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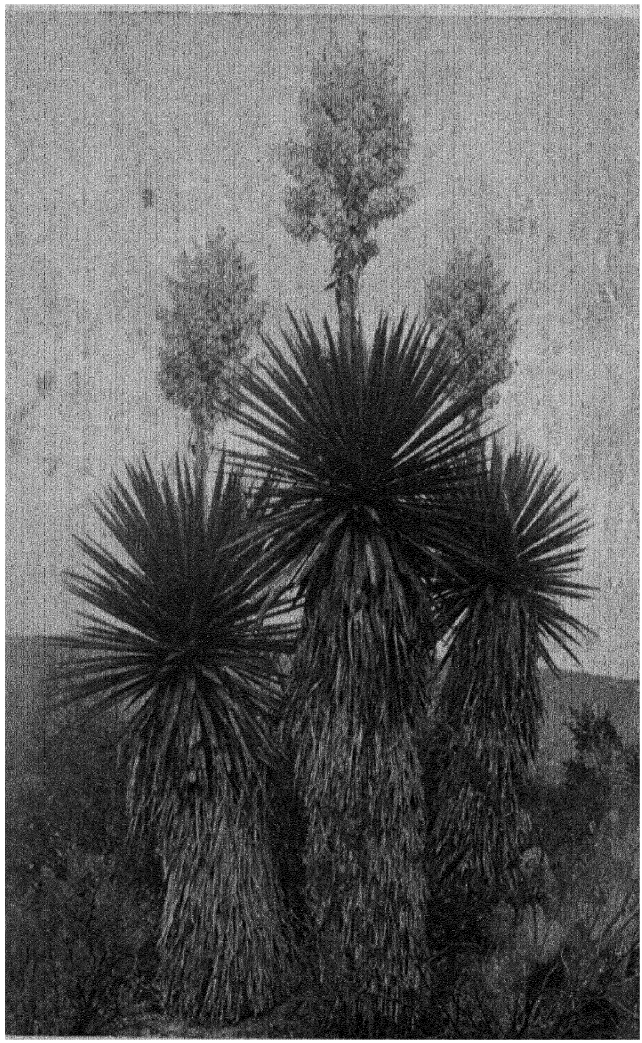
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Giant Dagger (*Yucca carnerosana*) in Big Bend National Park, Texas. Photograph by Omer E. Sperry.

PLANT ECOLOGY

BY

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FOURTH EDITION, THOROUGHLY REVISED,

WITH 118 ILLUSTRATIONS

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PREFACE TO THE FOURTH EDITION

PLANT ecology is still a vigorously healthy and growing science. This is attested both by the increasingly large number of publications on the subject and by the fact that there still are disagreements among ecological workers about some important principles and concepts. There is even disagreement about what a plant association is and there doubtless are many who will not agree with the concept of an association as presented in this book, but that is a healthy state of affairs for it means that critical thinking is being practiced.

Although many excellent papers and some books on ecological subjects have been published during recent years, most of them have not changed our fundamental thinking to any great extent. Thus, although it has been found necessary to make some changes in every chapter of this book in order to bring the facts up to date and in line with our present knowledge of the subject, it has also been possible to retain the same order of presentation that has been found so acceptable in former editions. Also, as in previous editions, every effort has been made to keep the text concise and easily understandable for it is believed that these qualities are essential in any book that is intended to be useful to beginning students in any branch of science.

In order to keep the lists of literature at the ends of the chapters from becoming too lengthy an effort has been made to add only those recent publications that have a direct bearing on the principles discussed in the chapter. This explains the omission of many excellent publications.

The author again expresses his gratitude to all who have offered suggestions and criticisms of previous editions of this book and solicits equally frank comments on the present edition.

W. B. McD.

TUPELO, MISSISSIPPI.

PREFACE TO THE FIRST EDITION

THE science of plant ecology has been badly in need of a text-book for a number of years. While there are many valuable books on various phases of the science there has been no single book in the English language that covered the subject in such a way that it could be used as a text in a comprehensive beginning course. The need of a text-book has been recognized for some time but the very rapid growth of the science has resulted in a great deal of disagreement about certain rather fundamental principles and has made the production of a book that would not be subject to severe criticism seemingly impossible.

The present volume is an attempt to supply the need of a text-book of plant ecology. Criticisms of it will be welcomed and are hereby solicited, for in the criticisms will lie the greatest hope of a better book in the future. The book is based on a course of lectures that has been given for several years to beginning classes in plant ecology at the University of Illinois. It is hoped that it will prove useful in other universities and, more especially, in colleges and normal schools where plant ecology is, or should be, taught. The text has purposely been made brief and probably many ecologists will not agree that a happy choice has always been made in deciding what to include and what to leave out. The entire field of plant ecology is covered, however, and as much material is included as can be given in a half year course with two lectures a week.

References to ecological literature are given at the ends of the chapters. No attempt has been made to include complete bibliographies on any subject. For the most part only some of the more recent publications are listed, very few that were published more than ten years ago being included. Usually the bibliographies in the publications listed will enable anyone to go much deeper into the literature of any phase of ecology in which he may be interested. An appendix, giving some suggestions concerning laboratory and field work, is added in response to numerous requests that have come from teachers for such information.

The author is greatly indebted to Miss Winona H. Welch, Miss Margaret C Jacobs, and Mr. W. C. Croxton, all of whom have read the entire manu-

script and have aided greatly in eliminating typographical errors, crudities in English and errors in the statements of facts. All illustrations obtained from individuals or used by permission of publishing companies are acknowledged in the legends of the figures. Illustrations not so acknowledged are by the author. Naturally, free use has been made of the published statements of numerous ecologists for which individual acknowledgement is not attempted. Sincere thanks are hereby expressed to all who have aided in any way, directly or indirectly, in the preparation or publication of the book.

W. B. McD.

URBANA, ILLINOIS.

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PLANT ECOLOGY

CHAPTER I

INTRODUCTION

Plants are among the most important objects on earth. Neither man nor any other animals could exist without them. They are the direct or indirect source of all foods, natural fibers and rubber, paper, most fuels and drugs, and very many other products without which the progress of civilization would have been absolutely impossible. They are also an important source of beauty. Whenever we think of a beautiful home or a beautiful city we think of one that is well supplied with trees, shrubs, grass and flowers. Whenever we think of a beautiful valley or a beautiful stream we think of one that is placed in a green frame formed by the green plants that border it. Indeed, the whole surface of the earth is made beautiful by the plants that grow upon it. It is because of these facts that the study of plants has long been considered an essential part of education.

1. **The Study of Plants in the Field.**—Although plants have been objects of study for a very long time, these studies have too often been confined largely to laboratories and books while field studies have been neglected.

The only practical way to become well acquainted with plants is to study them where they grow. The botanist who has limited himself largely to laboratory and library studies is usually considerably at a loss when he faces a field problem. He does not recognize the different kinds of plants nor does he know where to look for particular kinds nor why these kinds cannot be expected to grow in certain types of places. He does not understand the natural grouping of plants that he observes and is unable to make practical use of his field observations for solving problems. Many of the most important plant problems awaiting solution at the present time, problems that are of vital importance to the world's food supply, to the supply of lumber and other forest products, to the esthetic use of plants in landscaping, or to the conservation of natural resources, are field problems. It is, therefore, essential that those who are training themselves along botanical lines should place a reasonable emphasis upon field work.

2. **What Plant Ecology Is.**—Plant ecology is the science of the interrelations of plants and their environments. It is a part of general ecology, sometimes called bio-ecology, which deals with the interrelations of all living things and their environments. It is impossible to entirely separate plant ecology from animal ecology and this book will be found to overlap into the field of animal ecology in some instances. However, as long as biological science is organized in our colleges and universities as it is at present, with separate departments of botany and zoölogy, it will be neces-

sary to offer separate courses in plant ecology and animal ecology, and text-books will necessarily deal with these two branches of ecology as though they were distinct subjects.

Plant ecology is essentially a field study and this fact tends to distinguish it from plant morphology and plant physiology, which are essentially laboratory studies. It is also one of the most practical of the sub-divisions of botany, since ecological principles form the basis of practice in agriculture and forestry as well as in many of the modern phases of conservation. The

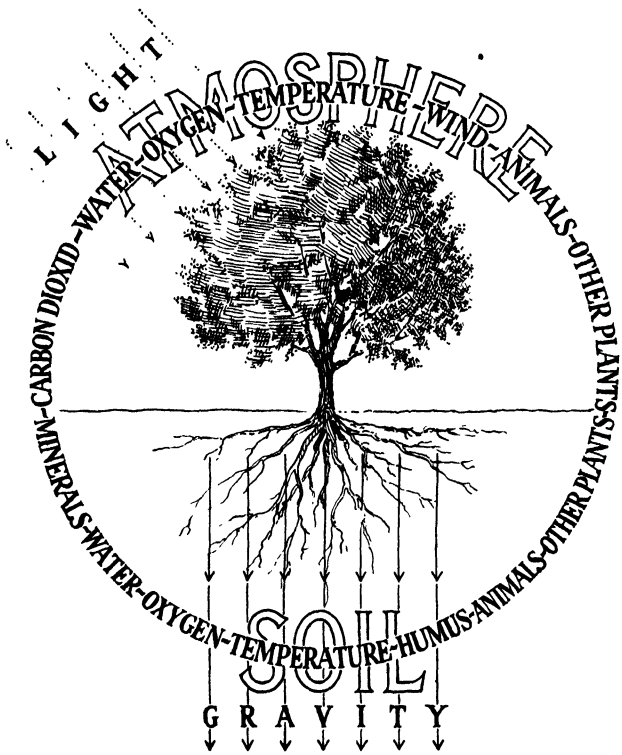


FIG. 1.—Diagram showing the principal factors in the environment of land plants. (From Transeau's General Botany. Copyright 1923 by World Book Company, Yonkers-on-Hudson, New York.)

problems of the farmer, the forester, the landscape architect, or the wildlife conservationist, and those of the ecologist are similar and often identical. They are concerned always with the relations of the plant or animal to its environment. Many of the ecological principles were practiced, though often in a haphazard and unscientific manner, long before the word ecology had come into use.

3. **The Environment of Plants.**—The environment of a plant consists of everything outside of the plant which influences in any way the life of the

plant. The environment is partly living and partly non-living. The living part of the environment consists of plants and animals. The non-living part consists of numerous influences such as light, heat, air, soil and water. Each part of the environment which may exert a specific influence upon the life of the plant is spoken of as a factor of the environment or as an ecological factor (Fig. 1).

4. **Autecology and Synecology.**—In the study of plant ecology we find it necessary to treat not only of the relations of individual plants to the environment but also of comparable relations of communities of plants. The ecology of individual plants is called autecology while the ecology of plant communities is designated synecology.

This book covers the entire field of plant ecology but the earlier chapters deal almost entirely with autecology while the later chapters treat more largely of synecology.

REFERENCE

CLEMENTS, FREDERIC E., and SHELFORD, VICTOR E.: Bio-ecology, New York, John Wiley & Sons, 1939.

CHAPTER II

THE ECOLOGY OF ROOTS

Roots are primarily the absorbing and anchoring organs of plants. Internally their structure is similar to that of stems. Externally they are distinguished from stems by the absence of nodes and internodes and especially by the absence of regularly arranged buds. They vary greatly in form and size. Some of the variations are due to inheritance while others are due to the environment and so are of ecological significance.

Because the root system of the plant is, for the most part, hidden within the soil, it has not received as much attention from students as the more obvious aërial portion. But the aërial portion of a plant cannot continue to live and grow without the root system, any more than the roots can live and grow without the stem system, and it is necessary to understand the ecological relations of all parts of the plant before we can successfully apply our knowledge to practical problems involved in the growing and utilization of plants.

5. **Absorption.**—The absorption of materials from soil takes place primarily through root hairs. Root hairs are extensions of cortical cells of roots. They are ordinarily from one to several millimeters in length and so small that as many as 300 have been counted on a single square millimeter of surface, though often they are not nearly so numerous as that. The numerous root hairs increase the absorbing surface of the roots from 2 to 10 times and sometimes even more and this is probably the chief advantage of these structures. Most root hairs have cell walls which are very thin and pliable and possess a mucilaginous material in the outer part of the wall, and this makes it possible for them to come into very close contact with the soil particles. They usually become very irregular in shape through this intimate contact with the soil particles and they cling to these particles so tenaciously that when roots are pulled from the soil the root hairs are for the most part broken off from the root rather than being pulled loose from the soil particles.

The ordinary thin-walled root hairs are rather ephemeral structures lasting only a few days or at most a few weeks, depending upon the kind of plant and upon the environment in which the plant is growing. As a root elongates, new root hairs are constantly being formed just back of the root tip and at the same time the oldest hairs farther back are dying off. There is thus an area of root hairs, rather definite in extent, which is constantly moving forward as the root elongates and so is coming into contact with fresh supplies of food materials in the soil (Fig. 2).

In the case of some plants that grow in very dry places such as deserts, the root hairs become thick-walled and persist for several months or even years. This is true also of a few plants that grow where the water supply is abundant, such as the honey locust (*Gleditsia triacanthos*) (Fig. 3), the Kentucky coffee tree (**Gymnocladus dioica**), the red bud (**Ceris canadensis**), and a number of species of the composite family. It is probable that in all of these cases the habit of producing thick-walled root hairs was formed at a time when the plants concerned grew only in very dry situations.

The rate of absorption from the soil, especially of water, depends not only upon the structural characteristics of the root system but also upon a number of external factors. One of these, of course, is the actual amount of water present in the soil. If there is a deficient amount of water present a state of physical dryness (actual absence of sufficient water) exists and the rate of absorption is reduced. A second factor concerned here is temperature. A high temperature, up to a certain limit, increases the rate of absorption while a low temperature decreases it. A third factor affecting the rate of absorption is the amount of salts, that is, of soluble materials, in the soil. Either a low temperature or a high concentration of salts in the soil brings about a condition that is spoken of as physiological dryness which means that while there may be an adequate amount of water present the plants cannot absorb it readily. The reason why the plants cannot get water readily from a salty soil is that the concentration of the soil solution is too nearly equal to that of the cell sap to allow the water to diffuse into the cells rapidly. Obviously the extent of the effect of this factor depends upon the concentration of the cell sap, which varies greatly in different kinds of plants.

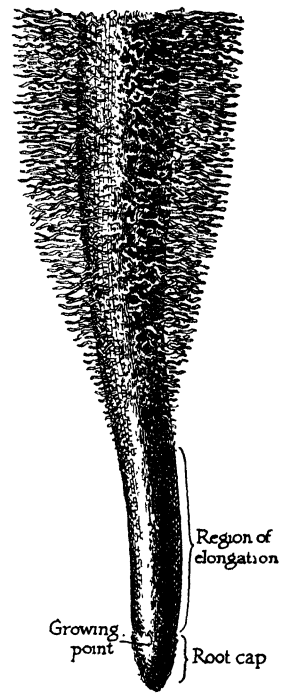


FIG. 2.—Root tip, showing root cap, growing region, and root hairs. (From Transeau's General Botany. Copyright 1923 by World Book Company, Yonkers-on-Hudson, New York.)

It was formerly thought that the absorption of nutrient materials from the soil took place almost entirely from the surface layer to a depth of only 6 or 8 inches. It is now known, however, that both water and mineral salts are absorbed from all layers of soil that are occupied by roots. For example, potatoes absorbed from all layers to a depth of 2.5 feet, barley to 3 feet, and corn to 5 feet. In all cases somewhat larger amounts were absorbed from the upper layers but this was probably due only to the presence of larger numbers of roots in those layers. Many native plants absorb their nutrients almost wholly below the first 2 or 3 feet of soil. This is necessarily so because there is practically no branching in the upper soil layers and the older parts of the root have lost the ability to absorb. These facts are very important in connection with the addition of artificial fertilizers to soils in which crop plants are to be grown.

6. **Anchorage.**—While the function of absorption is limited largely to the smallest roots and especially to the root hairs, anchorage is a function of the entire root system. That root systems in general are efficient in performing this function is shown by the infrequency with which plants are uprooted by the wind. It is seldom that even tall trees are uprooted except when a region is visited by a tornado. Experiments have shown that healthy corn plants four months old will offer a resistance of 200 to 360 pounds to a straight vertical pull. The efficiency of the root system

is well seen also along streams where the banks are being eroded by the water. The root system of a tree may be more than half uncovered and still hold the plant upright.

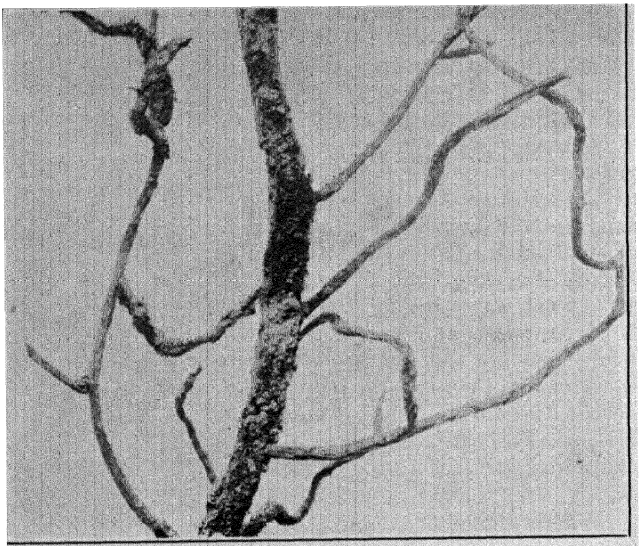


FIG. 3.—Roots of *Gleditsia triacanthos* showing persistent root hairs.

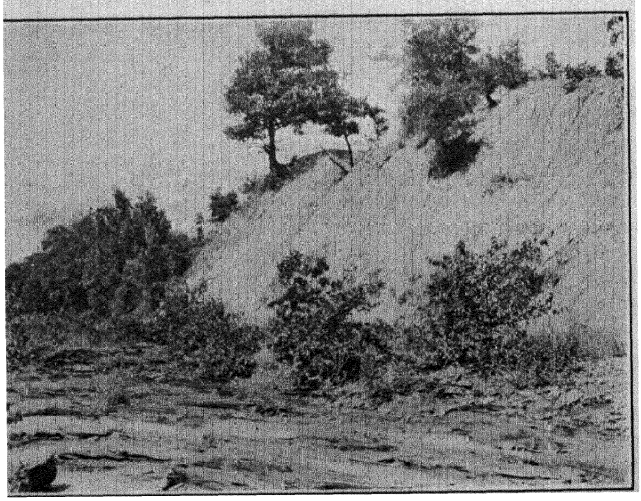


FIG. 4.—Trees and shrubs checking erosion on a hillside.

Where trees are growing along streams erosion is much less rapid than where there are a few or no plants as the roots tend to hold the soil in place (Fig. 4). In fact usually the simplest way to check erosion in such a place is to plant trees or shrubs. This is equally true of other places where

erosion is likely to occur, such as hillsides. Some kinds of plants are much more efficient than others in holding the soil. In sandy regions and especially in regions of shifting sand dunes, such as occur along sea coasts, there are certain plants, particularly some kinds of grasses, that are known as "sand binders" because of their ability to grow in the unstable sand and often to check its movements or even to stop it entirely (Fig. 5). The movement of the sand in such a place is of course due to wind action, and the sand binding plants are often planted along railroads and the borders of farms to prevent the encroachment of the sand through the agency of wind.



FIG. 5.—*Hudsonia tomentosa*. A sand binding plant. (Photograph by A. G. Eldredge.)

7. **Food Accumulation.**—Many plants have thick fleshy roots which serve the somewhat special function of store houses for accumulated foods. This is especially true of plants with tap roots such as beets, parsnips and dandelions. It is also true of many plants with fascicled or tuberous roots, as the dahlia and the sweet potato.

Most of these storage roots accumulate starch and in some, the sweet potato for example, there is not much except starch. Some, however, like the beet, accumulate sugar in addition to starch, and the dandelion and the dahlia as well as many other members of the composite family accumulate considerable quantities of inulin, a soluble carbohydrate. Practically all of these thickened roots also accumulate water and in many cases this is more important than the accumulation of food. Many desert plants have immense root systems which store up water in great quantities and the plants depend upon these supplies during rainless seasons. This is not true, however, of cacti which store their reserve water supplies in stems rather than roots.

Roots have obvious advantages as storage organs because of their position. They are better protected from animals than are aërial organs and are somewhat protected also from extremes of temperature or, perhaps of more importance, from sudden changes of temperature. Furthermore, and of still greater importance, they are very well protected from desiccation.

8. **Growth and Development.**—Certain factors in the environment of roots are more constant than corresponding factors in the environment of aërial organs. This is especially true of temperature. Some other factors, however, are as variable below the surface of the soil as above it. In the case of plants that live only during one season the roots ordinarily grow continuously from the time the seed germinates until the plant dies, although the rate of growth varies greatly from time to time as the factors of the environment, such as temperature and water supply, become more or less favorable. The roots of plants that live more than one year ordinarily cease growth at certain times during each year, at least in regions having warm and cold or wet and dry seasons. These periods of growth cessation are spoken of as dormant periods. The cause of these dormant periods is lack of sufficient water for growth. In the case of forest trees in the temperate zones, for instance, there is always a dormant period in winter when the soil becomes physiologically dry through low temperature, and in a dry year there may also be a dormant period in summer when the soil becomes physically dry. In a wet year, however, the roots of trees grow throughout the summer and this is probably the rule every year in the case of those roots that are so deep in the soil that the water supply never becomes inadequate.

The characteristics of a root system as to shape and extent depend in part upon inheritance and in part upon environment. Water is the most important environmental factor involved. In the tall grass prairies of eastern Iowa, Nebraska and Kansas, where the rainfall is sufficient to wet the soil to great depths, the most characteristic grasses, such as bluestem (*Andropogon*), wheat grass (*Agropyron*), and marsh grass (*Spartina*), all have root systems that extend from 5 to 8 feet into the soil. Some of the other important plants of the same community, such as sunflowers, asters, goldenrods, mints, and roses, send their roots even deeper and often absorb practically no water from the surface layers of the soil. Farther west, on the short grass plains, where, because of low precipitation and high run-off, the soil seldom becomes moist to a depth of more than 2 feet, the roots of the grasses and other plants are confined mostly to the first 2 feet of soil. Still farther to the southwest, in southern Arizona, where precipitation is very low, the roots of annual plants seldom penetrate more than 8 inches, although those of the perennial plants, such as cacti and more especially the shrubs, often penetrate to great depths.

In the case of several crop plants it has been found that the presence of fertilizers in the soil promotes vigorous growth and profuse branching of the roots. Considerable increases in yield of the potato crop have been obtained in certain regions by working fertilizers into the surface layer of soil and then plowing about 9 inches deep before planting the potatoes. The deep placing of the fertilizers causes the roots to develop abundantly in the deeper layers. If, then, there is a dry season while the crop is developing, and the surface layers of soil dry out, the plants are not affected as they would be if the greater numbers of roots were in the surface layers.

The rate of growth of roots varies greatly under different environmental conditions. It is sometimes remarkably rapid. The roots of corn, for example, have been known to grow at a rate of 2 to 2.5 inches per day during a period of several weeks. The roots of the common dogbane (*Apocynum cannabinum*) have been known to attain a verticle penetration

of 7 feet and a radial spread of 12 feet in a single growing season of about seven months.

9. **Aeration and Root Growth.**—Roots carry on respiration just as all other parts of the plant do. In this process they use up oxygen and excrete carbon dioxide. Therefore, either a deficiency of oxygen or an excessive accumulation of carbon dioxide is injurious to the root system. The commonest condition that results in a deficiency of oxygen is the presence of an excessive amount of water in the soil. When the soil is saturated with water, air cannot get in and a prolonged saturation often causes crop plants actually to drown. These facts need to be taken into consideration wherever irrigation is carried on. Care must be taken not to use too much water. The plants need both water and air and it is necessary for best results to strike a compromise between these two needs.

In swamps where the soil is constantly saturated with water the majority of roots grow horizontally rather than downward and sometimes even grow vertically upward. The horizontal roots of many swamp trees such as baldcypress (*Taxodium distichum*), tupelo gum (*Nyssa aquatica*), and swamp black gum (*Nyssa biflora*), produce upright branches which are called knees. Presumably the formation of these knees is induced by a deficiency of oxygen in the soil and a combination of abundant aerial oxygen and rather constant wetness above the soil, but it is doubtful whether the knees have any function. Their compact structure and covering of bark would seem to prohibit any free interchange of gasses. In the case of black mangrove (*Avicennia nitida*), however, the erect root branches called pneunatophores have well developed air spaces and stomata similar to those of leaves and are believed to be important organs of aeration.

In peat bogs the condition for aeration seem to be particularly bad. Such a place is practically if not entirely undrained and the deep layers of peat, constantly saturated with water, prevent the entrance of oxygen and facilitate the accumulation of carbon dioxide. The acidity that results from this accumulation of carbon dioxide brings about a condition of physiological dryness. Under such conditions many plants which flourish in ordinary swamps cannot grow at all. Many plants which are found in peat bogs have structural features that are characteristic of dry land plants and this has been attributed largely to the physiological dryness of the bog.

Another factor that prevents proper aeration of the soil, and so reacts unfavorably on root growth is compactness. In national and state parks many trees have been killed in picnic areas and camp grounds as a result of numerous automobiles running over the soil and compacting it to such an extent that neither water nor air could enter. Rainwater always contains a considerable amount of oxygen in solution and one of the benefits of a rainstorm comes from the oxygen that is carried into the soil but, if the soil is so compact that all of the water flows away instead of percolating into the soil, no aeration can result. One of the main reasons for preparing a deep, mellow seed bed is to maintain a porous condition of the soil in order that the roots may obtain sufficient oxygen for maximum growth.

10. **Root Duration.**—Some roots live for only a few weeks or months while others, as those of some trees, may live for hundreds of years. The classification of plants into annuals, biennials and perennials is based largely upon the length of life of the parts within the soil, though not in all cases on roots. An annual plant is one that completes its life cycle within

one vegetative season; a biennial one that lives during part or all of two vegetative seasons; and a perennial one that lives during more than two vegetative seasons. In many biennial plants, such as the parsnip, practically the only part that lives through the winter is the root. Many perennials, also, are annual above ground and live through the winter below ground. Some of these have perennial underground stems and in these the roots may be, and often are, annual, while others have perennial roots. Woody plants are perennial both above and below the surface of the soil.

Some plants may be annuals or biennials depending upon the time of germination. Spring wheat, for example, is an annual while winter wheat is a biennial. Some plants, likewise, that are annuals when grown in periodic climates may be perennials in uniform climates. The castor bean grows in Florida, for example, as a perennial and becomes a small tree, while in the northern part of the United States it is an annual.

11. **The Position of Roots in the Soil.**—We have already spoken of certain variations in depth and extent of root systems due to conditions of the environment. The position in the soil of the roots of any particular kind of plant, however, is governed in part also by inheritance. A maple tree, for instance, practically always produces a large number of roots in the surface layer of the soil. This is one of the main reasons why it is so difficult to get lawn grass to grow under a maple tree. On the other hand an oak tree growing under exactly similar conditions has a much smaller number of surface roots. Again, a corn plant, at germination, produces a primary root system from the seed and a more extensive root system is formed later by adventitious roots from the lower part of the stem. This latter root system is always produced at approximately the same depth whether the corn has been planted relatively shallow or very deep.

In a community of plants where a large number of kinds are growing together it is usually found that they vary greatly in the depths of the main parts of their root systems (Fig. 6). This is distinctly advantageous since it makes it possible for a much greater number of plants to occupy the area than would be the case if they all had their roots at the same level. A similar response to depth is found in underground stems. The underground stem of any particular kind of plant is always at approximately the same distance below the surface of the soil. If soil is piled up above the growing tip of such a stem it grows upward until it reaches the normal distance from the surface. Likewise, if soil is dug away from before it, or if it encounters a natural depression, it grows downward until it reaches its usual depth. This phenomenon, which is not well understood, has been spoken of as the "law of level."

Of considerable interest in connection with the position of roots in the soil is the phenomenon of root contraction. This again is not well understood but it is rather common nevertheless. A dandelion is often spoken of as a stemless plant. It, of course, is not stemless It has a short stem at the surface of the soil and the stem bears the leaves. This stem increases in length a little each year but, although the plant may live for many years, it never becomes any taller because every year the root contracts enough to pull the stem down as much as it has grown upward.

12. **Roots and Transplanting.**—When the end of a growing root is cut off an excessive number of branches is ordinarily produced back of the cut. It

is possible therefore to produce a compact and dense root system by cutting off the ends of all of the longer roots of a plant. Shrubs and trees that have been grown in a nursery usually do better than transplanted native plants, because in the nursery stock compact root systems have been induced by frequent transplanting. At each transplanting the longer roots are cut off and thus at the final and permanent transplanting there is a minimum of

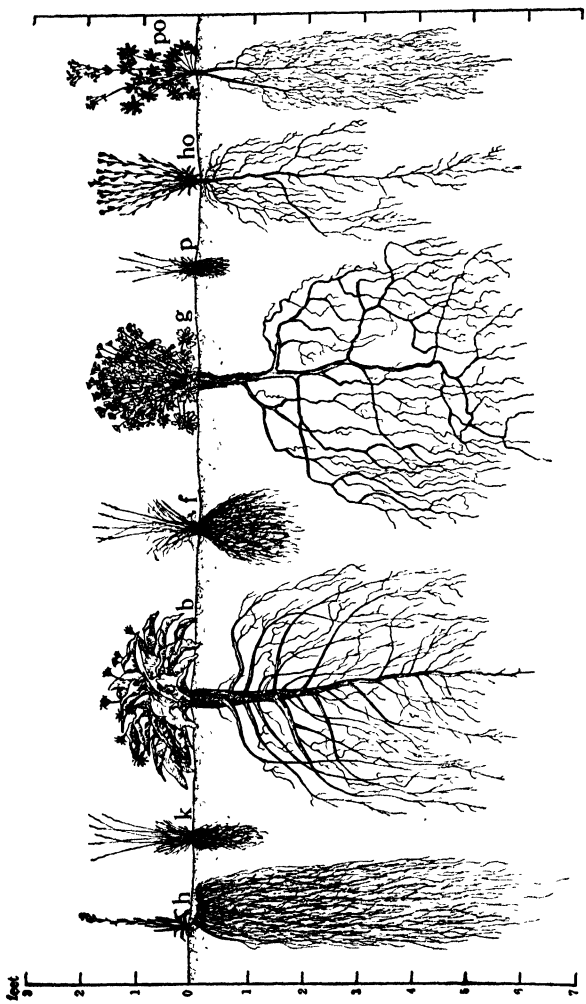


FIG. 6.—Bisect showing root systems of prairie plants at different levels. (After Weaver, Carnegie Inst. of Washington, 1919.) Drawn from photographs and data obtained by the excavation and examination of 325 root systems of these eight species: *h*, *Heracium scouleri*; *k*, *Kœleria cristata*; *b*, *Balsamorhiza sagittata*; *f*, *Festuca ovina ingrata*; *g*, *Geranium viscosissimum*; *p*, *Poa sandbergii*; *ho*, *Hoorebekia racemosa*; *po*, *Potentilla blaschkeana*.

disturbance of the root system. Even large trees may be successfully transplanted if their preparation for it is begun a year or two in advance. The preparation consists of gradually cutting off the roots a few feet from the base of the tree and loosening the soil near the tree so that a large number of short absorbing branches are produced. When the tree is finally transplanted these branches are ready to begin at once the work of absorption.

Of very great importance in connection with transplanting is the maintenance of a reasonable balance between root and shoot. If a considerable proportion of the root system has been lost in transplanting the shoot must be trimmed back in order that water may not be lost faster than it can be absorbed by the roots. On the other hand, if the shoot is trimmed back too much, growth will be retarded because the reduced leaf surface will prevent a sufficient amount of food manufacture to supply the needs of the more extensive root system.

13. **Water Roots.**—Roots of floating plants which grow entirely in water are much less extensively developed than are soil roots. There are usually few if any branches and no root hairs. Some floating plants have no roots at all, absorption taking place through stems or leaves. *Salvinia*, the water fern, for example, has two kinds of leaves, broad flat ones which float on the surface, and elongated, much dissected ones which hang down into the water like roots and perform the function of absorption. The duckweed, *Wolffia*, although it is a seed plant, has neither roots, stems, nor leaves but consists of a small football-shaped thallus through the entire surface of which absorption may take place. *Lemna*, another duckweed, has a single unbranched root only a few millimeters in length, while *Spirodela* has several such roots.

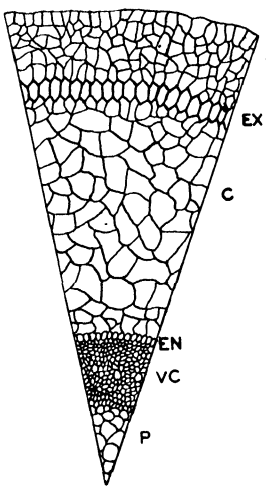


FIG. 7.—Sector of a cross-section of an air root of an orchid. *V*, velamen; *Ex*, exodermis; *C*, cortex; *En*, endodermis; *VC*, vascular tissue; *P*, pith.

Water plants which have roots extending in to the soil are intermediate between ordinary soil plants and floating plants in the relative development of their root system. When the roots of such plants are growing in water they ordinarily remain unbranched, but if they extend into the soil they branch freely and produce root hairs like ordinary soil roots.

14. **Air Roots.**—Air roots, like water roots, are relatively unbranched and without root hairs. Some climbing plants, such as poison ivy and Virginia creeper, produce innumerable air roots which grow horizontally around the support and so serve as anchoring roots. Such roots probably do not perform the function of absorption at all.

In corn and a number of other monocotyledonous plants roots are produced at some of the lower aërial nodes of the stem. These grow obliquely downward as unbranched air roots until they reach the soil. After entering the soil they branch freely and serve an important function as prop roots. In the banyan tree roots grow vertically downward and into the soil from horizontal branches. These roots become stiff and form a system of supports which make it possible for a single tree to continue to spread until it covers an enormous area.

Many tropical orchids which grow upon the branches of other plants where the conditions for absorption are difficult have specially modified air roots (Fig. 7). These roots are usually shining white. Structurally they differ from ordinary roots by having a layer several cells thick outside of

the cortex. This is called the velamen and it absorbs water with great rapidity by capillarity whenever dew or rain comes in contact with it. Between the velamen and the cortex there is a single layer of cells, the exodermis, the cell walls of which, in most cases, are more or less thickened. Some cells in this layer, however, called transfusion cells, have thin walls, and probably serve as passageways for water from the velamen into the cortex.

15. **Rhizoids.**—Roots are strictly organs of sporophytes. Gametophytes never have true roots but are supplied instead, in many cases, with rhizoids. Rhizoids are filamentous structures only one cell thick. In fern prothalli and in liverworts they are usually unicellular and unbranched while in mosses they are branches and multicellular but still only one cell thick. Many of the large marine algæ and some lichens are attached to the substratum by rhizoids. All rhizoids serve as anchorage organs and many are probably also of value in absorption.

The anchorage organs of most lichens are called rhizines and are not single filaments but are composed of a large number of filaments grown together. Their functions are the same as those of rhizoids and roots.

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CHAPTER III

THE ECOLOGY OF STEMS

UPRIGHT stems are largely concerned with the display of foliage and with the conduction of food materials from roots to leaves and of foods from the leaves to growing regions and to storage organs. Prostrate and other horizontal stems often have the more special function of vegetative reproduction. Stems may also serve as storage organs.

16. **Foliage Display.**—The efficiency of stems as organs of foliage display depends largely upon their ability to elongate and to branch. The direction of growth of both main shoots and branches is controlled largely by gravity and light. The amount of elongation is controlled partly by light and partly by water.

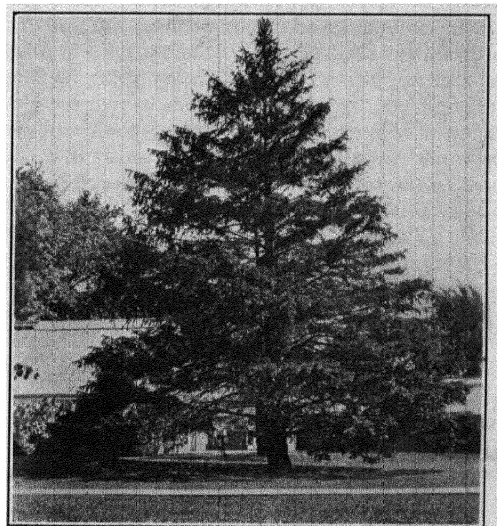


FIG. 8.—A pine tree, showing excurrent type of branching.

One of the most efficient types of stem systems from this point of view is that of excurrent trees well exemplified by pines and spruces (Fig. 8). In such trees the shape is that of a cone, the lowermost branches being the longest and the uppermost the shortest. Leaves are borne only near the ends of these branches so that the whole forms a sort of conical tent the walls of which are formed of green leaves. Such a stem system makes possible the display of an enormous number of leaves nearly all of which receive sufficient light to enable them to carry on a maximum amount of food manufacture.

There are many other types of stem systems which are nearly as efficient as those of the excurrent trees. Herbaceous plants exhibit a great variety of forms, many of them resembling those of trees. In places where these herbaceous plants are not shaded by larger plants they are fully as efficient

as trees except that because of their smaller size they cannot display so large a number of leaves.

17. **Vegetative Reproduction.**—Vegetative reproduction in the higher plants takes place almost entirely by means of stems. The commonest and most efficient type of stem from this point of view is the rhizome, or underground stem. In some kinds of plants, such as most ferns, the rhizome constitutes the whole stem system of the plant. In others there are annual aërial stems which bear the leaves. Some rhizomes are practically unbranched while others branch quite extensively. In any case it is characteristic of rhizomes that they elongate each year and so advance into new territory. Frequently the older parts die off each year about as rapidly as the newer parts elongate and this, in the case of branched rhizomes, results in the multiplication of individuals. This multiplication of individuals is not so important, however, as the advance into new territory. The fact that the rhizome is underground makes it possible for it to advance into an area that is already occupied by plants almost as readily as into one that is not so occupied. This is clearly shown whenever a field is plowed and then left undisturbed for several years. Such a field is practically always occupied first by annual plants, but within a few years the annual plants are crowded out and replaced by perennial plants which have entered for the most part by means of rhizomes. The conquest of such an area through the agency of seeds would take much longer because it is so difficult for the seeds to get down to the soil through a plant cover.

Runners are very much like rhizomes except that they grow above the surface of the soil. They are not so common nor so efficient as rhizomes, although some plants, such as strawberries, are able to spread very rapidly by means of runners. Somewhat similar to runners, at least in function, are such stems as those of the raspberry which bend over and take root at the tip and send up new shoots. Stem tubers, which are short and very much thickened rhizomes; corms, which are short and thick but vertical underground stems; and bulbs, which are large buds with very thick bud scales; are all of some importance in vegetative reproduction but are more important as storage organs.

18. **Conductive Tissues.**—The conducting elements in the higher plants are largely of four kinds: namely, tracheæ, tracheids, sieve tubes and parenchyma. Sap passes upward through the plant largely through tracheæ and tracheids. It passes downward mostly through sieve tubes, while lateral passage of sap is primarily through parenchyma tissue, such as that found in medullary rays.

Tracheæ are syncytes; that is, each one is made up of several cells placed end-to-end, but from which the separating walls have disappeared. They usually have pointed ends and are in most cases only a few centimeters in length, though sometimes they are as much as a meter or more long, especially in some climbing plants. Tracheids differ from tracheæ in being single cells. They have pointed ends like the tracheæ but are usually only a millimeter or less in length, though in some plants they are several centimeters long. Both tracheæ and tracheids function as dead empty cells. They both occur in the xylem of the fibro-vascular bundles.

Sieve tubes, which occur in the phlœm of the fibro-vascular bundles, resemble tracheæ in being syncytes; but they differ from tracheæ in functioning as living cells with protoplasmic contents, and in having perforated cross walls called sieve plates.

Water seems to be the chief external factor influencing the development of conductive tissues. The lower plants, most of which live where there is an abundance of water, if not actually in water, have no special conductive tissue. Also, conducting tissue is greatly reduced or practically absent in submerged seed plants.

In the case of amphibious plants different individuals of the same species, or even different parts of the same individual, may differ greatly in the relative amounts of conductive tissue, it being much less developed in those growing in water than in those projecting into the air. Furthermore, it is

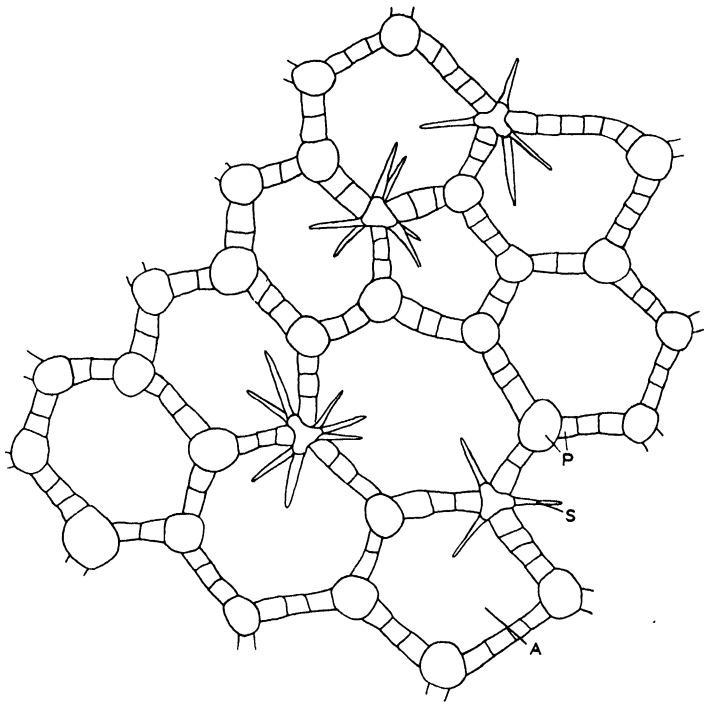


FIG. 9.—Portion of cross-section of water lily petiole showing sclereids. *P*, parenchyma cells; *S*, sclereid; *A*, air space.

found that in land plants the maximum amount of conductive tissue occurs in those growing in very dry situations and that the moister the environment the less is this tissue developed. This effect is also seen in the annual rings in the wood of trees, much thicker rings being produced in wet years than in dry years.

The attack of a plant by a parasite usually results in an increased development of conducting tissue. This is well seen in insect galls and root tubercles as well as in stems, leaves and roots that are attacked by fungi or other parasites. Such an effect might be expected since a parasitic attack increases activity and thus increases the use of water and other materials and the result of this should be comparable to the result of a lack of these materials in the environment.

19. **Mechanical Tissues.**—Mechanical or stiffening and strengthening elements in plants are mainly of three general types. These are fibers or elongated sclerenchyma cells; sclereids, or sclerenchyma cells that are not appreciably elongated; and collenchyma, or elongated cells whose walls are not uniformly thickened but are thickened primarily at the angles.

Fibers occur both in and around phlœm and in xylem. Those that occur in the phlœm or bark are called bast cells while those that occur in the xylem are called wood fibers. The commercial fibers such as flax, hemp, and jute, out of which thread, twine and ropes are made, are bast fibers. The individual fibers are only 1 or 2 mm. in length but they have pointed ends and are dovetailed together in such a way as to give great strength. When mature their walls are very thick; so thick that the lumen of the cell is extremely narrow.

Sclereids are formed by the uniform thickening of the walls of ordinary parenchyma cells and are therefore more or less isodiametric. They are found in the hard shell of nuts, in the seed of the date, and in the bark of trees. Sometimes isolated sclereids occur in places where they do not seem to be of any use, for example, the stone cells that occur in the fruit of the pear. In the petiole of the water lily leaf peculiar star-shaped or irregularly branched sclereids are found, their branches projecting into the large air spaces (Fig 9).

Collenchyma cells occur in many herbaceous stems, in petioles, and in young woody stems, usually just inside the epidermis. They are living cells, often contain chloroplasts, and may perform various functions besides those of mechanical tissue.

As a rule mechanical tissues are arranged in the plant in what seems to be the most efficient way. A vertical stem needs to have mechanical tissue placed where it will produce stiffness and prevent the stem from being too easily bent over by the wind. Now, when a vertical column is bent over, if it does not break, there must be a stretching on one side and a compression on the other. Both the compression and the stretching decrease toward the center until they become zero at the center of the column. Mechanical tissue right at the center, therefore, would not produce stiffness and it is a well known fact that mechanical tissue is very seldom found at the center of a stem. The center is filled with pith and the mechanical tissue is near the outside. Furthermore, it is well known to mechanical engineers that the most economical way to construct a column, that is, the way to get maximum strength in proportion to the material used, is to make it hollow but with a wall whose thickness is equal to about one-seventh the total diameter of the column. We find that many herbaceous stems closely conform to this mechanical principle by having the layer of supporting tissue equal in thickness to about one-seventh the diameter of the stem. Stems that are square, like those of many mints, often have most of the mechanical tissue in the angles and this is, of course, the very best place for it (Fig. 10).

Roots, on the other hand, do not need to be stiff. They need rather to be able to resist a pull and, since the pull is not always straight, they need to be able to bend without breaking. Accordingly we find that the mechanical tissue of roots is often largely near the center and that there is a thick cortex of thin-walled cells.

