.)

The Leafy Liverworts

Decaying logs along the banks of small streams frequently are completely covered with a lacework of leafy liverworts. In the tropics the surfaces of living leaves of trees may bear these small plants in a purely epiphytic manner. The gametophytes are often delicate and elaborate. The leafy forms belong to the order *Jungermanniales*. They spread by progressive growth and by gemmae. In some forms the sporophytes develop at the tips of the axes. In others the archegonia develop not at the tip but on the upper surface of the thallus, some distance back of the growing apex. The sporophyte has foot, stalk, and capsule. The stalk is usually long and delicate.

THE MOSSES

The mosses are world-wide in distribution. They grow in almost every kind of habitat. The most familiar ones form carpets on the ground in moist woodlands. Some of them grow in ponds and swamps. There is great diversity in size and form. They are mostly small plants not exceeding a few inches in height. They are typically green because of the presence of chlorophyll. In exposed locations red or brown pigments may obscure the chlorophyll. The tendency to grow together in densely compacted groups is a characteristic of the group. In some species cushions of unusual uniformity occur. This habit enables the slender individual plants to stand erect and is of significance also in the process of fertilization. Those that grow on the ground have no underground parts except the hair-like rhizoids. This fact explains why it is possible to strip large masses so easily

from the ground. Moss plants are differentiated into stem and leaves with a typical radial symmetry. In the land forms there is a central strand of elongated cells in the stem, but there are no vascular bundles of the type that occur in the sporophytes of ferns and seed plants. The leaves are often simple structures with blades consisting of a single layer of cells. Generally there is a midrib of elongated cells. In this discussion we have used the term stem for the axis and the term leaf for the lateral structures. This is done for convenience. These structures are stem-like and leaf-like, but it should be understood that they are not homologous with the stems and leaves of the higher plants. The sporophytes are borne terminally on the upright leafy axes. This fact, together with the development of a relatively long stalk which elevates the capsule, makes the sporophyte generation a conspicuous part of the moss plant. The group includes about 650 genera with some 14,000 species. Three subgroups are recognized. The account which follows includes two of these subgroups.

The True Mosses (Eubrya)

In the true mosses the leafy axis is gametophytic but it is not the whole gametophytic generation. When moss spores germinate they first produce a simple filamentous growth known as the *protonema.* This multicellular structure is distinctly algal-like. Buds or bulbils appear on the protonema and these in turn develop into the upright leafy shoots. The protonema may perish after the leafy shoot has established its independence. The gametophytic generation has its origin in the spores and includes both the prostrate protonema and the erect leafy shoots which are the gamete-bearing structures (*gametophores*). The gametophores may be simple; in some species they are branched. The gametophores grow apically with the young leaves always toward the tips.

The sporophyte of mosses has more complexity of structure than does that generation in the liverworts. The same parts—foot, stalk, and capsule —are present. The capsule shows a greater tendency toward sterilization of fertile tissue, and the sterile portion is differentiated into a variety of types of cells. The zygote begins its development in the venter of the archegonium. In its early growth the young sporophyte is a spindle-shaped embryo. The pointed lower end reaches down into the tip of the gametophore and becomes a well-developed absorbing organ or foot. For a while the archegonial tissues grow and keep pace with the growth of the elongated embryo. Finally the enlarged archegonial tissue is ruptured and lifted upward as a cap on the apex of the young sporophyte. This cap or hood is called a *calyptra.* This development constitutes an essential difference be-

tween the mosses and the liverworts. In many kinds of mosses the calyptra is a conspicuous structure. In *Polytrichum* the calyptra develops a felt of hairs which is responsible for both the common and scientific names of the genus. (See Figs. Introd.–3, 8–15.)

The stalk usually elongates considerably. Within the calyptra the complex capsule develops. Below the capsule is an enlarged region known as the apophysis. Above the capsule is a lid, or operculum, which eventually becomes detached and allows the spores to disseminate. The spores must sift through a circle of teeth-like structures, the peristome, which lie below the operculum and above the mouth of the spore cavity which they more or less completely cover. The teeth of the peristome are so variously shaped and marked that they furnish one of the most diagnostic features of the genera. The cells of the teeth are hygroscopic, closing the mouth of the capsule in wet weather and opening it and effecting a gradual scattering of the spores under dry conditions. The spore-bearing region surrounds a central columella. The entire outer surface of the capsule is covered by a well-developed epidermis. In the region of the apophysis there are stomata and intercellular air spaces. Here the chief photosynthetic activity of the sporophyte is carried on. The capsule and calyptra are variously shaped and assume different positions. In some mosses the capsule is erect and the calyptra covers it completely (*Polytrichum*); in others the capsule is inclined or pendulous and the calyptra covers only the side (*Funaria*).

The Peat Mosses (Sphagnobrya)

The peat mosses are included in a single genus, *Sphagnum*. There are more than 300 species. All the species grow only where water is abundant. They are common in bogs or swamps where the water has an acid reaction. Once established on the shore of ponds or morainal lakes, *Sphagnum* may spread until the whole area is occupied. The first result of the development of the mat of *Sphagnum* is a quaking bog. It is reported that there are several areas in the eastern United States which, according to maps made a hundred years ago, were lakes and which are now *Sphagnum* bogs without any open water. Certain other plants may grow in such boggy places. Among them may be mentioned pitcher plants, sundew, and some species of heaths, sedges, and orchids. Eventually the mat of organic material becomes drier, the *Sphagnum* disappears, and normal land plants invade the area. In the lower depths of such bogs there is an accumulation of dead moss plants and other organic material incompletely decomposed. This compact mass of material rich in carbon is known as peat.

The peat mosses have a pale green color and a soft texture. The leaves

are arranged in dense spirals around the stems. There are no rhizoids on the leafy plants. Water is taken in by direct absorption. Because of their peculiar cellular structure and arrangement the leaves take up water like a sponge. Some species are dioecious and others are monoecious. The capsule of the sporophyte is globose. There is a well-developed foot but a poorly developed stalk. The lack of stalk is made up for by the elongation of the upper part of the gametophore, which pushes the capsule well above the leaves into a position advantageous for spore distribution. The capsule breaks in an explosive manner which hurls the operculum and spores upward for several inches. Upon germination the spores produce a thallose protonema. One protonema may also give rise to another. In this way considerable vegetative multiplication may be brought about. (See Fig. 3–12.)

Economic Importance of the Bryophytes

The uses of liverworts and mosses in medicine and the arts are relatively few and unimportant. Certain species of *Sphagnum,* because of their superior absorptive capacity, are sometimes used for surgical dressings. Sphagnum moss finds considerable commercial use in the florist and nursery trade where it is used for keeping living plants fresh during shipment. The moss is gathered and dried and put in the market without further preparation. Since it takes up water readily it makes excellent packing material for plants or plant parts that must be kept moist. Peat moss is also used in orchid culture. A form of granulated peat moss is marketed in bags and is used by gardeners as a moisture-retaining humus. It may be incorporated with the soil or spread over the surface of the soil as a mulch. It prevents hard top crust and discourages weed growth. Peat, which is largely composed of dead *Sphagnum,* is cut from deposits, pressed into blocks, and used for fuel in some countries. Peat charcoal has been used for smelting iron and for working and tempering certain kinds of steel. In the economy of nature felts of mosses play a part through their water-retaining capacities, their contribution to soil reactions, and their effects on other vegetation.

THE FERNS

The abundance of ferns as wild plants of the woods and as cultivated plants of homes and gardens accounts for the fact that they are well known. Their beautiful leaves, commonly large and gracefully divided into small leaflets, are familiar sights. The use of the term "fronds" for fern leaves is widespread. Ferns are world-wide in distribution. Common in temperate regions, they attain their most luxurious development in the tropics.

While most frequent in moist habitats such as deep woods, marshes, and shady ravines, they are to be found in a variety of other locations. Some grow in the muddy bottoms of shallow pools, some are floating aquatics, some are epiphytes on branches and trunks of trees, some grow in crevices of rocky cliffs, and some on dry hillsides. They vary in size from tiny creeping forms that resemble the leafy liverworts in appearance to the tree ferns of the tropics which attain a height of 30 to 40 feet. Fossil records show that ferns are an ancient group extending far back into the geological ages. There are approximately 215 genera of living ferns and over 9000 species.