As in the case of conducting tissues the chief factor influencing the

development of mechanical tissue is water, or rather, lack of water. Many submerged water plants are almost entirely without mechanical tissue. Such plants may entirely collapse as soon as removed from the water. All seed plants that grow out of the water, however, have some mechanical tissue and this tissue reaches its maximum development in plants growing in desert regions.

20. **Protective Tissues.**—The greatest danger to which most land plants are subjected is too great a loss of water. While roots are better protected than most stems by virtue of their position, stems are better protected structurally than any other plant parts except seeds. The most important protective tissues of stems are the epidermis in herbaceous and young woody stems and cork in older stems. The epidermis ordinarily consists of a single layer of cells the outer walls of which are water-proofed by a deposit of cutin making up what is called the cuticle. Cutin is probably never deposited except on walls that are exposed to the air. The presence of air, however, is most likely an indirect factor, the direct factor being evaporation or desiccation since the cuticle is most strongly developed where there is free exposure in dry situations

In perennial stems the epidermis usually becomes ruptured during the second or third years and its function is taken over by a complex of tissues commonly called bark. Bark consists largely of phlœm and cork and it is the cork that makes it an efficient protective layer. Cork is a tissue the cell walls of which have been water-proofed by a deposit of suberin. The efficiency of suberin as a water-proofing substance is well known through the use of commercial cork, obtained from the bark of the cork oak, for bottle stoppers and many other purposes. Just as in the development of cuticle, the chief factor in the formation of cork seems to be desiccation. The initial step in cork formation is probably always a cutinization or suberization of walls, usually in the presence of air, which blocks the flow of sap and results in an accumulation of food. This accumulation of food brings about the formation of a growing tissue called a cork cambium which produces the cork tissue.

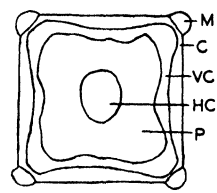


FIG. 10.—Diagram of a mint stem showing mechanical tissue at the angles. *M*, mechanical tissue; *C*, cortex; *VC*, vascular tissue; *HC*, hollow center; *P*, pith.

21. **Stem Habits.**—In plants with foliage the greatest loss of water takes place through the leaves. For this reason the various habits of growth and of foliage display result in varying degrees of protection from excessive loss of water. From this point of view woody plants may be classified as follows:

(*a*) *Tropical Evergreen Trees and Shrubs.*—These are the only plants that can be said to have unrestricted foliage display. They grow in the rain forests of the tropics where the uniform climate and ever abundant moisture make protection unnecessary. The conditions for growth in such a place are in many respects ideal and the vegetation is very luxuriant. The stems of the bamboo which grow in these forests are among the most rapid growers known. They sometimes grow nearly a foot in one day. On the other hand the great luxuriance of the vegetation brings about an intense competition for space.

(*b*) *Sclerophyllous Evergreen Trees and Shrubs.*—Sclerophyllous evergreens are those in which the epidermis of the leaves is composed of thick

walled (sclerenchyma) cells with a very heavy cuticle. Such an epidermis makes the leaf stiff and leathery. Sclerophyllous plants are of two general types. In regions having hot dry summers and warm wet winters, as in some parts of southern California, the sclerophyllous vegetation has broad flat leaves. Examples of this type are the holly, the live oak and the olive (Fig. 11). In regions with cold winters, on the other hand, we find sclerophyllous plants with the familiar needle-shaped leaves of the pines and spruces. In either case the advantage of the sclerophyllous habit is that with the protection afforded by the heavy epidermis these plants are able to display their foliage at all times and so to carry on photosynthesis throughout the year. At the same time there is the disadvantage that this type of leaf, which effectually reduces the rate of transpiration, also reduces the rate of gas exchange and so the rate of photosynthesis. The plants, therefore, are never able to manufacture food so rapidly as can the tropical evergreens.

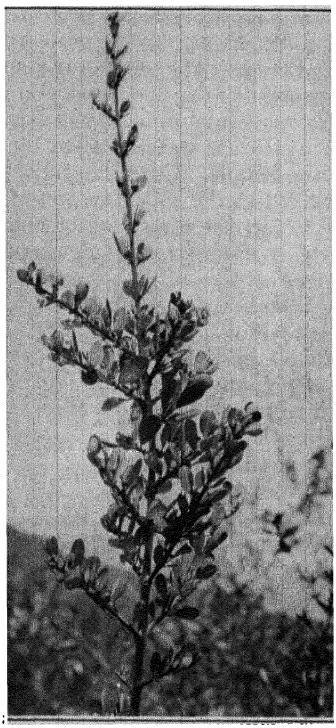


Fig. Alto, California. A broad leaf sclerophyll. (Photograph by W. S. Cooper.)

(*c*) *Leafless Evergreen Trees and Shrubs.*—These plants are still better protected than the sclerophyllous plants because the surface from which water may be lost is so very greatly reduced. Since they have no leaves all food manufacture has to be done by the stems and the surface for inter-change of gases for this work is also greatly reduced. Such plants cannot manufacture carbohydrates rapidly and so cannot grow rapidly. Examples of leafless evergreen trees are the giant cactus and other large cacti of the American deserts and the large spurges of the African deserts (Fig. 12).

(*d*) *Deciduous Trees and Shrubs.*—Woody plants that drop their leaves at the beginning of a dry or a cold (physiologically dry) season are said to be decidious. Such plants, during the favorable seasons, are as well fitted for maximum efficiency in food manufacture as are the tropical evergreens, while during the unfavorable seasons, they are better protected than any of the evergreens except, perhaps, some of the leafless ones. These of course are obvious advantages. On the other hand deciduous trees and shrubs are at some disadvantage in that they have to expend a lot of energy in constructing an entirely new set of leaves at the beginning of each growing season, and, also, in that they have absolutely no chance to manuacture any carbohydrates during the unfavorable season even though there may occur some very favorable days.

(*e*) *Evergreen Herbs.*—The distinction between shrubs and herbs is

rather artificial but is ordinarily based on the presence or absence of woody tissue in aërial stems. Thus perennial plants whose stems are entirely at or below the surface of the soil are usually classed as herbaceous even though their stems may contain some woody tissue. On the basis of such a definition there are various sorts of evergreen herbaceous plants. Some, as the wintergreens, have sclerophyllous leaves while others, as hepatica and dandelion, have leaves that are not protected by the sclerophyllous structure. In all cases these herbs are better protected than the corresponding evergreen trees and shrubs because of their low stature, and many of them grow in places where they receive some protection from fallen leaves of other plants or from a covering of snow.

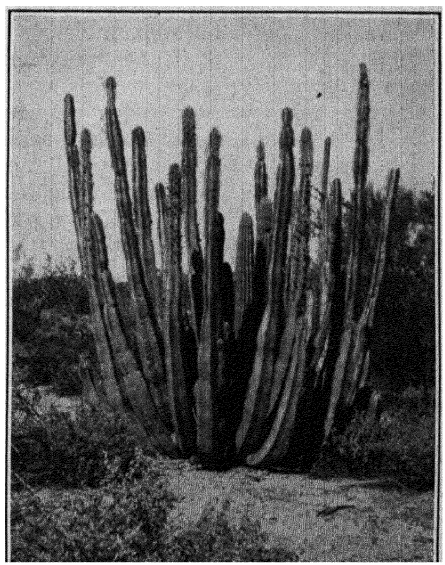


FIG. 12.—*Lophocereus sholtii*, a leafless evergreen. Organ Pipe Cactus National Monument, Arizona.

(*f*) *Deciduous Herbs.*—These are perennial plants in which all aërial parts die at the beginning of an unfavorable season. In some, as the bloodroot (*Sanguinaria canadensis*), only leaves are deciduous but in a greater number there are aërial stems which also die down to the ground each year. In connection with these latter it is proper to speak of stem fall as well as leaf fall. These plants, since they live through the unfavorable season as underground structures, are exceedingly well protected, but they have a considerable amount of construction work to do at the beginning of each growing season and, of course, they cannot display their foliage as efficiently as plants with perennial aërial stems.

(*g*) *Annual Plants.*—Annual plants are better protected during the unfavorable seasons than any other kinds because they live through those seasons only as seeds. During the growing season, however, these plants are practically without protection, but this is not disadvantageous. The

chief disadvantage of the annual habit is the necessity of reconstructing the entire plant each year.

22. **Stems as Storage Organs.**—Stems are nearly as important as storage organs as are roots. One of the most conspicuous structural characteristics of the stems of water plants is the presence of large air spaces where oxygen and carbon dioxide accumulate in considerable quantities. On the other hand, the cacti and many other plants that grow in places that are either physically or physiologically dry are characterized by fleshy stems which accumlate water. Such stems are spoken of as being succulent.

Food accumulates in greater or less quantities in practically all sorts of stems. It is found mostly in the parenchyma tissues of the cortex, medullary rays, pith, and wood. This food consists largely of carbohydrates, chiefly starch. In woody stems, especially, much of the starch is changed to sugar during cold weather so that the amount of sugar increases and the amount of starch decreases as the winter season progresses. Underground stems obviously have the same advantages as roots as storage organs.

Some families of plants are characterized by the presence of a milky juice called latex. This is usually white though in some cases it is some other color. The latex is entirely different from the sap of the plant and occurs in special latex receptacles. These receptacles differ in different kinds of plants. In the bloodroot and in the convolvulus and soapwort families the latex is found in single enlarged cells called latex sacs. These are usually arranged in longitudinal rows but they are not fused. In some members of the poppy and composite families the latex sacs become fused together either longitudinally only or, especially in the composites, both longitudinally and laterally. Thus a sort of circulatory system of latex vessels is produced. Structures such as these that are formed by the fusion of a number of cells are called syncytes. The mushroom genus *Lactarius* also has latex vessels of the syncyte type. Finally in the spurges and milkweeds the latex vessels are cœnocytes. This means that each latex vessel is composed of several cells which, however, have never been separated from each other by walls so that the vessel seems to be a single large cell with several nuclei. It starts as an ordinary cell in the embryo of the plant. This cell elongates, becomes multinucleate (cœnocytic), branches, and penetrates the tissues of the plant like a parasite until it finally forms a sort of circulatory system extending from one end of the plant to the other.

Very little is known about the function of latex and the probability is that it has no definite function. It is not characteristic of plants that grow in any particular kind of environment. While a majority of plants with latex are found in dry climates, many occur where the water supply is adequate and some even grow in the wet rain forests of the tropics. It does not appear, therefore, that the latex is of any particular advantage. There is usually found in the latex some of practically everything that is produced in the plant, including foods of various kinds and waste materials. This indicates that the latex receptacles are in a sense catch-all reservoirs into which anything that is produced in excess of demand may be dumped. In some species of spurge very interesting rod-shaped or soup-bone-shaped starch grains are found in the latex receptacles.

23. **Variations in Stem Form.**—The stems of different kinds of plants vary very greatly in shape and size. All gradations are found from a small fraction of an inch to 20 or more feet in diameter and from less than 1 inch

to 300 or more feet in length. These differences are to a large extent inherited. There occur also very great variations in the stems of individuals of the same species which are due to the external factors of the environment. A sugar maple tree growing alone in the open usually has a relatively short main stem with numerous large branches well down toward the base while an individual of the same species growing in a dense forest has a long trunk with no branches on the lower half (Fig. 13). The same statement is true of most species of trees and a similar statement would be true of many herbaceous plants.

The two factors that seem most likely as causes of these stem variations are light and moisture. Light has usually been regarded as having a retarding effect upon growth, and especially upon elongation, while absence



FIG. 13.—Sugar maple forest showing long trunks with the first branches far from the base.

of light favors elongation. Recent work has cast considerable doubt upon this general statement concerning light and in any case it is certain that light has often been overemphasized as a factor affecting the elongation of stems.

Moisture is much more important in this respect. Nearly all seed plants absorb water through their roots and lose water by transpiration from their leaves and stems. In general there must be a balance between these two processes and the height to which any plant can grow is limited by the height to which it can transport water rapidly enough to counterbalance the loss by transpiration. This fact is strikingly shown by certain water plants with floating leaves in which the conducting system is ordinarily poorly developed. There is, of course, no transpiration below the surface of the water but above the surface transpiration is rapid. The length of the stems of these water plants is thus governed by the depth of the water and very great variations in the same species are sometimes found.

Somewhat comparable to the variation in stem length in water is the elongation of certain kinds of stems that are being gradually buried by the sand of a moving sand-dune. Some woody plants, such as willows, poplars and dogwoods, grow very rapidly as the sand piles up around them and the stems may become several times as long as normally. Such plants, however, produce adventitious roots from the stem in the sand so that the distance from the top of the plant to the nearest roots, and thus to the water supply, is never excessive.

The dwarfing of plants is likewise to be explained largely on the basis of a balance between absorption and transpiration. All desert plants are more or less dwarf, that is, none of them grow very tall, but the most typical dwarf plants are found in Arctic and Alpine regions. In such places the low temperature of the soil makes absorption slow and difficult while the strong, dry winds tend to increase the transpiration rate. The result is

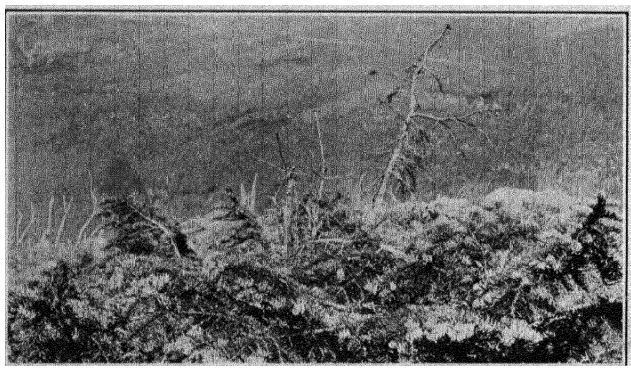


FIG. 14.—Engleman spruce dwarfed at timber line and showing upright branches killed during the winter.

that some plants which under more favorable conditions might develop into tall trees never become more than a few inches high although they may live for several hundred years. In many Arctic and Alpine regions the height of the woody plants is controlled largely by the depth of the snow. They grow upward as far as they can during the favorable season but during the winter all parts that project above the snow, and so are unprotected, are killed through desiccation (Fig. 14).

Tubers, such as those of the potato and many other plants, are very much shortened and thickened stems and are, therefore, somewhat comparable to dwarf stems. The causes of tuber formation are not well understood. Although tubers are most abundant in dry regions yet many tuber-producing plants grow where there is an abundance of water so that desiccation cannot be the only cause of tuber formation, and, until a great deal more experimental work has been done, it is not poss ble to go beyond the unsatisfactory statement that the production of tubers is an inherited characteristic of the plants on which they are produced.

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CHAPTER IV

THE ECOLOGY OF LEAVES

THE principal function of leaves is food manufacture. Many leaves are modified to perform other special functions and in some plants stems are more important than leaves as food manufacturing organs. In some cases, furthermore, leaves are reduced to mere scales and perform no function at all. As a general rule the greatest danger to which leaves are subjected is excessive transpiration and for this reason the structure of the leaves is in a sense a compromise between what would be best as a photosynthetic organ and what is necessary to safeguard against too rapid a loss of water.

24. **Structure and Arrangement of Tissues.**—The tissues of the leaf that vary most with variations in the environment are those that contain chlorophyll. Variations in the fibrovascular bundles and their sheaths, so far as our present knowledge of them goes, do not seem to be of much ecological significance.

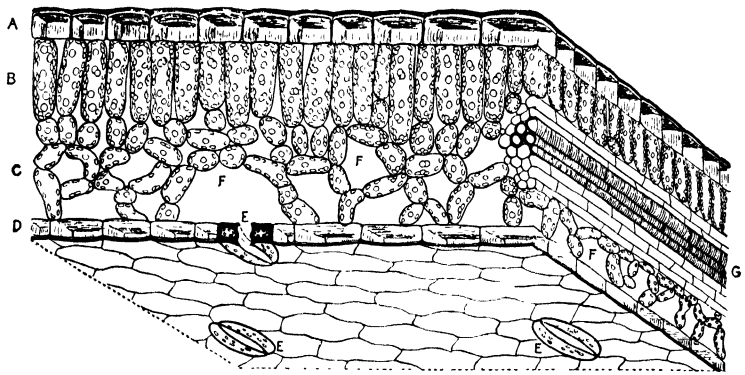


FIG. 15.—Sectional and surface views of an ordinary leaf. *A*, upper epidermis; *B*, palisade layer; *C*, spongy layer; *D*, lower epidermis; *E*, stoma; *F*, air space; *G*, vein. (From Sinnott's Botany—Principles and Problems, New York, McGraw-Hill Book Company, Inc.)

The majority of plants that grow in exposed places where there is an adequate supply of water have leaves with no chlorophyll in the epidermis except in the guard cells of the stomata, but with chlorophyll in all other cells except those of the fibro-vascular bundles and their sheaths. The tissues that contain chlorophyll are called, collectively, chlorenchyma. In the typical leaf of which we are speaking the upper half of the chlorenchyma is made up of elongated cells with their long axes perpendicular to the epidermis. These cells because of their shape are called palisade cells. The lower half of the chlorenchyma, on the other hand, is made up of irregularly-shaped parenchyma cells and has numerous intercellular spaces. For this reason it is called spongy parenchyma (Fig. 15).

If now we examine the leaves of plants growing in progressively wetter places we shall find a progressive decrease in the amount of palisade tissue and a progressive increase in spongy parenchyma until in the case of leaves

which are submerged in water there is no palisade tissue at all, the chlorenchyma being made up entirely of spongy parenchyma with very large intercellular spaces (Fig. 16). The leaves of plants that grow in wet places, and especially in dense shade, often have chlorophyll in the epidermal cells and for this reason are dark green in color.

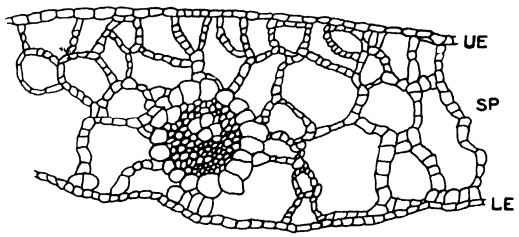


FIG. 16.—Section of a leaf of a water plant, pondweed (*Potamogeton*). *UE*, upper epidermis; *SP*, spongy tissue; *LE*, lower epidermis.

On the other hand if we examine the leaves of plants growing in progressively drier places we shall find that there is a progressive decrease in the amount of spongy parenchyma and a progressive increase in the amount of palisade tissue until in the case of plants growing in very dry places there is no spongy parenchyma at all and the chlorenchyma may consist entirely of palisade tissue (Fig. 17). There are, of course, many exceptions to these general conditions, especially in dry regions where very great variations in leaf structure occur.

There are three general types of these exceptions that are sufficiently common to be worthy of mention here, although this by no means exhausts the list. One of these is a leaf in which there is palisade both above and below with some spongy parenchyma between. This is most likely to be found in leaves that have a vertical or nearly vertical orientation so that the two sides of each leaf are about equally exposed. A second type is that found in plants with succulent, orfleshy, leaves. In these the chlorenchyma is oftenreduced to a few layers of cells and the larger part of the leaf tissue is made up of colorless water storage cells. This tissue is sometimes next the epidermis and in other cases occupies the central portion of the leaf. A convenient term that is often used to designate all of the internal tissues of a leaf, with the exception of the veins, is mesophyll. Thus in a succulent leaf the mesophyll is partly chlorenchyma and partly water storage tissue. In Arctic regions and at high elevations on mountains there is a third common type of leaf in which the mesophyll is made up entirely of chlorenchyma which can be said to be neither palisade nor spongy tissue. Rather it is a very compact parenchyma tissue of rounded or angular cells.

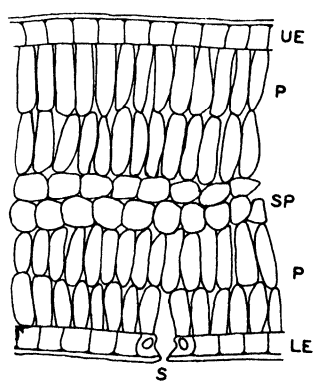


FIG. 17.—Section of a leaf of a desert plant, mesquite (*Prosopis velutina*), *UE*, upper epidermis; *P*, palisade tissue; *SP*, spongy tissue; *LE*, lower epidermis; *S*, stoma.

25. **The Causes of Palisade Development.**—The two factors that have usually been thought to have most influence on palisade development are light and transpiration. The amount of palisade tissue often varies considerably according to the relative exposure of the plant. A plant of wild lettuce (*Lactuca scariola*), for example, which has grown in a fully exposed place has relatively thick leaves, the mesophyll of which is all palisade tissue, while a plant of the same species, which has grown in deep shade, may have leaves only a third as thick as the former plant and with scarcely any palisade tissue. These different types of leaves from the same species are spoken of as sun leaves and shade leaves respectively. In the case of trees, such as the maple, it is often possible to collect leaves from the same individual plant which have the structural characteristics of typical sun and shade leaves; the sun leaves being taken from the south side of the tree where they are fully exposed to light and the shade leaves from the north side of the tree near the base where they are protected from the sun during practically the whole day.

The fact that palisade tissue is best developed in leaves that are fully exposed to the sun has led to the belief that the significance of the palisade shape of cells is concerned with the protection of the chloroplasts from intense light rays. Although chlorophyll is produced only in light and must have light in order to function, yet light that is too intense destroys chlorophyll by causing its disintegration. In a leaf that has been exposed to direct sunlight for some time the majority of the chloroplasts are found to be arranged along the walls that are perpendicular to the surface where they have a measure of protection from the direct rays of light. On the other hand, a leaf from the same species, but which has been for some time in diffuse light, usually shows many chloroplasts along the walls that are parallel to the surface where they may receive a maximum amount of the incident light. A similar response to varying intensities of light is seen in the alga, *Mougeotia*, in which there is a single rectangular, plate-like chloroplast in each cell. While this plant is in diffuse light the chloroplast of each cell ordinarily presents its broad side to the direction of the incident light but when the plant is placed in direct sunlight the chloroplast makes a half turn so that its edge is toward the light.

Although the evidence is strong that light is a factor in the development of palisade tissue yet its influence in this respect has probably often been overemphasized. When a plant is fully exposed to light it is also exposed to rapid transpiration. It has already been shown that palisade development reaches its maximum in dry land plants where transpiration, in proportion to the rate of absorption, is most rapid. The probability that transpiration is the principal cause of palisade development is also shown by many water plants that have both submerged and aërial leaves. In these cases there is an abrupt change in the degree of palisade development at the surface of the water, the aërial leaves having much palisade tissue and the submerged leaves none. The change in light intensity here is, of course, not abrupt while the change in transpiration rate is. Here, therefore, as in so many other cases, water appears to be the most important factor.

26. **Structure as a Basis for Classifying Leaves.**—Broad leaves, as opposed to needle-shaped leaves and reduced or scale-like leaves, are often classified into four groups on the basis of the structural differences discussed

in paragraph 24. Leaves which have palisade tissue toward the upper side and spongy tissue toward the lower side, so that the two sides of the leaf are very different in their photosynthetic and other relations, are called diphotophylls (Fig. 15). Those that have palisade tissue on both sides with spongy tissue between, so that the two sides of the leaf are essentially the same, are called diplophylls, meaning double leaves (Fig. 17). The term spongophyll is used for a leaf having spongy parenchyma all the way through (Fig. 16), while leaves that have compact tissue all the way through, whether it is composed of palisade cells or not, are called staurophylls.

27. **Air Spaces and Stomata.**—Gaseous exchange between leaves and the atmosphere takes place in connection with three physiological processes: respiration, photosynthesis and transpiration. By far the greatest volume of gas (water vapor) is involved in transpiration and by far the smallest volume in respiration, while photosynthesis is intermediate in this respect. This interchange of gases is rendered possible through the presence of stomata in the epidermis and intercellular air spaces within the leaf. There is usually a comparatively large air chamber beneath each stoma and this leads into intercellular spaces of varying sizes that form a connected system of passageways throughout the interior of the leaf. The cell walls that are adjacent to these passages and chambers are thin and are always wet, and the gases diffuse inward and outward through the protoplasmic membranes of the cells while in solution in the water.

The primary cause of the development of air spaces is probably just the opposite of that causing the development of palisade tissue, that is, lack of transpiration. Air spaces are always numerous and comparatively large in the spongy tissue of diphotophylls and they reach their highest development in submerged spongophylls and in the stems and petioles of submerged water plants. On the other hand, air spaces are small and inconspicuous in palisade tissue and are least developed in the staurophylls and succulent leaves of plants of dry and cold regions.

In submerged water plants the air spaces often exceed the tissues themselves in volume. In some cases they are undoubtedly of considerable importance as gas reservoirs. Oxygen is commonly present in abundance in ordinary lakes, ponds and streams but in swamps and other stagnant bodies of water it is present only in very limited amounts. For this reason, if there were not a supplementary supply to draw upon, the plants often would have difficulty in getting enough of this gas for respiration. But the oxygen that is liberated in photosynthesis during the day accumulates in the air spaces and is available for respiration during the night as well as in the daytime. Carbon dioxide is usually present in water in abundance so that its accumulation in the air reservoirs for purposes of photosynthesis is probably never really needed.

In some cases, also, the air spaces serve the function of giving buoyancy to the plant or plant part. For example the winter buds of such plants as the duckweeds and the bladderworts, when they are first formed during summer and autumn, are lacking in air spaces of any considerable size. They are heavier than water and in autumn they break off from the parent plants and sink to the bottom. In spring large air spaces develop in the buds and when these become filled with gases they cause the buds to rise to the surface of the water where they develop into mature plants. Water

hyacinth (*Eichhornia*) plants are caused to float and to hold their leaves just above the surface of the water by the large air spaces in an enlarged portion of each petiole. A somewhat similar function is performed in the case of some filamentous algæ, such as *Spirogyra*, by the bubbles of oxygen that become entangled in the mass of filaments. A rain storm will wash out this oxygen and cause the plants to sink to the bottom but with the

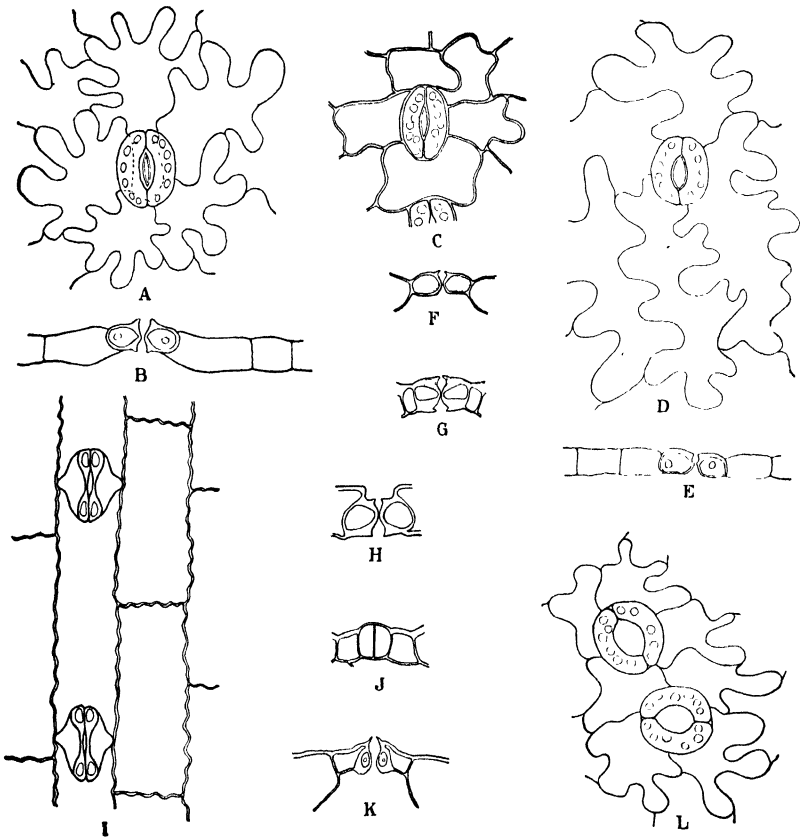


FIG. 18.—Stomata. *A*, *B*, from *Solanum tuberosum*, in face view and cross-section; *C*, from *Pyrus malus*; *D*, *E*, from *Lactuca sativa*; *F*, from *Medeola virginica*; *G*, from *Aplectrum hyemale*; *H*, from *Polygonatum biflorum*; *I*. *J*, *K*, from *Zea Mays*; *I*, face view; *J*, cross-section through end of stoma; *K*, median cross-section; *L*, from *Cucumis sativus* (*F*, *G*, *H*, and *J*, after Copeland). (From Eames and McDaniels—Introduction to Plant Anatomy, New York, McGraw-Hill Book Company, Inc.)

return of sunlight photosynthesis begins and the oxygen that is liberated soon causes the plants to rise again to the surface. This phenomenon is of considerable advantage to these plants since it brings them into a more favorable position with respect to light and to the necessary gases as well.

28. **Structure and Arrangement of Stomata.**—A stoma is a small slit-like opening through the epidermis (Fig. 18). It occurs between two modified epidermal cells, called guard cells, which, in surface view, appear kidney-

shaped and have their ends in contact. In cross-section the guard cells are seen to vary considerably in different kinds of plants. They are usually smaller than the other epidermal cells and in some cases the walls are uniformly thickened while in others they are unevenly thickened. In some guard cells the walls next the aperture are thicker than those on the opposite sides of the cells, while in others the outer and inner walls are thick and the lateral walls thinner. Many other modifications are found although the general structural features are practically the same for all stomata.

Most stomata have some capacity for opening and closing. This is done automatically by the increase or decrease of the turgidity of the guard cells. An increase in turgidity causes the cells to expand in the direction perpendicular to the surface. This straightens somewhat the walls that bulge out to form the aperture and so opens up the stoma. As the cells dry out the turgidity decreases, the cells collapse somewhat, and the walls that form the aperture come nearly or quite together, thus closing the stoma and greatly reducing the amount of water that may be given off by transpiration.

The arrangement of the stomata seems to be largely a matter of inheritance rather than environment. In the majority of monocotyledonous plants the stomata are arranged on the leaves in more or less definite rows and have their long axes extending lengthwise of the leaves. This is true also of some dicotyledonous plants that have long narrow leaves. In most dicotyledonous plants, however, the stomata are scattered irregularly and have their long axes extending in various directions.

The question as to whether stomata shall develop at all, however, is, to a certain extent at least, a matter of environment. The majority of plants that have their leaves fully exposed to the sun have stomata on the lower surfaces of their leaves only. This is true of most trees and many herbaceous plants although there are exceptions. Most grasses that grow in exposed places, for instance, have stomata only on the upper surface, but this is the surface that is most protected in dry weather when the leaves of these plants roll up. Plants that grow in the shade, on the other hand, usually have stomata on both surfaces. In water plants, leaves that are submersed are without stomata while leaves of the same plant that are above the water may have stomata on both sides. Floating leaves commonly have stomata on the upper surface only.

29. **Protection from Excessive Transpiration.**—It used to be said frequently that transpiration is a necessary evil. Certainly excessive transpiration is the greatest danger to which most plants are subjected. Its necessity has been considered as due to the fact that there must be openings for the interchange of gases in order that respiration and photosynthesis may be carried on and if there are openings of any sort it is not possible to entirely prevent transpiration. In other words, it would be a simple matter to construct a leaf that would not allow any transpiration but such a leaf would be useless as a photosynthetic organ. It is now believed, however, that transpiration is not entirely an evil but is often of considerable importance to the plant because of its cooling effect. It takes a considerable amount of heat to evaporate water and, just as evaporation of water from a canvas water-bag keeps the water inside the bag cool, so transpiration from a leaf prevents the internal temperature from going so high as to prove disastrous to the protoplasm. This is, of course, especially true of leaves that are exposed to the full light and heat of the sun since a great

deal of radiant energy is absorbed under such conditions. In spite of the obvious necessity of transpiration, however, the presence of an adequate amount of water within the plant is so vital that the possibility of losing it faster than it can be absorbed is an ever present and very real danger. For this reason we find a variety of structural modifications that appear to be designed to prevent excessive transpiration.

The stomatal movements described in paragraph 28 tend to control the rate of transpiration. In many cases, also, the stomata themselves are protected in one way or another. Sometimes they are merely sunken below the level of the epidermis, which protects them from air currents. Sometimes, as in the oleander, several stomata are grouped within a pocket-like depression which is clothed with hairs. Again, they may have extra well developed outer and inner vestibules, or a labyrinthiform passageway in place of the simple slit. Any of these devices tend to retard the exit of water.

In practically all leaves that are exposed to the air the epidermis itself is covered with a layer of cutin which renders it so nearly water-proof that transpiration is confined almost entirely to the stomata. Sometimes the cutin is reinforced, or in some cases replaced, by a coating of wax or of resin. This not only retards transpiration directly but also tends to check rapid heating of the leaf, which in turn influences the rate of transpiration. In the case of floating leaves, such as those of the water lily, the waxy covering has another use in that it prevents the surface from becoming wet. This facilitates the interchange of gases for respiration and photosynthesis by preventing the stomata from becoming clogged with water.

The surfaces of many leaves, as well as stems and other plant parts, are often covered with hairs. These may be simple or branched. Usually the simple hairs stand perpendicular to the surface but in a few cases, as on the bud scales of Norway maple, they are closely appressed, or, in other cases, as on the stems of Spanish moss (*Tillandsia*), they are scale-like and overlap like the shingles of a roof. The common mullein (*Verbascum thapsus*) has multicellular hairs that are much branched and form a woolly covering of the leaves. These various kinds of hairs have been thought to be rather efficient organs of protection against excessive transpiration. In many cases they doubtless do afford some protection, especially in windy weather, but experiments and observations that have been made seem to indicate that their efficiency in this respect has often been over-emphasized.

One of the most efficient means of protection against excessive loss of water is by reducing the transpiration surface. Most efficient of all, perhaps, is the periodic reduction brought about by leaf fall which will be discussed in paragraph 30 Many plants, however, have a permanently reduced transpiration surface The extreme condition is represented by leafless plants in which the photosynthetic function is performed by stems Among plants with leaves there are all variations from water plants with leaves that are only one or two cells thick to plants which have leaves that are freely exposed and which are round in cross-section and so have a minimum of surface in proportion to volume. Of course any reduction in transpiration surface reduces also the photosynthetic surface but the condition of each plant represents a compromise between two major needs—one for free gaseous exchange for photosynthesis and the other for protection from excessive loss of water.

Some plants, especially members of the legume family, exhibit interesting

leaf movements commonly called sleep movements. These consist of a closing up of the compound leaves during the night or sometimes during the hottest part of the day in time of drought. The leaves of the sensitive plant (*Mimosa*) not only close during the night but they close quickly whenever anything comes in contact with them. This movement is brought about by a mechanism at the base of the petiole (and also at the base of each leaflet) called the pulvinus. The decrease in turgidity of the cells in the pulvinus as the water suddenly passes from them into the adjoining intercellular spaces causes the leaves to close. They slowly resume their former position when the water reënters the cells. In some cases, as in bean leaves, the closing is due to an increase of turgidity which is greater on one side of the pulvinus than on the other. No satisfactory explanation of the causes of these increases and decreases of turgidity has yet been made. The closing of leaves during drought reduces the exposed surface and probably aids in checking water loss. The more common cases of night closing, however, and the sudden movements of Mimosa leaves are probably of no real benefit to the plants.

30. **Leaf Fall.**—A deciduous plant is one that drops all of its leaves at some time during the year, usually at the beginning of a cold or a dry season. Contrasted with these are the evergreen plants which drop their leaves only after a new crop has been produced and so always have some green leaves. In any case the fall of the leaf is brought about directly by the formation of a special separation layer, called the absciss layer, at the base of the petiole. The absciss layer consisting of two or more thicknesses of very thin-walled cells is formed during the development of the leaf. At the time of leaf fall the walls of these cells become softened and finally disintegrate. A gentle wind or the weight of a film of dew is then enough to cause the leaf to fall. In some trees, especially in the beech and some of the oaks, the absciss layer is very imperfectly formed and the leaves therefore hang on during the greater part of the winter. On the other hand, in some compound leaves an abscis layer forms first at the base of each leaflet and these drop off. Later the petioles also drop. In the bald cypress the abscis layer forms at the base of a twig and the entire twig, with the leaves on it, falls.

The cause of the formation of an abscis layer is not known. In regions with periodical dry seasons it is probably largely desiccation brought about by increased transpiration without any increase in rate of absorption. In regions with cold seasons, too, the cause may be desiccation since, for plants, a cold season is a dry season, that is, it is a season when transpiration continues but absorption is very greatly reduced because of the low temperature of the soil. Contrary to a rather common belief frost does not ordinarily cause leaf fall. In fact an early frost may delay leaf fall by interfering with the development of the abscis layer.

31. **The Forms of Leaves.**—Leaf form is to a large extent a matter of inheritance. So true is this that very many species of plants are easily identified by their leaves alone. To be sure there may be considerable variation in the leaves of an individual plant. The first leaves, or cotyledons, are always very different from the later ones. In the garden bean the second pair of leaves as well as the cotyledons are simple while the later ones are compound. A single mulberry tree may show all variations from an unlobed leaf to one that is very much lobed. The leaves of a single plant may also vary as much as 100 per cent or more in size. But with all

this variation a mulberry leaf never looks like an elm leaf. Inheritance is too potent a factor for that.

Nevertheless, there are some variations of leaf form that are more or less characteristic of certain types of environment. Plants that grow where there is an adequate supply of water have relatively thin and broad leaves, while plants growing where there is difficulty in getting sufficient water have smaller and thicker leaves. Furthermore, it has been shown by experiment in the case of many species that the same individual will develop larger and thinner leaves when grown in a moist environment than when grown in a dry environment. These facts seem to indicate that here again water, perhaps transpiration, is a very influential factor, though probably it is not the only one.

The influence of water on leaf form is brought out even more strikingly in the case of many water plants. In some of these, such as the mermaid weed (*Proserpinaca palustris*) and lake cress (*Radicula aquatica*), the aërial leaves, which are subjected to transpiration, are nearly or quite entire, while the leaves that are in the water are very much lobed or finely dissected. The water fern (*Salvinia natans*) has broad floating leaves that do the work of photosynthesis and very much dissected leaves that hang down into the water like roots and serve as absorbing organs. In these cases there can be no question of the influence of water on the form of the leaves.

32. **Leaves as Storage Organs.**—Food storage in leaves is usually only temporary. Permanent storage of food in these organs would seriously interfere with their photosynthetic function. Food usually accumulates in the leaves while it is being manufactured during the day because it is synthesized more rapidly than it can be transported to other parts of the plant. The transporation continues during the night, however, so that by morning the leaf is ordinarily without stored food.

Nevertheless, there are some plants whose leaves are the chief organs for permanent food storage. The century plant, which is a species of *Agave*, is a well-known example of such a plant. (Fig. 19). This plant grows vegetatively for from six to fifteen or twenty years, storing up food and water in its large, succulent leaves. It then sends up a flowering shoot which grows very rapidly and upon which a large number of flowers and fruits develop and mature. By the time this has been accomplished, the leaves have been drained of their stored materials and the plant dies.

Water accumulation in leaves, however, is often of considerable importance. This is especially true of plants with fleshy or succulent leaves (Fig. 19). Such plants are characteristic of some desert regions and of salt marshes and other saline areas where, because of the high concentration of the soil solution, absorption of water is difficult. The retention of water by succulent leaves, which in some cases is remarkably efficient, is accomplished by one or the other of two general methods. The first of these is by strong cutinization, layers of wax, or other modifications of the epidermis. The other method consists in maintaining a very high concentration of the cell sap, which effectively reduces the evaporation rate. Some succulent leaves when removed from the plant and freely exposed do not become entirely dry for weeks.

Crystals of calcium oxalate and sometimes of calcium carbonate, are often stored in leaves as well as in stems. These are to be regarded as waste materials. Since a plant has no regular excretory organs it is sometimes

necessary to store up certain products of metabolism in the form of insoluble crystals in order to get them out of solution. The leaf would seem to be a good place to store such crystals because when the leaf falls the crystals are gotten rid of. Crystals stored in the cortex or bark of a perennial stem are also disposed of eventually as the bark sloughs off from the outside.

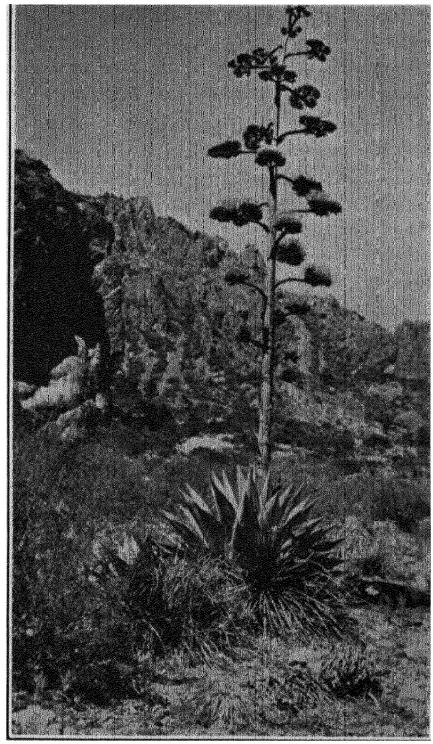


FIG. 19.—*Agave scabra*. A plant with succulent leaves. (Photograph by Dr. Omer E. Sperry.)

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CHAPTER V

SYMBIOSIS—DISJUNCTIVE

SYMBIOSIS means the living together of two or more unlike organisms, that is, organisms belonging to more than one species. It includes all such cases. While this is a broader definition than has been used by many authors it is the one that applied when the word was first introduced as a biological term and is considered the only one that is completely satisfactory. Any attempt to limit the definition of symbiosis leads one into the difficulty of trying to recognize lines of division between living phenomena where no lines exist. Hence it is much better to accept the definition as including all cases of the living together of two or more organisms of different species.

33. **The Classification of Symbiotic Phenomena.**—The various kinds of phenomena included under the term symbiosis are conveniently classified as follows:

I. Disjunctive symbiosis.
  1. Social
  2. Nutritive
    (*a*) Antagonistic
    (*b*) Reciprocal

II. Conjunctive symbiosis
  1. Social
  2. Nutritive
    (*a*) Antagonistic
    (*b*) Reciprocal

In disjunctive symbiosis the organisms concerned are not in actual contact, at least not all of the time, while in conjunctive symbiosis the symbionts are in actual contact throughout the time during which they are said to be in a state of symbiosis. Social symbiosis, whether disjunctive or or conjunctive, includes all cases in which dissimilar organisms are living together but without any direct food relation; that is, none of the symbionts derive food directly from the others. In nutritive symbiosis, on the other hand, one or more of the symbionts derives food directly from one or more of the other symbionts. Again, when only one or more but not all of the symbionts derive food from other symbionts, and these latter are in no way benefited but often injured by the relationship, the condition is said to be one of antagonistic nutritive symbiosis, but, when all of the organisms concerned obtain food or some other obvious benefit from the relationship, they are living in reciprocal nutritive symbiosis, either disjunctive or conjunctive. Examples of these various types of symbiosis will be discussed in succeeding paragraphs. Obviously our ability to properly place any given symbiotic phenomenon in the above classification depends entirely upon our knowledge of the relationship in question. In many cases our knowledge is still far from adequate.

34. **Social Disjunctive Symbiosis.**—This is the type of symbiosis in which the organisms concerned are not in actual contact, at least not all of the time, and in which there is no direct food relation. It includes, therefore, all of the ordinary interrelations of the various species of plants that are living together in any plant community, such as a forest, a swamp, or a meadow (Fig. 20). Since synecology is concerned almost entirely with these various kinds of plant communities they will constitute the subject matter of several later chapters and it will suffice here to point out

only a few of the social relations concerned. In a forest community, for example, the trees have very important symbiotic relations with all other plants in the forest. This comes about largely through the fact that the trees control to a large extent such factors of the environment as light, space relations, water supply, and to a certain extent available food materials.



FIG. 20.—A forest community with numerous kinds of plants living together in social disjunctive symbiosis.

Through this large measure of control of the environment they even determine what species of plants, and also what kinds of animals, may live in the forest. The social relations in such a community are in certain respects comparable to those of a human community where man controls the environment. There is usually a well-marked division of labor among individuals of a human community, some being engaged in supplying food,

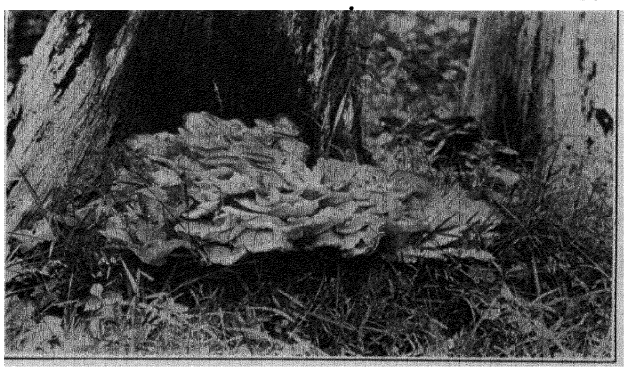


FIG. 21.—*Polyporus giganteus* hastening the decay of a stump.

others in supplying clothing or fuel, others in administering the law, etc. In the plant community there is a somewhat comparable division of labor among the various species, though not among the individuals of the same species. The function in the community of all individuals of the same species is the same, but some species have the function of manufacturing

food, some of supplying a ground cover to check evaporation of water from the soil, some to act as scavengers in getting rid of dead bodies (Fig. 21), etc. One important difference between the human community and the plant community, however, must be kept in mind. In the human community there are ordinarily more or less definitely organized activities carried on for the good of the community as a whole. In the plant community, on the other hand, there is no altruism. It is a case of every plant for itself. The activities of certain species do result advantageously for the community as a whole, but this is due to chance circumstances, and the activities would be carried on just as vigorously if they were resulting in harm to the community. This fundamental difference between the two communities, however, is the natural result of the presence of consciousness in the human species and the lack of it in plants, and as soon as we leave that fact out of consideration the two types of communities become strikingly similar.

Species in a plant community that are very different are often incidentally of very great service to one another. The trees, for example, furnish the shade necessary for some of the herbaceous plants and fungi, while the herbaceous plants furnish a living soil cover which at times prevents undue loss of the soil water which is needed in great quantities by the trees. The trees, likewise, as well as the shrubs, especially those near the border of the woods, serve as a windbrake which protects many smaller plants from the danger of too high transpiration rates.

The phenomenon of leaf fall, discussed in the preceding chapter, is of very great importance from the viewpoint of social disjunctive symbiosis since the fallen leaves form an efficient cover throughout the winter, thus greatly reducing evaporation from herbaceous perennial plants as well as from the surface of the soil. Closely connected with leaf fall, too, are the activities that bring about the decay of the fallen leaves. These are due mostly to bacteria and fungi. These bacteria and fungi are regular members of the community and are living in social disjunctive symbiosis with the higher plants. They are able to live in the community only as a result of the presence of the higher plants, and they render a distinct service to the community by preventing the accumulation of dead bodies and by releasing food materials through the decay of the organic matter.

35. **Antagonistic Nutritive Disjunctive Symbiosis.**—In this type of disjunctive symbiosis one or more, but not all, of the organisms concerned receive food from the other symbionts. A familiar example is the relationship between a grazing animal, such as a bison, and the grass upon which it feeds (Fig. 22). In exactly the same category, of course, is the interrelation between a herd of cattle and the grasses upon which the cattle feed, and a similar remark might be made about any species of herbivorous animals.

The interrelations between man and the plants that he cultivates for food are quite comparable to those between herbivorous animals and plants. These, therefore, also represent cases of antagonistic nutritive disjunctive symbiosis. Innumerable examples of this type of symbiosis between insects and plants might be cited. Only a few of the more interesting of these will be discussed in the remaining paragraphs of this chapter.

36. **Leaf-cutting Ants and Fungi.**—Sometimes when one is walking through a tropical forest he may chance to see a green line across the path in front of him. On stopping to observe the line he sees that it is in motion, and a closer inspection shows it to be composed of a large number of ants

each carrying over its back a green piece of leaf. These are leaf-cutting ants, often called umbrella ants because of their way of carrying the pieces of leaves over their backs. They have cut the pieces of leaves from some plant, probably a shrub, and are taking them to their nest. Often they entirely strip a shrub of its leaves within a few minutes. They will chew the pieces of leaves into a pulp and spread out the pulp on an area previosuly cleaned for the purpose. On this leaf pulp the ants plant the mycelium (or spawn) of a mushroom. The workers now take constant care of their mushroom garden, weeding out undesirable fungi, and producing, therefore, almost a pure culture of the fungus that was planted.

The fungus that is grown by the leaf-cutting ants is *Rozites gongylophora*, a toadstool-shaped mushroom. The ants, however, do not permit the

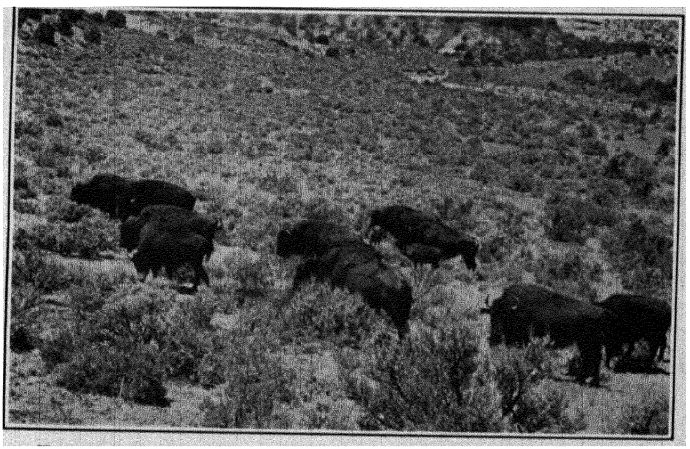


FIG. 22.—An example of antagonistic nutritive disjunctive symbiosis.

plant to produce mushrooms, which are its fruits. Cultivation for many generations, perhaps for centuries, has caused this fungus to produce abnormal vegetative structures just as many of the plants cultivated by man do. These abnormal structures consist of club-like, upward-projecting outgrowths of the mycelium and are called kohlrabies because their abnormal nature makes them comparable to the garden vegetable of the same name. The kohlrabies serve as food for the ants. This cultivation of mushrooms by ants is entirely comparable to the cultivation of vegetables by man and like the latter is an example of antagonistic nutritive disjunctive symbiosis.

37. **Termites and Ambrosia Beetles as Symbionts.**—Termites, commonly called white ants, cultivate fungi in a way comparable to that practiced by leaf-cutting ants. The termites, however, cultivate their fungi on excreta instead of leaf pulp. Several kinds of fungi have been identified from termite nests; species of *Xylaria*, *Collybia*, *Entoloma*, etc. The termites feed on the mycelium.

Still another somewhat similar symbiotic relationship is that between ambrosia beetles and fungi. The ambrosia beetles are wood-boring beetles as distinguished from bark-boring beetles. They bore tunnels into the

wood, sometimes rather simple and sometimes much branched. In these tunnels they plant the mycelium of a fungus. The fungi cultivated by the ambrosia beetles are not yet known but they probably are some of the lower fungi rather than mushrooms. The beetles feed upon the mycelium, which often grows so luxuriantly that it completely clogs up the tunnels, and beetles have been known to become imprisoned and to suffer death as a penalty for not being able to eat fast enough to gain an exit through their food supply.

38. **Insectivorous Plants.**—In all of the examples of antagonistic symbiosis so far discussed animal symbionts obtain food from plants. This condition is just reversed, however, in the case of a limited number of plants which have the power of digesting and absorbing animal food. These plants are called insectivorous or carnivorous plants. The best understood perhaps of these insectivorous plants is the sundew (*Drosera*). Several species of sundew are common in the bogs of the northern United States and Canada. *Drosera rotundifolia*, the commonest species, is a small plant with a rosette of radical leaves. In summer it sends up a stalk about 6 inches long which bears from one to two dozen small white flowers. The leaves are rounded or oval in shape, about a centimeter broad, and with hairy petioles of 2 to 5 cm. in length.

The leaves of *Drosera*, which are attractively red in color, are beset on the upper surface with glandular hairs which are rather short at the center of the leaf but progressively longer toward the outside. Each hair has on its knob-like end a sticky drop of semi-liquid substance which glistens in the sun like dew, thus giving the name, sundew, to the plant. When an insect, either by chance or attracted by the brilliancy of color or by the sweetish secretion, comes in contact with any of the hairs it sticks fast. The other hairs of the leaf now begin to bend inward toward the insect until a considerable number of them are in contact with it. The presence of the insect not only stimulates the hairs to bend inward but also to secrete protein-digesting enzymes. The digestible portions of the insect are thus rendered soluble and are absorbed by the leaf as food. After the insect has been digested the secretion of enzymes ceases, the hairs slowly bend back to their former positions, and the leaf is ready for the next victim. It is interesting to note that inorganic bodies, such as particles of sand, or anything not containing proteins, do not stimulate the hairs to secrete enzymes or to move in any way.

Quite comparable to the sundews so far as symbiosis is concerned, although belonging to a different family of plants, are the butterworts, or *Pinguiculas*. *Pinguicula vulgaris* grows on wet limestone rocks in the extreme northern part of the United States and in Canada. It is a small plant with a rosette of sessile, entire, spatulate or somewhat elliptical leaves, and sends up in early summer a scape with one violet-colored flower. The leaves are soft-fleshy and rather greasy to the touch, which accounts for both its Latin and common names. On the upper surface of the leaf are scattered glandular hairs to which insects adhere as in the sundew. When an insect is caught the hairs do not move as in the sundew but the edge of the leaf curves inward in such a way as to bring several hairs in contact with the insect. Between the glandular hairs are some shorter papillate or disk-like hairs which probably have the function of absorbing the digested proteins.

39. **Venus's Flytrap and the Bladderworts.**—Venus's flytrap (*Dionaea muscipula*) is a rather rare little plant that grows on wet sand in several places in North and South Carolina (Fig. 23). It has a rosette of leaves each of which possesses at its terminal end two oval-shaped lobes which are hinged together at the mid-rib and have long stiff teeth around the outer edge. On the upper surface of each lobe are three bristle-like hairs which are very sensitive. When one of these hairs is touched the lobes close suddenly like a trap. If an insect touches one of the hairs, therefore, it is almost invariably caught in the trap. The stiff teeth along the edges of the trap interlock like the teeth of a bear trap and the two lobes press together with such force that the outline of the insect can often be seen from the outside. The insect is digested by protein-digesting enzymes, secreted by glands on the surfaces of the leaves, and the digested portions are absorbed

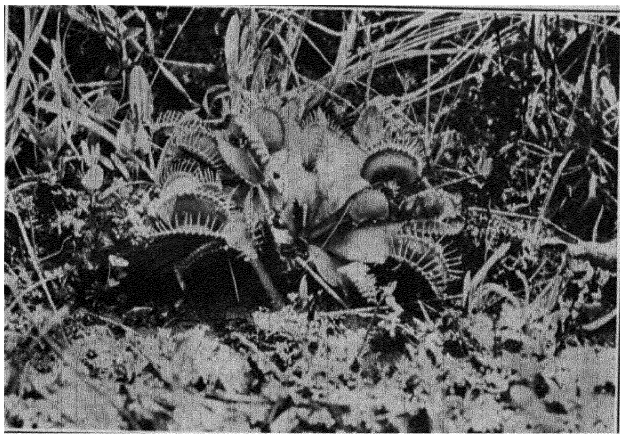


FIG. 23.—Venus's flytrap. (Photograph by B. W. Wells.)

by the leaf. The trap then slowly opens again. The whole process from the capture of the insect to the opening of the trap may take several days but there are sometimes victims in several traps of one plant at the same time.

The bladderworts (*Utricularia*) belong to the same family as the butterworts but they are quite different appearing plants. There are a considerable number of species, most of which grow in the water of ponds, swamps or bogs. Most of them are free-floating but a few are rooted in the mud along the edges of ponds. The floating forms are often entirely without roots but have very much dissected submerged leaves which serve as absorbing organs. On these submersed leaves are found numerous small bladders each with an opening at one end which is furnished with a valve-like lid and usually a few stiff bristles pointing inward, much like the entrance to an eel trap. When the trap is "set" for a catch the sides of the walls of the bladder are compressed. Any small animal that chances to swim into the vestibule may come in contact with the bristles and cause the walls of the bladder to expand and the valve to open. Then water is sucked into the bladder with a rush and any small animals in the vicinity

are carried in with it. The trap is then slowly set for another catch, the entire process taking about twenty minutes. There is considerable evidence that the animals thus captured are digested and absorbed by the plant. It is believed that a single plant, under favorable conditions, may capture several thousands of minute animals in a single day.

40. **Pitcher Plants** (Fig. 24).—There are several genera of plants that have pitcher-like leaves. *Sarracenia purpurea,* which occurs in peat bogs is our commonest native pitcher plant. It produces a cluster of radical, pitcher-shaped leaves, with a wing along one side and a rounded arching hood at the upper end. The leaves are usually attractively colored, yellowish-green and purple, and 10 to 20 cm. long. In June it sends up a flowering stem, 15 to 30 cm. high, bearing a single, large, deep purple flower. The leaves of *Sarracenia* are practically always partly filled with water, probably caught by them during rains. Entrance to the pitchers is easy and insects often go in, perhaps merely by chance or perhaps attracted by the bright colors. Once in, however, it is almost impossible for an insect to crawl out because of the numerous hairs near the entrance which point



FIG. 24.—*Sarracenia minor.* A pitcher plant. (Photograph by B. W. Wells.)

downward. The insects, therefore, sooner or later, get into the water and drown. It has been shown that digestive enzymes are present in the liquid in the pitchers of *Sarracenia* and that digestion of the dead insects takes place, although rather slowly. There are also certain bacteria present which appear to aid somewhat in the digestive processes. It has also been shown that the products of digestion are absorbed by the plant and, therefore, the symbiosis here is of the same type as that of other insectivorous plants.

There are several kinds of insects that live normally in the water in the pitchers of *Sarracenia purpurea.* One of these is a small mosquito which is harmless to man and is said to breed nowhere else. Another is a minute knat which is similarly limited in its breeding habits. These insects are believed to protect themselves from the digestive action of the liquid in which they live by means of antienzymes. In some species of *Sarracenia* frogs are often found resting in the pitchers and catching such insects as enter. Also, spiders sometimes spin webs across the mouths of pitchers for

the purpose of catching insects. These relationships are comparable to a squirrel inhabiting a hole in a tree and would be classed as social disjunctive symbiosis.

Darlingtonia californica, a pitcher plant which is limited in its distribution to Oregon and California, has a general growth habit similar to that of *Sarracenia,* but its pitchers are sometimes as much as 2 or 3 feet tall. There are no enzyme secreting glands in these pitchers and the liquid possesses no digestive ability, but bacteria bring about the decay of insects that drown in the liquid and the products of decay are absorbed through the inner surfaces of the pitcher.

Nepenthes is a genus of climbing or epiphytic plants of tropical Asia. The pitchers at the ends of the leaves of these plants have nectar glands just within the rim which serve to attract insects. The inner surface is extremely smooth and the insects in getting at the nectar usually slip and fall into the liquid below. The liquid in these pitchers has been shown to contain protein-digesting enzymes.

Dischidia, an epiphytic pitcher plant of the Malayan region, has two pitchers, one within the other. Soil and water collect in the outer pitcher and it thus serves as a sort of living flower-pot into which adventitious roots from other parts of the plant grow. The symbiotic relations of *Dischidia* have not been very thoroughly studied but they probably are similar to those of other pitcher plants.

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CHAPTER VI

POLLINATION

POLLINATION is the transfer of pollen grains to the stigma, or, in the case of gymnosperms, to the ovule. In the very great majority of cases it is brought about by some external agency. The principal agents of pollination are animals, wind and water. The cases in which pollination is brought about through the agency of animals represent our commonest examples of reciprocal nutritive disjunctive symbiosis and these will be discussed in Chapter VII. The present chapter treats of pollination through non-living agencies and, therefore, does not deal with symbiosis. It is interpolated here between two chapters on symbiosis for the sake of convenience in discussing all types of pollination in sequence.

41. **Cross and Close Pollination.**—When a flower is pollinated with pollen derived from a flower of a separate plant the phenomenon is called cross pollination or xenogamy, while, if the flower is pollinated with its own pollen, it is called close pollination or autogamy. A condition that is intermediate between autogamy and xenogamy is that in which the pollen is derived from another flower on the same plant. This is called geitonogamy.

In some plants autogamy is the only kind of pollination that is possible. This is obviously true of flowers that never open, such as the cleistogamous flowers produced by several species of violets and by a number of other plants. In other plants, and probably a much greater number, only xenogamy is possible. In the great majority of plants, however, it is probable that both autogamy, or geitonogamy, and xenogamy are possible. Xenogamy is never possible except through the aid of some external agent and with relatively few exceptions this is true also of geitonogamy. Even in autogamy gravity, wind, water, or animals often bring about pollination and in many cases one of these agencies is absolutely essential. In some cases of autogamy, however, pollination is brought about by actual contact between the stamens and stigmas. Strictly speaking these are the only cases of self-pollination. In practice, however, all cases of autogamy and geitonogamy are ordinarily called self-pollination as opposed to cross pollination which includes all cases of xenogamy, that is, all cases in which the pollen is derived from a separate plant.

42. **Wind Pollination.**—Flowers that are pollinated by the wind are ordinarily called anemophilous (wind-loving) flowers. Wind pollination is in certain respects the simplest form of pollination, although the flowers are often as perfectly adapted for it, structurally, as are the flowers that depend upon animals for pollination. The staminate flowers are often in catkins which hang downward and yield pollen, when it is ready, to the slightest breeze. Staminate catkins are especially characteristic of many trees and shrubs where they are well exposed to the wind. In most of the woody plants that are wind pollinated the flowers are produced early in the spring before the leaves expand so that there is very little in the way of the wind. In the southeastern part of the United States some of the anemophilous trees often begin blooming as early as January, the height of the blooming season for such plants occurs at about the time of the spring equinox in

March, and by the end of April the blooming season for anemophilous trees is at an end. In some wind-pollinated plants the pistillate flowers are also in catkins but in many they are not and probably there is no advantage in having the pistillate flowers in this type of inflorescence.

In many wind-pollinated flowers that are not arranged in catkins the stamens have such long and slender filaments that the anthers hang entirely outside of the flowers and so are freely exposed to the wind. Also, in the majority of wind-pollinated flowers, if we except the grass and sedge families, the pollen is produced in great abundance. It is important that this should be so because the wind is a very wasteful agent. It scatters the pollen indiscriminately, far and wide, and only a very small percentage of the pollen grains land by chance upon the stigmas of flowers belonging to the same species from which the pollen came. The pollen of anemophilous flowers is in most cases light, smooth, and dry, and thus is easily blown about by the wind. As a rule, they are not easily wetted; a fact of importance in rainy weather since wet pollen could not be blown about readily. It is these pollen grains, which are so easily blown about by the wind, that are the principal causes of hay fever. The stigmas of anemophilous flowers are usually large and well exposed and so are suitably fitted for catching wind-blown pollen.

As a rule anemophilous flowers are without color and nectar, contrasting with insect-pollinated flowers in these respects, and also, in the majority of cases, in a lack of showiness. The perianth is usually inconspicuous, either because of its greenish or brownish color or because of its small size, and in many cases it is absent entirely. When a perianth is present it usually consists of a calyx only, the presence of a corolla in wind-pollinated flowers being relatively rare.

43. **Cross Pollination in Anemophilous Flowers.**—Although wind-pollinated flowers are as a rule more simple structurally than are those pollinated by animals yet they are in many cases as well fitted for cross pollination as are the more complex insect-pollinated flowers.

Plants that have their stamens and pistils in the same flowers (perfect flowers) are said to be monoclinous, while those that have these essential organs in separate flowers (imperfect flowers) are diclinous. Diclinous plants are further subdivided into monœcious, those which have the stamens and pistils in separate flowers on the same plant, and dicœcious, those that have their stamens and pistils on separate plants.

Very many, probably a majority, of wind-pollinated plants are diclinous and many of these are dicœcious. In the dicœcious forms, of course, nothing but xenogamy is possible. In monœcious forms either xenogamy or geitonogamy is possible but in many cases the pistillate flowers are placed higher on the plant than the staminate and this makes geitonogamy very unlikely. The likelihood of geitonogamy is still further minimized in most cases by the fact that the pistillate flowers on any individual plant bloom earlier, sometimes several days earlier, than the staminate flowers of the same individual.

When the stamens and pistils of a monoclinous flower mature at different times the phenomenon is known as dichogamy. Dichogamy is subdivided into protogyny, the maturing of the stigmas before the anthers, and protandry, the maturing of the anthers before the stigmas. Both protandry and protogyny are found among monoclinous wind-pollinated plants and

make cross pollination rather certain among those plants that exhibit it.

Still another, and even more specialized, means of insuring cross pollination is found in a few anemophilous plants as, for example, in rye. In this plant the pollen is impotent, that is it will not germinate, on the stigma of the same flower in which was produced but will germinate readily on the stigma of any other plant of the species.

44. **Some Wind-pollinated Flowers.**—Many of our common trees and shrubs which produce their flowers, at least the staminate ones, in catkins, and which bloom early in spring, often before the leaves have developed, are wind-pollinated. Among these are the poplars, birches, oaks, hickories,

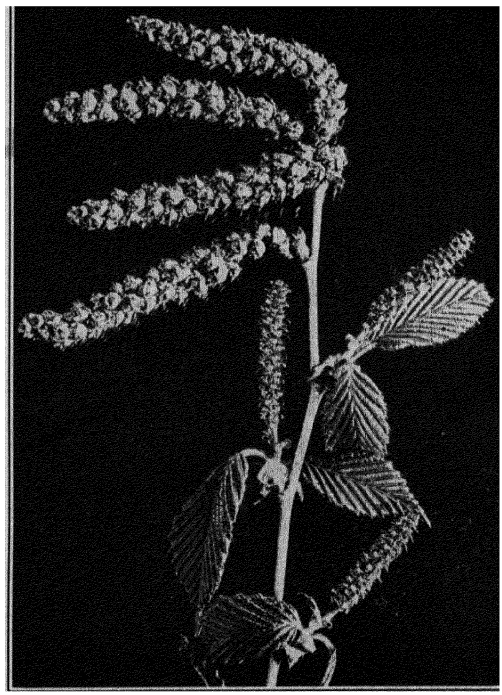


FIG. 25.—Yellow birch (*Betula lutea*). Wind pollinated. Staminate catkins above, pistillate below. (Photograph by John H. Lovell.)

walnuts, hazels and alders. The poplars are dioecious and it is necessary, therefore, that pollen be blown from one tree to another. The stamens of these plants are elastic and when the weather is clear and dry the pollen is discharged forcibly into the air to a distance of several inches. This gives it a good start on its journey. The birches, on the other hand, are monœcious, with both kinds of flowers in catkins (Fig. 25). The oaks, hickories, walnuts and hazels are also monœcious but have only their staminate flowers in catkins. The pistillate flowers are either solitary or only a few in a cluster.

Among other trees that are wind-pollinated are the beeches, elms and ashes. In the beech the pistillate flowers are in pairs while the staminate

flowers are clustered in globose heads, 2 or 3 cm. in diameter, which hang downward at the ends of long slender peduncles. The flowers of the elm are borne in small loose clusters. They are mostly perfect and close pollination is largely prevented by protogyny. Some species of ash are dioecious while others are monoclinous and still others are both, but in any case the flowers are all clustered on the branches.

All of the conifers are wind pollinated (Figs. 26 and 27). They are all diclinous and most of them are monoecious though a few are dioecious. Pollen is produced by coniferous trees extremely abundantly. Great clouds

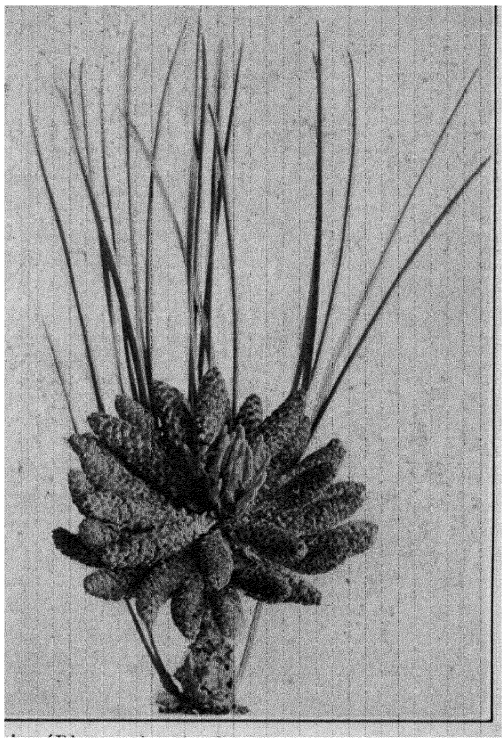


FIG. 26.—Red pine (*Pinus resinosa*). Staminate cones. (From The Flower and the Bee, by John H. Lovell; copyright, 1918, by Charles Scribner's Sons. By permission of author and publisher.)

of pollen sometimes arise from pine forests in such a way as to appear like smoke columns. Such immense numbers of pollen grains settle down on foliage, branches, grass and soil that the whole landscape is given a yellowish color. Such a phenomenon is often spoken of as a "sulphur shower." The pollen grains of pine are so well adapted to dissemination by the wind that some have been known to be carried more than 100 miles. Since everything in the neighborhood of the forest is covered with pollen some of the grains inevitably come in contact with the ovules in the pistillate cones and this constitutes pollination.

Two other important groups of plants that are anemophilous are the grasses and sedges. The majority of the grasses are monoclinous and self-pollination is often, though not always, prevented by dichogamy. Some, however, such as Indian corn, are diclinous and monœcious or, in a few cases, diœcious. Some of the sedges are monoclinous also, but probably a greater number are diclinous. Most of the diclinous species are monœcious but a few are diœcious. Many of the grasses bloom early in the morning, at sunrise or a little later, and it is an interesting phenomenon to watch. The bracts spread apart, the stamens elongate until the anthers hang outside of the flower, and then the pollen is shed, the whole process often

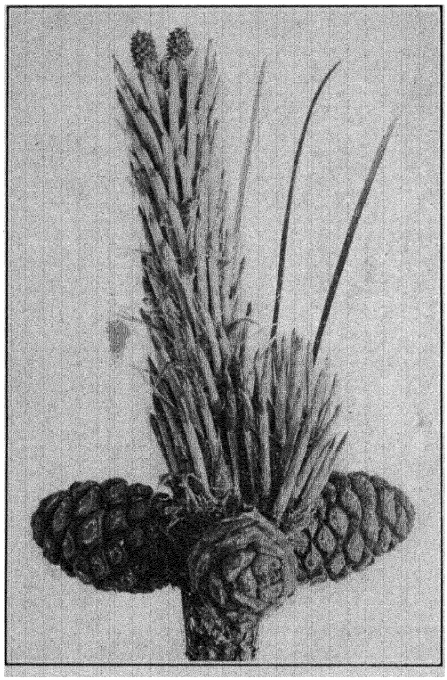


FIG. 27.—Red pine (*Pinus resinosa*). Ovulate cones. Wind pollinated. (From The Flower and the Bee, by John H. Lovell; copyright, 1918, by Charles Scribner's Sons. By permission of author and publisher.)

taking no more than fifteen or twenty minutes. As a rule each flower remains open but a short time but different flowers on the same plant may open progressively for several days. Sometimes unfavorable weather greatly retards or prevents the opening of the flowers and in that case self-pollination is likely to occur.

45. **Water Pollination.**—The majority of seed plants that grow in the water produce their flowers above the surface of the water and are pollinated by the wind or by insects. There are some interesting cases, however, in which water is the agent of pollination. In some of the pond weeds (*Potamogeton*), for example, the pollen grains are filamentous and without thick walls. They are just heavy enough to float below the surface of the water and may come in contact with the long exserted stigmas by chance.

In the tape grass (*Vallisneria spiralis*) the solitary pistillate flowers are borne on peduncles which elongate just enough to bring the flowers to the surface of the water. Sometimes these peduncles become as much as a meter in length, the growth continuing in any particular case until it is checked, probably, by increased transpiration at the surface of the water. The staminate flowers are produced in clusters of several hundred. Each one is about 1 mm. in diameter and consists of two stamens enclosed in a three-parted perianth. These staminate flowers become detached under water and rise slowly to the surface where they open and the segments of the perianth curve back in such a way as to support the flower on a little tripod. A pistillate flower resting on the surface of the water causes a slight depression of the surface film and when staminate flowers approach this depression by chance they shoot down into it and the stamens are very likely to come into contact with the stigmas. After pollination has taken place the peduncle coils up and draws the pistillate flower below the surface again, where the fruit matures.

Another interesting case of pollination in water plants is that found in some of the duckweeds. The duckweeds are among the smallest and simplest of flowering plants. One of these, *Lemna minor,* consists of a little green thallus from 2 to 5 mm. in diameter which floats on the surface of the water. Projecting into the water from the under side of the thallus is a single little rootlet, so reduced that it contains no vascular tissue. This simple little plant produces a cluster of 3 flowers, 2 staminate and 1 pistillate, in a notch in one side of the thallus. Each staminate flower consists of a single stamen and nothing else while the pistillate flower consists of a single pistil and the three are enclosed in a spathe in such a way as to appear like a single flower with two stamens and one pistil. The pistillate flower matures first and is ready to receive pollen several days before either of the staminate flowers is ready to expose its pollen. One of the stamens then elongates and the anther opens, the pollen remaining heaped in the open pollen sacs. Several days later the second stamen matures and exposes its pollen. Usually there are hundreds of individuals of these plants crowded together and they are constantly being jostled against one another by movements of the water due to wind or other causes. The open anthers are thus almost certain to be brought into contact with receptive stigmas. The dichogamy exhibited by this plant makes cross pollination almost certain but the stigma is still receptive when the first stamen matures so that if it has not already been pollinated self-pollination may take place at that time.

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CHAPTER VII

RECIPROCAL NUTRITIVE DISJUNCTIVE SYMBIOSIS

In reciprocal nutritive disjunctive symbiosis one or more, but not necessarily all, of the organisms concerned obtain food from one or more of the others, but those that lose food and get none in return are nevertheless benefited by the relationship in some other way so that the symbiosis is reciprocal so far as actual benefit derived from it is concerned. The outstanding examples are those concerned with pollination by means of animals, especially insects, and with dissemination through the aid of animals, especially birds and ants. The subject of dissemination, like that of pollination, falls under the general term symbiosis only in part. Furthermore it is closely related to the development of plant communities; a subject to be dealt with at length in later chapters. For these reasons it will be more convenient and also conducive to clearness to postpone all discussion of dissemination until we are ready to discuss vegetational development. The present chapter, therefore, will deal entirely with pollination by animals.

46. **Insect Pollination.**—Insects visit flowers, ordinarily, for the purpose of obtaining food, either nectar or pollen, and while accomplishing this purpose they incidentally effect pollination. These simple symbiotic relations between insects and the flowers they visit involve some of the most remarkable phenomena in the whole realm of Nature. No evolutionary facts are more astounding or more nearly inexplicable than that the flowers of many species of plants remain unpollinated unless they are visited by insects; in some cases by a particular kind of insect.

The great majority of insect-pollinated, or entomophilous, flowers are monoclinous. This is probably a distinct advantage since it makes possible twice as many acts of pollination for a given number of insect visits than if the flowers were diclinous. That is, in the case of diclinous flowers it is necessary for the insect to visit two flowers, a staminate and a pistillate, in order to accomplish one act of pollination, while in monoclinous flowers it is possible in each visit after the first one to deposit pollen on the stigma and at the same time collect more pollen from the stamens. Furthermore insects which were bent only on gathering pollen would, of course, not visit flowers that were only pistillate at all.

In many respects insect-pollinated flowers contrast sharply with those that are wind-pollinated (Fig. 28). The flowers as a rule are not in catkins but rather in inflorescences that are relatively inflexible in the wind. The stamens have relatively short filaments and are usually not prominently exerted. The pollen, instead of being dry and smooth, as in anemophilous flowers, is often rough with spines or other protuberances, or viscid, or both. This causes the grains to stick together in masses, renders them less easily blown about by the wind, and adapts them admirably to sticking to the legs and bodies of insects as well as to stigmatic surfaces.

Flowers that are wide open and have their parts freely exposed can usually be pollinated by most any kind of visting insect. They often have numerous stamens and produce pollen as abundantly as many wind-pollinated species. Those that have the pollen partly or wholly concealed

in tubular or otherwise partly closed corollas, however, usually have few stamens and do not produce pollen abundantly. The stigmas of insect-pollinated flowers as compared to those of wind-pollinated flowers are small and inconspicuous.

Insect-pollinated flowers are further characterized by showiness. This may be due either to color, size, form or arrangement, or to two or more of these features combined. In many cases, also, they are characterized by fragrance or by the production of nectar, or both.

47. **Cross Pollination in Entomophilous Flowers.**—The majority of insect-pollinated flowers exhibit dichogamy to a greater or less degree. In some cases the dichogamy is complete, that is, the stigmas are not receptive

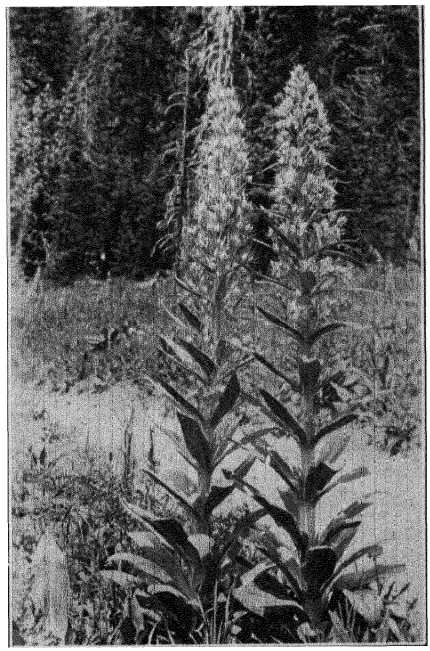


FIG. 28.—*Frasera speciosa*, with insect-pollinated flowers.

at any time when the stamens of the same flower are discharging pollen (Fig. 29). More often, however, there is some overlapping so that, if cross pollination has failed to occur, close or self-pollination is possible. Usually the stamens do not all mature at the same time and the stigmas are receptive when either the oldest or the youngest stamens are mature, depending upon whether the species is characterized by protandry or protogyny.

A less common but very interesting phenomenon facilitating cross pollination is that known as heterostyly. In various species of primrose (*Primula*), for example, some individuals produce long-styled flowers and others short-styled flowers. In the long-styled flowers the five stamens, which are attached to the corolla, are located half way down the corolla tube and the style is the same length as the corolla tube so that the stigma is near its

upper end. In the short-styled flowers, on the other hand, the stamens are placed at the upper end of the corolla tube and the style is only one-half the length of the tube. When an insect visits a long-styled flower, pollen from

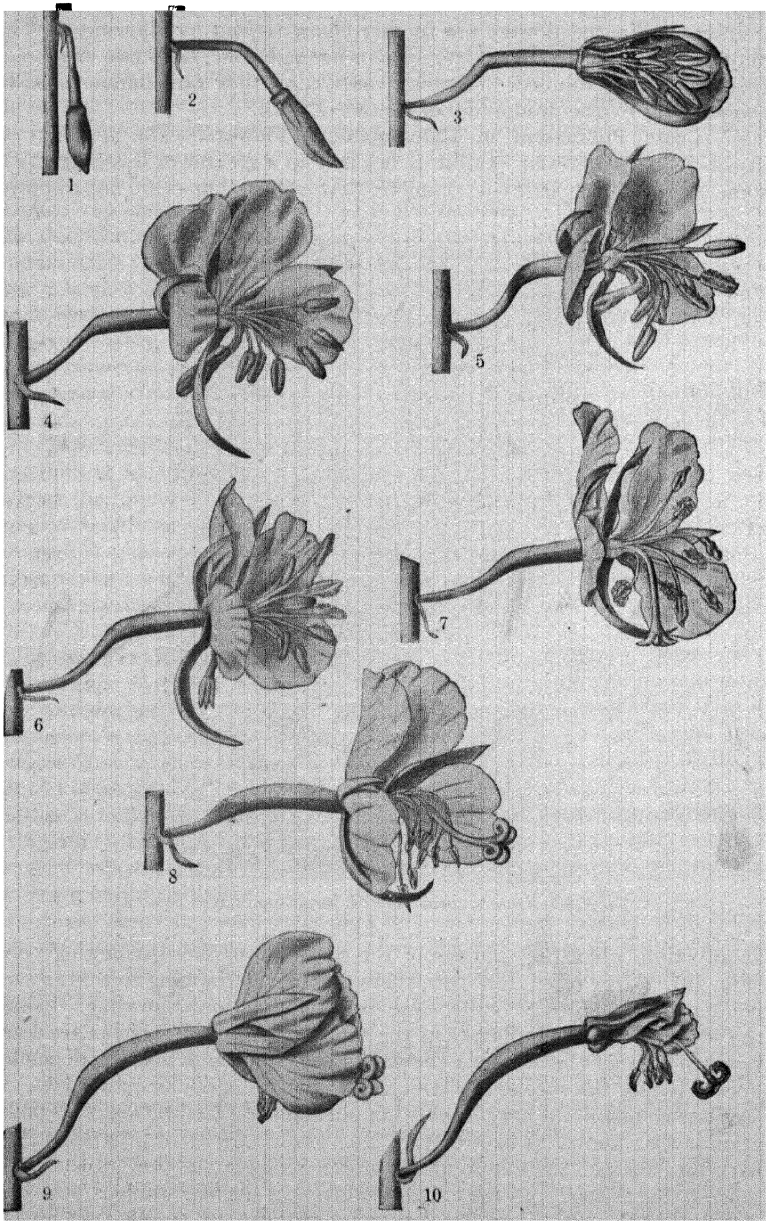


FIG. 29.—Fire weed (*Epilobium augustifolium*). Life history of flowers showing protandry. (After Clements and Long.)

the low anthers is deposited on the anterior part of the body and during subsequent visits to other flowers this pollen may come in contact with the stigma of a short-styled flower. At the same time, while the short-styled flower is being pollinated, pollen from the high anthers is deposited on the posterior part of the insect's body and this may later be rubbed onto the stigma of a long-styled flower. While this morphological phenomenon of heterostyly in itself makes cross pollination rather certain it is still further assured by the fact that pollen from low anthers will not germinate readily on the stigma of a long-styled pistil but will germinate readily on the stigma of a short-styled pistil. On the other hand, pollen from high anthers will germinate readily only on the stigmas of long-styled pistils.

Heterostyly is still further developed in the spiked loosestrife (*Lythrum salicaria*) which has flowers of three types: long-styled, short-styled, and intermediate-styled. Each of these three types of flowers has two sets of stamens, the short-styled flowers having intermediate and long stamens, the intermediate-styled flowers, short and long stamens, and the long-styled flowers, short and intermediate stamens. Thus pollen is readily transferred from any one of these types to either of the other two.

Flowers such as those of *Lythrum*, being of three forms, are said to be trimorphic. Other plants with trimorphic flowers are the swamp loosestrife (*Decodon verticillata*) and the pickerel weed (*Pontederia cordata*).

A phenomenon that is well-known among fruit-growers is that of self-sterility. Many of the common varieties of fruits, such as grapes, peaches, plums, cherries, pears and apples are either partly or wholly self-sterile, which means that they require pollen from some other variety in order to produce healthy fruits. For this reason it is not ordinarily recommended that orchards be planted with a single variety but that two or more varieties whose blooming seasons coincide or overlap should be used.

48. **Pollinating Insects.**—By far the greatest number of pollinating animals are insects and the most important group of insects from this point of view is the Hymenoptera which includes the ants, bees and wasps. The honey-bees and bumble-bees are in certain respects the most efficient of all pollinating insects. This is partly due to the fact that they work continuously from the beginning to the end of the flowering season; partly to the fact that they visit flowers for both pollen and nectar; and partly because of their remarkable precision which leads them to visit large numbers of flowers of the same species in rapid succession. A honey-bee, for example, visits only one kind of flower on any collecting trip and usually on any one day. It is for this reason that it is often possible to purchase pure clover honey, basswood honey, or buckwheat honey. Furthermore, the bees have hairy legs that are well fitted for carrying pollen, and their long, tongue-like probosces enable them to obtain nectar from irregular, tubular, and partly closed corollas. There are a considerable number of plants that can be pollinated only by bees and such plants are limited in their distribution to those regions that are inhabited by bees.

Ants are of no importance as pollinating agents and wasps, as compared with bees, are of minor importance, although there are some flowers, notably those of the figs, that are pollinated only by wasps.

Next to the Hymenoptera, in importance as pollinating agents, are the Lepidoptera, or butterflies and moths. These are nectar feeders only and their mouth parts are very greatly specialized and elongated to enable

them to obtain nectar from long corolla tubes. The butterflies which fly during the day and visit mostly showy and fragrant flowers are rather haphazard in their movements. They are apt to visit several different species of flowers within a few minutes and for that reason are not very efficient pollinators. Some of the moths, on the other hand, especially the hawk moths, are as precise in their movements as bees. The moths are night-flying insects and visit mostly night-blooming flowers. The hawk moths have very long mouth parts, sometimes as much as 7 or 8 cm. in length, which are coiled up when not in use. They visit mostly fragrant, white flowers with long corolla tubes.

The majority of the flies are of no importance as pollinating agents. The syrphid flies, however, which look a great deal like bees, feed largely upon nectar and pollen and so are of considerable importance. The carrion flies are also of some importance especially in connection with the pollination of ill-smelling flowers. They seem to be attracted particularly by odors that are offensive to human beings. A few kinds of beetles sometimes effect pollination but as a rule the floral visits of beetles result in more harm than good.

49. **Color, Odor and Memory in Insect Pollination.**—A great deal of work has been done during the past one hundred and fifty years in efforts to determine the relative importance of color, form, odor and memory in attracting or directing insects, especially bees, to flowers, and a great deal has been written on the subject. Much more needs to be done before we can speak with certainty on all phases of the question but certain facts are now fairly well established.

Many experiments have been performed for the purpose of determining whether bees can recognize colors, such, for instance, as removing the corollas of flowers, using artificial flowers, painting flowers unusual colors, or enclosing flowers in glass, and then observing the activities of the bees. While there has been some disagreement among different workers, the most reliable results show that bees do readily distinguish colors. Honey-bees show a decided preference for blue, but, when working on any particular species, they show a preference for the color of that species whatever it may be. It has also been shown, however, that they discriminate between colors only when it is of advantage to do so. In the case of a species with variable colors they soon learn that color discrimination is unnecessary and so they depend entirely upon form and odor. Charles Darwin once remarked that bees are very good botanists since they know that different varieties of the same species may differ widely in color. On the other hand, bees do distinguish species partly on the basis of color and they also depend on color to a certain extent to distinguish between fresh flowers and old withered ones or partly opened buds. When part of the flowers of a species are painted unusual colors the bees show a decided preference for the natural color until experience teaches them that such discrimination is unnecessary. It is pretty generally agreed also that the power of vision of bees is sufficiently developed to enable them to readily recognize differences in form and patterns of flowers. In fact they seem to be able to distinguish differences in surface and texture that are so small as to be unnoticed by man.

The sense of odor of insects has often been over-emphasized, although it differs greatly in different groups. Honey-bees do not have a sense of smell

that is especially highly developed and when they are in the immediate vicinity of flowers color and form are much more important than odor in guiding them. It is true also, of course, that bees cannot see for great distances. It seems to be true, therefore, that for distances greater than 20 meters odor is more important than color and form, while, for intermediate distances, color in mass is most used, and for distances of 1 meter or less the color and form of individual flowers are the guiding factors. For distances that are measured in miles, however, bees have simply to go hunting for flowers just as men do. But it is true also that memory and



FIG. 30.—White clover (*Trifolium repens*), a bee flower. After pollination the flowers all bend downward and turn reddish, then brown. (See Fig. 31.) (From the Flower and the Bee, by John H. Lovell; copyright, 1918, by Charles Scribner's Sons. By permission of author and publisher.)

habit play important roles and when bees have once found a field of clover or a basswood tree they make subsequent trips to the same place with apparently no more trouble than a man would have.

50. **Bee Flowers.**—Flowers which are wide open and have their pollen and often their nectaries freely accessible are visited by a variety of insect species any of which may effect pollination. There are many flowers, however, that are partly closed, that are very irregular in shape, or that have their nectar concealed, which can be pollinated by only one or a few species of insects.

Some of the violets are bee flowers, that is, they are pollinated almost entirely by bees. This is true especially of some of the yellow violets and

of the cultivated pansies (*Viola tricolor*). Most of the blue violets, on the other hand, are not much visited by insects and are often infertile. These species, in addition to the blue flowers, produce, usually later in the season, small green flowers (called cleistogamous flowers) which never open, are self-pollinated and produce seed abundantly.

The legume family contains a very large number of bee flowers, several of which never produce seeds unless visited by bees. Many members of this family have 9 of the 10 stamens united into a tube and the nectar, if any is present, is at the bottom of the tube. Four of the petals, the 2 forming the keel and the 2 wing petals, are inter-locked, around the stamen tube, while the fifth, called the standard, is broad and more or less erect.



FIG. 31.—White clover (*Trifolium repens*). Final stage, flowers all reflexed and brown colored. (Photograph by John H. Lovell.)

When a bee visits the flower for nectar it rests on the wing petals, which act as levers, and, bracing its head against the standard, depresses the keel enough so it can reach the nectar with its mouth parts. While it is doing this pollen is applied to the under side of its body. If the bee is not strong enough to depress the keel it, of course, does not get the nectar. Very few bees are strong enough to depress the keel of a sweet-pea flower and for that reason sweet-pea flowers are not much visited by bees and are usually self-pollinated.

The flower of alfalfa has the anthers and stigma held in the keel under tension and when a bee presses the keel down the anthers and stigma spring forcibly upward against the body of the insect. It is a curious fact that east of the Mississippi River alfalfa does not produce much nectar while in the western part of the United States it is one of the most prolific of honey plants. The honey-bees that visit alfalfa flowers, however, usually do not

effect pollination since they steal the nectar through a hole in the side of the corolla. In such a case the symbiosis is antagonistic and not reciprocal.