Ferns have a distinct alternation of generations. Both generations are independent. In the liverworts and mosses the growth which we call the "liverwort plant" or the "moss plant" is the gametophytic generation. Here the reverse is the situation; the growth which we call the "fern plant" is the sporophyte. The gametophyte of the ferns is a delicate structure so inconspicuous as ordinarily to be overlooked and unknown except to those who set about to make a study of the life history. The usual fern gametophyte, known also as a prothallium, is a green heart-shaped thallus that commonly bears both antheridia and archegonia (monoecious) on the under side. It has one layer of cells around the margins but is thicker in the center. There are numerous rhizoids on the under side in the older region near the tip.

Taken as a whole, fern sporophytes show great variation in form but they have in common roots, stems, leaves, and well-developed vascular tissue. The vascular system extends throughout the plant body, providing conducting and supporting tissues. Spores are borne in spore cases (*sporangia*). In the common ferns the sporangia are borne in clusters (*sori*) on the back or margins of the fronds. The sori are frequently covered by a membrane (*indusium*). Sporangial characters are of major importance in the classification of ferns; the position and arrangement of the sporangia and the structure of the sporangium itself are characters used in the separation of genera, families, and orders.

Common ferns are herbaceous leafy plants having stems that are creeping underground rhizomes with dorsiventral symmetry, rather than upright organs with a radial symmetry. The leaves or fronds have in general two distinctive features: (1) the veins branch in a forking manner (*dichotomous venation*), and (2) the young leaves unroll from the base toward the apex (*circinate venation*). The internal anatomy of fern leaves is much like that of seed plants. Simple leaves occur, but the compound frond is considered typical. Roots are mostly slender and fibrous. They may

be few but are frequently abundant. Vegetative reproduction takes place in some species by special buds or bulblets which form on the leaves and develop new plants after falling to the ground.

Our account would be incomplete without further consideration of the sporangia and sori. The leaves which bear sporangia may be called *sporophylls,* a term which means spore-bearing leaves. In many cases the leaves are green vegetative organs and also serve as sporophylls. In some cases the whole or part of a leaf is highly modified and given up to spore production. Such fertile leaves, or parts, are quite unlike the green leaves. The number of spores produced by a single plant may be very great. The number may be estimated this way: If there were 32 spores to a sporangium, 100 sporangia to a sorus, 1000 sori to a leaf, and 10 leaves to a plant, this would account for upwards of 30,000,000 spores. The number of spores per sporangium in some ferns is large, in others small.

In the majority of our common ferns the sporangium consists of a globoid capsule supported by a delicate stalk. The capsule has a jacket layer one cell in thickness. The jacket cells are thin-walled, except for certain cells forming the *annulus* by means of which the capsule is broken open and the spores discharged. The form of the annulus varies in different ferns. In a common type the annulus is a vertical row or ring of cells extending from the stalk over the capsule and part way down the opposite side. The cells of the annulus have walls which are thick on the inner and side surfaces but thin on the outside. When these cells dry out, the annulus is bent backward, the capsule jacket is ruptured, and the spores are exposed; then the annulus suddenly springs back to its original position, thus expelling the spores.

The character of the sporangium, especially the annulus, the form and arrangement of the sori, and the shape of the indusium if present, all constitute important criteria for identifying the different genera. The sporangia of the adder's-tongue fern (*Botrychium*) are large leathery structures borne in special spikes. The sori of the hart's-tongue fern (*Scolopendrium*) are linear with a lip-shaped indusium. In the shield fern (*Dryopteris*) the sori are round with a kidney-shaped indusium. The common polypody (*Polypodium*) also has round sori but they have no indusia. In the bracken (*Pteris*) the sori lie in an unbroken line along the leaf margin, which folds over, forming a continuous indusium. There is a group of water ferns (*Marsilia, Salvinia, Azolla*) which along with other special features develop two types of spores (*heterspory*), a condition not existing in other living ferns. The sporangia do not develop on the under side of the leaves, as in common ferns, but in special fruiting bodies.

The thin sporangial wall has no annulus. Where heterospory exists two gametophytes are produced, male and female. We find this condition in some club mosses and all seed plants. (Figs. Introd.-3, 6-23, 8-19, 8-20, 8-22, 8-23.)

THE HORSETAILS

The horsetails are rush-like plants with jointed, mostly hollow stems, and inconspicuous whorled leaves forming sheaths at the joints. They are mostly low-growing perennials that rarely exceed a foot in height. Many of them are evergreen. There is but a single genus (*Equisetum*) with about 25 species. They inhabit the cool temperate regions of most parts of the world except Australia and New Zealand. One species is tropical and reaches a height of 35 to 40 feet. They grow primarily in wet places, but there are some exceptions. The common or field horsetail may grow in dry sterile places such as open sandy banks or cinder embankments along railroads.

The jointed stems with the sheathed nodes give these plants a unique aspect. The stems may be simple but are often much branched. Since the leaves are whorled the branches are whorled, often with a large number in a whorl. Photosynthesis is carried on by the stems and branches, the leaves being mostly scale-like and without chlorophyll. The stems are noticeably ridged. There is an abundant deposit of silica in the walls of the epidermal cells. The silica is sometimes uniformly deposited or it may be in the form of granules. On account of the silica, certain species were used in early times for scouring purposes. In this way they acquired the common name scouring rushes. The stomata are located in the grooves. The aerial vegetative stems arise from a horizontal, branched, subterranean rootstock or rhizome. This rhizome is conspicuously jointed. The nodes bear both scale-like leaves and roots which usually function for a single growing season.

The sporangia are borne only on special organs (*sporangiophores*) which are arranged in a compact cone-like aggregation (*strobilus*) at the end of a stem. In most species the cone-bearing stems are of a special nature, without chlorophyll, unbranched, and often attaining full development in the early spring before the vegetative branches appear. In other species the cones develop at the tips of ordinary green shoots. A sporophyll has a stalk ending in a shield-shaped expansion which is six-sided because of contact with the adjacent sporophylls. The sporangia are elongated sacs on the under side of the shields. They split open at maturity by a longitudinal cleft. The mature spores contain numerous relatively large chloroplasts.

The structure of the walls of the spores is especially interesting. The outermost layer is formed into four spiral bands which at first are tightly coiled about the spore. Later these bands separate and appear as four strips attached at a common point and with spoon-like tips. They are hygroscopic and coil or uncoil according as the air is moist or dry. These strips are called elaters, but it should be noted that they are quite different in nature from the elaters of the liverworts, in which the elaters are sterilized sporogenous cells.

THE CLUB MOSSES

The club mosses are low, evergreen, herbaceous plants. They have many small moss-like leaves and many of them have conspicuous club-shaped strobili or cones; these two characters account for the common name of the group. The resemblance to mosses is purely superficial. They are common trailing plants of the forests. Some species have an upright bushy form suggestive of miniature pine trees and are commonly called ground pine. Some of the tropical species are epiphytes. The family consists mainly of one large genus (*Lycopodium*), with about 300 species of world-wide distribution. They are chiefly tropical or subtropical, but a few species are of common occurrence in temperate regions. Their generally attractive moss-like aspect coupled with the fact that they are evergreen makes them in demand for Christmas decorations.

The stems have well-developed vascular tissue but are mostly slender and weak. The main stem frequently creeps on or below the surface of the ground. If the stem branches, it does so in a forking manner (dichotomous). The leaves are small, simple, and numerous. They may be arranged in spirals, whorls, or opposite pairs. They are usually so close together as to cover the stem rather fully. The roots are not extensive and are chiefly adventitious, arising singly or in groups along the under side of the stem. The branching of the roots of some species is also regularly dichotomous.

The sporangia are relatively large, usually kidney-shaped, and yellowish when mature. They are borne one to a leaf, on the upper side near the base, in the axil, or on the stem just above the axil. In the simplest species all the leaves bear sporangia, or, to state it in different words, every leaf is both a vegetative organ and a sporophyll. In some species there are alternating regions of foliage leaves and sporophylls along the stem. In such cases the sterile leaves and the fertile leaves are much alike except that the latter are usually smaller. Fertile leaves of this sort continue to function as photosynthetic organs after the spores are shed. In most species the fertile leaves

are unlike the sterile leaves in shape, size, and color; they serve only as sporophylls. In these forms the sporophylls are grouped in terminal cones, or strobili. The cones in some species are directly at the top of the leafy stems, and in other species they are elevated on long erect stalks which have only separated scale-like leaves. The sporangia are leathery and open by longitudinal clefts. The spores are all of one kind and are produced in large quantities. The spore walls are thin, smooth, pitted, or with net-like thickenings. The spores bear evidence of their production in groups of four (quartets) by their tetrahedral shape and by the triradiate ridge along the edges where they were pressed together. (See Fig. 8–24.)