Red clover (*Trifolium pratense*) is pollinated almost entirely by bumble-bees and does not produce seed in the absence of bumble-bees, except in occasional years when *Tetralonia*, one of the solitary bees, is abundant. Honey-bees, as a rule, are unable to get nectar from red clover because their mouth parts are not long enough to reach it. Occasionally, in very dry years, the floral tubes of red clover are short enough so that honey-bees

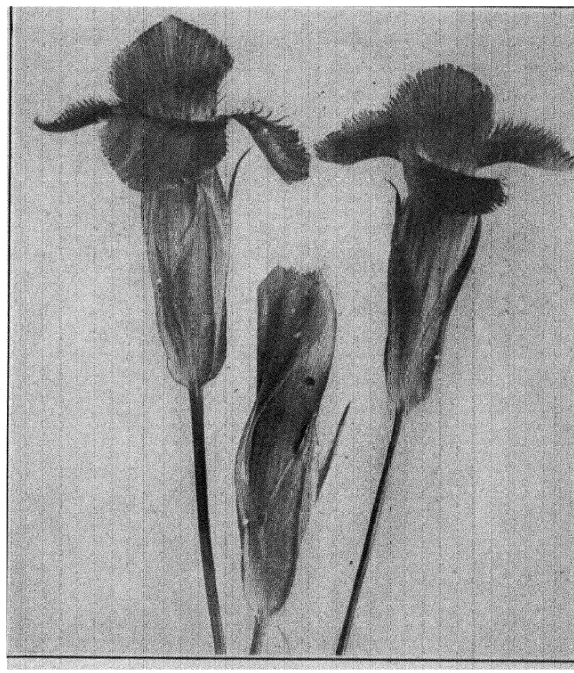


FIG. 32.—Fringed gentian (*Gentiana crinita*). A bumble-bee flower. (From The Flower and the Bee, by John H. Lovell; copyright, 1918, by Charles Scribner's Sons. By permission of author and publisher.)

can reach the nectar and red clover fields yield an abundance of honey, but ordinarily this plant is not a good honey plant. Recently, however, breeding experiments have been undertaken with domestic honey-bees for the purpose of producing a race capable of working on red clover flowers, and apparently with considerable success. White clover (*Trifolium repens*), which has smaller flowers than red clover, is well adapted for pollination by honey-bees and is one of the best honey plants wherever it grows (Figs. 30 and 31). Other common bumble-bee flowers are the larkspurs (*Delphinium*), the columbines (*Aquilegia*), the jewelweeds (*Impatiens*), the snapdragons (*Atirrhinum*) and some of the gentians (*Gentiana*) (Fig. 32). The mint family and the figwort family also contain many bee flowers. In these families the pollen is deposited on the backs of the insects instead of on the underside of the body as in the legume family.

51. **Butterfly and Moth Flowers.**—While blue seems to be the favorite color with bees there are a very large number of flowers pollinated largely by butterflies that are some shade of red. The pink family (*Caryophyllaceae*) contains a considerable number of butterfly flowers, some of which are almost entirely dependent upon butterflies for pollination since their nectar is hidden so deeply that it cannot be reached by other insects. The wild orange-red lily (*Lilium philadelphicum*) is another butterfly flower. It grows on dry uplands and produces flowers that are upright and well adapted to pollination by butterflies. Its relative (*Lilium canadense*) which grows in low places along streams has yellow flowers which are



FIG. 33.—Red phlox (*Phlox paniculata*). A butterfly flower. (From The Flower and the Bee, by John H. Lovell; copyright, 1918, by Charles Scribner's Sons. By permission of author and publisher.)

inverted. Because of their inverted position they are not easily visited by butterflies and are pollinated by bees almost entirely. Other butterfly flowers include several species of *Phlox* (Fig. 33) and numerous orchids. Many composites are pollinated by butterflies but they are not strictly butterfly flowers since they may be pollinated by various kinds of insects.

The hawk moths, being night-flying insects, visit mostly white, fragrant, night-blooming flowers. The Jimson weed (*Datura stramonium*) and the night-blooming tobacco (*Nicotiana noctiflora*) are good examples of hawk-moth flowers. Not all hawk-moth flowers are white, however. The evening primrose (*Œnothera biennis*), for example, which is yellow, is pollinated largely by these insects.

Perhaps the most interesting of all cases of pollination by moths is that of the yuccas which are pollinated by small moths belonging to the genus *Pronuba*. The flowers of the yuccas are pendulous and the style hangs down farther than the stamens but it is impossible for the pollen to fall from the anthers to the stigma because the stigma is cup-shaped and the stigmatic portion is on the inner surface only. The female moths begin work soon after sundown. Each one collects a considerable amount of pollen from the anthers and stores it in a sort of pouch on the under side of her head. She then usually flies to another flower, pierces the ovary with her ovipositor, and, after laying one or more eggs, creeps down the style and stuffs a ball of pollen into the stigma. It is difficult to image

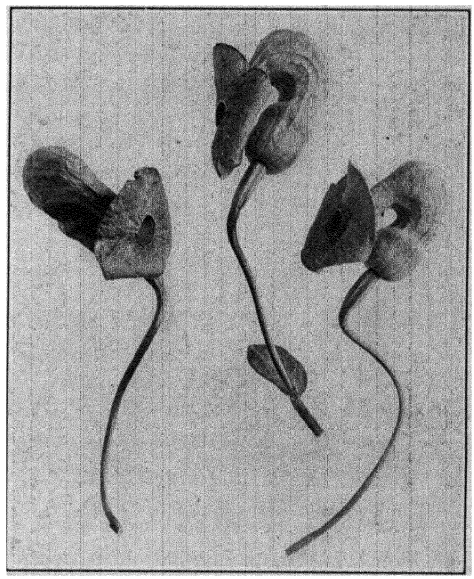


FIG. 34.—Dutchman's pipe (*Aristolochia macrophylla*). A fly flower. (From The Flower and the Bee, by John H. Lovell; copyright, 1918, by Charles Scribner's Sons. By permission of author and publisher.)

what would cause a moth to stuff pollen into a stigma for one hesitates to believe that she knows what the result will be. Yet this symbiotic relation is obligate for both the yucca and the moth, since in the absence of the moth the yucca produces no seed while without the yucca the moth cannot complete its life cycle, and if the moths should fail to pollinate the yuccas the result would ultimately be the extinction of both plant and insect. The yucca produces a very large number of ovules. Part of these are eaten by the moth larvae and the remainder mature into seeds.

52. **Fly Flowers.**—Syrphid flies, and some other nectar-feeding flies, visit many of the same flowers that are frequented by bees and such flowers cannot, of course, be designated strictly as fly flowers. Syrphid flies are especially important as pollinators of some fruit trees, though these trees may also be pollinated by bees. There are some flowers, however, that are pollinated almost exclusively by flies (Fig. 34). Many of these are ill-

smelling and attract mainly carrion flies. Familiar examples are the carrion flower (*Smilax herbacea*), the purple trillium (*Trillium erectum*), the skunk cabbage (*Symplocarpus fœtidus*) (Fig. 35) and the water arum (*Calla palustris*).

There are some fly flowers that are sometimes spoken of as prison, or pitfall, flowers. The spotted arum (*Arum maculatum*), a native of Europe, is one of these. This plant has its flowers on a spadix in a spathe, in a manner comparable to our Jack-in-the-pulpit. The pistillate flowers are near the base of the spadix. A little higher up are the staminate flowers and a short distance above the staminate flowers the spathe is constricted. There is a cluster of hairs on the spadix at the point where the spathe is constricted. These point downward and practically fill the spathe at that point. There is also a similar cluster of hairs between the group of staminate flowers and the pistillate flowers.

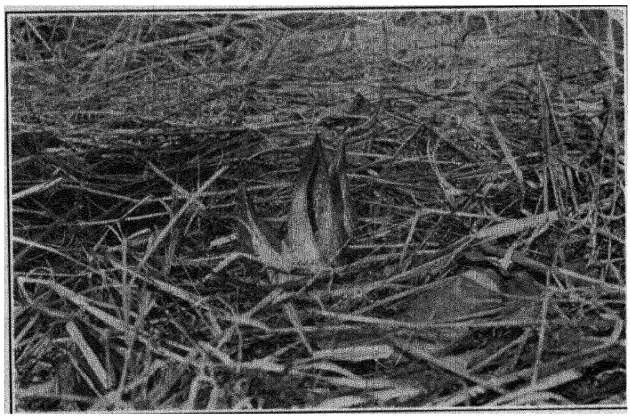


FIG. 35.—Skunk cabbage (*Symplocarpus fœtidus*). A fly flower.

The small flies which bring about pollination in this plant easily enter the spathe and pass down to the pistillate flowers where they feed upon the nectar. Their exit, however, is prevented by the stiff hairs. The pistillate flowers mature first and the lowest cluster of hairs then withers. This permits the flies to come up to the staminate flowers where they become dusted with pollen. Later the upper ring of hairs withers and the insects are liberated and are free to fly to another flower.

The Jack-in-the-pulpit (*Arisæma triphyllum*) which belongs to the same family as the *Arum*, is also somewhat of a prison flower. This species is dicœcious and the staminate plants mature a little in advance of the pistillate. The spathes are extremely smooth and slippery on the inner side. The flies are very likely to visit a staminate inflorescence first and once inside the spathe they are unable to climb up the smooth walls or the equally smooth spadix. As soon as the spathe begins to wither, however, it becomes less smooth and the flies escape and may chance then to visit a pistillate plant and so effect pollination. In the pistillate inflorescence they are again imprisoned until the spathe begins to wither. This does not take place so promptly as in the case of the staminate plant and often the insects perish before they are liberated.

In Bombay there are certain species of the genera *Ceropegia* and *Cryptocoryne* which are pollinated by carrion flies and fruit flies. The corollas are tubular and dark colored within but there are certain translucent areas which serve as windows to admit a small amount of light to the reproductive structures and it is believed that these are an adaptation for the guidance of the insect visitors.

53. **Pollination of the Fig.**—One of the strangest of the known cases of symbiosis between flowers and insects is that of the commercial fig and the wasps of the genus *Blastophaga* which pollinate it. The flowers of the fig are produced in composite inflorescences called syconia. A syconium consists of a fleshy receptacle which has developed into a hollow structure with a very small orifice at the upper end. The numerous flowers are arranged on the inner side, which is the morphological upper side, of the receptacle. The flowers are diclinous and the plants are essentially dioecious. The pistillate syconia, which are called figs, contain only normal pistillate flowers with rather long styles, while the staminate syconia, called caprifigs, contain both staminate flowers and small, short-styled, pistillate flowers, which are known as gall flowers. Pollination of the fig is accomplished by the female wasps. The orifices of the syconia are so nearly closed by overlapping scales that the wasps have great difficulty in getting in and often tear off their wings in the process. After a wasp has entered a pistillate syconium she creeps over the flowers searching for a suitable place to lay eggs and while doing this the pollen on her body is rubbed onto the stigmas. The styles of the flowers are so long, however, that the wasp is unable to reach the ovaries with her ovipositor and so is unable to lay any eggs. She cannot get out of the syconium, however, and soon perishes, but the flowers, having been pollinated, continue their normal develpment and the syconium matures into a fig.

If, on the other hand, the wasp chances to enter a caprifig she readily reaches the ovaries of the short-styled gall flowers and lays her eggs there. She then perishes in the caprifig. When the eggs hatch the young wasps feed upon the tissues of the gall flowers and, when mature, the males eat their way out of the ovaries in which they hatched and into those occupied by the females. After mating with the females the males soon die without leaving the caprifigs. The females now become dusted with pollen, make their way to the exterior, and fly to another syconium. Those that by chance enter figs will effect pollination but will not leave any offspring, while those that enter caprifigs will leave offspring but will not effect pollination. This symbiosis is obligate for both the plant and the insect yet the course of the evolution that has brought about so strange a relationship can scarcely even be imagined.

54. **Pollination by Birds and Other Animals.**—Next to insects, birds are the most important pollinating animals. Bird pollination seems to be more important in the southern hemisphere than in the northern. In South America the numerous humming birds are important pollinators while in Africa the sun birds are more important. The characteristics of bird flowers are in general similar to those that we are familiar with in bee flowers.

A few cases of pollination by bats have been reported, such, for example, as the century plant (*Agave scabra*) which is much visited by a species of nectar-feeding bat, but neither those nor any other mammals are important as compared with birds, and more especially with insects, as pollinating agents.

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CHAPTER VIII

SOCIAL CONJUNCTIVE SYMBIOSIS

CONJUNCTIVE symbiosis includes all cases of the living together of two or more unlike organisms in which the symbionts are in actual contact throughout the time during which they are said to be in a state of symbiosis. Any example of conjunctive symbiosis in which there is no direct food relation between any of the symbionts may be classed as social. The commonest examples of social conjunctive symbiosis are those of the various kinds of climbing plants and of plants that grow upon other plants for support but without deriving food from their hosts.

55. **Lianas.**—Lianas are plants that climb by one means or another (Fig. 36). They do not have a sufficient amount of mechanical tissue to maintain themselves in an upright position and so are forced to climb upon some support in order to display their foliage in an adequate way. If the support happens to be another plant, as it does in a great majority of cases, the phenomenon represents a symbiotic relation between the liana and its host.

The number of species of lianas in the north temperate zone is comparatively small but in tropical forests, where they reach their maximum development, the wealth of species is astonishingly great. Certain families, such as the legume, moonseed, soapberry, and Bignonia families are especially rich in climbing species, but a very large number of other families contain some lianas. In some tropical forests the lianas rank next to the trees themselves in conspicuousness. They vary greatly in size and in habit. They may be closely twisted around large or small stems or they may hang as streamers from the branches of trees. Some are stretched tightly from one tree to another while others loop downward to form great festoons from one branch to another. In many cases, too, they occur tangled together in masses on the ground.

The internal structure of the stems of lianas is characteristically different from that of upright stems. Especially is this true of twining plants the stems of which are necessarily pliable. In such stems the wood is seldom continuous but is separated into distinct wedges which frequently become much lobed and cleft as secondary growth proceeds. Sometimes the wood is also separated radially, the cambium being periodically renewed outward in the cortex, with the result that concentric zones of wood separated by rings of fundamental tissue are produced. In many lianas the internal structure shows an eccentric or a flattened arrangement due to the constant lateral pressure against the host.

The internodes of lianas are usually long, and the longest and largest known tracheæ occur in certain climbing stems. Such vessels appear to be correlated with the necessity of transporting water to great heights through a stem that is relatively small.

56. **Twiners.**—Twining plants are perhaps the most specialized of lianas. In these the tip of the shoot executes a rotating movement known as circummutation. This movement is induced and regulated by the response of the stem tip to the force of gravity and causes the stem to twine about any suitable support. The movement is due to a more rapid

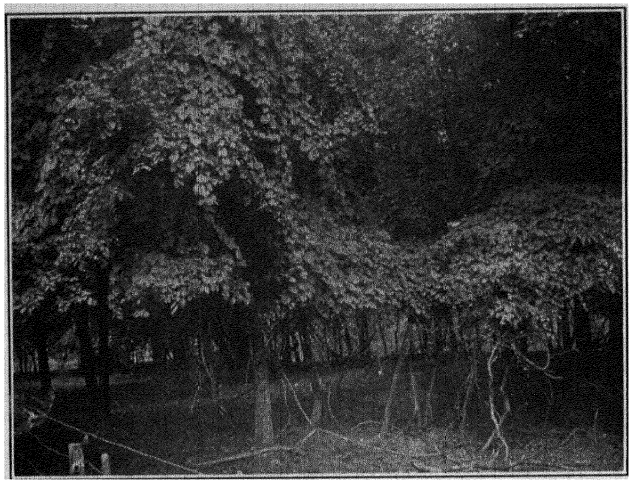


FIG. 36.—Wild grape climbing on *Cratægus*. Social conjunctive symbiosis.

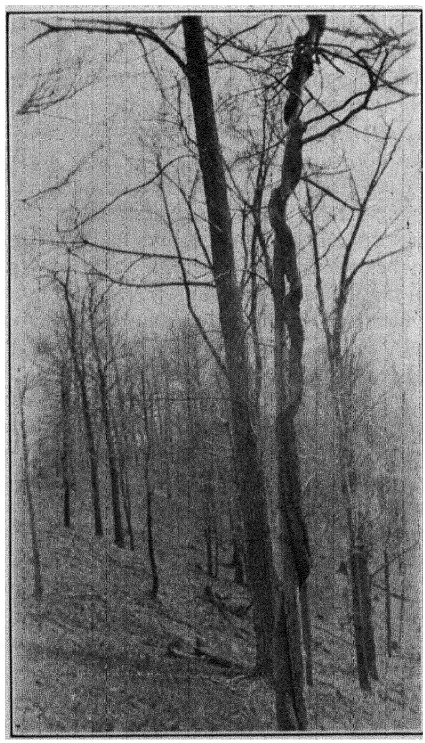


FIG. 37. Poison ivy on hickory, climbing partly by twining and partly by adventitious roots. Since the ivy grows more rapidly than the hickory it is rapidly becoming too heavy for the host.

growth on one side of the stem. Since the twining of the stem necessarily results in a twisting on its axis the place of rapid growth is constantly changing and migrating around the stem. Each complete revolution of the tip is accompanied by a complete twist on the axis of the stem and the most rapid growth of any given area on the stem is induced when that area is lowermost.

The direction of twining is specific, that is, with a very few exceptions, all individuals of a given species twine in the same direction. In the majority of cases the direction is counter-clockwise while in a smaller number it is clockwise. Among plants that twine in a counter-clockwise direction are the bean (*Phaseolus*), the bittersweet (*Celastrus*), the moonseed (*Menispermum*), and the bittersweet night-shade (*Solanum dulcamara*). The hop (*Humulus*) and the black bindweed (*Polygonum scandens*) twine in a clockwise direction.

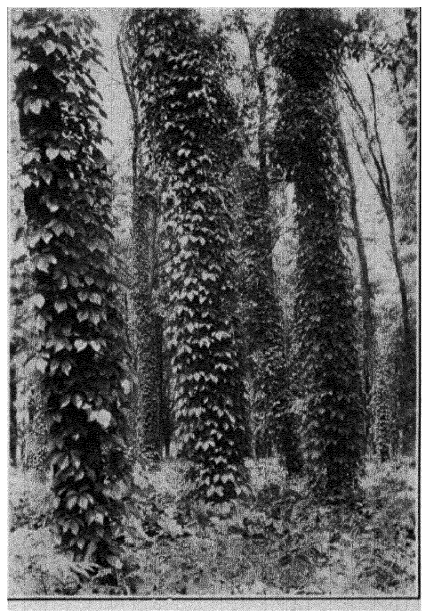


FIG. 38.—Trees covered with Virginia creeper (*Psedera quinquefolia*), a root climber.

57. **Tendril Climbers.**—Scarcely second to the twiners in specialization are the tendril climbers in which one organ or another is modified into a tendril which grasps any support with which it comes in contact. Tendrils are ordinarily extremely sensitive to contact with solid bodies. In some cases merely stroking the tendril lightly with a match-stick once or twice will cause a bending of the tendril at the point of contact within a minute or two. Even contact with a cotton thread, moved by light air currents, has been known to produce a reaction in a tendril.

The bending of the tendril is brought about through an increase in the rate of growth on the side opposite that stimulated, accompanied by a decrease in the rate on the side which receives the stimulus. As the tendril

bends around the support new regions make contact with it and are stimulated. Thus the encircling continues until the entire tendril is coiled about the support. Often that part of the tendril between the climbing plant and its supporting host coils into the form of a coil spring. This actually serves as a spring, stretching out and closing again during wind storms in such a way as to greatly diminish the danger of being broken or torn away from the support.

Tendrils may be formed from very diverse morphological parts of plants but usually they are either leaves or parts of leaves, or branches. In the climbing *Tropæolum* the petioles serve as tendrils and are practically unmodified except in their sensitiveness to contact. A comparable condition is found in various species of *Clematis* where the stalks (*petiolules*) of the leaflets serve as tendrils. In the sweet pea and some other members of the legume family some of the terminal leaflets of the compound leaves are modified into tendrils. In *Smilax* the tendrils have the position of stipules. Since stipules are normally absent in monocotyledons, however, these



FIG. 39.—Spanish moss, an epiphytic seed plant on bald cypress in North Carolina

tendrils are probably outgrowths from the leaf base. In the grape and other members of the Vitaceæ the tendrils are modified branches. In the squash and other members of the Cucurbitaceæ the origin of the tendrils is somewhat obscure, but it seems likely that, when they are simple, they are to be considered as modified leaves, and when they are branched, they represent shoots bearing leaves. Tendrils modified from roots are not common but are found in a few cases, as, for example, the orchid, *Vanilla*. In a few plants, especially some species of *Ampelopsis*, the tendrils do not twine about the support but form adhesive disks at their tips which cling to a solid surface with great tenacity.

58. **Root Climbers and Leaners.**—Climbing by means of roots is not very common among plants of the temperate zones but there are many tropical plants that climb by this means. Familiar examples in the north temperate zone are the poison ivy (Fig. 37) and some varieties of the Virginia creeper (Fig. 38). These produce very large numbers of adventitious roots along their stems and these roots grow horizontally about the hosts as well as into the cracks and softer parts of the bark. Such success as these plants have in maintaining their positions is to be attributed to the large number of anchoring organs rather than to the efficiency of individual roots.

Some plants, such as the bittersweet nightshade (*Solanum dulcamara*) do not have sufficient mechanical tissue to hold themselves erect and yet have no special means for climbing Such plants often lean upon neighboring plants and may be spoken of as leaners. There are many plants which are prostrate when unsurrounded by other plants but which become leaners when growing in dense vegetation. Some leaners are kept from slipping from their supports by the presence of spines or prickles as in roses and blackberries. These are especially effective if they point downward as in the species of bedstraw (*Galium*).

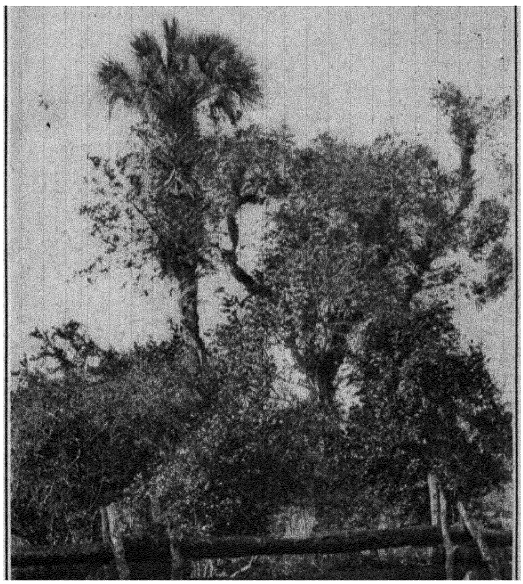


FIG. 40.—Epiphytic fig on a *Palmetto* tree. (Photograph by William Trelease. Courtesy of Dr. George T. Moore and the Missouri Botanical Garden.)

59. **The Liana Habit.**—The chief advantage of the liana habit is that it enables a plant to get its leaves up into the light without constructing a large amount of mechanical tissue. The chief disadvantage is that it makes the climbing plant dependent. If the liana does not chance to find a suitable support to climb upon it cannot succeed in elevating its foliage much above the surface of the soil. Furthermore, if such a plant climbs upon a slow growing host it may in time become too heavy for its supporting plant and this in time may result in the downfall of both symbionts (Fig. 37). Sometimes the leaves of the liana overtop those of the host and cut off so much light that the host is gradually weakened and thus the downfall of both is hastened. (Fig. 36.)

60. **Epiphytes.**—Epiphytes are plants that live upon other plants for support only. They are distinguished from parasites by the fact that they do not obtain food or food materials from the host plant. They manufacture their own food from carbon dioxide and water, and mineral salts

that are derived mainly from wind blown and water-borne materials. They thus differ from ordinary land plants only in their symbiotic relation with a host and in their lack of any connection with the soil.

Epiphytes are especially characteristic of moist tropical regions. In some tropical forests tree-trunks and large branches of trees may be found that are as completely covered with vegetation as is the surface of the soil itself, and the mass of roots and soil on such a tree-trunk may be as much as a foot in thickness. While there are certain families of plants, such as the Orchidaceæ and Bromeliaceæ, which furnish unusually large numbers

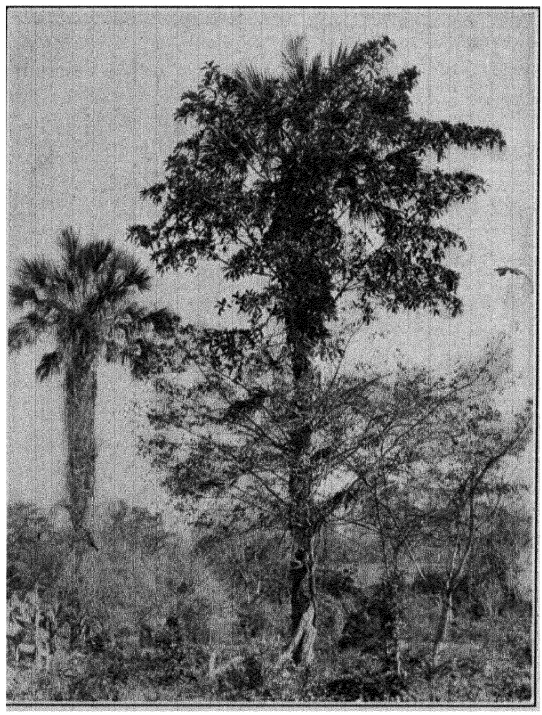


FIG. 41.—*Palmetto* with two well-established figs, showing strangling roots that have reached the soil. (Photograph by William Trelease. Courtesy of Dr. George T. Moore and the Missouri Botanical Garden.)

of epiphytes there are representatives among the epiphytes of many other seed-plant families as well as of ferns, mosses, liverworts, algæ, and lichens (Fig. 39.) In regions with winters or long dry seasons epiphytes are relatively much less abundant and are limited almost entirely to the lower forms of life, epiphytic ferns and seed plants being absent from most regions outside of the moist tropics.

Epiphytes very commonly possess certain structures that are characteristic of plants of dry climates, such as well-developed organs of absorption, structures for the storage of water, or modifications for preventing excessive transpiration. These characteristics are exhibited most markedly by epiphytes that occur near the tops of trees, where there is a high degree of

exposure and progressively less by those lower down. In tropical forests where epiphytes are abundant there are certain species that occur only near the tops of the trees, others that occupy intermediate positions and still others that grow only lower down where the air is constantly humid. The Spanish moss (*Tillandsia usneoides*), a common epiphyte of the coastal plain of southeastern United States, possesses a remarkable adaptation for preventing excessive transpiration. The plant has no leaves but the pale green stems are covered with hairs which are modified into scales. When these scales have been moistened by rain or dew they are somewhat elevated from the stem so that water readily gets to the stem and is rapidly absorbed. As the scales dry out, however, they collapse closely against the stem and, since they overlap like the shingles of a roof, they form a very effective covering to prevent loss of the water that has been absorbed.

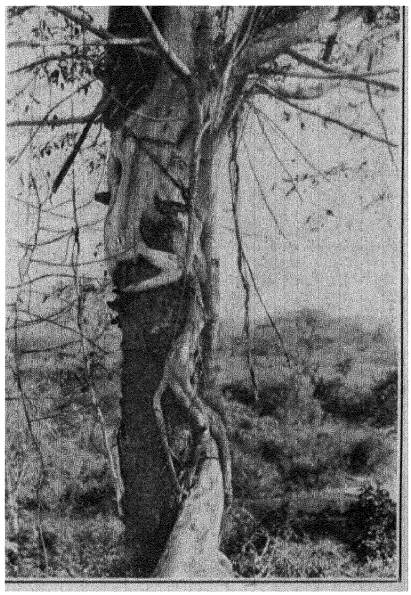


FIG. 42.—Strangling roots of an epiphytic fig. (Photograph by William Trelease. Courtesy of Dr. George T. Moore and the Missouri Botanical Garden.)

In moist tropical forests certain kinds of epiphytes occur on leaves. These, because of their position, are called epiphylls. Lichens, mosses, and even some vascular plants grow as epiphylls.

61. **Hemi-epiphytes and Pseudo-epiphytes.**—Hemi-epiphytes are plants that are epiphytic, and therefore symbiotic, during only a part of their lives. The strangling fig is a notable example (Figs. 40 and 41). The seeds of the fig germinate on the bark of a host and the young fig plant starts its life as an epiphyte. Soon, however, some of its roots begin to grow downward and around the trunk of the host. These roots become thick and flattened and the host plant is often actually strangled by them (Fig. 42). Eventually they reach the soil and the fig then becomes an independent plant, no longer epiphytic (Figs. 43, 44 and 45).

Ordinary soil plants are often found growing in crotches or knotholes of trees where a little soil has collected. These are called pseudo-epiphytes. Their symbiotic relations to the host plant are comparable to those of true epiphytes.

62. **The Epiphyte Habit.**—Many epiphytes seem to be capable of growing on most any supporting host. Some can even grow upon non-living supports. Spanish moss (*Tillandsia*), for example, may grow hanging from telegraph wires if the air is sufficiently humid, and many mosses and lichens grow equally well as epiphytes on living hosts or upon rocks. When growing upon rocks they are called lithophytes.

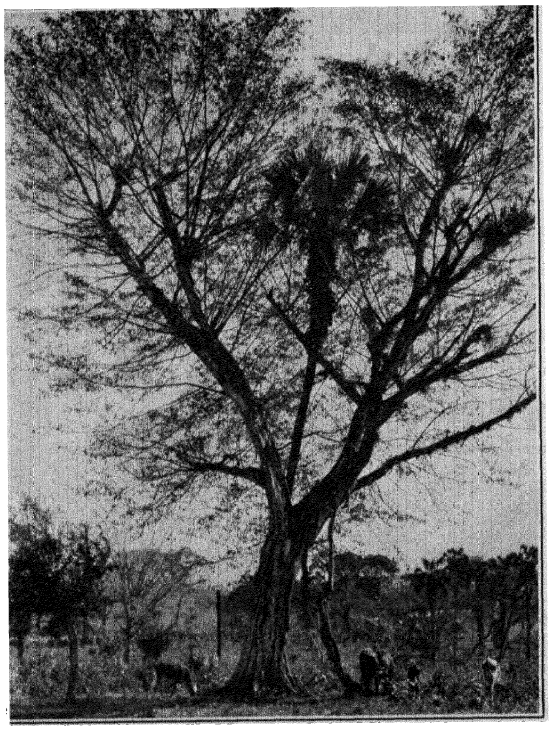


FIG. 43.—Large
Trelease. Courtesy of Dr. George T. Moore and the Missouri Botanical Garden.)

Some epiphytes, however, are more or less limited to certain kinds of hosts. The epiphytic fern, *Polypodium polypodioides* (Fig. 46), for example, is largely limited to trees having deeply-furrowed, soft bark which has a high water-absorbing capacity and loses water slowly. Such conditions are well provided by the American elm (*Ulmus Americana*) and the live oak (*Quercus virginiana*). In the case of epiphytic lichens it has long been known that the kinds that one may expect to find on a tree depends upon the character of the bark; whether it is rough or smooth, hard or soft, resinous or non-resinous, etc.

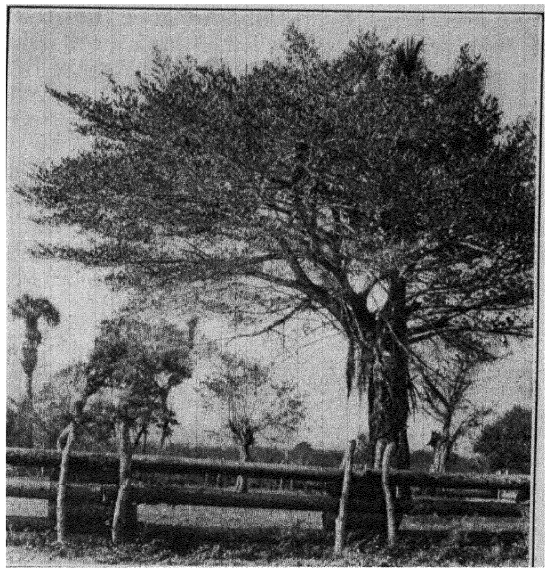


FIG. 44.—Large fig tree with *Palmetto* host almost killed. (Photographed by William Trelease. Courtesy of Dr. George T. Moore and the Missouri Botanical Garden.)

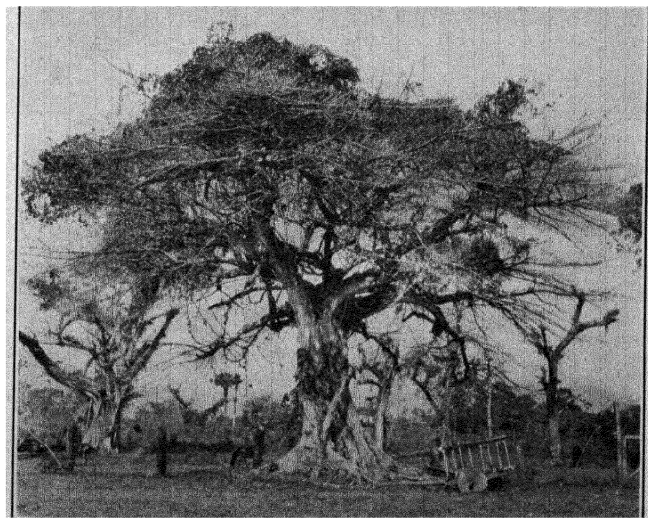


FIG. 45.—Large fig tree with the *Palmetto* host completely gone. (Photograph by William Trelease. Courtesy of Dr. George T. Moore and the Missouri Botanical Garden.)

It is doubtful whether any distinct advantage of the epiphytic habit can be noted. Often there is less competition for space than there is among land plants but it is open to question whether this is a real advantage, and in many cases, especially in the tropics, there seems to be fully as much competition for space among epiphytes as among other plants. A very obvious disadvantage is the unfavorable position with respect to water supply.

Epiphytism frequently results in harm to the host plant. The strangling action of the hemi-epiphytic fig has already been mentioned. Other epiphytes frequently break down their hosts by their increasing weight or weaken them by cutting off a part of the light or by interfering with the free interchange of gases. Epiphylls are especially injurious in these latter ways.

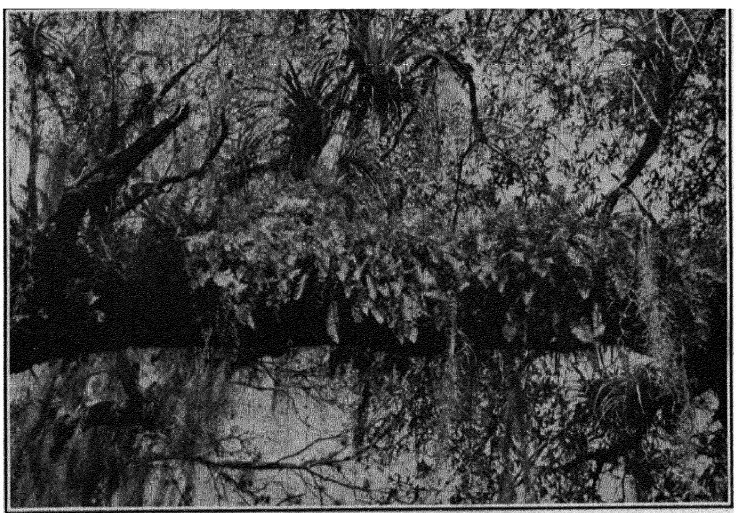


FIG. 46.—A variety of epiphytes, the polypody fern and three species of *Tillandsia*, growing on live oak in Florida. (Photograph by Alexander Sprunt, Jr.)

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CHAPTER IX

NUTRITIVE CONJUNCTIVE SYMBIOSIS

CONJUNCTIVE symbiosis is said to be nutritive whenever there is a direct food relation between two or more of the symbionts. It thus includes all interrelations of a parasitic nature. By parasitic nature we mean any case in which one organism absorbs food or food materials directly from another. It obviously includes, therefore, not only the ordinary parasitic relations that we commonly call disease but also the relations existing in all gall-like structures where the gall-forming organism is parasitic on a host and often

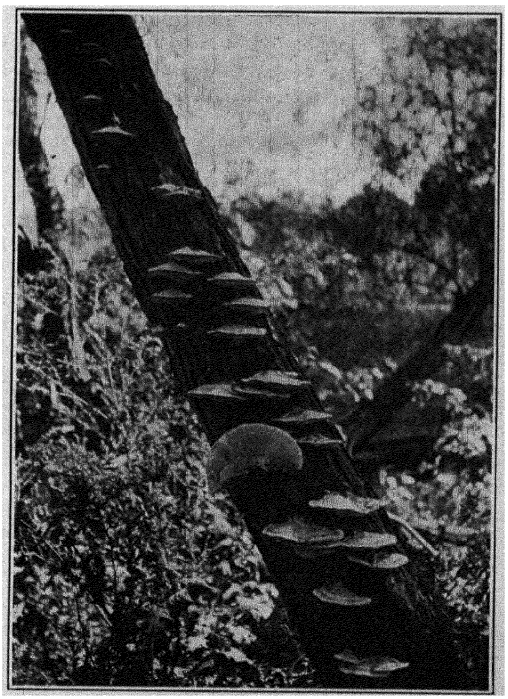


FIG. 47.—*Daedalea confragosa*, a facultative parasite on willow.

the host is in turn parasitic on the gall-forming plant or animal. Only some of the more common or otherwise interesting examples of nutritive conjunctive symbiosis can be discussed in this chapter.

63. **Antagonistic and Reciprocal Conjunctive Symbiosis.**—In antagonistic nutritive conjunctive symbiosis one or more, but not all, of the symbionts derive food or food materials from other symbionts while those from which the food is taken receive no benefit but often great injury from the relationship. Ordinary parasitism as exemplified by disease, some

mycorrhizas, and very many kinds of galls belong to this type of symbiosis.

Reciprocal nutritive conjunctive symbiosis differs from antagonistic symbiosis in that all of the symbionts receive benefit from the symbiotic relation, usually in the form of food. Any organism that receives food directly from another organism is parasitic. The symbionts concerned in this type of symbiosis are, therefore, parasites and our commonest examples are those in which two unlike kinds of organisms are living together in intimate contact and each is parasitic on the other. There is thus a double or reciprocal parasitism. Root and leaf tubercles caused by bacteria, lichens, and some mycorrhizas are examples of this type of symbiosis.

64. **Parasites.**—Parasites are plants or animals that derive food or food materials from other living organisms. Parasites which lack chlorophyll and so are dependent upon their hosts for all food are called holoparasites while those that have chlorophyll and thus are able to manufacture carbohydrates are called partial parasites. The latter obtain food materials rather than food from their hosts. It is not known in most cases whether parasites, either holoparasites or partial parasites, obtain proteins from their hosts or manufacture them themselves. It is not likely that they are all alike in this respect.

Plants that obtain their food from dead organic matter are called saprophytes. These, of course, are not symbiotic, but there are many fungi and bacteria that can live equally well as parasites or as saprophytes. Such organisms are called facultative parasites. Many of the bracket fungi, such as *Polyporus sulphureus*, are of this nature. (Fig. 47.) Such a plant gets into a living tree through a wound and may live as a parasite in the tree for many years, but after the tree is dead the fungus continues to grow as a saprophyte in the dead wood. Fungi of the genus *Cordyceps*, likewise, cause diseases of certain kinds of insects. They grow as parasites in the living insects until the hosts die and then continue to live as saprophytes on the dead insect bodies. Those fungi that are obligate parasites and must have a living host in order to complete their life cycles, and yet which habitually or periodically spend a part of their lives in a non-parasitic condition, are sometimes called tropoparasites.

Familiar examples of holoparasitic seed plants are the various species of dodder (*Cuscuta*). The dodders are twining plants which lack chlorophyll and have a yellowish color. The seeds germinate on soil, usually rather late in spring after other vegetation has sprouted and young shoots of host plants are therefore available. The young shoot of a dodder is a fine, yellow, thread-like structure whose tip rotates as it elongates. If it does not come in contact with a host plant it lives but a few weeks at most. If, however, it succeeds in finding a suitable host it grows vigorously, twining about the host and at the same time penetrating it with absorbing organs, called haustoria, which in this case are modified adventitious roots. Soon the dodder loses all connection with the soil and becomes purely a holoparasite. Some species of dodder may grow on various kinds of hosts while others are restricted to a single species. Sometimes these parasites are very destructive to crops such as clover and flax.

Other important holoparasites are found in the family Orobanchaceæ, a family of root parasites. The seeds of the broom-rape (*Orobanche*) germinate only when in contact with the root of a host plant. The seedling penetrates the host at once and produces in the soil a tuber-like body. Only

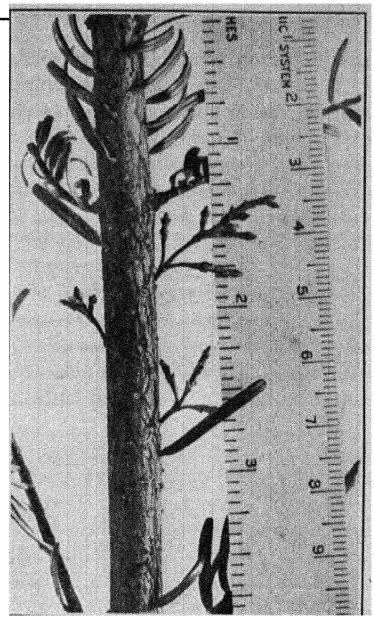


FIG. 48.—*Arceuthobium Douglasii* (dwarf mistletoe). Pistillate plants on *Pseudotsuga taxifolia*. (Photograph by James R. Weir.)

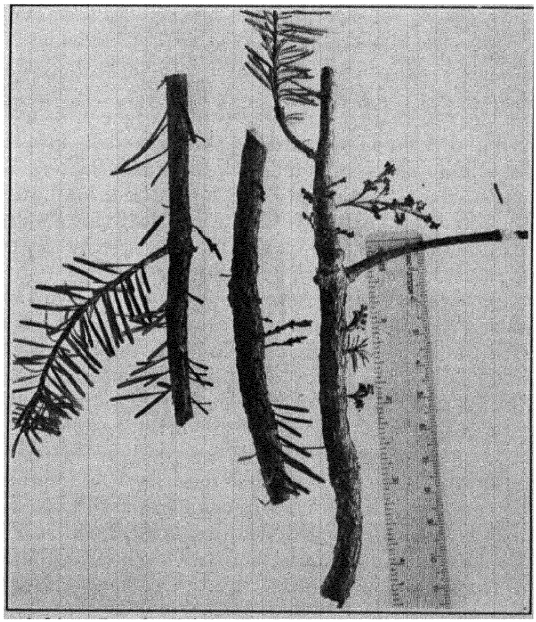


FIG. 49. *Arceuthobium Douglasii* (dwarf mistletoe). Staminate plants on *Pseudotsuga taxifolia*. (Photograph by James R. Weir.)

the flowering shoot comes above the surface of the soil. In some species the contact with the host is only at a single point which may be on a small lateral root at some distance from the main stem of the host.

The Rafflesiaceæ is a tropical family of root parasites. In the genus Rafflesia the entire vegetative part of the plant grows within the host, just as is the case with many parasitic fungi, so that the plant ordinarily is seen only when it is in flower. *Rafflesia Arnoldii*, one of these parasites, has the largest flowers that are known. They are sometimes as much as a meter in diameter.

Among the most familiar partial parasites are the mistletoes; *Viscum*, the European mistletoe, *Phoradendron*, the American mistletoe, and *Arceuthobium*, the dwarf mistletoe (Figs. 48 and 49). These plants contain chlorophyll and manufacture their own carbohydrates but they are parasitic on the trunks and branches of trees and obtain water and minerals from the host plants.

The family Scrophulariaceæ contains representatives of all gradations from complete independence to holoparasitism. Many of the common members of the family, as toadflax, *Linaria vulgaris*, are completely independent plants. Others, as some species of lousewort, *Pedicularis*, are mild root parasites. They contain chlorophyll and look like independent plants but they are able to augment their supply of water and minerals by robbing their neighbors. Often a single plant has numerous contacts with the roots of other plants, frequently of several species at the same time. *Tozzia*, another genus of the same family, with one species occurring in the Alps and another in the Carpathians, is much different. A plant of this genus lives for two or three years in a holoparasitic, entirely subterranean, condition. It then sends up an aërial shoot which becomes green, changing the plant, therefore, to a partial parasite, and in a few weeks produces flowers and fruits and then dies. Such a life history is strikingly similar to that of a two-year cicada in the insect world. Finally, there is the European genus, *Lathraea*, also belonging to the Scrophulariaceæ, which completely lacks chlorophyll and is thus holoparasitic throughout its life.

The examples of holoparasites among the fungi and bacteria are of course innumerable, their exact relations to the host plants and the amount of injury they do being very variable. There are also various kinds of holoparasitic animals, notably several species of scale insects, that exhibit this same type of symbiotic relationship with plants.

65. **Ectotrophic Mycorrhizas.**—A mycorrhiza, as the word suggests, is a structure composed of root and fungus. An ectrotrophic mycorrhiza is one in which the fungus mycelium is found on the outside of the root and between its cells, as contrasted with endotrophic mycorrhizas in which the fungus occurs inside the root cells. Ectotrophic mycorrhizas are found on various kinds of trees such as pines, oaks, hickories, beech, etc. They occur in the upper layers of the soil on the smallest rootlets. They usually form clusters of short, stubby branches often described as "coral branching" rootlets (Figs. 50 and 51). They vary in color from white to bright yellow, brick red, or dark brown, the color depending upon the kind of fungus.

As many as seven different kinds of fungi have been found producing mycorrhizas on the same species of tree and there is probably no arbitrary limit to the number that might be so found, just as there is no arbitrary limit to the number of diseases to which a species may be subject. There

is considerable evidence, however, that certain species of trees are more or less immune to the attacks of many mycorrhizal fungi while other species lack such immunity.

The internal structure of the mycorrhizas of dicotyledonous trees is characteristically different from that of coniferous trees. (Fig. 51.) In the case of dicotyledonous trees the cortical cells are ordinarily palisade-shaped on one side of the root and irregular in shape on the other side while such a condition has never been reported on a coniferous tree. No reason for this morphological phenomenon is known.

These mycorrhizas are caused by many kinds of summer and autumn mushrooms. The mycelium of the mushroom penetrates the outer cell wall of the rootlet and splits the wall by dissolving out the middle lamella. It then continues to grow and branch until it forms a fungus mantle which



FIG. 50.—Ectotrophic mycorrhizas of the hornbeam (*Carpinus betulus*) in leaf mold (Photograph by Somerville Hastings.)

completely covers the rootlet, tip and all. At the same time branches of the mycelium penetrate between the outer cortical cells of the rootlet splitting the walls and pushing the cells apart. Further growth of the rootlet is inhibited by the fungus mantle which covers it and excessive branching is induced just as when the tip of a root or shoot is cut off. The new branches, however, are in turn transformed into mycorrhizas by the mycelium, and the final result is the cluster of short stubby branches.

The ectotrophic mycorrhizas of forest trees, in the northern and northeastern parts of the United States, are produced during summer and autumn. They persist unchanged during the winter, so far as external appearance is concerned, and die in the spring. They are therefore annual structures. So far as dicotyledonous trees are concerned these mycorrhizas are probably of little importance. The fungi are parasitic on the roots, but ordinarily the percentage of the total number of rootlets of the tree that are affected is so small that the tree is not inconvenienced any more than when a few of its roots are broken off by a burrowing animal or some of its leaves eaten by insects.

For the other symbionts, however, that is, the fungi, the mycorrhizas are probably much more important. The roots of trees contain a large amount of reserve food at the time when mycorrhizas are being formed and this is undoubtedly made use of by the fungi Fungi, like all other plants, require a large amount of food for the production of their fruits. Some fungi store up the necessary supply of food, during their vegetative growth, in structures called sclerotia. The mycorrhiza-forming mushrooms, however, depend upon the food in the tree roots for their fruiting activity and the mycorrhizas therefore take the place of sclerotia for these fungi. In the

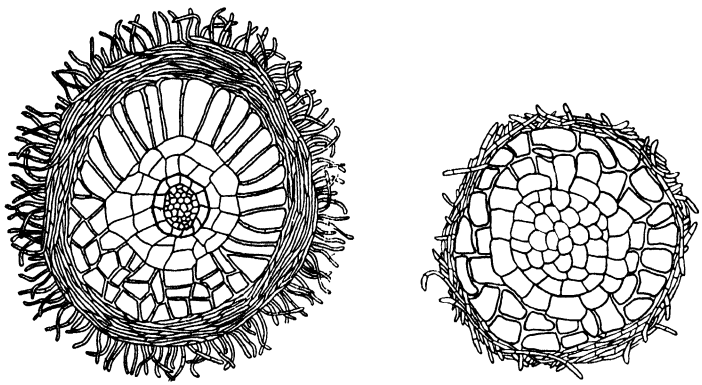


FIG. 51.—Cross-sections of ectotrophic mycorrhizas Left from *Carya ovata;* right from *Picea rubra.*

forests of eastern and northeastern United States and of southeastern Canada mushrooms are extremely abundant and ectrophic mycorrhizas, which are also abundant, appear to be very important in the nutrition of many of the late summer and autumn mushrooms. In the central part of the Rocky Mountain region mycorrhizas do not seem to play so important a part, though in some of the Pacific coast regions they are probably as abundant and important as in the east.

A number of cases are known in which the mycorrhizal fungus is partly ectotrophic and partly endotrophic. Such mycorrhizas are said to be ectendotrophic. In most cases they probably represent merely a difference in degree of parasitism. All ectotrophic mycorrhizal fungi are parasitic on the roots of the host plants. This leads to a resistance to the parasite on the part of the host cells. In most cases the fungus is able to penetrate between the cells but not to gain an entrance to them, and so remains ectotrophic. If, however, the fungus succeeds in entering the cortical cells of the root it becomes ectendotrophic.

There has been a great deal of disagreement among investigators concerning the relationship between mycorrhizal fungi and host plants and its significance. Some of this disagreement is undoubtedly due to the fact that some investigators have worked mostly with dicotyledonous trees while others have worked mostly with coniferous trees or with herbaceous plants and the relationship probably differs greatly in the different groups of plants or in different families within a group. In the case of coniferous

trees, especially some of the pines, evidence has been accumulating that growth of the trees, at least in the seedling stage, is much better where mycorrhizas are abundant than where they are scarce or absent. This may be due to the fact that an increased supply of nitrogen, and perhaps of such elements as potassium, phosphorus and calcium, are obtained by the tree through the fungi. Thus mycorrhizas may be of more importance in the practice of forestry than was formerly thought. A great deal more work will need to be done before we can speak with assurance concerning many of these forms but at present it seems likely that most ectotrophic mycorrhizas of dicotyledonous trees represent examples of antagonistic nutritive conjunctive symbiosis while those of many coniferous trees are reciprocal. In the case of the Indian Pipe (*Monotropa uniflora*) the relationship is almost certainly reciprocal. This little seed plant, which is entirely white,

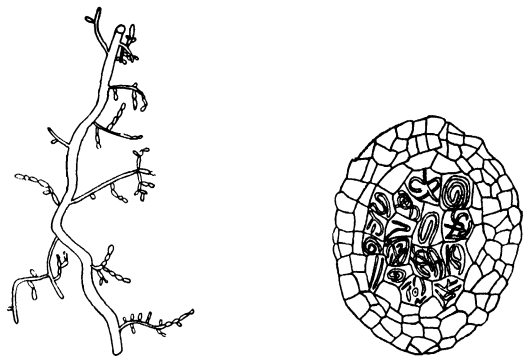


FIG. 52.—Endotrophic mycorrhizas of *Acer rubrum*. Left, external appearance; right, tangenital section.

was formerly thought to be a saprophyte. Usually, however, the entire root system of the plant is transformed into a cluster of ectendotrophic mycorrhizas and it appears that the seed plant must be parasitic on the fungus as well as the fungus being parasitic on the seed plant. It appears unlikely that any seed plants are ever saprophytic.

66. **Endotrophic Mycorrhizas.**—Endotrophic mycorrhizas differ from ectotrophic in that the mycelium of the fungus occurs inside the cells of the root rather than between the cells or on the outside of the root. In the case of the red maple, *Acer rubrum*, the rootlets containing the fungus are transformed into small bead-like galls (Fig. 52). There may be a single one of these in the case of a short rootlet or there may be several, arranged like a short string of beads, on a longer rootlet. The fungus is found only in the cortical cells of these bead-like mycorrhizas. Although these mycorrhizas of the maple are usually quite abundant on the roots in the superficial layers of the soil they are not thought to be of any great importance to the tree. No experimental work has ever been done on them, however, so that the exact relation between tree and fungus is not known.

Among the most interesting of endotrophic mycorrhizas are those of the orchids. Many orchids are entirely dependent upon mycorrhizal fungi. The seeds of some orchids, under natural conditions, will not germinate except in the presence of the mycelium of the mycorrhizal fungus. In other

species the seeds germinate but do not develop beyond the seedling stage unless they become infected with the proper kind of fungus. These facts have made the propagation of orchids for commercial purposes very difficult, and in some cases impossible, in the past. The mycorrhizal fungi concerned with most of these orchids, as well as with other endotrophic mycorrhizas, are not mushrooms but microscopic molds which for the most part are not well known although a few have been identified. *Gastrodia elata*, a non-chlorophyllous orchid of Japan, however, has as its endophyte the mycelium of *Armillaria mellea* which is a common edible mushroom.

Experiments have shown that the seeds of many orchids can be germinated, and the seedlings grown, without fungi by using a proper culture medium containing a sugar or some other chemical which supplies the necessary stimulus. This is the method now generally employed by florists.

Some orchids, as *Corallorhiza* and *Epipogon*, have no roots, the underground parts consisting entirely of branched rhizomes. These rhizomes always contain endophytic fungi, however, and the symbiotic relation is undoubtedly the same as in the case of orchids with roots. Such a combination of fungus and stem may be called a mycopremna.

Endotrophic mycorrhizas are nearly as common in the Ericaceæ as in the Orchidaceæ, and certain genera of this family, as *Calluna*, *Rhododendron*, and *Vaccinium*, the blueberry, are more or less dependent upon mycorrhizal fungi. These fungi can grow only in an acid medium and the blueberries and other mycorrhizal plants of the Ericaceæ, therefore, can flourish only in a soil that is kept acid by some means.

In *Calluna* it has been found that the mycelium of the fungus, which belongs to the genus *Phoma*, is not only present in the roots but throughout the aërial parts of the plant as well and is always present in the seeds. The germination of these seeds seems to be as dependent upon the presence of the fungus as is that of orchid seeds.

Endotrophic mycorrhizas are abundant in the composite, gentian, and legume families and probably in some others but nothing is known of their significance in these families. The fungi in the mycorrhizas of these families appear to belong to the group known as Phycomycetes but none of them have ever been isolated for identification.

A great deal of experimental work has been done on endotrophic mycorrhizas in the orchid and heath families and in many of these it is known that the fungus is parasitic on the root cells but that the root cells finally digest and absorb the hyphæ of the fungus. The relationship is, therefore, reciprocal. Outside of these two families, however, not much work has been done and it is not definitely known whether the various endotrophic mycorrhizal relationships are reciprocal or antagonistic.

67. **Galls.**—A gall is a structurally modified plant part caused by a symbiotic relation with some other organism. Usually the affected part is enlarged either through increase in size of the cells (hypertrophy) or increase in the number of cells (hyperplasy) or both. In some cases, on the other hand, there is decrease in size through a reduction in cell size (atrophy) or a reduction in cell number (hypoplasy). Usually the plant stores up quantities of food in the tissues of the gall and these are later used by the parasitic symbiont. Partly because of these large stores of reserve materials most galls are very resistant and if a plant bearing galls is cut down, the galls often remain fresh and green long after the other parts of the plant are dead.

Galls are found on all kinds of plant parts. They are most common on stems and leaves but occur on roots, flowers, and fruits also. They exhibit a great variety of form and color, some of them being very fantastic in form and appearance, and some of them are very beautiful. They are caused by many kinds of plants and animals but chiefly by fungi and insects and more especially the latter. The kinds of insect galls are almost innumerable (Fig. 53). The great majority are produced by gall-wasps (*Cynipidae*) or gall-gnats (*Cecidomyidae*). Each species of insect produces galls always on the same species of plant or on a few closely-related species and, while insect galls are widely distributed in the plant kingdom, there are some groups of plants that are peculiarly susceptible. Of about 450 known gall-wasps, for example, more than 350 are found on oaks and nearly 30 on roses. The gall-gnats are somewhat less restricted than the wasps but large numbers are found upon oaks, hickories, willows, roses, legumes and composites, especially goldenrods and asters.



FIG. 53.—Insect galls on white oak.

The exact nature of the stimuli that cause the production of insect galls is not definitely known in most cases and it probably is not the same in all kinds of galls. It has been believed that the stimulus was generally due to mechanical irritation caused by the feeding activities of the young insects after hatching. It has been found, however, that the formation of a certain type of leaf gall of witch-hazel is induced by repeated stinging of the leaf by the mother insect and that feeding activities have nothing to do with it. As the leaf is stung a minute quantity of a substance is injected and repeated stinging is necessary throughout the period of gall formation.

An interesting group of galls is that of the witches' brooms that are formed on various kinds of trees (Fig. 54). Those occurring on hackberry (*Celtic occidentalis*) are caused by mites, minute animals closely related to

spiders, while most other witches' brooms are caused by fungi. The formation of a witches' broom is quite comparable to that of an ectotrophic mycorrhizal cluster. That is, the attack of the parasite on a shoot inhibits the further elongation of that shoot and causes an abnormal number of branches to be produced back of the tip. These branches are in turn attacked by the parasite and still other branches are produced the final result being a thick broom-like cluster of short branches.

Other common galls caused by fungi are the "cedar apples" which occur on *Juniperus virginiana*, the "black knot" of plum and cherry trees, and some stem- and leaf-galls occurring on certain members of the family Ericaceæ.

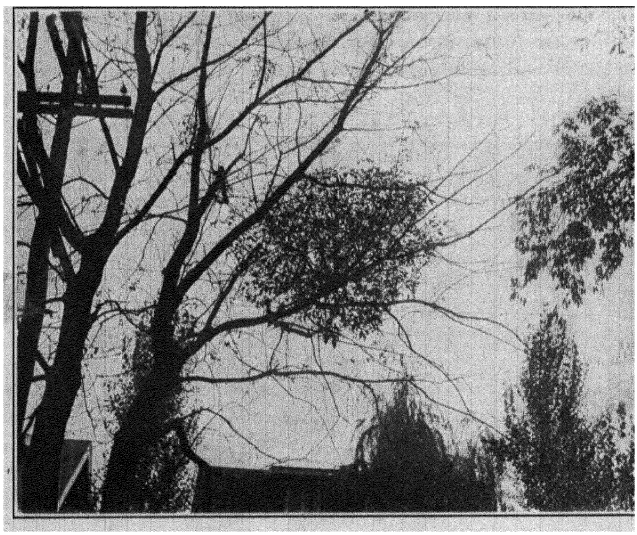


FIG. 54. Witches' broom on *Acer negundo*.

The gall-causing organisms, whether plants or animals, are parasitic on the host plants, and the galls, although composed of plant tissue, are of no benefit to the plants on which they are formed. The food that is stored in the galls can never be used by the host plant, but only by the parasite. These galls then are comparable to ordinary diseases and represent antagonistic nutritive conjunctive symbiosis. Usually they are not very harmful but when they become excessively thick on a plant they are seriously detrimental

68. **Root Tubercles.**—The best known bacterial tubercles are those found on the roots of many plants of the legume family. These tubercles are small galls, usually only a few millimeters in diameter, and are composed largely of parenchyma cells, like most other galls. Within the cells of the tubercle are found bacteria. The bacteria are facultative parasites which, in a saprophytic condition, are found rather commonly in soils. They enter the roots of leguminous plants through root hairs and become parasitic on the cells of the roots, and the roots are stimulated to produce the gall-tissues that form tubercles. At first the legume plants suffer

somewhat from the presence of these parasitic bacteria but eventually many of the bacteria are digested and absorbed by the root cells.

Root tubercles are also found in the families Cycadaceæ, Podocarpaceæ, Eleagnaceæ and Myricaceæ and in the genera *Alnus* and *Ceonothus*. In all of these cases the tubercles are produced through the modification of lateral rootlets. In this respect they differ from those of the Leguminosæ which are produced as out-growths of the cortex and not as modified lateral rootlets.

The bacteria that are concerned in the formation of these tubercles are spoken of as nitrogen-fixing bacteria because, unlike nearly all other organisms, they are able to use the uncombined nitrogen of the atmosphere, combining it with other elements to form nitrates. Nitrogen in the form of nitrate salts is readily utilized by legume plants and by other green plants. For these reasons the symbiotic relation between nitrogen-fixing bacteria and legume plants is extremely important to agriculture since it increases in the soil the available nitrates for other crop plants. As much as 250 pounds of nitrogen per acre may, under favorable conditions, be added to the soil through the activities of these bacteria. It is primarily because of this symbiotic phenomenon that a legume crop is nearly always included in any rotation of crops.

69. **Leaf Tubercles.**—Some tropical plants belonging to the family Rubiaceæ, especially the genus *Pavetta*, have small galls, or tubercles, on their leaves that contain nitrogen-fixing bacteria. These bacteria seem to be very closely related to those found in the root tubercles of legume plants and their relation to the host plant is in many ways comparable. The buds of these plants always contain a jelly-like material in which some of the bacteria are present. The bacteria enter the young leaves through stomatal openings while still in the bud. They at once become parasitic and even destroy some of the leaf cells but the formation of a tubercle by the leaf tissue appears to inhibit any further encroachment of the bacteria and many of them are finally digested and absorbed by the leaf cells.

Since the bacteria are always present on the growing tips of the plant in all of its buds, they are also present in the flowers and therefore on the seeds. When a seed germinates the bacteria are thus at once present on the growing tip of the plumule. These bacteria differ from the legume bacteria, in that they spend their entire lives on and in the host plant while the legume bacteria spend a part of their lives as saprophytes in the soil.

Pavetta plants which were grown for experimental purposes from sterilized seeds and thus were free from bacteria, showed typical "nitrogen hunger." When these plants were inoculated with the bacteria they soon recovered their normal health. This indicates that the symbiotic relation has become practically obligate for both organisms since the seed plants depend upon the bacteria for their nitrogen supply and the bacteria probably cannot live at all without the host plant.

70. **Lichens.**—A lichen is a symbiotic combination of fungus and one-celled algæ (Fig. 55). It used to be thought that lichens were single unit organisms and they were classified along with the liverworts. The green cells in them, which are known to be algæ, were called gonidia. The fact that the lichen is a plant complex rather than a single organism was discovered by growing the fungi and algæ separately. Later lichens were synthesized by placing lichen fungi among algæ that had been growing free

in nature. In these cases the mycelium enveloped some of the algal cells and lichens of the usual kind resulted. The algæ that are concerned in lichens commonly belong to a few well-known genera such as *Pleurococcus* and *Nostoc*. The fungi, however, appear to have been greatly modified by the symbiotic relation since they are very different from any fungi known outside of lichens.

Although lichens are dual organisms, that is they are made up of two distinct kinds of plants, yet they exhibit a high degree of unity and in many respects behave as single organisms. Perhaps the most striking indication of a high degree of unity is seen in the bodies called soredia. A soredium is a vegetative reproductive body consisting of a small amount of fungus tissue enclosing a few algal cells. It is the commonest and most efficient method of reproduction that a lichen has. The lichen fungi, of course, produce spores but these spores can never develop into lichens unless they chance to fall among algæ of a suitable species. The efficiency



FIG. 55.—Lichens on rock. (Photograph by Bruce Fink.)

of the soredium, therefore, is due to the fact that it keeps the two symbionts together. It is practically the only case known in which two symbionts have a common reproductive body.

Another feature that makes lichens seem like unit organisms is the fact that they are able to grow in extremely dry situations. Fungi, as a group, are characteristically plants of medium conditions with respect to water supply, while algæ as a group, are characteristically plants of very wet situations, many of them growing in water. But, when fungi and algæ live together in the intimate symbiotic relationship under discussion, the resulting organisms are more resistant to dry conditions than any other group of plants. It is for this reason that lichens form the outposts of the plant world in nearly every direction. In going toward the poles the last plants

one sees are pretty certain to be lichens. At the tops of the highest mountains the plants are almost exclusively lichens. At the tops of tall tropical trees, if any plants are found growing as epiphylls on the leaves that are fully exposed to the hot tropical sun, they are lichens.

The exact physiological relationship between the two components of a lichen is still very imperfectly known although it has been studied and discussed for a very long time. Some writers have thought that a lichen represents a sort of partnership between the fungus and the algæ each partner supplying to the other certain necessities of life. Others have taken a somewhat opposite view and have believed the algæ to have been enslaved by the fungus. Still others have considered the fungus as an ordinary parasite on the algæ, or have said that the fungus is diseased by the algæ. It is improbable that the physiological relationship between lichen-fungus and alga is the same in all cases. It is reasonably certain, however, that in the majority of lichens the fungus obtains organic food from the algæ, either as a parasite on the living gonidia or as a saprophyte on dead ones. Similarly, it is certain that the algæ obtain water, at least, from the fungus, either directly or indirectly. The relationship has apparently reached such a balance that it is more or less normal for both fungus and alga, and both can endure it, therefore, without suffering. This, however, must not be taken to imply a sort of reciprocity agreement under which each party supplies something to the other. Rather each party takes all it can get from the other. In other words the lichen represents a case of double, or reciprocal, parasitism, and must be classified as reciprocal nutritive conjunctive symbiosis.

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CHAPTER X

PHYSICAL FACTORS: LIGHT

ANY part of the environment of a plant that affects in any way the life of the plant may be spoken of as an environmental factor or ecological factor. The environment of any plant is partly living and partly non-living. The living part of the environment consists of plants and animals. These may be spoken of collectively as biotic factors. They have been discussed at some length in the chapters on Symbiosis and will be dealt with further in some of the succeeding chapters.

The non-living part of the environment consists of a variety of influences that may be spoken of collectively as physical factors. The more important of these will be discussed in the present and the immediately following chapters.

71. **Gravity.**—An environmental factor becomes important ecologically as it varies from place to place and in its effect upon different kinds of plants. If all factors produced the same effects on all plants everywhere there would be no science of ecology, just as there would be no science of human sociology if the environmental conditions in which human beings live were universally the same.

Gravity is the one universal factor. Its action is practically the same on all parts of the earth's surface. Since it is a universal factor it is not of very great importance ecologically, though it is very important physiologically. Generally speaking the effect of gravity is to cause roots to grow downward and stems to grow upward, but it is a curious fact that the directions of growth of the lateral roots and the lateral shoots are also directed largely by gravity. The advantage of this phenomenon is, of course, clear enough, since it would be a distinct disadvantage to a plant to have all its roots grow straight downward and all its stems straight upward. As long as the main shoot and the main root are intact the lateral branches seem to be inhibited from growing straight upward or straight downward, since if the main shoot is cut off one or more of the stronger lateral branches will then assume the vertical direction. This whole phenomenon is still very imperfectly understood and may not be due entirely to gravity.

The effect of gravity on the lower plants is comparable to that on seed plants. For example, the orientation of the fruit-bodies of fungi is due, for the most part, to gravity. In the case of the toad-stool type of mushrooms, with gills on the under side of the cap, the spores cannot be shed unless the cap is horizontal and the gills vertical. When such a mushroom grows from the side of a stump or log, the stem, through a response to gravity, always curves in such a way as to bring the cap into a horizontal position (Fig. 56).

72. **Light.**—Light is not, like gravity, a universal factor. The amount of light in different places and at different times varies greatly. The source of all light is the sun, and the amount of light received by any place on the surface of the earth depends upon the length of the day and the angle at which the sun shines. At the time of the spring equinox in March and again at the fall equinox in September the day is twelve hours long everywhere on the surface of the earth. But at all other times the days are twelve

hours long only at the equator and become either longer or shorter as one goes toward either pole. The intensity of light also varies greatly as the season advances because of the changing angle at which the sun shines, being most intense where the incident rays of light are most nearly vertical. The intensity of light is also greatly affected by the condition of the weather as everyone who has done photographic work well knows. The merest film of cloud in front of the sun brings about an appreciable reduction in the light intensity and the effect of thicker clouds is of course much greater. There are thus three variables that change the amount and intensity of light in any given place; namely, the time of year, the time of day, and the condition of the weather.

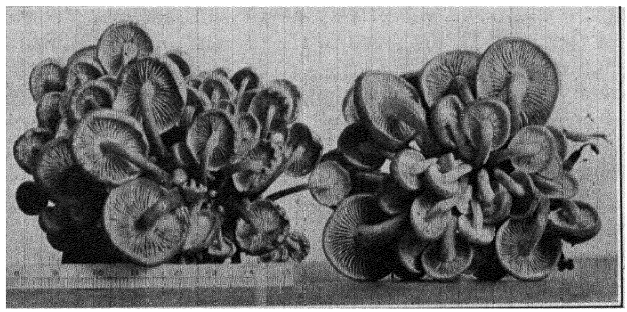


FIG. 56.—Clusters of mushrooms (*Collybia velutipes*) that grew on the lower side of a horizontal tree trunk. The curved stems are due to a response to gravity.

The quality of light is also an important factor. A beam of white light consists of many rays which differ in length and which, when separated, form the series of colors that are characteristic of a rainbow or a spectrum. The colors run in order through shades of red, orange, yellow, green, blue, indigo, and violet. Beyond the violet are the ultra-violet rays which are invisible to the human eye but which produce certain effects upon plants. These ultra-violet rays have very short wave lengths while the red rays have the longest wave lengths. The rays with long wave lengths, that is those at the red end of the spectrum, are the ones most used by the plant in the manufacture of carbohydrates. On the other hand the shorter wave lengths, violet and ultra-violet, are most important in checking vegetative growth. Since these short wave lengths are more readily absorbed by atmosphere, and especially by clouds, than the longer ones, the quality of the light varies greatly between high and low altitudes and between clear and cloudy weather.

73. **The Effect of Length of Day.**—At the equator the days are always twelve hours long and during the summer of either hemisphere the length of the days increase toward the pole until at the pole light is continuous throughout the mid-portion of the summer. The long days of the north, during the summer of the northern hemisphere, enable plants to develop rapidly and mature quickly. It is largely because of the longer days that oranges are ripe and ready for the market several weeks earlier in the northern part of the Central Valley of California than they are 400 miles

farther south. It is also primarily due to the long periods of sunshine during the growing season that large crops of hay, wheat, potatoes, and other vegetables can be grown in some parts of Alaska.

Experiments have shown that some seed plants normally produce flowers only when the days are relatively long and so may be spoken of as long-day plants. Others come into bloom only when the days are relatively short and are called short-day plants. Long-day plants, such as evening primrose, red clover and radish, can be made to bloom earlier than they normally would by lengthening the day by means of artificial light. Short-day plants, on the other hand, such as tobacco, dahlia and ragweed respond in just the opposite way from the long-day plants and, therefore, in order to bring them into bloom earlier it is necessary to shorten the period of illumination by placing the plants in a dark place during a part of each day.

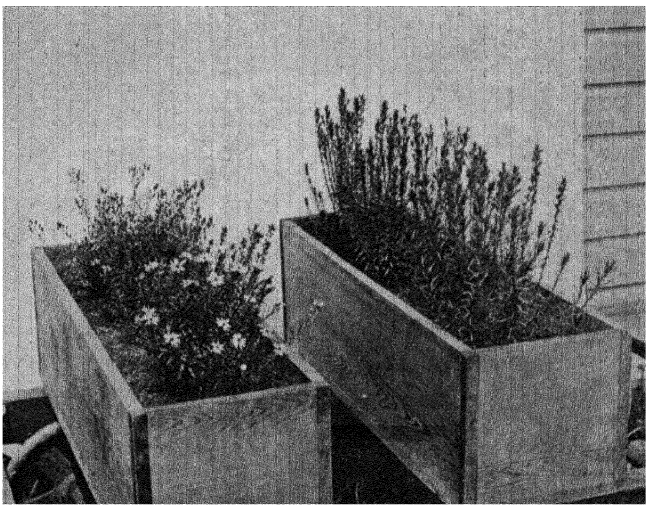


FIG. 57.—*Aster linariifolius* L. Plants in box on left exposed to light from 9 A.M. to 4 P.M. daily. In full bloom when photographed, June 21. Plants in box on right left out of doors during the test. Showed no indications of flower heads when photographed, June 24. (After Garner and Allard.)

Length of day is by no means the only factor concerned in determining the time of flowering and fruiting. In many cases it has been shown that the critical length of day for reproductive activities may be altered by changing the temperature. Plants have also been caused to bloom early by a process called vernalization, which consists of soaking the seeds and then subjecting them to chilling temperatures above freezing for several days.

Many plants, such as buckwheat, chickweed, and dandelion, are neither long-day nor short-day plants but belong to an intermediate or neutral group which is little, if any, affected by length of day. In fact, the number of species belonging to this group is probably far larger than that of either

of the other two groups. The group to which any species belongs can usually be determined quite readily by growing it under daily light exposures of ten and eighteen hours and observing under which, if either, its reproductive phenomena are accelerated.

Usually vegetative growth is favored by a length of day that is just the reverse of that most favorable for flowering and fruiting. The light period most favorable for the production of reserve food in such structures as tubers, bulbs, and thickened roots, however, may differ from both that

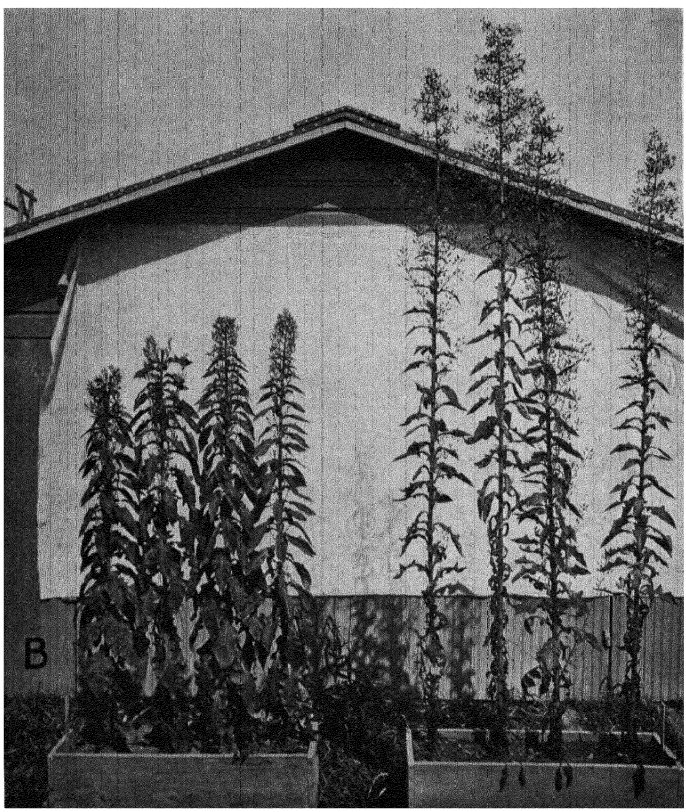


FIG. 58.—Wild lettuce (*Lactuca spicata*). Plants at left, exposed to a ten-hour day beginning March 29, produced much larger, coarser leaves than the control plants (at right) exposed to the full summer length of day. Under the short-day exposure both leaf and stem were far more hairy than under the long-day conditions. The stature was greatly reduced, but the time of flowering was not affected. (After Garner and Allard.)

which is most favorable for vegetative growth and that which induces reproduction. These facts have great practical value because with an adequate knowledge of the responses of plants to length of day it should be possible to plant field and garden crops at such times as will bring the development of those plant parts that are to be utilized at the season when

the length of day is most favorable. It should also enable florists to bring plants into bloom at any desired time during the year. (Figs. 57, 58 and 59.)

74. **The Requirement of Light by Plants.** There is no place in the world where there is not enough light for plant life. Even in the depths of the ocean and in underground caves there are saprophytic bacteria and molds that bring about the decay of any organic matter that may be there. Some of these saprophytic plants can spend their entire lives in total darkness and some of them are readily killed by exposure to light. All green plants, however, require a certain amount of light. Chlorophyll, except in a few cases, is formed only in light, and it cannot function for carbohydrate synthesis without light. Many saprophytic and parasitic fungi which can flourish vegetatively in the dark require light at the time of fruiting.

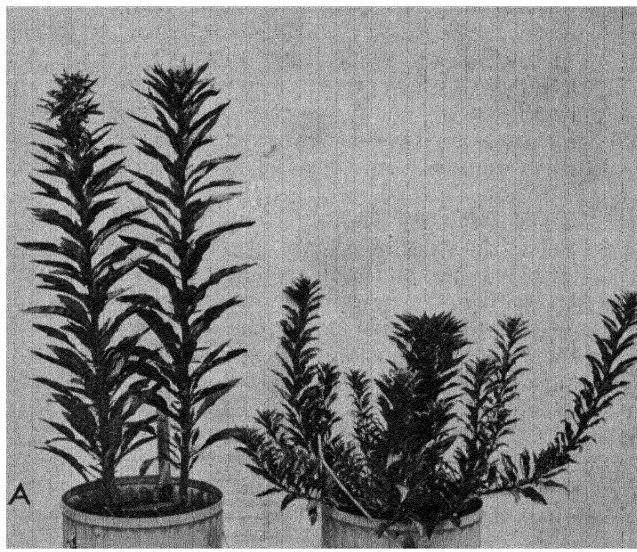


FIG. 59.—*Oenothera biennis*. Plants at left were exposed to the full daylight period of the spring months. The individual at right received only ten hours of illumination beginning March 19. It is seen that the short-day conditions caused a decided weakening in power to elongate the primary axis, resulting in development of numerous basal shoots. In this case dominance of the apical bud is lost, a characteristic response to a suboptimal light period for elongation of the stem. Photographed June 21. (After Garner and Allard.)

Light is also an important factor in the formation of anthocyanin, the pigment which gives the red colors to flowers and other plant parts. Fall coloration of leaves is due largely to two pigments, yellow xanthophyll and red anthocyanin. The xanthophyll occurs in leaves in plastids similar to chloroplasts and it is present all summer, masked by the green chlorophyll. When the chlorophyll disintegrates in the autumn the xanthophyll becomes visible. Anthocyanin, on the other hand, occurs in solution in the cell sap and it is produced, in the presence of bright sunlight, especially in the leaves

of trees that normally contain large amounts of sugar or tannin. Fall coloration, therefore, is always most brilliant in those years in which there are many bright, sunny days during early autumn.

Most plants actually use only a small part of the light that they receive. Many of them could probably get along with less than 1 per cent of the light that is normally available for them. Yet there is for each species an optimum amount as well as an upper zero point or maximum and a lower zero point or minimum. In general, low intensities of light favor the growth of vegetative structures. The largest leaves and the fullest development of many kinds of stems are found in partial shade. Many vegetative crops, such as potatoes, beets, carrots and turnips, yield best in regions where there is a high percentage of cloudy days. Ginseng, when grown commercially, is covered with slat frames so that it will not be fully exposed to the light, and tea is usually planted in alternate rows with taller trees, the shade causing the tea leaves to become large and of good quality.

On the other hand, intense light favors the development of flowers, fruits, and seeds. The best regions in which to grow fruits and grains, therefore, are those in which there is a high percentage of bright, sunny days, provided there is also a sufficient amount of moisture. Furthermore, the brightest colors and the greatest profusion of flowers are found in Arctic meadows where the light is very intense, while in the shade of a dense forest flowers are scarce.

75. **Tolerant and Intolerant Plants.**—Plants that are able to survive, grow and develop in the shade of other plants are said to be tolerant while light-demanding plants are intolerant, that is, intolerant of shade. Light is not the only factor involved in tolerance but it is an extremely important one. Tolerance is particularly important in a forest. Some trees, such as sugar maple, beech, and hemlock, are very tolerant. The seedlings of such trees can develop and grow very slowly in the shade of other trees for many years and then make a very rapid growth later if the shade is by some means removed. Such trees as soft maple, bur oak, poplars, and many of the pines, on the other hand, are very intolerant and cannot develop successfully in the shade of other trees. This difference between species becomes very important when tolerant and intolerant trees are growing together. The seeds of both may germinate but only the seedlings of the tolerant species can continue to grow. Whenever any of the old trees die or fall, therefore, their places are certain to be taken by tolerant trees. The obvious result of this is that finally the forest comes to be composed of tolerant trees only.

This relation between tolerant and intolerant trees is well exemplified in the southeastern pine belt. Both short-leaf pine (*Pinus echinata*) and loblolly pine (*P. taeda*) are much less tolerant than most of the hardwood trees that grow in the same region. Often when a pine forest is cut there are numerous hardwood seedlings already established and, in absence of fire, they become more vigorous after the cutting. The low shade produced by these hardwoods is fatal, usually in about five years, to any pine seedlings that may develop on the area, and so the forest that matures is a hardwood forest. Pine seedlings that start in the shade of tall hardwood trees may survive longer, often for ten to twenty years or longer, but they grow slowly, their bark is thin, and their root systems are not well developed. As a result they are at all times very susceptible to drowth or to

fire. On the other hand when a hardwood forest is clean-cut and there are no established seedlings, any pine seedlings that get started within a year or two may successfully compete with hardwood seedlings, or hardwood shoots that may develop from the old stumps, because of their more rapid growth. Such seedlings grow vigorously and develop a thick bark and a well developed root system. They soon become fire resistant and drowth resistant and may develop into a pine forest. In all cases however, in the absence of fire and cutting, the intolerant pines are eventually replaced by the more tolerant hardwoods.

Not all trees can be classified as very tolerant or intolerant since some species, such as the white oak (*Quercus alba*) and the white pine (*Pinus strobus*), are intermediate in this respect, that is, they can endure some shade but not so much as such trees as sugar maple and hemlock. The relative tolerance of species can often be determined fairly accurately merely by observing their manner of growth and degree of success under varying conditions. More accurate results are obtained by measuring the light in various forests where the seedlings are growing or fail to grow. The minimum amount of light necessary for continued growth varies from about 2 per cent of full sunlight for very tolerant species to about 25 per cent for intolerant species. A still more accurate method is to actually grow the species under varying amounts of controlled shade but this method involves a long period of time. In using any of these methods, however, it must be remembered that light is not the only factor involved in tolerance. Such factors as soil fertility and temperature are often very important and soil moisture is often more important even than light.

76. **Adaptations for Securing Light.**—Plants are adapted in various ways for procuring the necessary amount of light. Our early spring flowers which live in forests, for example, carry on those activities that require an abundance of light before the trees have leaved. Many of them are active only about three months and, becoming dormant soon after the leaves of the trees are out, remain so until the following spring. The habits of twining plants and of other climbers are significant primarily because they serve to bring the foliage into such positions that it may be displayed to the light.

The foliage of many plants has a mosaic arrangement, often called a leaf mosaic, in which the leaves are arranged in such a way that there is a minimum of overlapping, consecutive leaves never being directly above one another. In many trees the branches are progressively longer from the top toward the base so that the leaves, which occur only near the outer extremities, are not shaded by the leaves of higher branches. This is especially true of coniferous trees which are often nearly perfectly cone-shaped but it is more or less true of many other trees and also of many herbaceous plants. When trees grow close together as in a forest the lower branches which receive insufficient light soon die and drop off (Fig. 60). This is especially true of intolerant trees. Such trees are no longer cone-shaped, but their leaves are produced only near the top and so are all well exposed.

Some kinds of leaves are much more sensitive to light than other kinds. Leaves that are not very sensitive to light, as those of the tulip tree, *Liriodendron tulipifera*, are apt to assume a great variety of positions with respect to light, but those that are more sensitive, as those of the sugar

maple, *Acer saccharum*, practically always have their blades at right angles to the direction from which they receive the greatest light, their petioles being twisted in such a way as to bring this about. Some plants, as the common mallow, *Malva rotundifolia*, have leaves that are so sensitive to light that their blades turn toward the east in the morning and follow the sun toward the west during the day, keeping the broad face always at right angles to the source of light.

77. **Protection from Excessive Light.**—Although all green plants must have a certain amount of light, that which is very intense may disintegrate chlorophyll. Most plants are able to protect themselves from such a calamity by moving the chloroplasts out of the direct light. That is, if a plant remains in direct sunlight for a time, its chloroplasts are usually found to be arranged mostly along the walls that are perpendicular to the leaf surface, where they are somewhat protected from the light rays. On

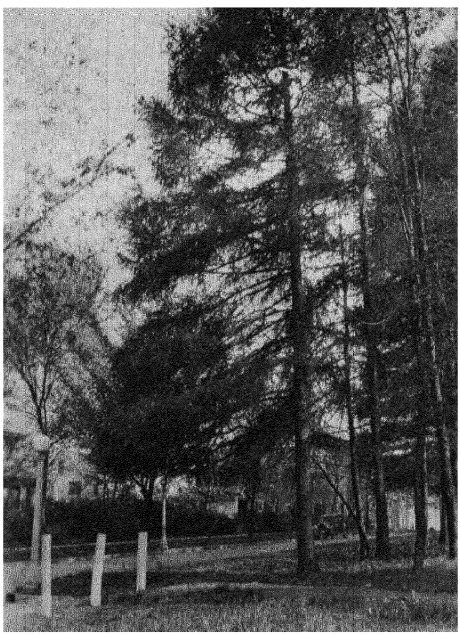


FIG. 60.—A larch tree the branches of which have been mostly self-pruned from the side toward the forest but not from the side toward the street. A light relation.

the other hand, if the same plant is exposed to dim light, its chloroplasts gradually assumed positions mostly along the walls that are parallel to the surface, where they receive as much light as possible. One of the filamentous algæ, *Mougeotia*, shows somewhat comparable chloroplast movements. In this alga there is a single large chloroplast in the shape of a rectangular plate in each cell. When this alga is in diffuse light the chloroplasts present their broad faces to the incident rays of light but when in bright light they turn so that the edge of the plate is toward the light.

Certain plants, especially *Lactuca scariola* the prickly lettuce, and *Silphium laciniatum*, the rosin weed, are called compass plants because most of their leaves are edgewise and in a north and south plane. This condition holds, however, only for plants growing in full sunlight, the leaves of the same species growing in partial shade being horizontal. It is fairly certain, therefore, that the vertical position of the leaves of compass plants is a result of light conditions. It is probable that this position protects the chloroplasts from too great an intensity of light, since the sun's rays are perpendicular to the flat side of the leaves only in the morning and the evening when the light is much less intense than during the middle of the day.

A similar protection is had by such plants as *Iris*, *Typha*, and many grasses, the leaves of which are vertical. The position of such leaves, however, is probably not a response to light conditions entirely since they are held in position by their sheathing bases, and probably a greater advantage than that of protection from intense light is that light is permitted to penetrate nearly or quite to the bases of the leaves. This enables the entire length of the leaf to be utilized for photosynthetic activity.

78. **Measurement of Light.** Measurements of light are usually relative rather than absolute, that is, the result of such measurements are expressed in units which represent, not the absolute amount of light, but the amount as compared to some other amount which is used as a standard. The method that has been used more than any other is the tinting of silver chloride paper ("printing out" paper) to a standard tint and noting the time required to reach that tint. The chief objection to this method is that the silver paper is not sensitive to the longer wave lengths of light, the ones most used in photosynthesis. For making comparisons between different habitats, however, the method has considerable value.

The Clements photometer is the instrument that is most used in light measurements by the silver chloride method. This consists of a circular metal box around which a strip of "printing out" paper may be fastened. The "cover" is slipped on outside of the paper and fastened at the center by a thumb-screw in such a way that it may be revolved. The cover has an opening at one side which is closed by a shutter. When an exposure is to be made the shutter is withdrawn for a definite length of time as measured by a stop-watch and the cover is then revolved one unit-space in preparation for the next exposure. Twenty-five exposures may be made with one strip of paper. The paper is later removed from the instrument in diffuse light and compared to a strip of standard tints. One model of this instrument is of vest-pocket size and has a stop-watch attached. All the operations are automatically made by pressing a plunger.

The Weston Sunlightmeter is an instrument which in some respects is more convenient for field work than the photometer. It consists of a special photo-electric cell with a sensitive ammeter calibrated directly in foot-candles so that it is only necessary to expose the instrument to the light and read the light values in foot-candles on the instrument scale The range covered by this instrument is approximately that of the visible spectrum and, since a large number of readings can be made in a short time the instrument is very useful for comparing various habitats. Full light in the open may be used as a standard and the light in other habitats may be expressed as percentages of the standard.

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CHAPTER XI

HEAT

HEAT is a factor that is of very great importance to plants but one that is difficult to study in such a way as to yield tangible results. There seems to be little, if any, relation between structure and temperature. For this reason we cannot readily see the effect of heat or lack of heat upon the plant, and it is very difficult to separate heat as a factor from other factors that are acting at the same time. There are many structural features of plants that were formerly attributed to heat that are really due, for the most part at least, to other factors.

Plants may be compared, in a sense, to cold-blooded animals. Their internal temperatures vary with the external temperature and their greatest activity takes place at an optimum temperature, while at very low or very high temperatures they are sluggish or dormant. Each species of plant has a maximum temperature and a minimum temperature beyond which activity ceases, as well as an optimum temperature at which it is most active.

79. **Minimum Temperatures.**—In general plants are adapted to temperatures ranging from 0° to 100° C. The reason for setting these rather arbitrary limits is simply that plants, in order to carry on their functions, must have liquid water, and, of course, water ordinarily solidifies at 0° and vaporizes at 100° C. There are a few of the lower plants, however, that are active at temperatures below zero. Some of the algæ that occur in Arctic waters appear to be active at temperatures below zero. The water in which they live is still liquid, however, since there is salt enough in the water to lower the freezing-point several degrees below zero. Certain algæ grow quite luxuriently on the permanent ice in certain caves in the lava bed near Grants, New Mexico. The "black spot" fungus which is found on meat in cold storage is able to grow and even produce spores at temperatures as low as 6° below zero. This growth is not luxurient, of course, and very little water is required.