THE LITTLE CLUB MOSSES

The so-called little club mosses have the same general habit as the species of *Lycopodium*. They are also similar in aspect but are smaller and more delicate. There is but one genus, *Selaginella,* with about 600 species. They are world-wide in distribution, most of them occurring in humid tropical forests. Of the comparatively few that grow in temperate regions, some are found in moist, shady habitats, while others are xerophytic, growing on dry cliffs or dry sandy soil. The resurrection plant of the southwestern United States and Mexico is a xerophytic *Selaginella.* When dry the rosette-like branches curl up into a ball and the plant lies dormant for months but will revive and expand when moist conditions return. Such plants will unfold and spread out even after they are dead. Some species are grown as decorative plants in greenhouses and are prized for the delicacy of their foliage. In most species the leaves are arranged along the dorsiventral stems in four rows, with two rows of large leaves and two rows of smaller leaves on the upper surface. The roots arise from the under side of the branches and are frequently distributed over much of the plant. Often the roots develop from the tips of naked branches that extend from the stems to the ground.

The sporangia are borne in the axils of sporophylls which are grouped in cones, or strobili. In some species the cones are so loosely arranged that they are not readily distinguished from the vegetative shoots. *Selaginella* differs significantly from *Lycopodium* in that two kinds of spores are produced, small spores or microspores, and large ones or megaspores. The production of two kinds of spores is known as *heterospory,* in contrast to *homospory* where the spores are all alike. The sporangia are called *microsporangia* and *megasporangia* respectively. The microsporangia are commonly small, reddish or brownish, and oval; the megasporangia are gen-

erally larger, whitish, and four-lobed. The microsporangia occupy the upper part or one side of a cone and bear many spores (several hundred); the megasporangia are generally formed at the base of the cone or on the other side and have a single megaspore in each of the four lobes. Both kinds of spores have triradiate ridges as in *Lycopodium,* and the walls are often ornamented with spines or net-like ridges. (See Fig. 8–25.)

Economic Importance of the Pteridophytes

The rootstocks of some ferns contain a sufficient store of starch to serve as a possible source of food under primitive conditions. A large species of bracken known as the tara fern is said to have been one of the principal articles of food of the natives in New Zealand before the settlement by the British colonists. The rootstock was steeped, dried, and then roasted. Survivals of this use, or reversion to it, are probably not common today. Some of the tree ferns yield a kind of sago. The young uncoiling leaves (fiddleheads) of several ferns are eaten as greens or salads. In northern Maine the ostrich fern is considered very delicious. It not only is used locally but is shipped to Boston and New York markets. A species in tropical Asia is used as a potherb. Some ferns contain active principles which have been used in medicine. From the male fern a preparation is made which has long been used to expel tapeworms. A cough syrup is prepared from one of the European species of maidenhair fern. Other ferns possess astringent principles which have a limited use in pharmacy.

Ferns are not widely used in the arts, although at one time the bracken was employed in dressing kid and chamois leather. Bracken is used for thatching and for bedding cattle, and may be mixed with hay for cattle. It is a favorite shelter for deer and other game. In parts of Brazil a large species of bracken fern is a serious weed. The chief economic use of ferns is as ornamental plants. As house plants, in greenhouses, and in the florist trade ferns are valued for their beauty. The best-known kind is the Boston fern (*Nephrolepis*). The maiden hair (*Adiantum*), the shield fern (*Dryopteris*), and polypody (*Polypodium*) are also common. In tropical gardens and parks, tree ferns are cultivated. The little club mosses (*Selaginella*) are also used for indoor culture. Club mosses and ground pine (*Lycopodium*) are used for Christmas wreaths and festoons.

The club mosses produce spores in abundance which are sometimes used for pharmaceutical preparations to prevent chafing of the skin and to dust on pills to keep them from adhering. These spores under the name "vegetable sulphur" or "lycopodium powder" entered into the manufacture of fireworks in former times. They burn with a bright flash and produce little

smoke. The stems of some species of horsetails are encrusted with silica and have been used in polishing woods and metals. Poisonous substances are contained in some horsetails, and hay containing them is injurious to cattle. We have previously called attention to the fact that the element gold has been found in plant tissues. According to a recent report made to the American Institute of Mining and Metallurgical Engineers, a considerable gold content has been found under certain conditions in the common horsetail. The suggestion was made that a "geobotanical" method might be developed to provide clues as to the presence of gold-bearing ore bodies below the surface through the amount of gold extracted from the soil by these plants. Our account of the economic importance of ferns, horsetails, and club mosses would be incomplete indeed if we did not refer to the fact that all these plants were large, often tree-like, plants in past geological ages and that they contributed much to the formation of coal.

THE GYMNOSPERMS

In the gymnosperm group seven orders are generally recognized. Three of these orders (*Cycadofilicales, Bennettitales, Cordaitales*) are known only as fossils. The Cycadofilicales are fern-like plants of the coal-measure deposits. The form and veining of the fossil leaves resemble ferns so much that they were formerly thought to be ferns. Four orders (*Cycadales, Ginkgoales, Gnetales,* and *Coniferales*) include both living and fossil forms.

The Cycad Order (Cycadales)

These plants are commonly called cycads. The fossil forms prove that they were once abundant and world-wide in distribution, but the few living forms survive only in tropical and subtropical regions. They are palm-like plants with tuberous or columnar stems which are covered by leaf bases and terminated by a crown of large compound leaves. Species with cylindrical stems may reach a height of 40 to 50 feet or even more. The young leaflets of the genus *Cycas* are rolled up in a circinate manner similar to the young leaves of ferns. Cycads are grown as ornamentals in all parts of the world where the climate is warm enough for their culture. They are long-lived plants. *Cycas* is the conspicuous genus of the eastern hemisphere, *Zamia* the conspicuous genus of the western hemisphere. The living cycads are dioecious. The strobili usually become soft at maturity and soon decay. The staminate strobili are cone-like and relatively large. In *Zamia,* the ovulate strobili are in the form of a compact cone. In

Cycas, the ovulate strobili are loose and rosette-like. The pollen is wind-distributed. Fertilization is made possible by pollen tubes that penetrate the nucellar tissue and provide a watery fluid in which the large ciliated sperms swim. The cycads and ginkgo are the only seed plants having motile sperms.

The Ginkgo Order (Ginkgoales)

The only living representative of this order is the maidenhair tree, *Ginkgo biloba.* The resemblance of the leaves to the leaflets of the maidenhair fern (*Adiantum*) is responsible for the common name. The tree is extensively cultivated in China and Japan, particularly in temple grounds. It is often seen in cultivation in Europe and the United States. It is a handsome tree, having the general habit of the conifers. The species is dioecious. The staminate strobili are borne in clusters. The ovulate strobili have long stalks bearing as a rule two ovules, only one of which usually ripens into a seed.

The Gnetum Order (Gnetales)

In this order there is but a single family with three genera: *Ephedra,* shrubby plants of the warm regions of the Mediterranean basin and nearby Asia, and of similar regions in the Americas; *Welwitschia,* woody plants with a peculiar conical body, from the deserts of western South Africa; and *Gnetum,* trees or woody vines in the tropics of both hemispheres. The species of *Ephedra* have small scale-like leaves and jointed stems. These characters give them a superficial resemblance to the horsetails and are responsible for the common name, joint firs, sometimes applied to them. An alkaloid, ephedrin, which is used in medicine for the treatment of the nasal passages, is isolated from one of the species of *Ephedra.*

The Conifer Order (Coniferales)

This is the largest group of living gymnosperms. There are approximately 350 species belonging to 40 genera. The group was well represented in past ages, as is proved by the fossil record. In contrast to the cycads which inhabit the tropics, the conifers inhabit chiefly the temperate regions. The species that grow in the tropics are mostly confined to mountainous elevations. Some species are found in the arctic regions. The conifers vary in form and size from straggling shrubs to large trees. The best-known members of the group are evergreen forest trees such as the pines (*Pinus*), spruces (*Picea*), firs (*Abies*), hemlocks (*Tsuga,* Fig. 6–25), and redwoods (*Sequoia*). The redwoods of California (Fig. 2–1) are known as the "big

trees." Some of them attain a height of 300 feet, a diameter of 40 feet, and an age of 3000 years. The American yew (*Taxus canadensis*) is a low straggling bush. One of the junipers (*Juniperus horizontalis*) is a prostrate or creeping shrub. The bald cypress (*Taxodium distichum*) is a deciduous tree of southern swamps. It is known for the peculiar "knees" which develop on its roots and project above the water, often at some distance from the trunk (see Fig. 10–15).