Plants apparently have no protection against low temperatures. Their internal temperature rises and falls with the external temperature. To be sure, heat is liberated by respiration within the plant as in an animal, but the plant cannot keep up its internal temperature by respiration, as a warm-blooded animal can, because the optimum temperature for respiration is rather high and the rate of respiration decreases with a lowering of the temperature. Therefore, when the plant most needs extra heat it cannot supply it through respiration. The internal temperature of the plant often is somewhat higher than the external temperature during the day. The internal temperature of pine leaves, for example, has been found to be from 2° to 10° higher than that of the surrounding air during the day. This, however, has been attributed to the absorption of radiant energy rather than to respiration.

The death of plants by winter-killing, or from cold at any time, is very frequently the result of desiccation rather than directly from low temperature. Thus, plants that are protected from drying winds can endure much lower temperatures than those of the same species that are fully exposed.

There is no place in the world that is too cold for plant life. There are, however, places that are too continuously cold. Many plants, when in a dormant condition, can live for a considerable time at temperatures far below zero, but they cannot grow and reproduce in such temperatures. It is not known for many plants what the minimum temperature beyond which life ceases is. It varies greatly at different times of the year and with different conditions of the plant, especially as to the amount of moisture present in the plant.

For some plants temperatures below zero are necessary periodically. Some seeds, for example, will not germinate until they have been subjected to freezing temperatures and this is true also of the spores of some fungi.

Plants can often be made more resistant to low temperatures artificially by a process of hardening. This is usually done by subjecting the plants to a temperature a few degrees above freezing for several days and watering sparingly. Seedling vegetables are often hardened in this way by placing them in a cold frame for several days before transplanting to the field. When plants freeze water is withdrawn from the cells and ice forms in the spaces between cells. Death of the cells results from this desiccation of the protoplasm or possibly in some cases from the rupturing of the cell through the mechanical pressure of the ice. The hardening process seems to increase the water-retaining power of the cells so that a larger proportion of their water is prevented from being withdrawn and remains in an unfrozen state. Perennial plants can often be hardened by subjecting them to drought, the results being much the same as those brought about by subjection to low temperatures. Tree seedlings may be hardened by this method in nurseries before transplanting.

80. **Maximum Temperatures.**—No plants are active at temperatures of 90° C. or higher. The maximum temperatures that can be endured, however, like the minimum temperatures, vary greatly with different species of plants and with different internal and external conditions. Certain species of yeast have been shown to be capable of enduring a temperature of 114° C. when in a dormant condition. Many very dry seeds can endure temperatures above 100° C. while the same species in an active state would be killed by a much lower temperature. Certain algæ found in hot springs live and carry on their various functions at 77° C. and there are a few fungi which can endure as much as 89° C. Some lichens, and perhaps even seed plants, that live in tropical deserts, where the air temperatures, and more especially the surface soil temperatures become exceedingly hot, must endure temperatures of 70° C. or higher frequently.

Most of the plants we are familiar with, however, live where the temperature never goes much beyond 50° C. and if subjected to higher temperatures when in an active condition, since they cannot quickly go into a dormant state, they suffer death.

81. **Optimum Temperatures.**—The optimum temperature for any plant is the temperature at which the plant gets along best in the conditions under which it is living. There is an optimum temperature for each physiological function of the plant and these various optima, for the most part, do not coincide. The ecological optimum is thus a temperature at which the plant as a whole is most nearly in harmony with the environment and it may not coincide with a single one of the physiological optima. The ecological optimum varies greatly for different plants and for the same

plant at different ages and at different times during the year or even at different times of day. For example, the optimum temperature during the day, at least for plants of temperate climates, is always higher than that for the night. For many plants the optimum temperature becomes progressively higher from the time of germination to the time of fruiting, though it must be admitted that we have accurate knowledge of these variations for only a very few plants. Probably no plant, in its natural environment, ever enjoys its ecological optimum of temperature throughout an entire year. However, a plant may be said to be successful if it can reproduce each year, and plants vary so greatly in their adaptations to heat as well as to other factors that they are found to flourish under extreme conditions. Some Arctic and Alpine plants produce their flowers while the ground is still partly covered with snow and continue to flourish even though the temperature goes below freezing each night, while some tropical species carry on their activities at temperatures so high that many plants, if subjected to them, would perish in a very short time. Some plants, such as certain trees, can endure a very wide range of temperature, while others especially some algæ, are active only within a very narrow and very definite range of temperature.

82. **Soil Temperatures.**—The temperature of the soil is very important to the plant largely because of its effect upon the rate of absorption of water. Seeds cannot germinate until the soil has been warmed up to a certain temperature, depending upon the species, nor can perennial plants become active in spring until the soil is sufficiently warm so that water can be absorbed readily by the roots.

Soil temperatures vary greatly in different situations. The soil of a bottomland is usually considerably cooler than that of the adjacent upland, particularly if the two are supporting comparable types of vegetation. The soil of a south-facing slope warms up much more rapidly in spring than does a north-facing slope and therefore, dandelions, hepaticas, and other spring flowers bloom earlier on a south-facing slope than elsewhere.

Soil temperature depends in part on the color of the soil surface. A dark-colored soil absorbs heat and so warms up more rapidly than a light-colored soil which reflects the heat rays. A cold soil can be warmed to a certain extent by spreading over the surface a layer of dark-colored soil. The soil temperature also depends to a certain extent upon the water content, a wet soil being colder than a drier one of similar type, and one result of drainage, though not the most important one, is the increase in temperature through a decrease in water content.

83. **Temperature and Plant Distribution.**—The distribution of plants is governed to a certain extent by temperature. Thus, broad belts of vegetation may be recognized between the equator and the poles extending parallel with the equator and corresponding roughly to temperature belts. One also encounters somewhat similar belts in going up a mountain and the corresponding belts are usually somewhat higher on the south side of the mountain than on the north side, because of the difference in temperature. The kind of vegetation, however, is not so much affected by temperature as is the flora. By the flora of a region we mean the species of plants that occur there, while the kind of vegetation refers to the general type, such as forest, grassland, or desert. For example, we find forests in every one of the great temperature zones of the earth but the species of trees that make up

the forests are different in each zone. The relation of temperature to floral distribution is well expressed by what we may call Schimper's First Law. This states that "The type of the flora in so far as it depends on existing factors is determined primarily by heat."

84. **Temperature and Crop Plants.**—While we must not make the mistake of over-emphasizing temperature as a controlling factor in the distribution of crop plants, yet it is to be expected that Schimper's First Law applies to specific crop plants to the same extent that it does to uncultivated species except as its action is modified or prevented by man. A definite amount of heat is required to mature each crop and various attempts have been made to find an approximate measure of this amount of heat. There is for each crop plant, as well as for every other kind of plant, a minimum temperature at which activity begins. Any temperatures below this minimum are entirely ineffective in advancing the crop toward maturity. Therefore, there must be a considerable number of days during which the temperature rises above the minimum if the plants are to mature.

A summation of the day-degrees of temperature in excess of the minimum from the date of planting to the date of maturity is known as the "thermal constant" and may be used as an approximate measure of the heat required to mature the crop. For example, if 40° F. be taken as the minimum effective temperature, then any day on which the temperature reached 50° F. would count as ten day-degrees, one on which the temperature reached 54° F. would count as fourteen day-degrees, and so on. The thermal constant would then be found by adding together all of these excess day-degrees for the season during which the crop was developing and maturing. Such thermal constants are of considerable practical value since they enable one to determine whether a given locality is favorable for the maturing of a given crop. If the climate of the locality is such that the necessary number of excess day-degrees to make up the thermal constant for the crop under consideration cannot be expected, then it is useless to attempt to grow such a crop in that locality.

In deriving the thermal constant the minimum effective temperature has often been chosen arbitrarily and the same one used for all crop plants. Such a method is obviously unsuitable since the minimum temperature for germination, or for any other activity, varies greatly with different species of plants. A somewhat more satisfactory method is to use as the minimum effective temperature the mean daily temperature at planting time since the two may be shown to approximately correspond. Farmers ordinarily plant each crop at about the same time each year without much reference to any thermometer, but they have, quite unknowingly, hit upon dates that correspond to the minimum temperatures of which we are speaking. Therefore, by noting the average time of planting each crop for a long series of years it is readily possible to determine the mean daily temperature at planting time, and this has been done for a number of crops.

By using the above method it has been found that the planting of spring wheat begins when the temperature has risen to about 37° F., spring oats are planted when the temperature is at 43° F., early potatoes at 45° F., corn at 55° F. and cotton at 62° F. The temperature for the planting of each crop is fairly uniform wherever the crop is grown. For example, early potatoes are planted in some of the southern states as early as the middle of February while in some of the northern states planting does not begin

until about May 1, but in each locality the planting begins when the mean daily temperature has risen to about 45° F.

The thermal constants have not been actually worked out for many plants but they could readily be computed from data that have been accumulated by the United States Department of Agriculture and the United States Weather Bureau. The thermal constant for corn computed from the mean daily temperature at the average date of planting to the beginning of harvest is about 1600° to 1800° F., depending on the variety of corn grown, in the principal corn-producing regions. The thermal constant for cotton is about 1900° F. and temperature is the principal limiting factor in determining the northern limit of successful commercial production of cotton. If a variety of cotton could be developed which would mature with a few hundred day-degrees of temperature less than 1900 the area of cotton production in the United States could be very greatly extended.

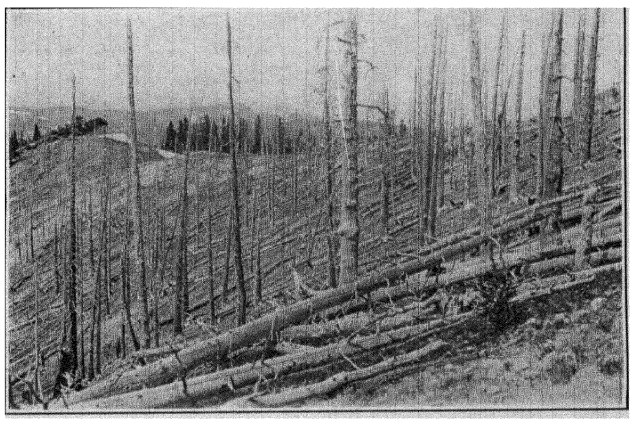


FIG. 61.—A "cemetery" forest of Engleman spruce. Killed by fire.

85. **Fire.**—Fire produces very high temperatures for short periods of time in very local areas. Its most common effect is the destruction of vegetation. The greatest losses from fires occur in forest regions where hundreds of acres of valuable timber are destroyed each year (Fig. 61). In forests where the humus layer is deep and very dry, fire may destroy the entire layer of organic matter and may thus convert a dry forest into a swamp or shallow lake. Forest fires are started by various agencies. Fires are left unextinguished by campers, or smokers throw away burning matches or cigarette stubs, but many fires are also started by electrical storms.

It should not be assumed that all fires are detrimental. Fires started by electrical storms are just as natural as rain or sunshine and, from the ecological point of view, many such fires are beneficial. In past times lightning-caused fires must have constituted a very important factor in maintaining a biological balance between plants and animals. In a fully mature forest there often are very few plants other than trees and, therefore, very little food for many kinds of the larger animals. A fire in such a forest may produce an opening in which brush and herbaceous plants,

furnishing suitable animal food, can develop abundantly. Furthermore, certain plants are dependent upon fire for essential functions. The seed-bearing cones of the lodge pole pine (*Pinus Murrayana*) often remain closed and hang on the tree for years. The heat from a forest fire, however, will frequently cause these cones to open up and allow the seeds to fall. This phenomenon is often a deciding factor in determining the type of reproduction on a burned-over forest area. The longleaf pine (*Pinus palustris*), which can endure complete defoliation by fire without any lasting ill effects, is dependent upon fire to prepare a suitable seed-bed by removing accumulated materials which prevent the seeds from getting to the soil and also to check the competition of invading tree species by periodic burning of the forest floor. The use of fire is considered good silvicultural practice in the regeneration of longleaf pine forests and comparable practices could be used in the regeneration of loblolly and shortleaf pine forests. The vegetative growth of many grasses is stimulated rather than injured by periodic burning but at the same time there may be effects upon the soil fertility and upon animal life that are detrimental.

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CHAPTER XII

AIR

ALL plants need air for respiration and green plants need it also for photosynthesis. Air in many of its relations to plants is nearly as universal as gravity. We shall not deal with it, therefore, in many of its physiological relations but only in those relations that are variable enough to be of ecological significance.

86. **Atmospheric Composition and Pressure.**—The composition of the atmosphere does not vary materially from place to place except in the amount of dust and smoke that it contains. In large cities there is often enough dust or smoke, or both, in the air to exclude certain kinds of plants entirely. Most evergreen trees, for example, are unable to endure urban conditions and remain healthy for any great length of time. This is perhaps even more true of the majority of lichens and for that reason lichens ordinarily are not found in or near cities of even moderate size.

In the vicinity of volcanoes and hot sulphur springs, and also in the vicinity of smelters and other places where large quantities of coal are burned, there are often poisonous gases, mostly sulphurous acid, in the atmosphere which are very injurious to vegetation. The areas thus affected, however, are relatively limited.

Experiments have shown that ordinary air pressures are not at the optimum for vegetative growth of common green plants used in the experiments. It was found in all cases that a decrease in atmospheric pressure, other conditions remaining the same, was accompanied by increased growth. We have no experimental data, however, to indicate whether the normal atmospheric pressure is at the ecological optimum for the sum total of the plant's activities. Probably it is. A decrease in atmospheric pressure increases the relative humidity of the air and by so doing has a tendency to check transpiration. The decreased pressure at higher altitudes, however, is ordinarily more than counterbalanced by a decrease in temperature, and thus has the opposite effect on humidity. Altogether, therefore, atmospheric pressure is not of very great importance from an ecological viewpoint.

87. **Air in Water.**—Air dissolves in water very slowly when the latter remains still but much more rapidly when the water is in motion. Therefore, running water is usually well aërated, while standing water often is not. Practically all seed plants that grow in water possess well-developed air spaces but this characteristic is much more conspicuous in plants growing in standing water than in those growing in running water.

The presence of algæ and other water plants often influences very greatly the amounts of oxygen and carbon dioxide in water. In lakes and ponds where algæ are abundant the water sometimes becomes supersaturated with oxygen as a result of photosynthesis. The amount frequently reaches a saturation of 300 per cent or more. The same process prevents the accumulation of large amounts of carbon dioxide. In this way the algæ become very important in furnishing a supply of oxygen to the submerged roots of higher plants. This phenomenon is of especial economic importance in rice fields where the algæ have been shown to be valuable for the aëration of the roots of rice plants.

88. **Soil Aëration.**—Roots of different plants vary considerably in their oxygen requirements. The roots of swamp plants, for example, require much less oxygen than the roots of drier land plants. All roots, however, must carry on respiration in order to live and so must have some oxygen. The aëration of the soil, therefore, is very important to the plants growing in it.

The carbon dioxide that is present in the soil is derived almost entirely from respiration and decay processes that take place within the soil. Therefore, as would be expected, it regularly increases in amount with the depth of the soil, since at the greater depths it is more difficult for it to escape into the atmosphere. The oxygen of the soil, on the other hand, is obtained from the atmosphere and decreases with an increase in depth of soil. The amounts of carbon dioxide and oxygen in the soil vary greatly at different times of year, with varying conditions of temperature and rainfall, with different types of soil, and with varying kinds and numbers of plants growing in the soil. As would be expected the greatest amount of carbon dioxide is found in the soil in summer and the smallest amount in winter. Ordinarily sand contains the most oxygen and the least carbon dioxide while peat soil is just the opposite in these respects and clay holds an intermediate position. An increased amount of plant growth augments the carbon dioxide and decreases the oxygen supply and similar effects are produced by an increased amount of dead organic matter in the soil.

Since oxygen dissolves very slowly in water a soil that is saturated with water is almost invariably poorly aërated. Plants which ordinarily do not grow in water may be actually drowned if the soil is saturated and there is standing water on the surface for too long a time. This often happens to such crop plants as corn and wheat. These facts are extremely important in irrigation projects. Common practice in irrigated regions has often involved the use of more water than is best for crop production. The plants need both air and water and in general the amount of air increases as the water is decreased. Therefore the most economical practice in irrigation is one that strikes a compromise between these two needs of the plant. The water should be applied in such a way as to interfere as little as possible with the aëration of the soil since otherwise an actual reduction in yield per acre is likely to result.

89. **Atmospheric Humidity.**—The amount of moisture present in the atmosphere, as water vapor, varies greatly from time to time although there is always some present. When the air becomes completely saturated with water condensation begins and some of the water is precipitated as rain or snow. When the atmosphere is saturated with moisture the loss of water from plants by transpiration is negligible and the drier the atmosphere the more rapid is transpiration. The amount of water that the air can hold at any given atmospheric pressure, however, varies directly with the temperature. Therefore, from the ecological point of view, the absolute amount of moisture in the air is not nearly so important as the difference between the amount present and the amount necessary to completely saturate it. This difference is called the saturation deficit. It is a measure of the capacity of the atmosphere for taking up water and thus, indirectly, of the rate at which evaporation or transpiration may take place. The amount of moisture present in the air is expressed, not as an absolute amount. but as a percentage of the amount necessary for saturation at a given temperature. This is called the relative humidity. Every change of

temperature, of course, changes the relative humidity, without changing the absolute humidity. The saturation deficit, on the other hand, is expressed as weight per cubic foot of air or, more often, as pressure, in inches or centimeters of mercury.

In the measurement of atmospheric humidity use is made of a psychrometer. This instrument consists of two thermometers mounted in such a way that they can readily be whirled to facilitate evaporation. The mercury bulb of one thermometer is covered with cloth which is saturated with water. The evaporation of the water cools the thermometer and the difference between the readings of the two thermometers is called the depression of the wet bulb. Tables have been worked out for nearly all possible combinations of air temperatures and wet bulb depressions showing relative humidities and dew points, the dew point being the temperature

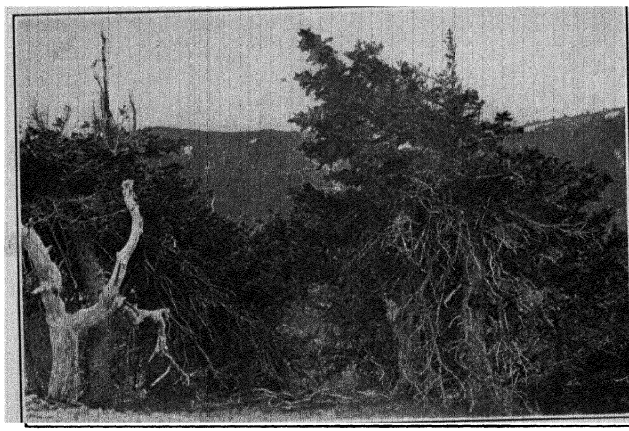


FIG. 62.—"Elfin timber." Engleman spruce at timber line in the Arapaho National Forest, Colorado.

at which condensation would take place with the existing water vapor, that is, the temperature at which the air would become saturated without any increase in the absolute humidity. The tables most used in America are the "Psychrometric Tables" of the United States Weather Bureau, contained in its Bulletin 235. From these tables the relative humidity may be obtained directly and the saturation deficit is obtained by taking the difference between the saturation pressure at the current dry bulb temperature and the saturation pressure at the current dew point. Such data, when extended over a long period of time, are very useful in determining whether the environment is suited to plants that are well protected from excessive transpiration or to those that are relatively unprotected.

(9). **Wind.**—Wind is moving air and is more important from an ecological viewpoint than is still air. Its effect on plants is both physical and physiological. The breaking-over and uprooting of plants and the breaking of branches are familiar examples of the physical effect of wind. Wind is also important as an agent of pollination and of dispersal. It has already been discussed as an agent of pollination in Chapter VI and its action in the dispersal of seeds and fruits will be taken up later in connection with the subject of plant succession.

The physiological effect of wind consists almost entirely in increasing transpiration, and in this capacity it is very important. As a rule, the velocity of the wind increases with the height above the ground. Therefore, the tallest plants, such as trees, suffer most from the drying effects of the winds, while low plants, such as many grasses, get along very well in windy regions. Furthermore, the height to which many plants can grow is limited by their ability to transport water upward fast enough to counteract the loss through transpiration. For this reason, in the most windy places, such as exposed mountain ridges and flat windy sea-coasts, tall plants are entirely absent. A similar reason accounts for the absence of tall plants in desert regions. The very high temperatures and exceedingly low relative humidity in such regions plus frequent winds combine to produce evaporation rates that are almost unbelievably high and, since the supply of soil water is very limited to begin with, the necessity of a balance between transpiration and absorption makes it impossible for any desert plants to become very tall.



FIG. 63.—Dwarf vegetation at the top of Specimen Mountain, Colorado. *Silene acaulis* in the center.

Because of this drying effect of the wind the trees are smaller on the windward side of an exposed grove than on the opposite side. A single tree growing in the open is almost invariably one-sided; that is, a larger part of its crown is on the side opposite that from which the prevailing winds blow. So true is this that one can determine the direction of the prevailing winds of a region by examining the trees.

At timber line on mountains the same species of woody plants, which a few hundred feet further down are upright forest trees, grow as gnarled and sprawling, much-branched shrubs, known as elfin-timber or krumholz (Fig. 62). The short growing season, the low temperature of the soil, and the drying effect of the winds, make conditions here so difficult for growth that a tree may be several hundred years old yet only a few inches in diameter of trunk and a foot or so in height. Above timber line on the higher mountains a similar effect is seen in the herbaceous vegetation, all of the plants being very dwarf (Fig. 63).

91. **Cold-air Drainage.**—Cold air is heavier than warm air. It therefore has a tendency to settle down into low places and displace the warmer air that is there. This takes place to a certain extent each night as the air is cooling after sundown. For this reason there are usually frosts later in spring and earlier in autumn in the lowlands than on the uplands. Peaches, strawberries, and other crop plants that are subject to late frosts in spring, are more profitable on highlands than in valleys, because they more often escape the effects of late frosts.

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CHAPTER XIV

WATER

WATER is the most important single factor in the environment of plants. The amount needed by different kinds of plants varies greatly but some is necessary for every living organism. It is of vital importance to the plant in several ways. For example, it is a necessary constituent of all protoplasm as well as of cell sap. It is a food material necessary in carbohydrate synthesis. All inorganic food materials are absorbed and transported in a water solution. The resistance of a plant to heat or cold is largely determined by the amount of water present. Finally, water has more influence on the external and internal structure of plants than any other factor.

Several phases of the water factor have been discussed in preceding chapters. There are a number of other facts about the water relation, however, that it is necessary for us to understand and these will be taken up in the present chapter.

102. **The Classification of Plants on the Basis of Water Relation.**—Plants are found growing in all sorts of conditions with respect to water supply. Some live on rocks where the amount of water available is extremely limited, others are immersed in water where the supply is inexhaustible, while others are found in all degrees of gradation between these extremes. Those plants that can get along with small amounts of water are called xerophytes. Those that can endure large amounts of water are called hydrophytes. Those that get along best with medium amounts of water are called mesophytes. The majority of plants are readily classified into one of these three groups. There are, however, large numbers that are intermediate between two groups and rather difficult to classify satisfactorily. For this reason we frequently find it convenient to use such terms as xero-mesophyte, to indicate a plant that is somewhat more xeric (characterized by scanty moisture supply) than a typical mesophyte, meso-zerophyte, for one that is somewhat less xeric than a typical xerophyte; hydro-mesophyte, for one that is somewhat more hydric (characterized by abundant moisture supply) than a typical mesophyte. etc, It is also customary to use such combinations as shade-mesophyte, sun-hydrophyte, alpine-xerophyte, etc., in order to more accurately define the type of plant under discussion.

There are some plants that change from one group to another at different seasons. Familiar examples of this phenomenon are the deciduous trees of the temperate zones. The majority of these trees, such, for example, as *Acer saccharum*, the sugar maple, are typical mesophytes in summer when they have leaves but are xerophytes in winter when they are leafless. Such plants are classified as mesophytes because that is what they are throughout the important growing season but in order to express the fact that their water relation is quite different during the winter they are also called tropophytes.

Some of the characteristic differences between xerophytes, mesophytes, and hydrophytes have been brought out in the discussion of the ecology of stems and leaves and others will be taken up in a later chapter. It is

necessary to point out here, however, that this classification of plants does not depend so much upon the actual amount of water present in the immediate environment as upon the relation between absorption and transpiration. In some cases the cause of xerism is an actual inadequate water supply, as in deserts, but in other cases it may be due to physiological dryness; that is, to difficulty of absorption, as in saline regions or in peat bogs; or it may be due more largely to high transpiration as in some alpine regions. The chief causes of hydrism, on the other hand, are a saturated atmosphere or an abundance of soil water, or both.

103. **Transpiration.**—When a land plant is in an active condition there is a more or less constant stream of water passing through it. The water is absorbed into the roots, transported upward through the xylem, and transpired from the surfaces of the leaves. The plant actually uses a considerable amount of water but it absorbs and transpires a great deal more than it needs for its ordinary metabolic processes. The amount passing through the plant varies greatly at different times and sometimes is surprisingly large. It has been estimated for example that a beech tree, one hundred years old, transpires about 60 barrels of water during a season, and that a field of corn transpires during its entire season of growth as much water as would amount to 5 inches of rain on the field. Actual measurements during a period of ten days of dry weather have shown that corn transpired from 6 to 9 times its own dry weight daily while alfalfa transpired from 36 to 56 times its own dry weight. On the basis of 1 ton of dry matter per acre this would amount to a daily loss of 0.05 to 0.08 of an acre inch of water daily from the cornfield and of 0.32 to 0.49 of an acre inch from the alfalfa field.

Of course all plants do not transpire so rapidly as those we have cited. It has been estimated that sun mesophytes, such as alfalfa, often transpire at least 175,000 times as rapidly, per unit area, as some of the desert shrubs, such as *Fouquieria splendens*, the ocotilla, when they are leafless. It has been shown in the case of several kinds of emersed water plants that water is lost more rapidly from a given area occupied by plants than from an equal area of free water surface. In the case of water lilies, however, the reverse was true.

The process of transpiration is thought to be of very great importance to the plant because of its cooling effect. Yet the greatest danger to which many plants are subjected is that of too great a loss of water. The various ways in which plants are protected from this danger are discussed in Chapter IV.

104. **The Mechanical Effects of Water.**—Water sometimes has destructive effects upon plants. Heavy storms of rain or hail may beat down and destroy seedlings or they may tear or knock off leaves, flowers, or fruits. Snow, which is a form of water, may break down plants or plant parts by its weight. In some places in mountainous regions snow collects near the mountain top and when thawing starts in spring the snow comes down the mountain in a gigantic snow-slide, breaking down the woody plants in its path. When this is repeated in the same path year after year the development of a forest is completely prevented. Such snow-slide paths are often several hundred feet wide. Snow, on the other hand, may be of very great value to plants by serving as a protective covering during the winter. A sleet storm is very destructive in breaking down woody plants. There

is also danger of trees being smothered when sleet remains on them for a long time, though probably this does not happen often.

Water is of considerable importance as an agent of pollination and in the dissemination of seeds and fruits, but these matters are discussed elsewhere.

105. **Rainfall.**—Whenever air is cooled to such an extent that it cannot hold in a vaporous state as much water as it contains, the water falls as rain, hail, or snow, or is deposited as dew. These forms of precipitation are the chief source of water for most plants. Some plants, such as numerous epiphytes and many lichens and mosses, especially those growing upon rocks, absorb all of their water directly from atmospheric precipitations.



FIG. 69.—Forest vegetation, Norway and jack pines, Minnesota. (Photograph by A. G. Gaskill. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

Ordinary land plants, on the other hand, get most of their water indirectly from rainfall after it has penetrated into the soil.

The annual amount of rainfall varies greatly in different places and from season to season. The locations of large bodies of water and of mountain ranges and the direction of the prevailing winds are important factors in determining the amount of annual rainfall in any region. In the continental United States the regions of greatest rainfall are found in the northwest and in the extreme southeast. Leaving out of consideration the effects of local topographic features the amount of rainfall gradually decreases

from Florida toward the north and west, and from Washington and Oregon toward the south and east. The region of least rainfall, on the other hand, is found in the southwestern part of the United States and, in general, it increases in amount from New Mexico and Arizona toward the north and east. In much the greater part of the United States the larger part of the



FIG. 70.—Grassland vegetation, Oregon. (Photograph by H. L. Shantz. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

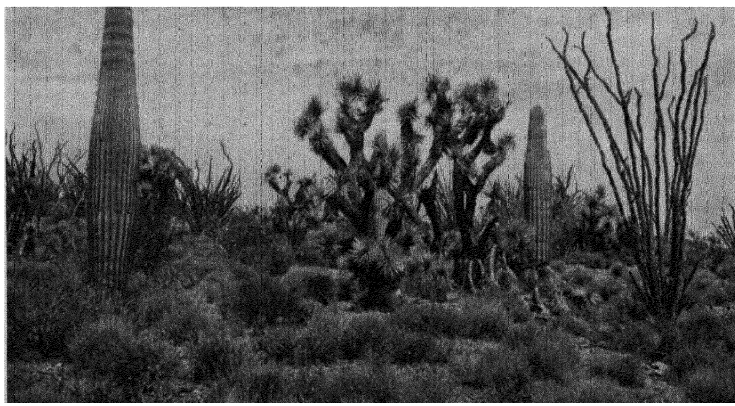


FIG. 71. Desert vegetation with *Carnegia gigantia*, *Yucca brevifolia*, and *Fouquieria splendens* most prominent. Western Arizona.

rain falls in summer. In some regions of the southwest, however, especially in southern California, the larger part, in some cases more than 80 per cent, falls in winter. The seasonal distribution of rain not only has a marked effect upon the distribution of the types of vegetation, as will be

brought out in the following paragraph, but is also one of the chief causes of certain periodic phenomena in plants such as dormant periods. An adequate supply of moisture is absolutely necessary for active growth and, therefore, if at any time it becomes inadequate it may bring about a dormant period, or it may cause death.

106. **Water as a Factor in the Distribution of Plants.**—If we disregard small local areas and consider only large regions, a birds-eye view of the land surface of the earth shows three general types of vegetation; namely, forest (Fig. 69), grassland (Fig. 70) and desert (Fig. 71). These rather distinct types are determined largely by the amount of rainfall, the seasonal distribution of the rainfall, and the frequency of rainy days or of effective rains. By effective rains we mean rains that actually supply water to the

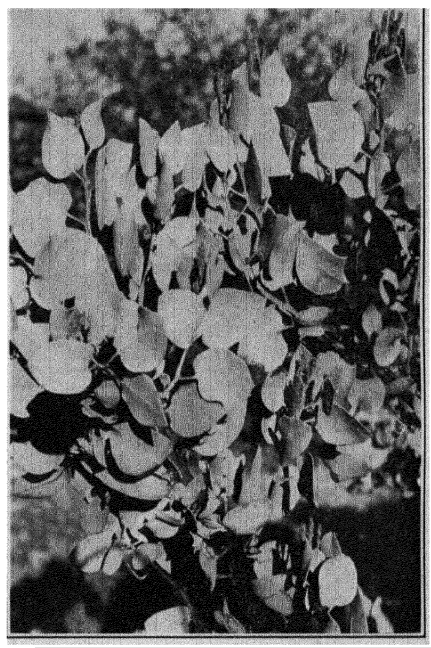


FIG. 72.—*Arctostaphylos viscida*, a broad-leaf sclerophyll. Grass valley, California. (Photograph by W. S. Cooper.)

plants. Light showers are often entirely ineffective because the water evaporates before it has penetrated the soil far enough to be available to the roots. On the other hand, during a torrential rain there may be such a great run-off that only a small fraction of the water that falls becomes available to the plants. If, therefore, a large percentage of the rain falls in light showers or torrential storms it may be considerably less effective than a much smaller total precipitation which falls in such a way as to be largely absorbed by the soil. The frequency of effective rains and the seasonal distribution of the rainfall are, therefore, usually more important than the amount of the annual precipition.

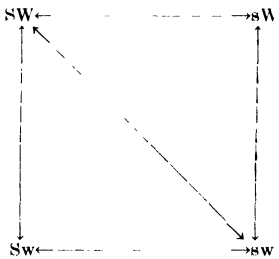
In general, forests occur in regions where there is adequate rainfall during all seasons of the year. There must also be a warm vegetative season and, if there is a winter, the atmosphere must be reasonably moist in order that transpiration may be reduced, since the trees are always exposed to transpiration and they cannot absorb water from a frozen soil. In regions of high winter rainfall and low summer rainfall, such as occurs in parts of southern California, the sclerophyllous type of forest, composed of low trees or shrubs with broad, sclerophyllous, evergreen leaves, is found (Fig. 72).

Grasslands occur chiefly in regions of high summer rainfall and low winter rainfall, while deserts occur where there is low rainfall both winter and summer. If we represent the summer season by the letter S and the winter by W, using a large letter for a high rainfall and a small letter for a low rainfall in each case, the amounts of rainfall needed by the different types of vegetation may be represented symbolically as follows:

SW-ordinary forest. Sw-grassland.

sW-sclerophyllous forest. sw-desert.

It may be seen by the following diagram that there may be transition from one to another of the types in all cases except between sclerophyllous forests and grasslands.



The influence of water on the distribution of the vegetation types is well brought out by what we may call Schimper's Third Law. This states that the type of vegetation in the tropical and temperate zones is determined by the amount and seasonal distribution of the rainfall and by the humidity of the air.

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CHAPTER XV

GROWTH HABITS OF PLANTS

VARIOUS attempts have been made from time to time to classify plants into life-form groups and to interpret these groups in terms of the environment. These classifications have been founded, for the most part, on the role played by a particular species in vegetation and its life history under the conditions prevailing in its habitat, with special reference to duration, propagation and protection during unfavorable seasons. These classifications have not proven so useful as their authors hoped, largely, perhaps, because we still are unable to interpret ecologically many of the growth-forms that we find, but such classifications are of considerable value in certain types of ecological work.

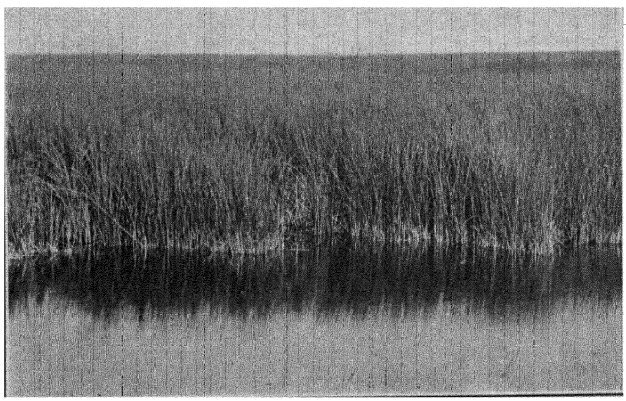


FIG. 73.—A marsh in California. The vegetation is almost exclusively *Scirpus validus* (great bulrush), a typical hydrophyte. (Photograph by H. L. Shantz. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

The simplest classification of this sort is the one we have already given; namely, the classification into xerophytes, mesophytes, and hydrophytes, although it is based only on a single relation, that of water supply. In this chapter we shall first discuss some of the characteristics of these three general types of plants and then consider briefly two other classifications that have been used.

107. **Plants of Hydric Habitats.**—The habitat of a plant consists of the sum total of the environmental conditions under which it lives. It is the place of abode of the plant together with all the environmental factors that are operative within the abode. Hydric habitats are those occupied by hydric plants (Fig. 73). They may differ from one another in various ways but all agree in containing an abundance of available water. In response to a degree of uniformity of environment plant forms have developed with certain characteristics that may be taken as more or less distinctive of plants of hydric habitats.

A pond or small lake may be taken as typical of extreme hydric habitats. Characteristic plants of such a habitat are many algæ, duckweeds, pond lilies, etc. Root systems are much reduced both in length and in amount of branching. Root hairs are absent in the water though they may be present where the roots extend into the mud below. Leaves often equal or surpass roots as absorbing organs. Those of submerged plants are thin and often finely dissected. Air spaces often exceed the tissue in actual volume. Stomata are absent in submerged leaves and are present only on the upper surfaces of floating leaves. Such stomata as are present have but

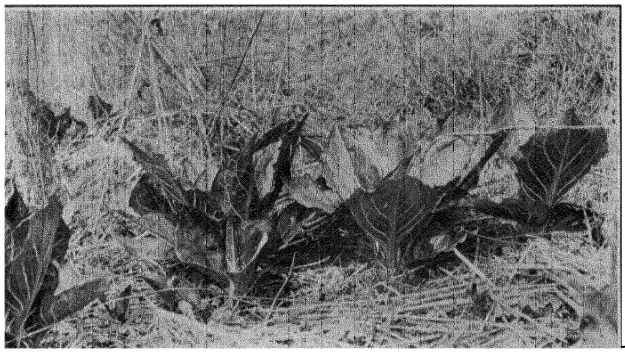


FIG. 74.—Skunk cabbage (*Symplocarpus fœtidus*). Plants of swampy places.

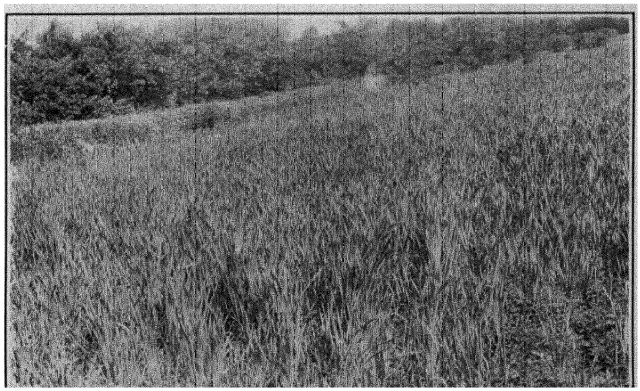


FIG. 75.—A cat-tail swamp. The most abundant plant is *Typha latifolia*, a hydrophyte.

slightly cutinized walls and are almost always open. Protective features are few or wanting. Cutin and cork rarely are developed below the surface of the water, hairs are scarce, and the cell sap has a low osmotic pressure. Conducting and mechanical tissues are also greatly reduced. The absence of protective features is, of course, not disadvantageous to the plants because absorption is easy and below the surface of the water transpiration is practically absent. The submerged portions of seed plants are usually covered with slime which harbors communities of bacteria and other low

organisms. The aërial surfaces of floating organs, on the other hand, are usually coated with wax and so are not easily wet. Vegetative reproduction is highly developed in hydric habitats, while flowers and seeds are less abundant than in most habitats.

A swamp (Figs. 74 and 75) is a hydric habitat which differs from a pond or lake in that the water table is just about at the surface of the soil, though it may be a little above during wet seasons or a little below during dry seasons. Some characteristic swamp plants are the cattails (*Typha*), the reed (*Phragmites*), the bulrush (*Scirpus*), etc. The structural features of swamp plants are in part like those of pond plants, especially in the reduced root systems and prominent air chambers, but ,in general they are less extremely hydric and have a tendency to approach a resemblance to mesophytes. Roots of swamp plants are frequently horizontal, or even ascending, rather than descending. Rhizomes are greatly developed and there is an abundant development of vertical chlorophyll-bearing organs, whether stems or leaves.

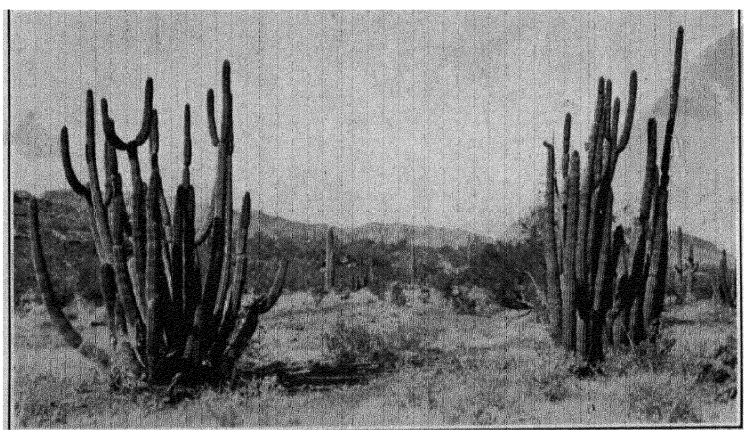


Fig. 76.—(*Lemaireocereus thurberi*), Organpipe cactus a desert xerophyte.

108. **Plants of Xeric Habitats.**—There are two general types of xeric habitats, those in which there is an actual dearth of water and those which contain an abundance of water but are physiologically dry. The latter will be discussed in Paragraph 109.

The most typical of the true xeric habitats are found in desert regions where such plants as sage brush and the various kinds of cacti are characteristic (Fig. 76). The roots frequently are strongly developed, possessing either considerable length or great size, though this is generally not true of cacti. Roots that have great size serve to accumulate large amounts of water. Root hairs are abundant, often extending far back from the root tip, and in some cases having thick, rigid cell walls. Palisade tissue is strongly developed and the chlorenchyma in both leaves and stems is often deep-seated so that these organs have a pale green color. There is a marked reduction in the size of all cells including the guard cells of the stomata.

Protective features are remarkably well developed and of course are needed because of the great exposure of xerophytes to transpiration. The transpiring surface is usually relatively reduced, the leaves, if present, being small and thick. Many species are leafless, their cylindrical stems exposing a relatively small surface to transpiration while their vertical orientation affords some protection from the intense rays of sunlight during the middle of the day. In many cases there is a temporary reduction of transpiring surface, as in the leaves of grasses which roll up and those of legumes which fold during the hottest and dryest parts of the day. Temporary reduction is exhibited also by those deciduous plants which shed

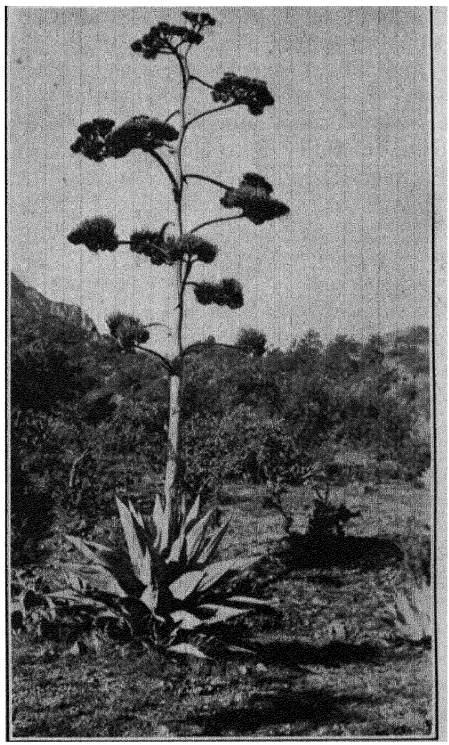


FIG. 77.—*Agave scabra*, a succulent xerophyte.

their leaves at the beginning of each period of dry or cold weather. Annuals, which live through the critical season only as seeds, represent the extreme of temporary reduction of transpiration surface. Dwarfness of habit is a prominent xeric feature and the resulting compactness in arrangement of branches and leaves, as well as the closeness to the ground, afford considerable protection.

The more minute structural features of xerophytes are no less significant than are the more obvious characteristics. Commonly the epidermis is thick and highly cutinized, and often it is superficially coated with wax, resin, or varnish. In woody stems there is a prominent bark development,

the cork layers, in particular, being of great significance in checking transpiration. The leaf and stem surfaces frequently are covered with hairs, and spinescence is also common. Spinescence is of no significance in protection from transpiration but in some plants the spines probably do afford protection from herbivorous animals. Stomata occur only on protected surfaces, chiefly the undersides of leaves, and often are placed at the bases of pits or other depressions and may be further protected by hairs or heavy cutinization or both.

Many xerophytes are succulent (Fig. 77); many contain latex; and oils and resins often are abundantly developed. The osmotic pressure of the cell sap usually is very high, especially in woody plants and in plants of alkaline soils and in most xerophytes there is a marked ability to endure wilting without suffering death. Conducting tissues are well developed, as is lignification, and annual rings are prominent. Bast fibers and other mechanical elements reach their highest development in xerophytes. Among the most severe of xeric habitats are the alkali plains and basins where excessive climatic aridity is supplemented by a soil in which highly concentrated salts make absorption extremely difficult. Succulents with sap of high osmotic pressure seem to be best fitted for existance under such conditions but there are some places where the alkalinity is so great that plant life is practically excluded.

Some xerophytes, especially rock lichens, are entirely lacking in the ordinary xeric structures but are able to withstand prolonged desiccation and then quickly revive with the coming of rains. Aside from lichens, mosses and a few club mosses absorption through aërial organs is relatively rare in xerophytes. Tubers, bulbs, and corms are especially characteristic of xeric habitats and are of great advantage because of their ability to develop rapidly at the beginning of a rainy season. Vegetative reproduction, however, is not prominent and the production of flowers and fruits is favored by xeric conditions.

It is believed that solar radiation and an actual shortage of water are the two principal external factors that induce xeromorphic structures. A shortage of water in the embryonic tissues appears to prohibit the normal development of cells during the period of enlargement and leads to the production of small cells with thick walls. This decrease in the size of cells leads to the production of small leaves with a close network of veins and closely spaced stomata. Intense solar radiation induces the production of palisade tissues. The increase in the amount of palisade tissue increases the capacity for photosynthesis while the closely spaced stomata increases the rate of transpiration per unit area. It has been found by experiment that when a mesophyte and a xerophyte are grown under identical conditions with an abundant water supply and a humid atmosphere they may transpire at identical rates but as the aridity of the atmosphere is increased the xerophyte will lose more water than the mesophyte because its stomata will remain open longer, but it will suffer less because it can endure wilting so much better and after its stomata are closed it will lose almost no water because of its protective features. It is also believed that intense insolation and water deficiency are the chief factors that lead to higher osmotic pressures in xerophytes and that the high osmotic pressures are in some way related to the power of resistance of the protoplasm to injury during wilting.

Xerophytes, for the most part, are plants that have been derived from mesophytes through responses to adverse environmental conditions. Most of them will grow better if their water supply is increased, within certain limits, and their xerophytism is measured by their ability to resist drought and to endure wilting rather than by their morphological structures.

109. **Plants of Habitats that are Physiologically Dry.**—Plants that grow in saline soil or in salty water are called halophytes and they are strikingly xeric. Perhaps the most characteristic feature of halophytes, as a group, is their succulence which is accompanied by very high osmotic pressure. We have already spoken of alkali plains, which are usually physically as well as physiologically dry, and we are concerned now only with those habitats which contain an abundance of water. The oceans are, of course, halic (characterized by physiological dryness) habitats but the majority of plants in them are algæ which are for the most part submerged and, therefore, not subject to transpiration. Because of this protection from transpiration these algæ do not show xeric features.

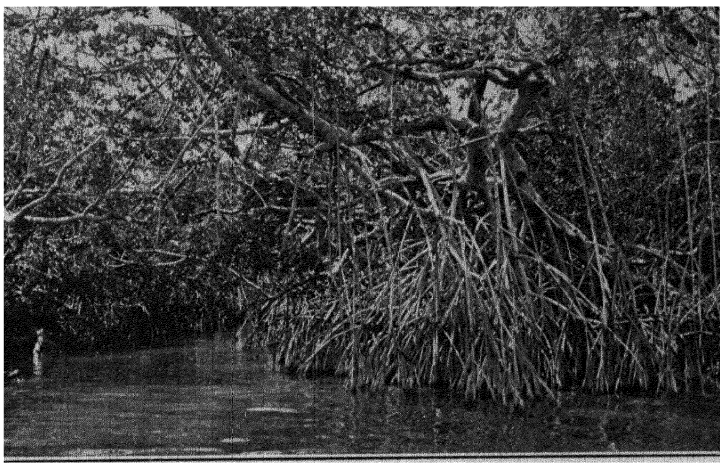


FIG. 78.—A mangrove in a halic habitat in Florida. (Photograph by Alexander Sprunt, Jr.)

Much more interesting from our point of view are the salt marshes which contain strikingly xeric plants comparable to those occurring on saline soils. In temperate regions the most representative salt-marsh plants are erbacheous, but in tropical and subtropical regions there are extensive mangrove forests occupying halic habitats. Few plants show more marked xeric features than the mangroves (Fig. 78). They have evergreen leaves which have water storage tissue, prominent palisade cells, and thick cutin. Often there is a network of roots extending from the branches down through the water and into the soil below. Frequently, also, there are ascending "knees" comparable to those found in bald cypress swamps.

Another very interesting type of habitat which seems to be physiologically dry, although there is an abundance of water present, is the bog (Fig. 79). Bogs are formed in places where lack of drainage, and conse-

quently lack of aeration, leads to an accumulation of carbon dioxide and of undecayed or only partly decayed organic matter. One result of this is a rather high degree of acidity of the water. Possibly some other substances which may be somewhat toxic to the roots of plants also accumulate. The habitat is not well understood but it seems to be difficult for plants to absorb water from it and undoubtedly the acidity is one of the factors causing this. Low temperature may also be an important factor since both the air and soil temperatures in a bog are usually lower than in neighboring habitats. The peat moss (*Sphagnum*) is especially characteristic of bogs and it is probable that the cooling effect of the rapid transpiration of water from this moss is a factor in the production of the low temperatures in the bog. There are also many orchids, insectivorous plants, and such woody plants as cranberry (*Vaccinium*), leather leaf (*Chamædaphne*), bog rosemary (*Andromeda*), and tamarack trees (*Larix laricina*). Many of these plants,

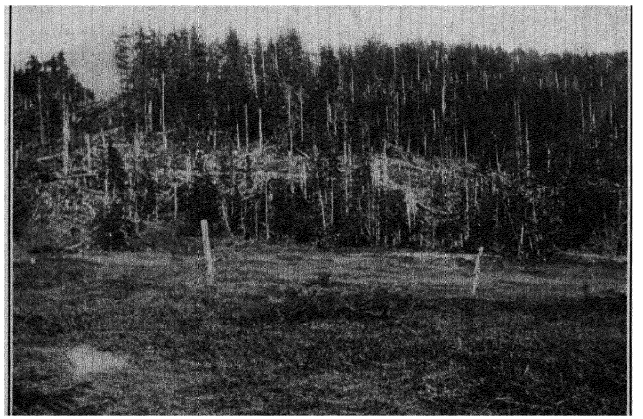


FIG. 79.—Cordova bog, Alaska. (Photograph by George B. Rigg.)

especially the woody ones, show marked xeric features. Some of them, the tamarack for example, like many plants of saline habitats, grow better elsewhere if given a chance, indicating that they "tolerate" rather than "prefer" these physiologically dry habitats. This means only that, under ordinary conditions, they are not able to compete with other plants in more favorable habitats but are able to meet competition in the unfavorable ones.

110. **Plants of Mesic Habitats.**—The most typical mesic habitats are found in deciduous forest regions. In many respects the structural characteristics of mesophytes are more or less strictly intermediate between those of the xerophytes and hydrophytes that we have discussed, but, of course, all degrees of gradation could be found between the few typical habitats with which we are dealing.

In the typical mesic habitats there is usually a prominent development of vertical roots with abundant root hairs. The foliage reaches a maximum development and the leaves are relatively large and thin. The thin, transparent layers of epidermis and an abundance of chlorophyll cause the leaves to appear dark green, in contrast to the pale green leaves characteristic of xeric plants. Stomata usually occur on both surfaces of the leaves,

except in the case of trees where they ordinarily are on the lower surface only. The guard cells have a maximum capacity for movement and cutinization of walls is usually moderate.

111. **The Life-forms of Raunkiaer.**—Raunkiaer is a Danish botanist. His classification of plants into life-forms is the result of an attempt to find some method of estimating the relative values of the climates of various parts of the world by means of some standard that would have a direct bearing on plant life. The ordinary physical methods of measuring climatic influences are unsatisfactory because very different physical factors may have quite similar effects on plant growth and various combinations of factors may produce essentially the same growth-forms. The measurement of any single climatic factor or group of factors, therefore, does not give us an accurate estimate of the value of the climate for plant life.

For these reasons it was felt by Raunkiaer that the plants themselves should be the recorders of the biological value of any climate. The factor that was selected was the nature and degree of protection of the perennating bud or shoot apex during the critical season. A perennating bud is one that lives through a critical season and may develop into a shoot during the next growing season. It was necessary first of all, therefore, to classify plants on the basis of bud protection. The classification as finally used by Raunkiaer is as follows, the symbol used for each life form following the name in parentheses.

1. Stem succulents (S).

2. Epiphytes (E).

3. Megaphanerophytes and mesophanerophytes (MM). The megaphanerophytes are trees that are over 30 meters high while the mesophanerophytes are trees from 8 to 30 meters high. Since the buds are freely exposed in both they are grouped together.

4. Microphanerophytes (M). These are small trees and shrubs from 2 to 8 meters high.

5. Nanophanerophytes (N). Shrubs that are less than 2 meters high. All trees and shrubs may be spoken of simply as phanerophytes.

6. Chamaephytes (Ch). These are plants that have their buds or shoot apices perennating on the surface of the ground or just above it, so that in regions with snow they are protected during the winter and in regions with dry seasons some protection is afforded by plant remains. The buds are thus better protected than in phanerophytes. Plants with runners, cushion plants, etc., belong in this group.

7. Hemicryptophytes (H). These plants have dormant buds in the upper crust of the soil just below the surface. The aërial parts of these plants are herbaceous and die down at the beginning of the critical season so that they form an additional protection. Most rosette plants belong here.

8. Geophytes (G). The geophytes have their dormant parts subterranean. They are plants with bulbs, rhizomes, tubers, etc.

9. Helophytes and hydrophytes (HH). The helophytes are marsh plants with their buds at the surface of the water or in the subjacent soil. The hydrophytes are water plants with perennating rhizomes or winter buds. It is unfortunate, of course, that the term hydrophyte is used here in a much narrower sense than ordinarily. The geophytes, helophytes and hydrophytes are collectively called cryptophytes.

10. Therophytes (Th). These are the plants which live through the critical season as seeds; that is, they are annual plants.

It is readily seen that this classification does not take into consideration any of the lower forms of plant life. It is further seen that, leaving out of consideration the first two groups, the stem succulents and epiphytes, which in a sense stand apart by themselves, the remaining groups, beginning with the phanerophytes in Group 3, form a series in which each type has its buds better protected than has the type preceding it. In using this classification for the evaluation of a climate the species of the flora are listed and the percentage of species falling in each group is determined. This list of percentages is spoken of as a biological spectrum and is compared with a normal spectrum which is supposed to represent the average conditions for the entire earth. The normal spectrum used by Raunkiaer is as follows:

S	E	MM	M	N	Ch	H	G	HH	Th
1	3	6	17	20	9	27	3	1	13

In comparing the biological spectrum of any region with the normal spectrum the important feature is the place of greatest deviation from the normal. For example, a study that was made of the flora of New York and vicinity gave the following spectrum:

S	E	MM	M	N	Ch	H	G	HH	Th
0	0	4.55	7.18	3.51	5.29	33.29	20.23	11.74	13

The greatest deviation from the normal in this spectrum is found in the large percentage of geophytes and of helophytes and hydrophytes. Since these three groups together are called cryptophytes, the climate of the region may be called a cryptophytic climate. Some other, rather incomplete, studies that have been made in this country have indicated that the climate of the plains region in the vicinity of Akron, Colorado, is hemicryptophytic, that in Tooele Valley, Utah, chamæphytic, and that of Death Valley, California, therophytic.

112. **Vegetation Forms.**—A simple classification into vegetation forms which may be made to include the whole plant kingdom is sometimes found useful. Such a classification, based upon the methods of increase and the character and length of life of the vegetative shoots, consists of four large groups; namely, annuals, biennials, herbaceous perennials, and woody perennials.

Annual plants pass the unfavorable season in the seed or spore form, and the vegetative shoots live during only one growing season, the entire length of life of the plant being about one year. Biennials pass one unfavorable season as seeds or spores and the next as a vegetative propagating organ of some form. There is no accumulation of aerial shoots and the plant lives during two or parts of two years. Herbaceous perennials pass each unfavorable season both in the seed or spore form and in the form of vegetative propagating parts. There is no accumulation of aerial shoots but the plant lives several or many years. Woody perennials pass each unfavorable season in the form of seeds or spores or as plants with aërial shoots.

For more accurate description of vegetation types the last two groups, herbaceous perennials and woody perennials, may be sub-divided as shown in the following list.

1. Annuals.
2. Biennials.

Herbaceous perennials.

3. Sod-grasses.
4. Bunch-grasses.
5. Bush-herbs.
6. Cushion-herbs.
7. Mat-herbs
8. Rosette-herbs.
9. Carpet-herbs.
10. Succulents.

Woody perennials.

11. Half shrubs.
12. Bushes.
13. Succulents.
14. Shrubs.
15. Trees.

113. **The Evolution of Growth-forms.**—Our knowledge is not yet sufficient to enable us to arrange all of the growth-forms of plants in an evolutionary sequence which we can be sure is correct, and perhaps it never will be. But a beginning has been made by a number of workers, and it is now believed that among the angiosperms the woody type is more ancient than the herbaceous. Probably the most primitive type of tree is the sparingly branched, rain-forest type with large, undivided leaves. During the course of evolution more xeric forms have been produced and there has been a tendency toward reduction in size of plant and of leaf, an increase in the amount of branching of the plant and of the veins in the leaves, the production of compound leaves and of deciduous leaves, and the development of thorns and of succulence. Climbing plants, epiphytes, parasites, and herbaceous shade plants, all of which may occur in primitive habitats along with trees, are probably all much more recent than the trees. Probably all of the angiosperms of desert and semi-desert conditions are relatively recent. Extreme hydrophytes or aquatic plants are also thought to be derivative. The annual type of flowering plant is considered the most recent of all.

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CHAPTER XVI

PLANT COMMUNITIES

PLANTS ordinarily live with other plants in communities that consist of many individuals (Fig 80). When an ecologist goes into a forest he does not see merely a number of trees, shrubs, and herbaceous plants with no relations one to another except that they happen to be growing in close proximity. What he sees is a plant community which is just as simple and understandable but with its multitude of activities just as complex, just as inevitable in its structural make-up but with its succession of life problems just as intensely interesting as any city or other human community. Actually practically every plant community contains many individual animals as well as plants and the animals are important components of the community. In other words the community is a biocommunity rather than merely a plant community. However, since we are studying plant ecology rather than bioecology, it is necessary that we largely ignore the animals and deal with plant communities as though they were composed of plants only.

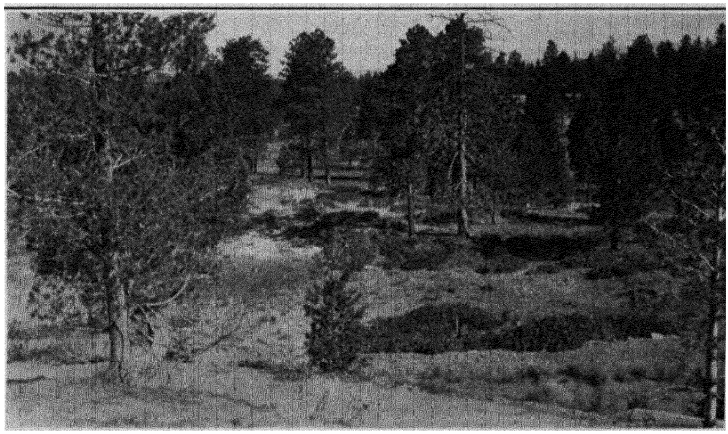


FIG. 80.—A plant community consisting of many individuals.

The kinds of plants that one may expect to find in any community depend upon the factors of the environment, for just as we, in order to live and be healthy, must have homes that are adequately supplied with heat, light, water and food, so the plants in their homes are affected by these same factors of the environment. For this reason various kinds of plants that require the same type of environment are habitually found living in the same community. So true is this that often when an experienced field man sees a certain species of plant he almost instinctively looks for other species that he has learned are usually associated with this one.

The ecology of plant communities is called synecology and will be discussed in this and the following five chapters.

114. **The Plant Community an Organism.**—The individual plants that make up a plant community are living together in a state of social disjunctive symbiosis but they are so intimately associated that the community as a whole may be considered as an organic entity; that is, an individual organism. As an individual the plant community is born, it grows and developes, it matures, reproduces, and may finally die like any other organic individual.

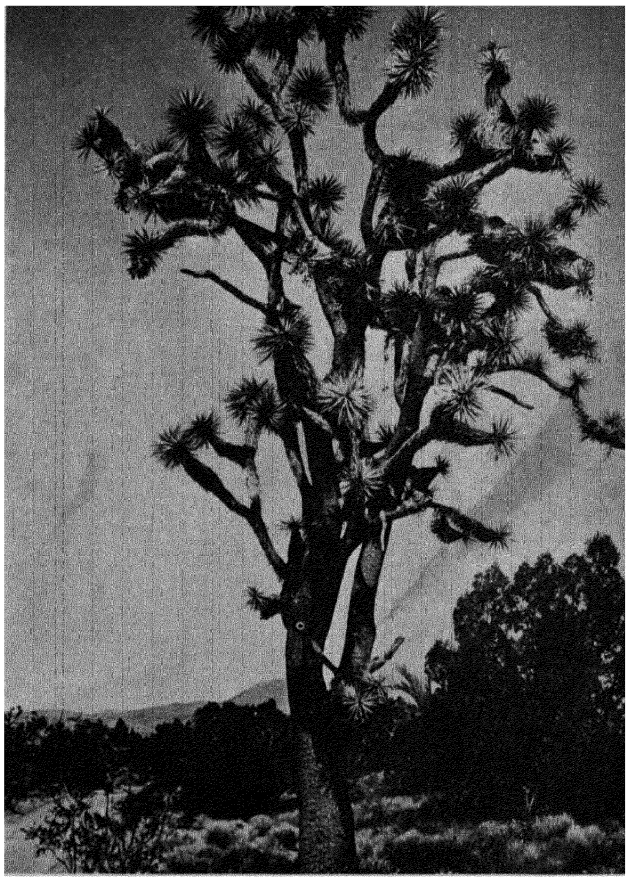


FIG. 81.—A Joshua tree, an individual of the second type which is composed of millions of cells or individuals of the first type.

If we consider the plant community as an individual organism then we can recognize three distinct types of individuals. The first of these is the single cell. This was the first kind of individual that appeared on earth and at first, of course, there was only the one type. The single cell performed all of the functions that it is necessary for a plant to perform and, of course, there was no such thing as division of labor. After a while, however, some of these

one-celled organisms began to cling together and so form little colonies or communities of cells. They were still all alike, each one performing all functions, but from these little colonies have evolved the much larger communities of cells that we call the higher plants and animals. Thus a higher plant, such as a joshua tree (Fig. 81), is a community of millions of individuals of the first type of which we have spoken. It is a representative of the second type of individual. In this individual, which is really a community of cells, there is a decided division of labor and a differentiation of form and structure among the component individuals.

Just as the second type of individual is a community composed of individuals of the first type, so a plant community, which we consider as the third type of individual, is composed of individuals of the second type, largely, though some of the component individuals may be of the first type. It is a little difficult at first to think of a plant community as an individual in the sense that a tree is an individual, because we have not been in the habit of so considering it, but there is no greater degree of difference between a tree and a plant community, such as a forest, than there is between a tree and a one-celled alga, and we shall find that the forest community has a life cycle and can do practically everything that the tree can do. It has sometimes been said that we should not consider plant communities as individual organisms because it is often nearly impossible to tell where one community ends and another begins. It is quite true that certain kinds of plant communities overlap at their margins in such a way that their delimitation is not easy but if this fact were to be accepted as a valid argument against considering plant communities as individuals the argument would have equal force against considering certain kinds of plants as individuals. For example a single plant of wild ginger (*Asarum canadense*) may reproduce by means of rhizomes until it forms a circular patch several feet in diameter. No one would consider this patch a single plant and yet it is practically impossible to tell how many plants there are or where one plant ends and another begins. The same thing is true of many other plants that spread by rhizomes or runners. But this difficulty in delimiting individuals need cause us no worry. In the majority of plant communities, as in the majority of plants, the difficulty is not encountered.

In every plant community there are certain species of plants that are called dominant plants because they largely control the environment and so determine what other species may grow in the community. In a forest the dominant species are trees. They have very important symbiotic relations with all other members of the community through their direct or indirect control of light, space relations, water supply, and to a certain extent available food materials. From this point of view it is of interest to compare a plant community with a human community. In a human community man is the dominant species. As the dominant species he controls the environment to such an extent as to determine what other species may live in the community. Some of the other species usually found in a human community are the horse, dog, cat, mouse, fly, etc. Some of these are not present because man wants them to be, but because man is present and is controlling the environment in such a way as to make it possible for the other species to live in the community. These facts are just as true of the plant community. The presence of some of the species is distinctly advantageous to the dominant plants, while that of others is just as distinctly disadvantageous, as for example the parasitic fungi, but they are all present

because dominant plants have made it possible by control of environment.

115. **The Migration of Plants.**—As we examine various plant communities growing in very different environments we are impressed by the fact that nearly all plants seem to be growing in places to which they are very well suited. Where did they all come from and how did they succeed in finding a congenial environment? The answer to this question is to be found largely in the efficient means that most plants have for disseminating their propagating bodies.

Fruits that open at maturity, such as capsules and pods, are called dehiscent fruits while those that do not open at maturity, such as berries and akenes, are called indehiscent. In the case of plants with indehiscent fruits usually the entire fruits are disseminated while plants with dehiscent fruits commonly scatter the seeds only. In some plants the seeds are forcibly expelled by the act of dehiscence. The seeds of the violet and of the lupine are thus hurled out to a distance of several decimeters and those of the witch hazel are often scattered for several meters. In the *Geranium* the carpels separate from the base of the main axis of the fruit and curl upward with such suddenness as to discharge the seeds. In the touch-me-not (*Impatiens*) the mature fruit is under such tension that a mere touch causes it to dehisce violently and so scatter the seeds. The fruits of the dwarf mistletoe (*Arceuthobium*) explode at maturity and hurl the seeds for several meters, and, since the seeds are sticky, they readily adhere to the bark of trees on which the mistletoe is parasitic.

Many capsules and pods do not dehisce violently but open up and remain in such a position that their seeds are easily shaken out by wind or brushed out by animals. In many mints the nutlets may be shot out if the calyx is pressed down and then released, and in the smartweed (*Polygonum virginianum*) the akene is attached to an elastic cushion in such a way that when it is pressed back and then released it bounds off to a distance of two or three meters. These means of dissemination are of course relatively inefficient because the seeds are never scattered more than a few meters from the parent plant.

The spores of many fungi are forcibly discharged at maturity. The fungus *Pilobolus* grows only on dung piles and when the spores are mature they are discharged in masses which usually fall on the grass or other vegetation surrounding the dung pile. They can never germinate and grow on the grass but if the grass is eaten by an animal the spores pass through the alimentary canal and are deposited in a suitable substratum for germination and growth. The spores of many Ascomycetes and Basidiomycetes are discharged into the air and are then caught by air currents and carried away.

Many plants with rhizomes or runners depend more upon growth than upon the dissemination of seeds or fruits for migration. Migration by growth is a very slow but otherwise efficient means of advance into new territory.

116. **Migration Through the Aid of Wind.**—Wind is probably the most efficient of disseminating agents, at least as to the numbers of seeds or spores carried. Spores being lighter than seeds are often carried much farther, though very small seeds, such as those of orchids, may be carried for great distances.

Many adaptations for wind dissemination are found. In the maple (*Acer*), the hop tree (*Ptelea*), and the elm (*Ulmus*) the fruits, called samaras,

are provided with wing-like appendages which often contain air spaces of considerable size. These prevent the fruits from falling rapidly to the ground. The seeds of *Catalpa* are similarly provided with wings. Very characteristic wind-scattered fruits are found in many members of the composite family. In the dandelion for example, the involucre closes after the flowers have bloomed, remains closed while the fruits are maturing, and opens again when the fruits are ready for dissemination. Each fruit is provided with a crown of hairs, the pappus, which spreads out like a parachute and prevents the fruit from falling quickly while being carried by air currents. In the milkweeds (*Asclepias*), the willows (*Salix*), and the poplars (*Populus*), the seeds are provided with tufts of hairs which render them as well adapted to wind dissemination as are the akenes of the dandelion and other composites. The abundant hairs on the seeds of the cotton plant (*Gossypium*) are, from the point of view of the plant, an adaptation for wind dissemination. Somewhat similar cottony hairs are found on the seeds of some of the anemones and of the cotton grass (*Eriophorum*).

Remarkably interesting adaptations for wind dissemination are found in the so-called tumble weeds. These are plants which, at maturity, break off from the roots and are tumbled along over the ground by the wind, scattering their seeds as they go. In the case of the Russian thistle (*Salsola Kali tenuifolia*) and the tumble weed amaranth (*Amaranthus græcizans*) the entire shoot breaks off at the surface of the soil, while in the old witch grass (*Panicum capillary*) only the panicle breaks off. Sometimes the panicles of old witch grass become attached to other tumble weeds and are carried along with them.

Many kinds of bacteria and the spores of lower plants are scattered principally by the wind. Samples of air taken almost anywhere at any time are found to contain greater or smaller numbers of these minute organisms.

117. **Migration Through the Aid of Water.**—Water is less efficient than wind as far as the numbers of propagating bodies carried are concerned, but it is an important disseminating agent largely because it may carry fruits or seeds for long distances. In streams and ocean currents the propagating bodies are carried in a definite direction but in lakes and ponds the direction often varies with the changing direction of the wind.

All seeds are heavier than air and therefore the distance to which they can be carried in that medium is necessarily limited. Many seeds and fruits, however, are lighter than water and so may float almost indefinitely. This is especially true of the fruits of many water plants which often have large air spaces in the ovary walls or the seed coats. The seeds of many land plants, however, sink in water, some quickly and others after a longer time, so that the distance to which they may be carried is limited. The length of time that a seed may float on water and still be viable is closely connected with its resistance to the infiltration of water. Many seeds that are capable of floating rather quickly lose their ability to germinate because of the entrance of water which institutes decay. This is likely to be especially true if the water is rough and still more so if it is salty as well as rough. For example, the cocoanut, which is often seen floating on tropical waters, has frequently been cited as a typical example of water dispersal to distant islands. This fruit, however, usually loses its viability within a few days through the infiltration of water so that it is doubtful whether it could populate a very distant land unless it were carried on

driftwood or by some comparable means. On the other hand, there are some fruits and seeds that can float on water for a very long time without becoming injured. The fruits of *Suriana maritima*, a common tropical plant, have been shown by experiment to be uninjured after floating on rough, salty water for one hundred and forty-three days, and the seeds of *Hibiscus tiliaceus* were viable after floating in a similar way for one hundred and twenty-one days. The seeds of some species of *Asparagus* may be viable after soaking in water for a year, and those of the arrow-leaf (*Sagittaria*) and of the mermaidweed (*Proserpinaca*) have been shown to be uninjured after soaking at the bottom of a pond for seven years.

Fruits and seeds are often carried great distances on driftwood or other articles floating on water. Furthermore the seedlings of some kinds of plants may float for days on water and then, if stranded in a suitable place, take root and grow. The seedlings of some species of bur marigold (*Bidens*) are sometimes seen floating on water by the hundreds and many of them later succeed in finding suitable places to grow. In the case of duckweeds and many algæ the mature plants float on water and may be carried from place to place.

118. **Migration Through the Aid of Animals.**—Many indehiscent fruits, especially bur fruits and others that have hooked appendages, are involuntarily distributed by animals. The cocklebur (*Xanthium*), burdock (*Arctium*), bur marigold (*Bidens*), hound's tongue (*Cynoglossum*), sweet cicely (*Osmorhiza*), bed-straw (*Galium*) beggar's lice (*Lappula*), and bur grass (*Cenchrus*) are familiar examples of animal disseminated fruits.

Another interesting class of fruits that are scattered by animals consists of those that are fleshy or possess a more or less juicy, edible pulp. Such fruits are eaten abundantly by birds and other animals and the seeds are likely to be disseminated. On the other hand, fruit-eating animals do not always facilitate dispersal, since they eat and digest many seeds. Acorns and nuts of various kinds are eaten in large quantities by squirrels. Occasionally nuts that are buried by squirrels are not eaten and so may germinate, but as a means of dissemination this method is, to say the least, very precarious. Ants are dissemination agents of considerable importance in the case of seeds, such as those of blood-root (*Sanguinaria*), ginger (*Asarum*), and the false mermaid weed (*Flœrkia*), which have oily or albuminous appendages. The ants feed upon these appendages and often carry the seeds considerable distances.

Wading birds often carry seeds in the mud that adheres to their feet. This undoubtedly accounts for the wide distribution of many aquatic plants since such birds often fly for great distances and almost always from one body of water to another. The efficiency of animals as disseminating agents lies primarily in the fact that each species of animal frequents the same type of vegetation most of the time. Animals that live in forests, for example, either stay in the same forest or go from one forest to another so that any seeds or fruits that they carry are likely to be dropped in places that are suitable for their growth.

Man is a very important agent of dispersal. He acts in the same way as other animals to a certain extent but is more important because of his common carriers. Railroad trains, for example, may carry seeds for long distances and scatter them along the right of way. So true is this that one almost always finds a flora along a railroad that is rich in the number of species.

119. **Plant Succession.**—The discussion of the means of dissemination in the preceding paragraphs is enough to answer the question as to where the plants that we see came from and how they happened to find suitable places in which to grow. They came from already existing communities and the seeds of each species were scattered everywhere, but only those that fell into suitable communities were able to grow. The developement of plant communities from birth to maturity is called plant succession. This will be discussed at length in later chapters but it will aid us in grasping the significance of the individuality of plant communities if we trace briefly the development of one at this time.



FIG. 82.—A mature forest community of birch, beech, maple and hemlock. (Photograph by A. G. Vareka. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

Let us take for example a beech and maple forest such as may be found in Indiana or Ohio as well as in a number of the other states east of the Mississippi River. Let us suppose that after the glacial period an area of bare rock of fairly high elevation was left exposed somewhere in Indiana or eastern Illinois. The bare rock was, of course, not a suitable place for trees to grow, but, since it was a bare area, that is, an area unoccupied by plants, it was a good place for the birth of a plant community. The first plants that appeared on the rock were some xeric mosses and lichens. This was the birth or beginning of the new plant community.

These plants grew very slowly, but gradually they corroded the surface of the rock, causing it to crumble somewhat and they also collected dust and other materials blown upon the rock by the wind, so that after a number of years they had formed a small amount of soil upon the rock. Because of this soil, which would hold a certain amount of moisture, it was now possible for some of the more xeric herbaceous plants to grow here. Probably the first ones were some of the common weeds and these were later followed by grasses and the perennial plants that usually grow along with the grasses. Notice, now, that as more plants grew here and more soil was formed the place was becoming less and less xeric. Finally, after many years, there was soil enough and water enough in the soil so that woody plants began

to appear. Perhaps the first was the juniper, or some xeric shrubs, but later other and larger trees came, especially the black and white oaks and the hickories. Our plant community had now developed into a real forest and, because of the shade and the increasing layer of leaf mold, it was becoming quite mesic but it was still too dry for the beech and maple for these trees are confirmed mesophytes. Of course the oaks and hickories had many other trees, shrubs, and herbaceous plants associated with them, each of which had its part to play in the community, and they flourished for many years. But gradually the place became more and more mesic, the oaks and hickories gave place to the beeches and maples, and the community had at last reached its maturity (Fig. 82).

We shall see that the development of such a community is just as definite as is that of any other type of individual. In other words, it was just as certain that this would in time develop into a beech-maple forest and not into some other kind of community as it is that an acorn will develop into an oak tree and not into a hickory or some other kind of tree.

120. **A Tree and a Plant Community Compared.**—We have stated that a plant community is born, it grows and develops, matures, reproduces, and may die, like any other individual. It will be profitable now, before taking up the details of the structure of plant communities, to compare the life cycle of a plant community with that of a tree (a cell community). In order to make the comparison less abstract we will compare a beech-maple community with an oak tree.

A plant community always starts on some kind of a bare area and a bare rock surface will serve as well as any. This bare area then represents a sort of potential plant succession—a possible place for the birth of a plant community. But a plant community will never develop here until something comes in from the outside. Turning to the oak tree we may compare the egg cell before fertilization with a bare area. It represents a potential plant; but it will never develop until something, the male gamete, comes into it from the outside.

We are using birth here only in the sense of a beginning or an origin. Therefore, we may take the fertilized egg (a single cell) as the beginning or birth of the new individual that is to develop into an oak tree. Corresponding to this on the bare area we would have first a single moss plant. In order that these young organisms may grow they must both receive something more from the outside. The fertilized egg must receive food and the young community must receive plants. The fertilized egg now develops into an embryo, and the young community develops into a lichen-moss community; the embryo develops into a seedling, and the lichen-moss community develops into a perennial herbaceous plant community; the seedling develops into a shrub, and the perennial herbaceous plant community develops into a shrub community; the shrub develops into a sapling, and the shrub community develops into a xeric tree (oak-hickory) community. These are mere progressive steps in the development of these two organisms. The sapling now matures into a tree, and the xeric tree community matures into a mesic tree (beech-maple) community.

The mature oak tree, which is a representative of the second type of individual, is a community of individuals of the first type, and it reproduces by giving off single individuals of the first type (cells or gametes). The plant community, on the other hand, is a community of individuals of the second type, and it reproduces by giving off single individuals of the second

type (plants, usually in seeds). As to death, there seems to be no reason why a tree should ever die unless it gets diseased or meets with an accident. Some of the big trees of California have lived for several thousand years and there is no reason to suppose that they will not keep on living unless they become diseased or meet with an accident. The same thing may be said of a plant community. It may die from disease or from an accident, but otherwise it will continue to live indefinitely. It is a little hard at first to visualize the phenomena concerned with this third type of organism only because we have not been used to doing so. It is necessary to keep in mind the bigness of these organisms and of the phenomena concerned and to learn to think in terms of bigness. For example, some organisms of the first type (bacteria) may complete their life cycles in a half-hour, for some of those of the second type (a tree) it may take a hundred years, but for those of the third type (a plant community) it may, in some cases, take a million years. The following tabular comparison may help to make clear the comparison discussed above.

Bare area	Egg cell	Bare rock
Birth	Fertilized egg	Moss plant
Growth and	(Take in food)	(Take in plants)
Development	Embryo	Lichen-Moss Community
	Seedling	Herbaceous plant community
	Shrub	Shrub community
	Sapling	Xeric tree community (Oaks and hickories)
Maturity	Oak tree	Mesic tree community (Beech and maple)
Reproduction	Gives off cells	Gives off plants (seeds)
Death	From disease or accident	From disease or accident

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CHAPTER XVII

THE STRUCTURE AND CLASSIFICATION OF PLANT COMMUNITIES

A ONE-CELLED plant, or individual of the first type as described in the preceding chapter, has certain definite morphological parts which are usually readily recognized and to which names are applied. The cell wall, cytoplasm, nucleus, and nucleolus are such parts. Likewise an oak tree, or individual of the second type, has easily distinguishable morphological parts such as roots, stems, and leaves. We may reasonably expect, therefore, to find somewhat comparable structural parts in the case of an individual of the third type, the plant community. This we shall be able to do, but, just as leaves, stems or roots may be so reduced or so modified that they are very difficult to recognize, so the structural parts of a plant community, while very readily recognized in many cases, are often so reduced or modified that their recognition is by no means easy.

121. **Technical Terms Applied to Plant Communities.**—Plant community is a non-technical term which may be applied to any assemblage of plants growing together in a natural habitat. Such terms as plant formation, plant association, consociation, society, and colony are technical terms which should be used only after the vegetation has been sufficiently studied so that its climatic and successional relationships are reasonably well known. In order to understand the structure and classification of plant communities it is necessary to be familiar with the technical terms used in describing them and, therefore, these terms will be defined in the following paragraphs.

It should be remembered that the kind of individual that we have been calling a plant community is really a biome, or biotic community. The animals are just as vitally important in its structural make-up as are the plants. Since we are studying plant ecology, however, and it is obviously impossible to cover the field of animal ecology at the same time, we will continue largely to disregard the animal constituents of the communities.

122. **Plant Associations.**—An individual, adult plant community is called a plant association. A plant association, therefore, is an individual of the third type, just as a plant is an individual of the second type, and a cell an individual of the first type.

As stated in the preceding chapter, there are in each plant association certain species of plants that are called dominant species because they in a large measure exert a controlling influence upon the environment. There may be only a single dominant species or there may be several and the other species that are growing along with the dominant plants are called secondary species. The associations are named from the dominant species. Thus we may speak of the sage brush association, meaning an association in which sage brush is dominant, or we may speak of an oak-hickory association (Fig. 83), or of a beech-maple-hemlock association. The scientific names of the dominant plants may be used instead of the common names, as for example, the *Artemisia* association, the *Fagus grandifolia-Acer saccharum* association, or the *Quercus-Carya* association.

The term, plant association, may be used in either the concrete or the abstract sense. For example, we may speak of a particular plant commu-

nity as an oak-hickory association in which case we would be using the term in the concrete sense, or we may say that the oak-hickory association is characteristic of the drier uplands throughout Indiana in which case we are using it in the abstract sense. This practice is, of course, no different than the common usage of the names of individual plants. In speaking of an individual tree, for instance, we may say that it is a white oak, using the name in the concrete sense, but if we say that the white oak is common in eastern Illinois we are using the same name in an abstract sense.

A plant association, viewed in the concrete, may be defined as a plant community characterized by its essentially homogeneous physiognomy and ecological structure and by its essentially homogeneous floristic composition, at least with regard to dominant species. In the abstract the association may be defined as a vegetation-unit characterized by an essentially constant physiognomy and ecological structure and by an essentially constant floristic composition, at least with regard to dominant species.



FIG. 83.—An oak-hickory association.

Physiognomy, as used in the above definitions, refers to the general outward appearance, or external morphology, of the association. This is determined almost entirely by the nature of the more prominent plants that enter into its structural composition and more particularly by the nature and abundance of the dominant species. Thus, when we refer to an association as deciduous forest, or evergreen forest, or prairie, we are speaking in terms of physiognomy.

Ecological structure includes all peculiarities of vegetation that are of ecological significance. It is to the plant association what morphological and physiological structure are to a plant. It takes into consideration not only those peculiarities that are visibly expressed in the growth forms of the plants but also those that are not so expressed. For example, the behavior of the various plants that make up the association in relation to various conditions of light, heat, water, soil, and other factors of the environment

would be included under ecological structure. Thus, when we speak of plants as being xeric, hydric, or mesic, or when we speak of them as being tolerant or intolerant of shade we are speaking of characteristics that come under the head of ecological structure but which may or may not be expressed in the growth forms of the plants. Furthermore, while physiognomy is concerned primarily with the dominant species only, ecological structure takes into consideration all of the secondary plants as well.

Floristic composition refers, of course, to the species of plants that make up the association, but it is the relatively common and conspicuous species, that is, the dominant species, that are of most importance.

123. **Consociations.**—A consociation is a morphological part of a plant association and is characterized by having a single dominant species (Fig. 84). There are as many consociations in each association, therefore,



FIG. 84.—Yellow pine consociation in a yellow pine-douglas fir association. (Photograph by A. G. Varela. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

as there are dominant species. Theoretically there is no reason why there should not be some associations with but one dominant species. In such a case the single consociation would be coextensive with the entire association. Practically, however, all associations have several dominants. In many cases the dominant species are mixed throughout the association and therefore the consociations are mixed and are coextensive with the association as well as with one another. In all of these cases, however, there is no practical reason for recognizing consociations at all and it is probably better, on the whole, not to do so. The recognition of consociations becomes of value, however, in case a part of an association is dominated by a single species to the exclusion of other dominants. For example, in an upland oak-hickory association in which the dominant species are white oak, black oak, and shag-bark hickory, we may find a portion of the community in which the white oak is the only dominant that is present, or the only

one that is present in sufficient numbers to have any real share in the control of the community, and it becomes convenient in such a case to speak of this morphological part of the association as a white oak consociation.

It should be understood that when we say a consociation is characterized by a single dominant we do not mean that it consists of the dominant species only. It consists of the dominant species and all of the secondary species that occur along with the dominants. That is, just as an association is made up of the dominant and secondary plants that are growing in the community, so the white oak consociation mentioned above would consist of all of the plants that were living in that part of the association dominated by white oak alone.



FIG. 85.—A spring beauty society in a forest association. (Photograph by A. G. Eldredge.)

124. **Faciations.**—Some associations have as many as ten or more dominants. In such cases there are usually portions of the association that are characterized by the grouping of dominants. That is, because of slight differences in environmental conditions, various combinations of two or more of the several dominants may occupy certain areas within the association. Such morphological parts of the association are called faciations. They may be characterized by any number of dominants above one and below the total number in the association.

125. **Societies.**—A plant society is a morphological part of an association characterized by one or more subdominant species (Fig. 85). A subdominant species is one that exerts a measure of control over a portion of an association where, of course, the environment is already controlled by the true dominants. It is thus a dominance within a dominance. More often it is the aspect rather than the environment as such that is controlled by the subdominant species. The growth habits of the subdominants are ordinarily different from those of the dominants. For example, in a forest, where the dominant species are trees, the subdominant species

are shrubs, herbs, or cryptogamic plants, and in a prairie, where the dominant species are grasses, the subdominants are herbs or low shrubs.

Three kinds of plant societies are ordinarily recognized. The first of these includes what are called aspect societies. These represent the commonest and most important type of society. They are ordinarily composed of subdominant herbs and they become conspicuous only during a certain season of the year, usually when they are in flower. Thus in a deciduous forest one may find in early spring a spring beauty (*Claytonia virginica*) society or a blue-eyed Mary (*Collinsia verna*) society, either of which may control the aspect or appearance of a portion of the association very completely during a few weeks while the flowers are in bloom. By midsummer this same area may be occupied by a wood nettle (*Laportea canadensis*) society. Likewise in a desert community there are frequent aspect societies dominated by California poppies or lupines or other annual or perennial



FIG. 86.—A bottomland forest associes in southern Illinois.

herbs which come into bloom during or immediately following a rainy season. In a prairie association some of the societies may completely mask the dominant grasses for a time. This is especially true of some of the late summer and autumn societies that are composed of subdominant, coarse herbs of the composite family.

The second kind of society that we may recognize is the layer society. In a forest very definite layers in the vegetation are reconizable. These are usually the tree layer, the shrub layer, the herb layer, and the cryptogamic layer. Societies may occur in any of these layers except the tree layer. Every aspect society, of course, occurs in one or another of these layers and so might be called a layer society. There are some societies, however, especially in the shrub and crytogamic layers, that are evident at all seasons and these are best spoken of as layer societies. There is also in every association a subterranean layer and this undoubtedly contains societies, especially of bacteria, but it is not well enough known to merit discussion.

The third type of society is represented by cryptogamic societies. These, again, are often seasonal and so might be called aspect societies, and they

are also layer societies. They are sufficiently distinct, however, to merit separate classification. The subdominants are usually mosses, liverworts, lichens, or, sometimes, fungi.

Societies are usually smaller and of a lower morphological rank than consociations, but a society is not a part of a consociation in the sense that the consociation is a part of the association. It is rather a part of the association, just as the consociation is, and a single society may extend over portions of more than one consociation.

126. **Climax and Seral Communities.**—The fully mature plant associations of any climatic region represent the most mesic vegetation that can be supported by the climate of that region. For this reason the mature communities are called climax associations. Often the majority of the communities in any region are not climax but represent one or another of the developmental stages of the climax communities. These may be called seral communities from the series of stages that lead from bare area to climax.

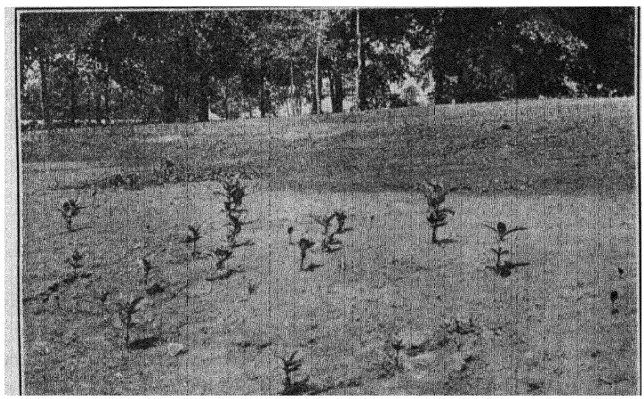


FIG. 87.—A pigweed colony on a bare area created by man.

Most ecologists prefer to use two distinctive sets of terms when dealing with climax and seral communities. Thus the terms association, consociation, faciation, and society are applied only to climax communities while corresponding terms with different endings, namely, associes, consocies, facies, and socies are applied to seral communities. These seral terms have the same relation to the climax terms as the word boy has to the word man. Obviously, neither the seral nor the climax terms should be used until a community has been sufficiently studied so that it is known whether it is a climax community or not. Until such study has been made the vegetation should be referred to simply as a community.

A colony is a small group of plants occurring on an otherwise bare area (Fig. 87). It, therefore, is a morphological part of an associes in a very young stage of its development. The term family is sometimes applied to such a morphological part of a very young community when it is composed of plants belonging to a single species and especially when the plants are all descended from a single ancestor. Since family is used in taxonomic

botany in an entirely different sense its use here is unfortunate and it seems better to call all of these parts colonies whether they are composed of one or more than one species.

A colony is usually easily recognized because it occurs on an otherwise bare area. However, a colony is not necessarily of small extent. An entire abandoned field may be occupied by a colony of Russian thistles and a field of corn or of any other crop plant may properly be considered a colony. More typical, however, is a colony of sand binding grass on a wind-formed sand dune, a colony of fireweeds on a burned forest area, or a colony of lichens or mosses on a rock surface.

127. **Plant Formations.**—In dealing with any group of objects, living or otherwise, it is often convenient, or even necessary, to classify them in some logical way. The particular kind of classification that is best depends largely upon the use that is to be made of it. For example, we may classify seed plants according to growth form, or on the basis of relation to water supply, or into natural families and orders, and each of these classifications has valuable uses.

There has been a considerable amount of discussion and disagreement among ecologists concerning what is the best scheme of classification of plant communities. If, however, we recognize that plant communities are individuals we should be able to classify them in any way that may suit our purpose, just as we do in the case of individual plants, without being subjected to undue criticism.