The conifers are profusely branched. In many cases the trees are symmetrically cone-shaped, with a main trunk that is larger and more rapidly growing than the lateral branches. This is particularly true of young trees; older trees are likely to be more irregular in outline. For the most part the leaves are small, simple, firm, flat, or needle-like. They may be borne singly as in firs and spruces, or several in a bundle as in pines. The leaves usually function for several seasons. This fact accounts for the name evergreen which is so commonly applied to the members of this group. The larch (*Larix*) loses all its leaves annually.

Coniferous woods are used extensively in almost every wood-utilizing industry. The wood from the members of this group is rather uniform in texture. Large ducts or vessels are not present. The majority of the species have resin present in all parts of the plant including the wood. Under the microscope the wood cells (*tracheids*) of the conifers show bordered pits, especially in the radial walls. Reference has been made previously to interesting studies of the annual rings of some of the very old trees, principally redwoods and pines.

The coniferous tree is a sporophyte. The cones are the spore-bearing structures. There are two kinds of cones: *staminate,* bearing the microspores, and *ovulate,* bearing the megaspores. In some species the form of the ovulate structure can hardly be said to be cone-like, but in most cases both staminate and ovulate structures are distinct cones. The following account presents the life cycle of a pine as an example of the coniferous group.

The two kinds of cones, staminate and ovulate, are borne on the same sporophytic plant. The staminate cones are small. They are borne in clusters at the base of the new growth that develops in the spring. These cones drop off soon after the pollen is shed. The microspores, later called pollen grains, develop in two pollen sacs on the under side of each scale of the cones. The walls of a pollen grain develop so as to form two sacs or wings. The pines shed pollen in such quantities as to cover the soil and nearby objects with films of yellow sulphur-like powder; hence the expression "showers of sulphur" which is heard in some localities. At the

time the pollen grains are shed the microspore has already begun internally the development of the male gametophyte.

The ovulate cones develop in groups of two or three, or singly, near the upper end of the new growth. At first they are small but they persist and grow for two years while gametophytic and embryonic development is going on. In some species of pine they become large and conspicuous at maturity, and may hang on the trees indefinitely. Two ovules are borne on the upper side of each scale near its place of attachment to the axis of the cone. An ovule is a small oval nucellus surrounded by an integument in which there is an opening or micropyle. The female gametophyte develops within the nucellus. It consists of an extensive cellular development (prothallus) with a small group of archegonia at the end toward the micropyle. The archegonia are surrounded by jacket cells, have a short neck, and contain the egg nucleus.

Pollination takes place in the spring. At the time the pollen grains enter the micropyle the male gametophyte is partially developed, as has been explained. Fertilization does not occur until the next spring. By that time two non-swimming sperms have formed and the pollen tube has grown through the nucellus to the neck of the archegonium. The union of one sperm with the egg forms the zygote. The embryo develops slowly. It is usually another year before the seed is mature, and still longer before it is disseminated. The embryo has several cotyledons. During the process of ripening of the ovule a thin layer separates from the upper surface of the scale in such a way as to form a wing of the mature seed. The seed consists of an interesting combination of generations. The embryo is the new sporophyte, a part of the female gametophyte still persists, and some of the nucellus remains; this, the integument, and the wing are tissues of the old sporophyte.

This account of the life cycle of the pine should bring to mind some of the fundamental features of reproduction already presented but which need reviewing. There are two distinct generations: a sporophyte, which develops spores, and a gametophyte, which develops gametes. The sporophyte is heterosporous, i.e., develops two kinds of spores, microspores and megaspores. The microspores develop into gametophytes which bear only sperms. The megaspores, only one of a quartet maturing in each megasporangium, develop there into female gametophytes which bear only eggs. The retention of the megaspore and female gametophyte within the megasporangium is a most important step toward seed production. Another step is the surrounding of the megasporangium with an integument. Fertilization takes place within the megasporangium. The zygote is formed there

and grows into an embryo there. The embryo surrounded by the integument and sometimes provided with stored food (endosperm) is the seed; the endosperm is gametophytic tissue in the pine. The seeds germinate after a resting period. The sporophyte generation in the gymnosperms lives for long periods and during its lifetime may produce many generations of spores. The gametophyte generations are of relatively short duration and produce only one set of gametes.

THE ANGIOSPERMS

The angiosperms are commonly called "the flowering plants." They are also called "the higher seed plants." The group is large in numbers of species; it is estimated that about 200,000 are known. Here belong plants of great importance to man, used by him for food, shelter, clothing, medicine, and in the arts. The common plants of the fields, orchards, and gardens are angiosperms. Most of the plants of the plains and deserts belong in this group. Angiosperms are also important in the forests both as part of the tree population and also in the undergrowth.

There are two primary classes of the angiosperms, the Dicotyledons and the Monocotyledons. These two groups are separated by combinations of characters of the embryo, the leaves, the stems, and the flowers. The dicots (this abbreviated form is frequently used) have embryos with two cotyledons, leaves with netted venation, stems usually differentiated into bark, wood, and pith, and flowers with members usually in sets of five or four. The monocots have embryos with a single cotyledon, leaves with parallel venation, stems with vascular bundles usually lacking cambium, and flowers with members in sets of three. These characters are not of equal value nor are they always definitive in distinguishing the two groups. The cotyledon character is the only one that holds without serious exception.

Gymnosperms and angiosperms differ in the way in which the ovules are borne. It follows that the manner of fertilization is also different in the two groups. In the gymnosperms, where the ovule is exposed on the surface of a scale, the pollen grains can come in contact with the surface of the ovule. Some of them pass through the micropyle. From this position only short pollen tubes growing through the overlying nucellus are necessary to carry the sperms to the eggs. In the angiosperms the pollen grains cannot reach the ovules which are enclosed in the ovary. In connection with the ovary there is a stigma for the reception of the pollen. In some flowers there is a style of considerable length between the stigma and

the ovary. The pollen tube spans the distance from the stigmatic surface to the micropyle of the internal ovule.

Flowers are characteristic structures of angiosperms. In an earlier account (Chapter 9) it was pointed out that a common type of angiosperm flower has its parts in whorls, a colored perianth, and both stamens and pistils. There are many exceptions. In some flowers the stamens and carpels are spirally arranged. In many flowers the sepals are green and only the petals are colored, in others both are colored, in others neither is colored, in others the perianth may be lacking. Some flowers do not possess both stamens and pistils. The members of the same set of floral structures may be separate or united. There are often recognized two subclasses of the Dicotyledons, the Archichlamydeae and the Sympetalae; the notable character which distinguishes them is the condition of the corolla. In the former the petals (if present) are separate or free, while in the latter the petals coalesce so as to form tubes or bells.

There are flowers in which the sepals, petals, and stamens arise beneath the carpels. This type of flower is hypogynous. There are other flowers in which the outer floral parts arise from an urn-like structure surrounding the carpels. Such flowers are perigynous. In other flowers the sepals, petals, and stamens seem to arise from the top of the ovary, and the flower is said to be epigynous. Another modification involves the symmetry of the flower. The flowers may have either radial or bilateral symmetry. There are also great variations in the arrangement of flowers in clusters or inflorescences. The differences in flower structure are important in determining relationships and in working out classifications. Attention has been called to the fact that certain floral characters are regarded as representing relatively low or primitive development and others as representing relatively high or derived development.

THE DICOTYLEDONS

The dicotyledons are a varied and extensive group. Their variations have adapted them to a great range of conditions. They are the dominant and conspicuous members of the plant world. So successful are their modes of life that among the angiosperms they outnumber the monocot species four to one.

The stems of dicotyledons are characterized by vascular bundles arranged in the outline of a truncated cone surrounding the pith and surrounded by the cortex. Because the taper of the truncated cone is usually slight it may seem to be almost cylindrical. This accounts for the frequent statement

that the vascular bundles are arranged in the form of a cylinder. In a cross-section they appear to be in a circle around a central pith and surrounded by a cortex. At the top of the truncated cone is the meristem of the stem tip. Another way to state this is to say that the three regions—cortex, bundles, and pith—diverge downward from the meristematic tip. It will be recalled that the cambium is between the phloem and xylem of the bundles. It therefore is in the outline of a truncated cone. In annual stems the cambium builds up secondary xylem and phloem, but all tissues die at the end of a single growing season. In perennial woody stems the cambium becomes active with each succeeding growing period and builds up both a new layer of xylem over the preceding layer and a new layer of phloem inside the preceding one. In this way the stems increase annually in size. In cross-sections these annual increments appear as concentric rings, hence the expression annual rings. They are in reality annual layers. Lateral branches of a stem have the same structure and develop in the same manner.

The leaves of dicotyledons are highly differentiated. Typically, they have blade, petiole, and stipules. The blade varies in form and complexity. As a rule the blades have a network of veins that branch repeatedly, becoming smaller and smaller, the veinlets ending freely in the margins which are often toothed or lobed. Such an arrangement is called an open venation. The cotyledons, the leaves of the embryo, are two in number and opposite. The leaves of the plant may be opposite, alternate, or whorled. The flower parts are ordinarily in sets of five or four; an increase or decrease in the number of stamens and carpels is common. Five whorls—one of sepals, one of petals, two of stamens, and one of carpels—is a common arrangement, but there are many deviations in the number of whorls, and spirals may prevail instead of whorls, especially in the stamens and carpels.

The Buttercup Order (Ranales)

This is a large, interesting, and important order. It is regarded by some botanists as the great genetic alliance. This is a way of saying that the higher groups are thought to have been derived from this order by evolutionary processes. The group includes several familiar families, some of them herbaceous and others woody. Chiefly herbaceous is the buttercup or crowfoot family (*Ranunculaceae*), with the buttercups, windflowers, anemones, hepaticas, larkspurs, and columbines. The magnolia family (*Magnoliaceae*), including the magnolias and the tulip tree, is woody, as is also the laurel family (*Lauraceae*), which includes the spicebush, the bay tree, the camphor tree, the cinnamon tree, and the edible avocado or alligator

pear. The barberry family (*Berberidaceae*) includes the herbaceous May apple and the shrubby barberry. The water lilies (*Nymphaceae*) are herbaceous. The representative flower of the order has a combination of characters that stand for relatively low or primitive development—radial symmetry, hypogyny, separate parts, numerous stamens and carpels spirally arranged. Buttercup flowers have these characteristic features. There are variations from this simple structure. The sepals and petals may be few or many in number. In some species there may be bilateral symmetry. This is the case in the larkspur and monkshood, which are regarded as the highest types of the order. (See Figs. 7–19, 9–5, 9–11, 9–21.)

The Pink Order (Caryophyllales)

The true pinks are herbs with swollen nodes, opposite leaves, and radially symmetrical, hypogynous flowers. The parts of the flowers are in fours or fives. The stamens are distinct and as many, or twice as many, as the perianth parts. The chickweeds belong here, also the pinks and carnations of gardens and greenhouses. Many of the cultivated varieties have double flowers that are attractive in both form and color. The pinks represent a group that has diverged from the buttercups in a different direction than that of the roses.

The Buckwheat Order (Polygonales)

This order includes a series of forms allied to the preceding order. The flowers are small and radially symmetrical, and the perianth parts are commonly not distinguishable as sepals and petals. The stipules of the leaves form a sheath above the swollen nodes of the stems. The cultivated representatives are buckwheat and rhubarb. The wild species include a number of species of dock, knotweed, and bindweed. (See Fig. 5–12.)

The Heath Order (Ericales)

The heaths, or heathers, are chiefly shrubs, or small trees, with evergreen leaves. The flowers most frequently have five whorls of five members each. The anthers usually open by terminal pores. The corolla is sympetalous in the higher forms. The order contains many plants notable for the beauty of their flowers, and also some that are valued both in cultivation and in the wild state for their edible fruits. Here are included azaleas, rhododendrons, laurel, trailing arbutus, wintergreen, blueberries, huckleberries, and cranberries. The Indian pipe is a low herb with a pipe-like shape when in bloom. The leaves are reduced to scales and are without chlorophyll; the plant is parasitic or saprophytic. (See Figs. 1–14, 9–23.)

The Gentian Order (Gentianales)

The plants of this order are characterized by their opposite leaves and by the twisting of the petals in the flower bud. There is a single whorl of stamens; the ovary is superior and consists of two carpels. The gentian family (*Gentianaceae*) includes many species with beautiful flowers. The common name "fringed gentian" is derived from the conspicuous fringed corolla lobes. The olive family (*Oleaceae*) includes shrubs and trees of importance. Here belong the privets, the lilacs, the jasmines, and the ashes. The olive is widely cultivated in the warmer climates of both hemispheres. The milkweed family (*Asclepiadaceae*) includes plants with milky juice and opposite or whorled leaves. The stamens are inserted on the corolla; the filaments are united into a tube; the anthers are adherent to the stigma; the pollen grains adhere in waxy masses.

The Phlox Order (Polemoniales)

The phloxes and their relatives constitute a group of families that show relationship to the pinks and some of the other orders placed lower in the series. The typical flowers are radially symmetrical, have parts in fives, are sympetalous, have stamens inserted on the corolla, and have a superior ovary (hypogynous). The phlox family (*Polemoniaceae*) is well known through both the wild species and the cultivated ornamental forms. The convolvulus family (*Convolvulaceae*) includes the morning glory, parasitic dodders, and the sweet potato. The borage family (*Boraginaceae*) includes the forget-me-nots, the common heliotrope, and the borages. The nightshade family (*Solanaceae*) includes many food, drug, ornamental, and poisonous plants. The best-known food plants are the Irish potato, the tomato, and the eggplant. In this family are included also tobacco, belladonna, Jimson weed, nightshade, ground cherry, and the petunias. The figworts and the mints are treated in some classifications as families of the phlox order, but we present them as separate orders. (See Fig. 9–7.)

The Figwort Order (Scrophulariales)

The flowers of this order have much in common with those of the phlox order. They are hypogynous and distinctly bilaterally symmetrical, and the number of stamens is usually less (2 or 4) than the number of corolla lobes. The flowers resemble the mints, but the fruit is different. In the figworts the fruit is a two-celled, many-seeded capsule; in the mints the fruit consists of four, more or less separate, one-seeded nutlets. The figwort family includes many of our common wild plants and also some of our

showy cultivated flowers. Here belong toadflax, mullein, beardtongue, speedwell snapdragon, and foxglove. The latter is an old-fashioned ornamental; it is also cultivated for the drug, digitalis, which is prepared from the leaves. Digitalis is widely used for heart disease. The bignonia family (*Bignoniaceae*) includes catalpa trees of the temperate regions, jacaranda tree of the tropics, trumpet vine, and flame vine. (See Figs. 12–11, 14–6.)

The Mint Order (Lamiales)

The mints are related to the figworts and the phloxes. They are like the figworts in having bilaterally symmetrical flowers; they differ from them in having a fruit of four separate bony nutlets instead of a capsule. The flowers are hypogynous; the corolla is typically two-lipped; there are four stamens, two long and two short, or only two, and they are inserted on the corolla tube. The stems are ordinarily square and the leaves opposite. Many of the species are characterized by aromatic oils. From species of the genus *Mentha* are obtained peppermint, spearmint, and menthol. From other genera are derived rosemary, lavender, and thyme. Among the wild forms are ground ivy, catnip, skullcap, and pennyroyal. Several are cultivated for their foliage or flowers, such as coleus, scarlet sage, and bergamot. The order is higher than the figwort order. It may be regarded as the culmination of a series branching from the buttercups which includes the pinks, heaths, gentians, phloxes, and figworts. (See Fig. 6–9.)

The Mallow Order (Malvales)

The mallows have flowers with radial symmetry, a superior ovary, and separate or little-fused petals. The stamens are numerous; their filaments are joined to form a tube which sheathes the pistils and is more or less united with the petals below. They have many of the characteristics of the buttercups. The mallow family (*Malvaceae*) includes such well-known ornamentals as hibiscus and hollyhock. Here also is the cotton plant. The cotton of commerce is made from the hairy coverings of the seeds. The linden or basswood tree is the typical representative of the linden family (*Tiliaceae*). That very important tree, widely known as cacao, from which we get chocolate and cocoa, is a member of the cacao family (*Sterculiaceae*). The commercial products are prepared from the roasted seeds. The trees are widely cultivated in the tropics. The flowers arise from dormant axillary buds on the main stem and older branches. A tree with the large woody fruits hanging close to the trunk and older branches is an interesting sight.

The Geranium Order (Geraniales)

This is a large and varied order containing many plants of economic importance. Typical flowers are hypogynous, perfect, radially symmetrical or in some species bilaterally symmetrical; there are five or ten stamens, and five carpels, united. True geraniums and the cultivated "geraniums," which belong to the genus *Pelargonium,* are members of the geranium family (*Geraniaceae*). This order includes the flax family (*Linaceae*). The value of flax is well known. The flax plant has been cultivated for ages. The ancient Hebrews and Egyptians made linen cloth from flax fibers 5000 years ago. Here belongs also the citrus family (*Rutaceae*), with the oranges, lemons, limes, and grapefruits. Another important group is the one known as the spurge family (*Euphorbiaceae*), which includes such plants as poinsettia, croton, castor-oil, and the Para rubber tree (*Hevea*). Rubber is prepared from the milky juice (latex) of different kinds of trees and shrubs, but most of the present supply comes from the Para rubber tree. A native of Brazil, it is now extensively cultivated in the oriental tropics. (See Fig. 9–8*A*.)

The Insectivorous Order (Sarraceniales)

This is a small order of both popular and scientific interest because of the capacity of many of its representatives for catching and digesting insects. The sundew (*Drosera*), Venus's-flytrap (*Dionaea*), and the pitcher plants of North America (*Sarracenia*) and of tropical Asia (*Nepenthes*) belong here. Their leaves are variously modified for the insectivorous habits. Many of the species occur in peat bogs. (See Figs. 6–17, 6–18.)

The Poppy Order (Papaverales)

This order includes two well-known families, the poppies (*Papaveraceae*) and the mustards (*Cruciferae*). The poppies are herbs with a milky juice which is sometimes brightly colored. The opium poppy has been cultivated since ancient times. Opium is prepared from the milky juice of the fruit. Morphine is one of the principal constituents of opium. Other members of the poppy family are celandine and bloodroot. The mustard family is large and important. Here belong cabbage, Brussels sprouts, cauliflower, broccoli, radish, turnip, cress, white and black mustard, and such familiar ornamentals as sweet alyssum and candytuft. In the mustards there are four sepals and four petals. The petals have a cross-shaped arrangement which accounts for the family name, *Cruciferae*. There are six stamens in two sets, two short and four long. The family is widely distributed in the temperate and colder regions.

The Violet Order (Violales)

This order is here called the violet order, its name being taken from the violet family (*Violaceae*) which it includes. Because of violets and pansies this family is one of the best known of all the dicotyledonous families. The flowers are hypogynous and have a strong tendency toward bilateral symmetry. In the violet genus the lower petal is spurred at the base. There are five stamens, cohering with each other and surrounding the ovary. In this order is included the tea family (*Theaceae*). The tea of commerce is prepared from the leaves of several species. The tea family is made up of trees and shrubs found in the tropics or warmer temperate regions. The camellias, known for their beautiful showy flowers, belong here. The papayas, or papaws, of the tropics belong in a family (*Caricaceae*) which is included in this order. The common papaya is cultivated for its edible fruits.

The Rose Order (Rosales)

It is estimated that this great group may have as many as 15,000 species in it. Among them are many plants of great agricultural and horticultural value. The simpler form of flowers of the rose order indicates a close relationship between this order and the buttercup order. In the rose family (*Rosaceae*) the flowers are cyclic, radially symmetrical, perigynous, or epigynous. The sepals and petals are in sets of five; the stamens are usually numerous. The distinguishing feature of this family is the arrangement of the sepals, petals, and stamens on the rim of a disc or cup-shaped structure. The fruits are varied. In the strawberry the receptacle is enlarged and fleshy, bearing numerous dry achenes spirally arranged on its surface. In apples, pears, quinces, and hawthorns the fleshy fruits develop from an inferior ovary (epigynous flower). In the rose family, as it is treated by most botanists, belong also plums, cherries, prunes, apricots, peaches, almonds, blackberries, and raspberries, in addition to the great group of roses. Closely related to the rose family is the saxifrage family (*Saxifragaceae*). The stonecrops belong to the family *Crassulaceae*. In the live-forever (*Sedum*) of this family we find radially symmetrical, hypogynous flowers with five sepals, five petals, five to ten stamens (one or two whorls), and five carpels. This flower is sometimes cited as the typical flower of the dicotyledons. The largest group of the rose order is the bean or legume family (*Leguminosae*). Here belong many species of tremendous economic importance as foods, ornamentals, drugs, and dyes—beans, peas, peanuts, lentils, clover, alfalfa, sweet peas, wistaria, locust, redbud, licorice, and logwood (source of haematoxylon dye). The flowers of the legume family are characterized by

their bilateral symmetry. The sweet pea is a good illustration of this type of flower. There are five petals—the upper one is the "standard," the two lateral ones are the "wings," and the two lower ones are more or less united to form a "keel"—the ten stamens are united by their filaments to form a sheath about the single pistil; in many species nine stamens are united and one remains free. Insect pollination prevails. The dry fruit is a legume. The storage of food in the seeds is in the cotyledons. Most all legumes have alternate compound leaves with stipules. (See Figs. 6–12, 9–2, 9–8*B,C*, 9–12*A*, 9–22.)

The Beech Order (Fagales) and Other Tree Orders

This group includes some of our important forest trees. In the beech order are the beeches, birches, oaks, and chestnuts. The flowers are imperfect, but the two kinds are usually borne upon the same plant. The staminate flowers are developed in spike-like, many-flowered clusters known as catkins. The pistillate flowers may be solitary or in few-flowered clusters. In the oaks they are surrounded by a scaly cup-like growth which becomes the cup of the acorn when the fruit is ripe. In the birches the pistillate flowers are in short cone-like spikes.

In the willow and poplar order (*Salicales*) both kinds of flowers are in catkins. The flowers are without perianth, but there is a bract associated with each flower. In the walnut order (*Juglandales*) belong the walnuts, butternuts, and hickories. These trees have large compound leaves which contain aromatic oils. The flowers and inflorescences resemble those of the beech order. In the fruit the outer part of the ovary wall becomes a fleshy rind and the inner part forms a bony nutshell. (See Figs. 6–26, 9–6, 9–12*B*, 13–2.)

The Nettle Order (Urticales)

This order has many features in common with the beech order. The flowers are small, inconspicuous, and densely aggregated in the inflorescence. The plants are woody or herbaceous and are distributed in both temperate and tropical regions. There are several families. The elm belongs in the elm family (*Ulmaceae*). The mulberry family (*Moraceae*) includes a number of trees or shrubs with milky juice. Here belong the mulberry and the osage orange. Interesting tropical species are the breadfruit and the edible fig. The so-called "rubber plant" that is grown as a house plant belongs to the fig genus. The banyan tree of India is another species of the same genus. The nettle family (*Urticaceae*) includes the herbaceous stinging nettle. It is characterized by glandular stinging hairs.

The Maple Order (Sapindales)

The members of this order are principally shrubs and trees, such as the box, sumac, holly, horse chestnut, buckeye, and maple. The cashew family (*Anacardiaceae*) includes the mango, whose edible fruits are so highly esteemed in the tropics. It is cultivated in both hemispheres. The pistachio nut is a near relative. The well-known plants—poison ivy and poison sumac—belong to the same family.

The Carrot Order (Umbellales)

This is a large group of herbaceous and woody plants of world-wide distribution. As a rule the inflorescence is an umbel, which may be simple or compound. The flowers have one whorl of stamens and the ovary is inferior. The ginseng family (*Araliaceae*) includes ginseng, wild sarsaparilla, and the English ivy, which is prized as a wall-climber in some regions. The dogwood is a well-known representative of the dogwood family (*Cornaceae*). In the dogwood each flower cluster, or umbel, is surrounded by four petal-like bracts, making the inflorescence have the appearance of a single flower. The parsley family (*Umbelliferae*) contains mostly herbaceous plants. They are widely distributed in temperate regions. Several valuable economic plants belong to this family, among them celery, carrot, parsnip, anise, and caraway. The poison hemlock is a member of this family. Hemlock was used by the ancient Greeks in carrying out capital punishment. (See Figs. 6–16, 9–12*C*.)

The Madder Order (Rubiales)

Trees, shrubs, and herbs are included in this order. The flowers are epigynous and the petals are united to form a more or less tubular corolla. The parts are generally in fives, though the carpels may vary in number. The flowers have a simplicity of structure. They are regarded as relatively high in development. The madder family (*Rubiaceae*) includes coffee and cinchona. The bark of cinchona trees yields quinine. In the honeysuckle family (*Caprifoliaceae*) are a number of ornamental shrubs and vines—snowberries, elders, and honeysuckles. (See Fig. 2–7.)

The Composite Order (Asterales)

In this order we find a combination of floral characters which are regarded as representing a high evolutionary position. Tendencies toward this high development have been evident in the preceding orders. The composite group marks the culmination of these tendencies. Here there is

cyclic arrangement, small and definite numbers of parts, undiverged (i.e., not distinct) parts, and an inferior ovary (epigyny). The flowers may be radially or bilaterally symmetrical. An inflorescence in the form of a head of many small flowers is characteristic. This type of inflorescence was called a compound flower by the older botanists. It is true that a compact head does simulate a single flower, especially when there are non-showy disc flowers surrounded by showy ray flowers. The group is not only one of the highest but also one of the largest of the angiosperm orders. The representatives are chiefly herbaceous; some are shrubs; and in the tropics a few are low trees. The thistle family (*Carduaceae*) comprises a great array of plants, many of which are troublesome weeds. Here belong sunflowers, asters, goldenrods, thistles, ragweeds, dahlias, marigolds, zinnias, and chrysanthemums. Plants of the chicory family (*Cichoriaceae*) are characterized by their milky juice. In this family the heads do not have a central region of disc flowers but are composed entirely of ray flowers. The familiar plants of this family are lettuce, endive, chicory, hawkweed, and dandelion. (See Figs. 5–9, 9–12*D*, 9–26, 12–10, 12–12, 13–4.)

THE MONOCOTYLEDONS

The majority of the members of the monocotyledons have vascular bundles which do not possess a cambium. The arrangement of bundles in the stele may conform to the dicotyledon type, but steles in which the bundles are distributed in a central mass of pith are common. By expansion many monocot stems become hollow, a condition frequently seen in the grasses. The embryo produces only one cotyledon, in contrast to the two in dicotyledons. The single cotyledon of the monocot embryo is often so modified that it is not leaf-like in structure or function. In many species it remains within the seed during germination, functioning as an organ of digestion and assimilation. The leaves are usually simple and parallel-veined. The veins do not end freely in the margin, which is entire. Such a system is called closed venation. The flower parts are ordinarily in sets of three, i.e., three sepals, three petals, three or six stamens, and three carpels. In some groups the flowers are incomplete or imperfect.

The Lily Order (Liliales)

The members of the lily order are frequently cited as typical examples of the monocotyledons. The flowers are cyclic, perfect, complete, and hypogynous (superior ovary). The perianth consists of a calyx with three sepals, and a corolla with three petals, commonly colored alike. There are

two whorls of stamens of three each. The ovary is formed of three carpels. The plants are herbaceous, mostly perennial, with underground shoots in the form of scaly bulbs or rhizomes. The common name lily is often used for plants belonging to other orders such as calla lily (*Arales*) and water lily (*Ranales*). The Easter lily, the tiger lily, the madonna lily, and the Turk's-cap lily are true lilies (*Liliaceae*). In the lily family are included also onions, leek, and garlic. Asparagus, lily of the valley, and Solomon's seal are included by some botanists in the lily family and by others in the lily-of-the-valley family (*Convallariaceae*). The rushes, plants which are sedge-like in aspect and texture but which have flowers liliaceous in structure, are included as a separate family, the *Juncaceae*. These are not to be confused with the bulrushes, members of the sedge family. (Figs. 8–4, 9–3.)

The Aroid Order (Arales)

The plants of this order are generally characterized by large leaves and showy inflorescences and fruits. Notable exceptions are the duckweeds (family *Lemnaceae*), which are small leafless floating aquatics. Representative aroids have the small flowers densely grouped on a fleshy spike (*spadix*) more or less overarched by a large bract (*spathe*). The spathe is variable in form and often of bright color, features which are associated with insect pollination. In a popular sense the whole inflorescence is called a flower. The cultivated calla lily is a good example. Other cultivated representatives are the species of *Caladium,* often with variegated leaves, and the large-leaved *Colocasia,* known as the elephant's-ear. Some varieties of these genera produce large edible tubers and are cultivated in the tropics. They are known by the common names dasheen, taro, and yautia. The order is represented in temperate regions by such familiar plants as jack-in-the-pulpit (*Arisaema*), skunk cabbage (*Spathyema*), and sweet flag (*Acorus*). In recent years there have appeared newspaper accounts of the blooming of a strange plant in the conservatories of the New York Botanical Garden with a gigantic "flower" four to six feet in diameter and six to eight feet in height. It is an East Indian genus of the aroid order (*Amorphophallus*) and the so-called flower is really an inflorescence.

The Palm Order (Palmales)

The palms are characteristic plants of the tropics and subtropics. For the most part they attain the size of trees. Although variable in form they usually have a stout simple trunk terminated by a dense crown of large evergreen leaves. In some species the leaves are palmate (fan palms), in others pinnate (coconut and date palms). The flowers are usually green-

ish, and although they are small the inflorescences are conspicuous among the leaves. The fruit is a one-seeded berry or drupe, sometimes large in size. The palms are familiar as ornamentals wherever they are hardy outside, and they are widely grown elsewhere in greenhouses for use as decoration and display. The date palm (*Phoenix dactylifera*) and the coconut palm (*Cocos nucifera*) furnish the dates and coconuts of commerce. Some palms are a source of oils and fibers. Palm leaves are widely used in the tropics for thatching roofs. "Panama" hats are plaited from the leaves of a species of palm.

The Cattail Order (Pandanales)

The common cattail (*Typha*) is the representative of this group in temperate North America. These plants live in marshy places. The main stem is a rootstock which branches through the mud and sends up leafy stems in the spring. The erect leafy stems live only during the growing season. The leaves are long and sword-like. The flowers are small, imperfect, and densely crowded in terminal spikes, the staminate flowers being grouped in the upper portion of the spike and the pistillate flowers in the lower portion. The brownish fruiting spikes persist in the fall and winter and are often used for decorations. The screw pine (*Pandanus*) is the tropical representative of the order. It is a peculiar tree with spiral clusters of sword-like leaves and well-developed prop roots. Specimens are frequently seen in conservatories. (See Fig. 6–31.)

The Grass and Sedge Order (Graminales)

The grasses and sedges are classified as two families, *Gramineae* and *Cyperaceae,* within this order. Except for the bamboos, which become shrubby or tree-like, the grasses are herbaceous. The sedges are grass-like in aspect. The grasses usually have cylindrical, jointed stems which are hollow except at the nodes. Many sedges have triangular stems and most of them have solid stems. Both families are characterized by leaves that are flat and linear, by flowers in the axils of chaffy bracts, and by fruits that are one-seeded and dry. A perianth is entirely lacking or is represented by a series of scales or bristles. They are wind-pollinated. The fruit of grasses is a grain; of sedges, an achene. Both families are world-wide in distribution and are found in a great variety of soil and climatic conditions. The sedges usually grow in wetter localities than grasses. The grass family is of outstanding economic importance. Here belong the cereal grains—wheat, rice, barley, rye, oats, and corn—which furnish the most essential foods of man. Their cultivation has for ages been one of the chief human

industries. In addition to the cereals the grasses include sugar cane, sorghum, millet, and many meadow and pasture species important as forage for animals. The plains of North America, the llanos of South America, and the steppes of Russia are vast areas where grasses are the dominant plants. Most grasses are comparatively low herbs, but there are notable exceptions. Maize, sugar cane, and broom corn reach heights of six feet or more; the giant bamboo attains a height of 100 feet. The strong woody stems of bamboo are widely used in many tropical countries for the building of houses and furniture, and for a variety of other domestic and economic purposes. An interesting sedge is the papyrus, the Egyptian paper plant. It is commonly grown in aquaria and pools. A close relative is the umbrella plant, which is similarly cultivated. The bulrushes or club rushes are also sedges. (See Figs. 8–2, 9–25.)

The Iris Order (Iridales)

Here belong several interesting families of land plants of diverse habits. The flowers resemble the lilies but differ from them in being epigynous (inferior ovary). In the iris family (*Iridaceae*) are included many of our most popular cultivated ornamentals—iris (called also flags and fleur-de-lis), crocus, freesia, and gladiolus. The amaryllis family (*Amaryllidaceae*) includes the genera *Amaryllis* and *Narcissus*. In the genus *Narcissus* are the variable forms known under the common names paper-whites, daffodils, and jonquils. This family also includes the century plant (*Agave americana*). Sisal hemp is produced from one of the agaves, and the liquors, pulque and mescal, are made from the juices of other species. The pineapple family (*Bromeliaceae*) includes the pineapple and also many epiphytic plants of the tropics. The pineapple of the market is a multiple fruit formed by a fleshy axis covered with spirally arranged ovaries. Spanish or long "moss" (*Tillandsia*), that commonly hangs from the trees in the southern states and the West Indies, is a member of the pineapple family. (See Fig. 10–15.)

The Banana Order (Scitaminales)

This order is largely tropical in distribution. In addition to the banana it includes the traveler's tree, ginger, and canna. The flowers of the ginger and canna families are not radially symmetrical but are dorsiventral or asymmetrical. The inflorescence of the banana is a nodding spike two or three feet in length; the lowest flowers are pistillate, the central ones are perfect, and the upper ones are staminate. Seeds do not develop in the edible banana. The plants are propagated by shoots which develop from

underground rhizomes. A shoot dies after bearing fruit. The leaves are large; and the shoot, which appears as a large trunk of considerable thickness, consists chiefly of thick overlapping leaf sheaths. The banana plants are sometimes called herbaceous trees because they look like trees; however, they are woody only at the base. (See Fig. 8–1.)

The Orchid Order (Orchidales)

The orchids are commonly regarded as the highest of the monocotyledon orders. They are outstanding because of their unusual floral characteristics. In the words of C. C. Curtis, "Their flowers are a source of wonder and admiration, owing to the singular beauty and delicacy of their mechanical construction." In the orchid family (*Orchidaceae*) the flowers sometimes have such extreme variations that it is difficult to recognize the usual floral parts although they are all present. They have bilateral symmetry and are insect-pollinated. The most striking feature is the labellum, which is a modified petal. It is remarkably varied in form and color. The stamens and pistils are united to form a column. The style often ends in a beak at the base of a single anther or between two anthers. The pollen grains are united in waxy masses. The construction is such in many species that cross-pollination is insured through the agency of one particular insect. Orchids are widely distributed in both temperate and tropical regions. They are herbaceous perennials; some are terrestrial but many are epiphytic. Vanilla is prepared from the pods of a climbing epiphyte. While too much cannot be said about the beauty of orchid flowers, it is only fair to call attention to the fact that many species have inconspicuous flowers. The ornamental species are much cultivated in public, private, and commercial conservatories. Their successful cultivation requires skill and patience. The seeds are extremely small and rudimentary. In recent years methods have been developed for the germination of seeds in flasks on bacteriological culture media. (See Figs. 6–30, 9–10, 14–9.)

RÉSUMÉ OF CLASSIFICATION OF THE ANGIOSPERMS

We have given attention to some selected orders and families of the flowering plants. In considering these various groups it has been our objective to present something of interest about the members of the different groups, to set forth their distinctive and attractive features, and to bring about an appreciation of their usefulness to man. We must strive, however, not to become overwhelmed with a mass of details. It is theoretically possible to construct a genealogical tree which will reflect our

conception of relationships in pictorial form; the construction of such a tree is the ultimate aim of all botanists who study classification.

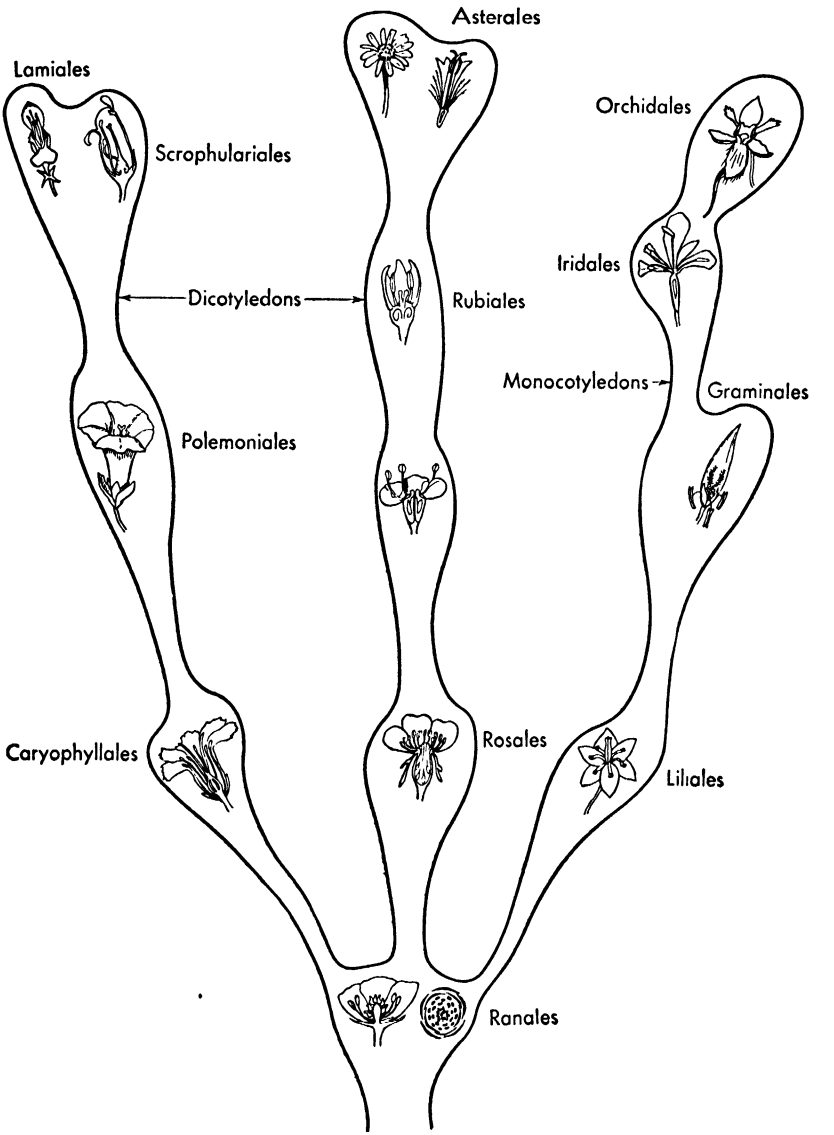


FIG. App.–1. Relationship of angiosperm orders in the form of a genealogical tree. Further explanation given in the text.

Reference to the genealogical tree here presented reveals the following general course of development. The buttercup order (*Ranales*) is the great genetic alliance; from it arise two major branches or series of dicotyledons.

The first of these branches ends in the figworts (*Scrophulariales*) and mints (*Lamiales*). It includes groups whose flowers have separate petals and radial symmetry, and finally ends with the figworts and snapdragons which have a sympetalous corolla and decided bilateral symmetry. A superior ovary (hypogyny) is characteristic. The second of these series includes the rose order (*Rosales*) and terminates in the composite alliance (*Asterales*). Here are groups having flowers with separate petals and radial symmetry, but the tendency in the higher groups of the series is toward a sympetalous corolla and bilateral symmetry. Development of the floral parts from a disc around the ovary (perigyny) or from above the ovary (epigyny) is characteristic. The monocotyledons are represented as having their origin in the buttercup complex. They constitute a third branch of the angiosperm tree. From the lily order (*Liliales*) there are two lateral branches, one ending in the grass order (*Graminales*) with their inconspicuous chaffy flowers, and the other in the orchids (*Orchidales*), with their showy, bilaterally symmetrical flowers.

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