One of the most used as well as most useful of the methods of classifications is that of grouping the plant associations into plant formations. A plant formation consists of all of the associations within a climatic region. Since it is a product of the climate and is controlled by it all of the component associations present similar physiogonomies and have similar climatic requirements. For example, all of the deciduous forests of the eastern portion of the United States are considered as belonging to one formation although the various deciduous forest associations differ from one another considerably floristically. Likewise, the various grassland associations of the central United States may be grouped along with the bunch grass association of California and that of the northern portion of the Great Basin into one grassland formation.

Unfortunately it cannot be said that all ecologists agree that the above conception of plant formations is the correct one. Many consider the formation as the individual of the third type and the associations as morphological parts of the formation. It seems more logical, however, to consider the formation a group of individuals rather than a single organic entity. The pinyon-juniper woodland of the western states, for example, is all considered as belonging to the same formation but there is a pinyon-juniper community in the Chisos Mountains of southern Texas, another in northern New Mexico, and still others in several other western states. These are all separate, individual plant associations and not parts of a single individual but they may all be grouped together into one woodland formation.

128. **Successional Series of Communities.**—The vegetation of a region cannot be thoroughly studied without taking into consideration the dynamic or developmental phenomena. For this reason it is necessary sooner or later to classify the plant communities according to their genetic

relationships. This is often much more difficult than classifying them according to formations because it involves determining the relative maturity of each community and this frequently cannot be done by observation alone.

The phenomenon that furnishes a basis for a genetic classification of plant communities is plant succession. This process has been briefly outlined in Chapter XVI and will be discussed in more detail in Chapters XVIII and XIX. The development of a climax association from its beginning on a bare area results in an orderly sequence of communities ,each member of the series being replaced by a more mature community until the climax is reached. This is brought about through a progressive change in the habitat due largely to the reactions of the vegetation upon the environment. All of the communities concerned in the development of a climax from beginning to maturity may be grouped together into a successional series or, as it is sometimes called, a sere. Usually in every region some examples of all of the developmental stages may be found so that by careful study it is possible to group them in their proper genetic relationships.

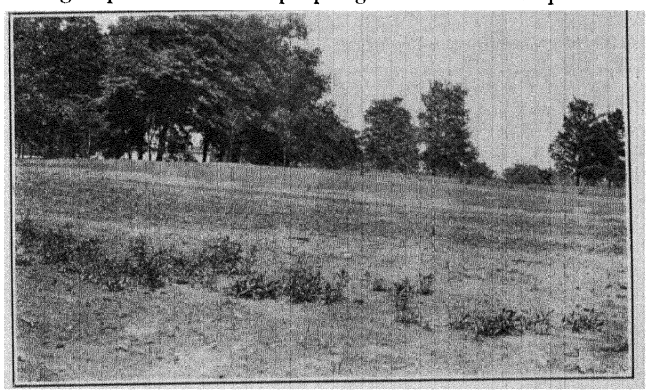


FIG. 88.—Ruderal plants on a secondary bare area. The first stage of a xerarch secondary sere.

Several types of successional series or seres may be recognized on the basis of their origin. A sere always starts on a bare area. A bare area may be either primary or secondary. A primary bare area is one which has not supported plant life before and so contains no plant parts or remains, either living or dead. The substratum of a primary bare area is usually sand, rock, or water. A secondary bare area, on the other hand, is one on which the plant community has been destroyed by one means or another. On such an area there is almost certain to be some humus and there may be seeds or other propagating organs that are alive. Any bare area is almost certain to be either wetter or drier than the habitat of the climax association. If it is wetter than the climax the succession will in general progress from hydric roward mesic. Such a successional series is said to be hydrarch. On the other hand, if the bare area is drier than the climax the succession progresses from xeric toward mesic and the successional series is said to be xerarch. A successional series or sere that starts on a primary sand area

is called a psammosere, one that has its origin on bare rock is called a lithosere, one that starts in fresh water is called a hydrosere, and one that starts in salty water is called a halosere. These facts lead to the following classification of seres.

Primary seres:	Secondary seres:
Hydrarch:	Hydrarch
Hydrosere	Xerarch
Halosere	
Xerarch:	
Psammosere	
Lithosere	

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CHAPTER XVIII

PLANT SUCCESSION

PLANT succession is a universal process by which all plant associations develop from beginnings on bare areas to maturity. As a general rule succession is from xerism toward mesism or from hydrism toward mesism. This is necessarily true because the mature, or climatic climax, vegetation is the most mesic that the climate can permanently support. There are some exceptions to the general rule, however. For example, in a region where the climax is a xeric type of vegetation, a sere that starts in water, as at the edge of an ox-bow lake or other inland depression, may develop progressively from a hydric condition to the xeric climax but in so doing it would necessarily pass through a mesic stage so that the last part of the sere would be from mesism toward xerism. We may say, therefore, that developmental plant succession always proceeds toward the climax and usually, though not necessarily, toward mesism.

More often, when succession is away from, rather than toward, mesism it is also away from the climax and is destructive rather than developmental in nature. For this reason it is necessary to distinguish between development and succession, or rather between developmental succession and succession that is not developmental. Succession that is not developmental is in general due to some change in the habitat that makes it less mesic. Such a change may take place rapidly or it may take place very slowly. In any case it is destructive in its effect since it cuts back the association to a younger stage. It is comparable to cutting back a tree, such as a willow, and so making a shrub of it. If such a willow tree, after it is cut back, is left undisturbed it will proceed at once to grow up again into a tree. Likewise, when a plant association is cut back to a younger stage by some means and then the cause ceases to act, developmental succession begins at once and proceeds toward the climax. The cutting back process, or succession away from the climax, has been called retrogression by some ecologists. Over-grazing, which has a tendency to make a habitat more xeric by destroying part of the living plant cover and preventing an accumulation of litter, is a very common cause of retrogression in many parts of the United States.

129. **Initial Causes of Succession.**—A sere always starts on a bare area. Therefore, the causes of bare areas are the initial causes of succession. Bare areas may be produced in a variety of ways. For example, erosion by the action of water may produce an area that is entirely without plants (Fig. 89). This frequently takes place at the upper end of a ravine or along a stream bank. Excellent examples of this type of erosion may be seen in the "bad-land" regions of North and South Dakota. In some regions ice is even more important than liquid water as an agent of eroison. This is true especially where there are glaciers. The ice mass of the glacier usually grinds up and removes all plants and plant parts as well as the upper layers of the substratum so that with the later retreat of the ice large areas of virgin soil or rock are laid bare. Sometimes when the water of a pond or lake freezes the expansion that takes place causes the ice to push against the shore and bring about erosion which results in bare areas. Wind is also

an important agent of erosion, especially in regions of sandy soil where it may produce moving sand dunes or may dig out depressions in the sand known as "blow-outs." Gravity may produce a crumbling or slipping of land masses, bringing about land slides which result in bare areas.

Deposit is, is a sense, implied when we speak of erosion, since materials removed from one place must eventually be deposited somewhere else. However, as an agent for the production of bare areas, deposit is quite distinct from erosion. Running water may build flood plains, and sand bars may be built in a similar way by waves and tides. Wind, glaciers, and gravity are all agents of deposit since they must deposit the materials which they have moved by erosion. Volcanic dust is sometimes carried by the wind and deposited in such quantities that existing vegetation is buried and a bare area produced. Lava flows and other volcanic deposits



FIG. 89. A bare area of shale produced by the erosive action of water.

form bare areas in the vicinity of their source. The water from hot springs and geysers often forms deposits of considerable extent. Water from hot springs is often heavily charged with lime and this is deposited as travertine. Rock Island in Utah Lake near Provo, Utah, was built up entirely by deposits of travertine from hot springs and extensive terraces in Yellowstone National Park have been built up by the same means. The typical deposit from the hot water of geysers, on the other hand, is siliceous sinter or geyserite. Both travertine and geyserite are rock and the successions that take place on them are similar to those on other types of rock.

The elevation or subsidence of a land mass, if great enough and rapid enough, will produce a bare area. There are also many climatic and biotic factors that may produce bare areas, though these are, for the most part, secondary rather than primary bare areas. For example, a drought may be severe enough to kill all vegetation on an area, a wind storm may destroy

a forest, a snow slide may destroy the vegetation on a mountain side, a hail storm or a late frost may kill herbaceous plants, or lightning may start a fire which will destroy a forest (Fig. 90). In arid regions evaporation may cause a pond or lake to completely disappear and so expose a bare area of soil. Man is the most destructive of the biotic factors and destroys vegetation over the largest areas (Fig. 91). Other animals such as ants or prairie

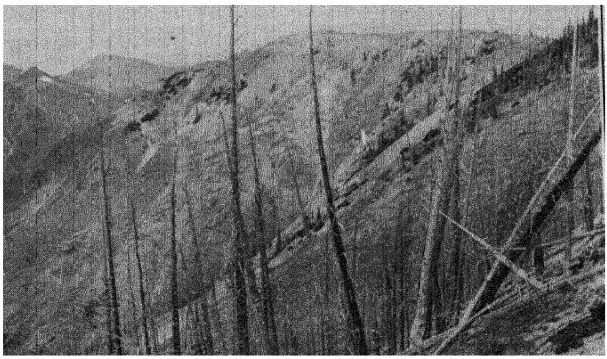


FIG. 90.—A mountain side on which the forests have been largely destroyed by fire

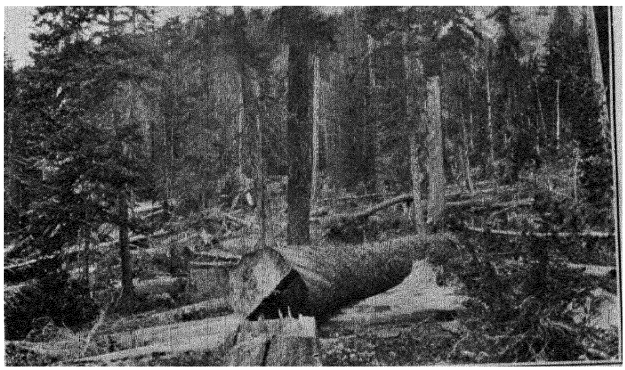


FIG. 91.—A forest of spruce and pine showing the destructive activity of man acting as a biotic factor.

dogs often destroy the plant life of small areas. Parasitic plants such as the dodder or a disease-producing fungus may become so abundant as to completely destroy the plants on a limited area.

Bare areas may be classified as sand, clay-gravel, rock, and water. Sand consists essentially of disintegrated rock. It is usually composed largely of grains of quartz and silicates but may have other minerals and even organic matter mixed with it. A clay-gravel sub-stratum also consists of

disintegrated rock. The soils classed under this head are extremely variable since they consist of varying proportions of sand, gravel and clay. Bare rock also varies greatly, both in hardness and in chemical composition. Water is of course always the same in chemical composition but it varies in the materials that are in solution in it and also in depth.

130. **Continuing Causes of Succession.**—After a sere is once started there are various factors that cause it to continue. A change of climate in a region changes the climax vegetation and so brings about a succession of plant communities. Climatic changes are usually so slow, however, that, while they are valuable in the interpretation of the past history of vegetational changes, they are of little importance in the study of current seres.

On every part of the earth's surface that is not already level there is a tendency for the action of physiographic factors to result in a leveling of the land. This is brought about largely through erosion from the higher places and deposit in the depressions. These processes are influential in causing plant successions to continue because they make the habitats more mesic.

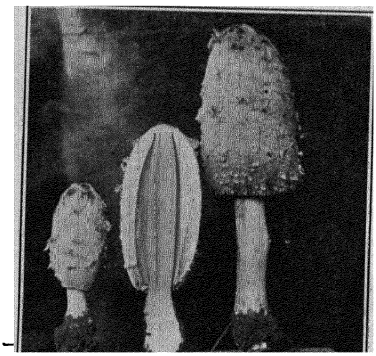


FIG. 92.—*Coprinus comatus*. One of these mushrooms may produce more than 5 billion spores.

By far the most important causes of succession, however, are biotic. Each plant community in a sere changes the environment in such a way that the habitat gradually becomes better suited to the component species of the immediately succeeding stage and less suited to the existing one. The processes that are concerned in the biotic causes of succession may be grouped under three headings; namely, invasion, competition, and reaction. Invasion means the movement of plants from one area into another and their colonization in the latter. The movement from one area to another constitutes migration and the colonization of plants in a new home is known as ecesis. The various means by which plants migrate were discussed in Chapter XVI. Migration, however, must be followed by ecesis if the invasion of the new area is to be successfully completed.

Most plants produce a great excess of disseminating bodies. A single pigweed (*Amaranthus retroflexus*) has been known to produce 2,350,000 seeds. A single specimen of the pasture mushroom (*Agaricus campestris*), according to an estimate based on results obtained with a counting appara-

tus, may produce 1,800,000,000 spores, while a large specimen of the shaggy mane mushroom (*Coprinus comatus*)(Fig. 92) may produce 5,240,000,000 spores. Some conception of this immense number may be obtained from the statement that, although these spores are microscopic in size, if the number from the above shaggy mane mushroom were placed end to end they would extend a distance of about 41 miles. But the world is full of plants now, so that, on the average, there is a chance for only one disseminule from each plant to grow. Thus, the great waste of seeds and spores through migration to unfavorable places is not a serious matter. The whole surface of the earth is bombarded with seeds and spores of innumerable kinds each year but after migration is completed ecesis can take place only under favorable conditions.

Although migration often proceeds over great distances the proximity of the young community to parent vegetation, or feeder vegetation as it may be called, is an important factor in controlling the rate at which invasion may proceed. As a rule the greater numbers of seeds and fruits fall within a few hundred feet of the parent plants so that the greater the distance of the feeder vegetation from the new area the less likely is migration to it to be attained. For this reason certain stages in the succession, those for which feeder vegetation is near by, are likely to develop much more rapidly than those that must be fed from a greater distance. Furthermore, the topography of the intervening area indirectly influences migration. High hills or a forest may act as barriers which more or less effectually prevent migration where it would take place quickly over a level, unbroken area.

Migration must be followed by ecesis before invasion can be said to have been completed. Ecesis is the establishment of a plant in a new home after it has migrated. It consists of three processes, germination, growth, and reproduction.

In the great majority of seeds there is a period of arrested development after the embryo has been formed during which the seed is said to be in a state of dormancy. At the end of the dormant period growth is resumed and the seed is said to germinate. Dormancy and germination are also characteristic of other propagating bodies such as bulbs, tubers, and spores. However, there is a great deal of variation among the various species of plants in the length of the period of dormancy. In viviparous plants, such as the mangrove, the development of the embryo is continuous from the beginning. There is no dormant period and, therefore, no germination, properly speaking. Some seeds, such as those of cottonwood and willow, can remain dormant only a few days or, at most, a few weeks and if they do not find conditions favorable for germination during this time they permanently lose their ability to germinate. Some seeds, such as those of cultivated oats, will germinate as soon as produced, under favorable conditions, but will remain dormant for months if artificially stored and then germinate readily when placed under favorable conditions. Wild oats, on the other hand, normally lie dormant until the following spring after their production no matter what the conditions of their environment may be. Seeds of certain mustards and plantains have been known to lie dormant in the soil for twenty to forty years before finally germinating and the reason why some farmers believe that under certain conditions wheat will "turn to chess" is that the seeds of chess, or cheat, may lie

dormant in the soil for years and then, when conditions are favorable for chess but not for wheat, may germinate and grow in a field where wheat was planted.

The most common factors of the habitat that cause dormancy of seeds are unfavorable temperature and lack of sufficient water. There are other factors, however, such as enzymes, light, and certain nitrogenous compounds, that may be important in some cases. Some seeds, however, such as those of certain mints and legumes, have seed coats that are so impermeable to water or to oxygen that they can never germinate until the seed coat is made permeable either by natural deterioration or by some means of artificial scarification. The latter can usually be done very quickly by the use of acids or by some mechanical means while the former may require a period of several years.

After a seed has germinated and the embryo has developed sufficiently to free itself from the seed coat the plant is said to have reached the seedling stage and this is likely to be the most critical period in its life cycle. Seedling mortality is often exceedingly high. Seedlings may be destroyed by insects, birds, rodents, or larger animals; they may be destroyed by excessive competition; or they may be killed by drought or by low temperatures. Often the entire crop of seedlings of woody plants may be killed by desiccation and this phenomenon may be repeated several years in succession. This is attested to by the fact that where young trees are developing it is often found that they are all of the same age or that only a few age classes are represented, indicating that seedlings survive only when there is an unusually favorable year.

If a plant survives the seedling stage it is very likely to grow to maturity. The size that it finally attains and the rate at which it grows depend upon various environmental factors, such as water, light, and temperature, as well as upon inherited characteristics.

The final process in ecesis is reproduction. Obviously annual plants could not endure more than a single season unless they were able to reproduce and perennial plants, while they might persist for several or many years, could not be said to be wholly successful in establishing themselves in a new area unless they could complete their life cycles by carrying on sexual reproduction. Therefore, ecesis can be said to be fully complete only when reproduction has been successfully accomplished.

Competition, the second process involved in the biotic causes of succession, is a universal characteristic of plant communities. It occurs whenever two or more plants make demands in excess of the supply, increasing as the population increases until the community approaches the climax in maturity and then decreasing. It can exist, however, only between plants that are more or less equal in their demands. There is no competition in this sense between a parasite and its host, nor between a tree and an herb, but there may be competition between two trees or two herbs or between a tree seedling and an herb. Those species which compete in any way are called competitive species while those which can live in the same community without competing are called complementary species. In the younger stages of the succession competition is largely confined to the soil where the roots compete for water or nutrients or both. As the population increases, however, competition may be as acute above the surface of the soil as below it. The competition that takes place in the air is largely for light.

In a forest there is an apparent root competition for moisture between the trees and the herbaceous vegetation and tree seedlings. Where the forest canopy is very dense there is often practically no undergrowth and this was formerly attributed to the inability of plants to grow in the dense shade. It has been found, however, in some places, that by digging a trench around a small area in such a forest in such a way as to cut off all roots entering the area an abundant undergrowth may develop, thus proving that lack of soil moisture is more important than lack of light in such a case. This, however, is somewhat different than competition between plants that make similar demands upon the environment. The trees, as the dominant plants, are in control and the undergrowth never has a chance to compete with them on anything like equal terms. Tolerance, or the ability of plants to grow under a forest canopy, is a complex phenomenon which is dependent upon several factors, the most important of which are probably the light and moisture relations It is not, however, so much a question of competition as of enduring the conditions imposed by the dominant trees.

Competition may take place between individuals of the same species or between those of different species. In either case it is of great importance both in the development of native vegetation and in crop production. When a large number of seedlings are growing together on a small area there is often intense competition for light. The difference of only a small fraction of an inch in height between two seedlings may determine which will succeed and which will fail to grow to maturity. The first leaves of the taller seedling will overshadow those of the shorter one and this will immediately give the one a decided advantage over the other in the amount of photosynthetic activity and, therefore, in the rate of growth, and, as other leaves are formed, this advantage will increase. If the seedlings belong to the same species or to the same growth form it is likely that the one that started at a disadvantage will soon die but if one is a tree seedling and one an herb seedling both may eventually reach maturity since the tree seedling will soon become dominant and the herb seedling subordinate and competition between the two will cease.

Competition is an extremely important consideration in the growing of crop plants since if too many plants are grown on a given area the actual yield will be reduced because of too much competition while if too few plants are present the yield will again be reduced because the available water, light, and nutrients will not be used to greatest advantage. The most important reason for the cultivation of growing crop plants is to prevent the development of weeds which would compete with the crop plants.

Reaction, the third biotic cause of succession, refers to the effects of the plants upon the habitat. These effects are quite variable in nature. As soon as the first plants appear on an area the soil-forming reactions begin. The weathering or disintegration of the rock, if the substratum is composed of rock, is hastened by the excretions from the plants and by the growth of roots in cracks and crevices. Wind-blown materials and water-borne detritus are caught by plants and added to the soil. Dead plant bodies or parts of plants are also accumulated and become a part of the soil. The structure of the soil is also changed by the plants, in part by the same reactions that produce soil. The addition of humus, for example, decreases the average size of the soil particles and usually has a tendency to make the soil more mellow. Sometimes the addition of humus results in making

the soil more compact. The precipitation of the humus substances by the soil salts may even produce a "hard-pan" layer which is impervious to water and even to roots

The reactions which affect the water content of the soil are extremely important. As a general rule, during the entire course of the succession the soil-water content is either increasing or decreasing. These effects are brought about indirectly through the building-up of soil, the increase in shade, etc., or directly through transpiration. In the case of a xerarch succession the soil-water content increases while in a hydrarch succession it decreases so that in either case development is toward mesism. The nutrients that are in solution in the soil water are also modified by the reactions of the plants. They may be increased through the addition of humus by leaf fall or by other means or they may be decreased through the plants being eaten by animals or being removed from the land by man. The soil organisms, both parasites and saprophytes, are usually increased both in number of individuals and in number of kinds as the plant community develops.

The reactions above the surface of the soil usually increase the amount of shade and the relative humidity of the air and decrease the temperature and the wind velocity. The local climate is often actually changed by the development of climax vegetation, especially if the climax is a forest. This is brought about by the large amount of water that is transpired by the plants. This increases the rainfall and results in a somewhat more humid climate. The number and kinds of aërial organisms are affected in ways quite comparable to those of the soil organisms.

The reactions of a plant community as a whole are more important, in a way, than the reactions of individual plants because they are more effective. The leaves that fall from an isolated tree are likely to dry up and blow away but the leaves from a similar tree in a forest remain to form a mulch and later humus. The shade under the isolated tree is intermittent because of the changing position of the tree with respect to the sun but the shade under a similar tree in a forest is continuous because of the shade produced by neighboring trees. Thus, while the reactions of the community are the resultant of the reactions of the individual plants, it is usually much more than the mere sum of these reactions.

The result of all these various reactions is that the vegetation is kept in a dynamic state and succession proceeds toward the climax. Vegetation is never entirely stable, but, since the climax association is the most mesic community that the climate will support, it cannot become any more mesic and as compared to the earlier stages of the sere, it is relatively stable and will persist indefinitely unless there is a change of climate or the community is destroyed by one means or another.

Successions that are brought about by the reactions of the plants themselves are sometimes called autogenic successions while those caused by climatic or physiographic factors are called allogenic successions. It is probable that a succession is never entirely autogenic or entirely allogenic but it is frequently possible to recognize that a given case is largely the one or the other.

131. **Pioneer Stages of Succession.**—The environmental conditions on a bare area are extremely difficult for most plants. There is no protection from the light and heat of the sun during the day and nothing to check

radiation at night. Also there is no protection from wind, and, therefore, evaporation is very rapid. Moisture conditions are extremely variable. After a rain there may be pools of water on rock or soil surfaces but these may dry up quickly and the substratum become very hot and dry. There is usually a complete lack of humus and many of the essential mineral salts may be lacking, or present in an unavailable form. The character of the

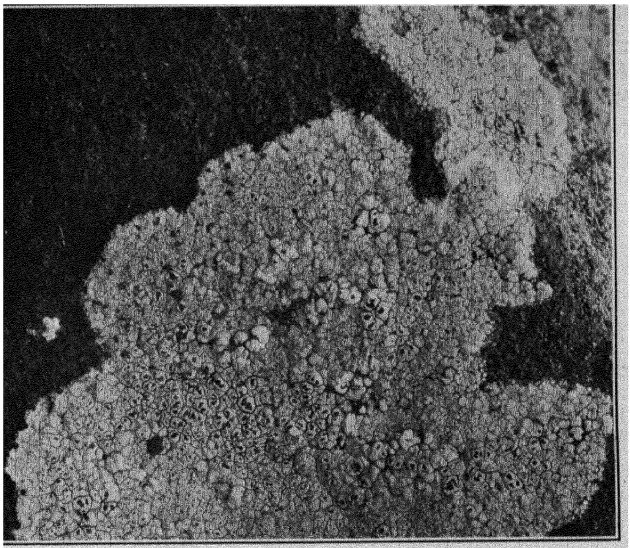


FIG. 93.—A crustose lichen. (Photograph by Bruce Fink.)

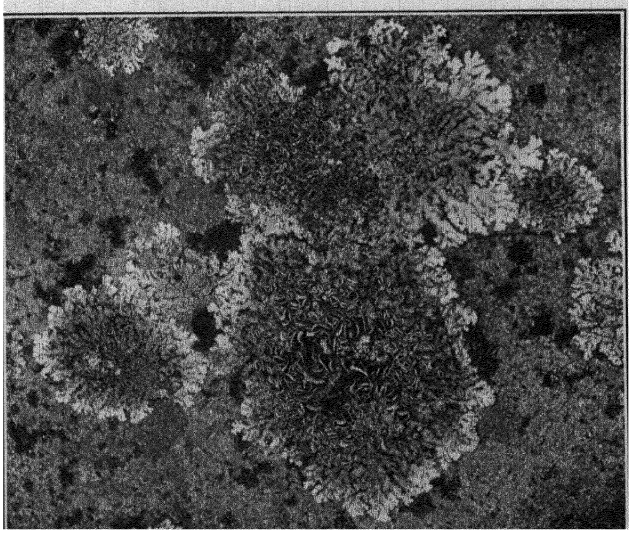


FIG. 94.—A foliose lichen. (Photograph by Bruce Fink.)

surface is often such as to make it very difficult for plants to gain a foothold, either because of its hardness or its instability.

Due to these extremely severe conditions the pioneer plants in all xerarch successions are very xeric. On bare rock the first plants are lichens and mosses. Lichens are divided into three groups based on their growth-forms. These are crustose, foliose, and fruticose lichens. The crutose lichens (Fig. 93) are so-called because they form thin crusts on the surface of the substratum. They are probably the most xeric of all and are often the first to appear on a rock surface. The foliose lichens (Fig. 94) are more or less leaf-like. They are as a rule somewhat less xeric than the crustose forms but they too may be pioneer plants on a rock surface along with xeric mosses. The fruticose lichens (Fig. 95) are upright forms and usually

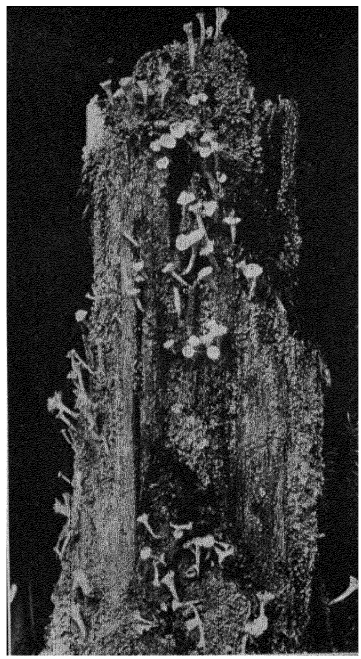


FIG. 95.—A fruticose lichen. (Photograph by Bruce Fink.)

appear later in the succession. On sand or clay-gravel the pioneer plants are ordinarily annual xeric herbs. The pioneer plants of a hydrarch succession are, of course, hydric, often floating or submerged, plants, but even here the conditions are much more severe than in later stages of the sere.

132. **Intermediate Stages of Succession.**—The intermediate stages include all of the stages between the pioneer community and the climax. In the pioneer community there are relatively few species and few individuals and the community is, therefore, more or less open because the soil is not entirely occupied. The presence of the pioneer plants, however, by checking the wind velocity, producing shade, adding humus to the soil,

etc., makes the habitat less extreme and prepares it for the invasion of other species. The number of individuals increases from the pioneer stage to the climax and the community becomes less and less open. When the soil becomes fully occupied by plants the community is said to be closed. The number of species also increases until the climax is nearly reached and then it decreases. The duration of the pioneer stages is relatively short and the duration of the intermediate stages increases until the climax stage is reached. This is relatively permanent.

The increase in population as the sere progresses is possible because the reactions of the plants are constantly making the habitat more mesic and less severe. The first plants following the pioneer species are likely to be herbaceous perennials. After the herbaceous plants have rather thoroughly occupied the soil, shrubs usually begin to appear and there develop one or more definite shrub stages. This is likely to be true whether the sere is xerarch or hydrarch, though the kinds of shrubs will be different in the two



FIG. 96.—A young tree stage of a hydrarch succession. Willows and soft maples.

cases. Trees may begin to come in at about the same time as the shrubs or soon after, and they increase in numbers until they become abundant enough to constitute a tree stage. In a xerarch succession the first trees may be conifers or they may be such xeric trees as the black and the white oaks (*Quercus velutina* and *Quercus alba*) and the hickories (*Carya ovata*, etc.). In a hydrarch succession the first trees are likely to be willows (*Salix*) and cottonwood (*Populus deltoides*) (Fig. 96). These first trees are followed by increasingly mesic species until the climax is finally reached.

133. **The Climax Stage of Succession.**—When the habitat becomes as mesic as is possible under the existing climatic and physiographic conditions the dominant species of the climax association appear and in time gain control of the environment. The climax association is the mature, adult organism of which the pioneer and intermediate communities are developmental stages. The climatic climax is the same throughout a climatic region whether it develops through a xerarch or a hydrarch succession. The course of development of a sere and its ultimate climax can usually be predicted, therefore, with perfect definiteness if the climax of the region is known.

The dominant species of the climax association exercise such a complete control over the environmental factors such as light, space, food materials, etc., that they prevent the entrance into the community of many other species of plants. For this reason, while the number of individuals in the climax community may be as great as in the intermediate stages, the number of species is ordinarily much smaller than in some of the earlier stages. The adjustment between the dominant species of a climax association and the environment approaches so near to perfection that the community is relatively stable and is likely to persist as long as the climatic and physiographic conditions remain unchanged.

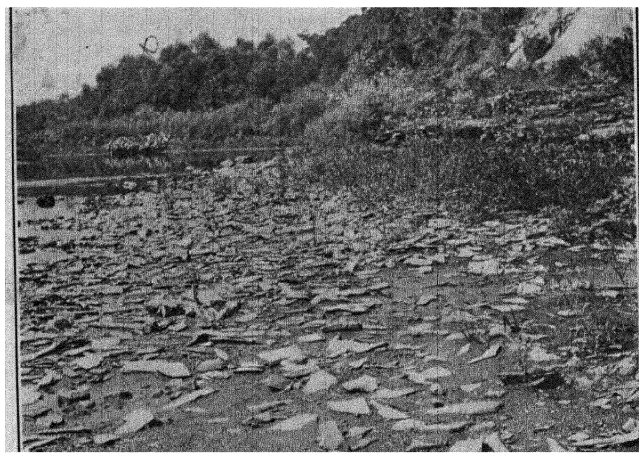


FIG. 97.—A shingle beach. Plant succession is very greatly retarded in such a place because of the unstable nature of the substratum and frequent flooding.

134. **Factors Which Modify the Typical Succession.**—There are various topographic, physiographic, and biotic factors which modify the typical or ideal succession. Most often these factors affect only the rate; either accelerating or retarding the succession. In some cases, however, the succession is reversed temporarily so that its direction is away from, rather than toward, mesism, a phenomenon that is comparable with the cutting back of a small tree to a shrub stage. Such a shrub if left undisturbed under ordinary conditions will develop again into a tree and in a comparable way the plant community which has been cut back by one means or another will, as a rule, develop again toward the mesic climax.

A topographic factor that influences the rate of development is the degree of slope. As a rule, the more nearly horizontal and level an area is the more rapid can the succession take place. With an increasing angle of slope the succession is more and more retarded and if the slope approaches too near the vertical no development can take place at all. The direction of slope is also of some importance in this respect. In a dry, hot region the vegetation of a north-facing slope will usually develop more rapidly than on a south-facing slope while in a cool, moist climate just the reverse is true.

An extremely important physiographic factor is erosion. This may either hasten or retard development or it may destroy vegetation and so put the sere back to a younger stage. Deposit is more likely to hasten than to retard a succession, though it may do either (Fig. 97).

Parasitic plants or animals may retard a succession by destroying certain kinds of plants or they may cut the sere back to an earlier stage, especially if they attack the dominant plants of the community. Grazing animals often produce similar effects. Man has, of course, caused very great modifications in successions over extensive areas, these changes being too numerous and far-reaching to be discussed here. Fire, which may be either a biotic or a climatic factor, is largely destructive though it may be only retarding in its effect.

135. **Past Successions Determined by Pollen Analysis.**—The determination of past successions by the pollen analysis method has become so important in recent years that it cannot be neglected by any student of ecology. The walls of pollen grains are of such a nature that when they become embedded in soil, and especially in the peat accumulations in bogs, they are often preserved unchanged for thousands or even millions of years. Furthermore, the pollen grains of the various kinds of plants are so characteristic that they can usually be readily recognized by microscopic examination. This is especially true of the pollen of wind-pollinated trees. Therefore, by observing the pollen that is present at various depths in the peat of a bog it is possible to determine what kinds of trees were growing in the vicinity of the bog at the time the peat was accumulating.

The technique that must be learned before one can successfully carry out pollen analyses differs somewhat with different workers. In general, however, the method is as follows. Samples of peat are collected at known depths by means of a soil sampler. Each sample is treated with a ten per cent solution of potassium hydroxide for 24 hours or longer, then is centrifuged and the clear liquid is decanted off. After the material has been stained with an organic dye such as safranin a bit of the concentrated liquid that remains with the centrifuged material is placed on a slide and, after drying, mounted in glycerin jelly. Usually from 100 to 150 pollen grains are counted and identified in each sample, and the numbers of each kind of pollen are recorded as percentages. These percentages are then plotted as bars of varying lengths on graph paper and the resulting graphic illustration is called a pollen spectrum.

Since it is presumed that the relative abundance of a particular kind of pollen in a peat deposit is an indicator of the relative abundance of the kind of tree that produced the pollen, a pollen spectrum may tell us when that kind of tree first appeared in the region under consideration, when it reached its maximum development and when, if ever, it began to decline. Although some valuable studies have been made of pollen found in some of the Tertiary deposits, the pollen spectra that are of greatest practical value in connection with studies of existing vegetation are those made from deposits formed since the end of the Wisconsin glaciation some 25,000 years ago. Such spectra not only give us a picture of the successions and climatic changes that have taken place since the end of the glacial period but they also help us to understand the origins of the present floras and the successions that are taking place at the present time.

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CHAPTER XIX

TYPICAL EXAMPLES OF PLANT SUCCESSION

HAVING discussed plant succession in general in the preceding chapter we will describe in the present chapter some specific seres. Lack of space will not permit us to discuss the many different successions that are progressing in different parts of the world. We will therefore describe one typical sere for each of four general types of bare areas, sand, clay-gravel, rock, and water, and make brief mention of only a few of the better known modifications.

136. **Plant Succession on Sand.**—Sand areas are found in North America along the shores of the Alantic and Pacific Oceans, along the shore of Lake Michigan, in parts of the desert region of the southwest, in the sand-hill region of Nebraska, and in several other limited regions in the Mississippi Valley. We shall discuss the development of the beech-maple-hemlock association along the shore of Lake Michigan in Northern Indiana since this has been more thoroughly studied than any other sand succession.

An area of sand that is unoccupied by plants is exceedingly unstable. Sand which is thoroughly wet is not readily moved by the wind but after each rain the superficial layer quickly dries out and is then subject to being blown about by the wind. Any small object or an unevenness of the surface may serve as a slight check upon the wind and cause it to deposit the sand in a mound. This mound increases in size and becomes what is called a sand dune. Often the sand is more or less constantly being blown away from one side of such a dune and deposited on the opposite side so that the dune as a whole slowly moves with the wind and is spoken of as an active dune. Such a dune, while very dry at the surface, usually contains an adequate amount of moisture a short distance beneath the surface. There is usually an almost total lack of organic matter and the essential mineral elements may also be practically lacking or present only in unavailable forms.

Under these unfavorable conditions there are but a few plants that can gain a foothold. In the xerarch succession the most successful pioneer is the beach grass (*Ammophila arenaria*) (Fig. 98). This grass and the wormwood (*Artemisia*) (Fig. 99) seem to be the only plants that can grow to full maturity in pure dune sand. They have extensive root systems which are composed of slender, much branched roots and they grow better in pure sand than where organic matter is present. Along with these are often found the sand-reed grass (*Calamovilfa longifolia*), the sea-rocket (*Cakile edentula*), the puccoon (*Lithospermum canescens*), sometimes the false heather (*Hudsonia tomentosa*), etc.

The hydrarch succession usually starts in a shallow depression. The pioneer is usually either the baltic rush (*Juncus balticus*) or the cottonwood tree seedlings (*Populus deltoides*). The cottonwood is especially efficient in enduring partial burial in sand. The trees keep on growing upward as fast as the sand piles up around them so that a cottonwood dune may be built up where there was originally a depression. Where the rush is the pioneer the filling of the depression is likely to take place more slowly. Gradually, however, hydric grasses, sedges, and mosses come in and with

them, or following them, are such herbs as the water smart-weed (*Polygonum amphibium*), the marsh cinquefoil (*Potentilla palustris*), etc., and later such shrubs as the sandbar willow (*Salix longifolia*) and the button-bush (*Cephalanthus occidentalis*).

In the xerarch succession the soil is so unstable that although the *Ammophila* may check the movement somewhat it is not able to stabilize the



FIG. 98.—*Ammophila arenaria*, a sand pioneer, being replaced by *Arctostaphylos uva-ursi* in the foreground and *Juniperus virginiana* in the background. (Photograph by A. G. Eldredge.)

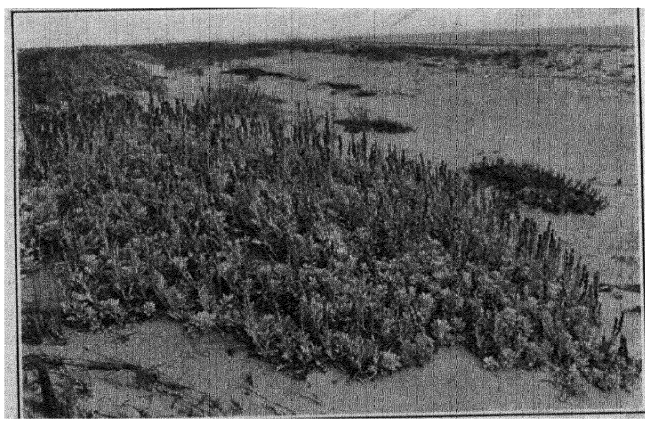


FIG. 99.—Wormwood (*Artemisia stelleriana*), a sand pioneer. (Photograph by A. G. Eldredge.)

dune entirely. It seems to grow best when sand is constantly being piled around it and as the dune advances the grass community moves with it, advancing in front and being torn out by the wind behind. The pioneer stage may be repeatedly formed and destroyed, therefore, and it is not until the dune gets far enough from the lake shore and the force of the wind is somewhat checked that the sand becomes less unstable, the pioneer plants die out, and the species of the intermediate stages begin to appear.

Some of the plants of the intermediate stages that appear rather early are the Solomon's seal (*Polygonatum commutatum* and *P. biflorum*), the bastard toadflax (*Comandra umbellata*), the bird-foot violet (*Viola pedata*), the dogbane (*Apocynum androsaemifolium*), the horse-mint (*Monarda punctata*), the blazing-star (*Liatris cylindracea* and *L. scariosa*), and some asters and goldenrods. Later some shrubs, woody lianas and trees begin to appear. The first trees are usually jack and white pines (*Pinus banksiana* and *P. strobus*). The herbaceous and shrub vegetation becomes abundant and is composed of a variety of species. Among the shrubs there are a number belonging to the heath family such as the bear-berry (*Arctostaphylos uva-ursi*), the shin leaf (*Pyrola elliptica*), and the aromatic wintergreen (*Gaultheria procumbens*).

Seedlings of oaks and other trees develop in this pine community and the next stage is a black oak community. The black oak is the dominant and sometimes almost the only tree. The evergreens disappear and are succeeded by such shrubs as the blueberry (*Vaccinium pennsylvanicum* and *V. vacillans*), various species of sumac (*Rhus*), the pin cherry and choke cherry (*Prunus pennsylvanica* and *P. virginiana*), sassafras (*Sassafras variifolium*), and the maple-leaved haw (*Viburnum acerifolium*). There are also many herbaceous plants such as goldenrod (*Solidago speciosa* and *S. hispida*), the milkweed and butterfly weed (*Asclepias syriaca* and *A. tuberosa*), the prickly pear (*Opuntia rafinesquii*), and the false Solomon's seal (*Smilacina racemosa* and *S. stellata*).

The black oak community may persist for a rather long time but is gradually replaced by a more mesic oak community in which the red oak (*Quercus borealis*) is a prominent dominant. Finally the habitat reaches the highest degree of mesism, a thick layer of humus has formed over the sand, the water-holding capacity of the soil has greatly increased, the evaporation rate has decreased, and the climax forest, dominated by the beech (*Fagus grandifolia*) and the sugar maple (*Acer saccharum*), appears and persists indefinitely unless destroyed by one means or another.

137. **Successions on Clay or Clay-gravel.**—The clay gravel successions that are best known are those that take place on glacial deposits. These have been studied in various places in the northeastern quarter of the United States and in southeastern Canada. The glacial deposits throughout these regions are very variable, some areas being almost pure clay and others consisting of more or less complex mixtures of clay, gravel and other materials. They are practically all occupied by plants at the present time so that opportunities for actually observing primary successions in the early stages are extremely rare. The best that are available for this purpose at present are the striplands of Illinois, Indiana and Ohio where the vegetation has been completely destroyed in the process of surface coal-mining.

As a result of stripping the soil is left as bare alternating ridges and furrows, the ridges varying from 3 or 4 feet to 30 or 40 or more feet in height (Fig. 100). In many cases these areas are left undisturbed for a long term of years and their revegetation takes place without any artificial interference. In Vermilion County, Illinois, these striplands are mostly on bottomland areas along streams. Here the pioneer plants are usually annual and perennial herbs. In the bottoms of the furrows the knotweeds (*Polygonum aviculare* and *P. persicaria*) are often the dominant and sometimes the only plants. In the more shallow furrows the barnyard grass

(*Echinochloa crusgalli*) takes the place of the knotweeds or occurs along with them, and often scattered individuals of the giant ragweed (*Ambrosia trifida*) are present also. On the other hand, some of the deeper furrows, which lack adequate drainage, have water standing in them a greater part of the time. Here are found cat-tails (*Typha latifolia*) and occasionally water plantain (*Plantago alisma-aquatica*). Just above the water there is usually a zone of cocklebur (*Xanthium commune*).

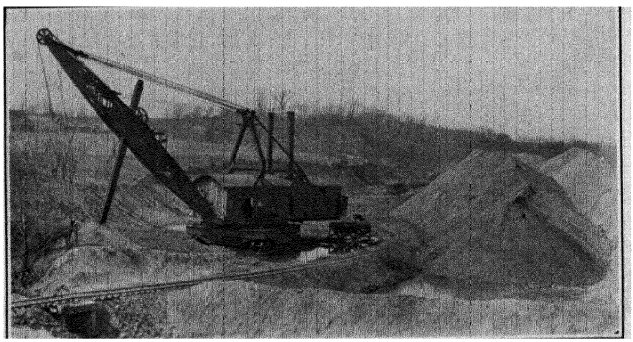


FIG. 100.—Creating a bare area. Striplands, Vermilion County, Illinois.

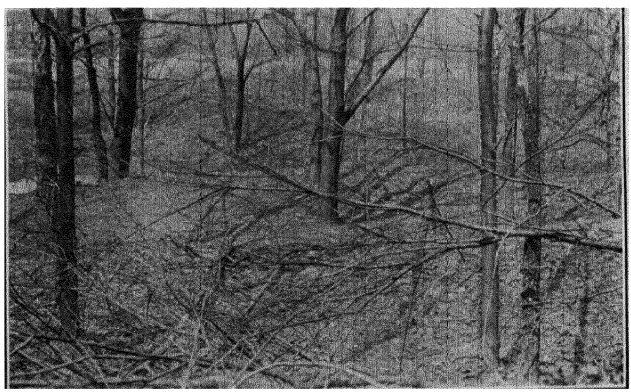


FIG. 101.—Mixed forest on striplands, Vermilion County, Illinois, twenty-five years after stripping.

The ridges present somewhat more variety in their floras, although some of them are occupied almost exclusively by sweet clover (*Melilotus alba*) which grows 7 feet high and so thick that it is difficult to walk through. Other ridges are covered with such plants as wild aster (*Aster ericoides*), sunflowers (*Helianthus hirsutus* and *H. decapetalus*), ragweed (*Ambrosia artemisiifolia*), evening primrose (*Œnothera biennis*), black mustard (*Brassica nigra*), and prickly lettuce (*Lactuca scariola*).

The first woody plants are usually willow (*Salix nigra*) and cottonwood, but this depends upon the proximity of communities from which these

plants may migrate, and sometimes the buttonbush (*Cephalanthus occidentalis*) and the soft maple (*Acer saccharinum*), the white elm (*Ulmus americana*), the green ash (*Fraxinus lanceolata*), and the sycamore (*Platanus occidentalis*) come in almost as soon as the typically hydric pioneers (Fig. 101). In any case they are sure to come sooner or later and are likely to be accompanied by honey locust (*Gleditsia triacanthos*) and such lianas as wild grape (*Vitis cordifolia*) and poison ivy (*Toxicodendron radicans*). The elm, sycamore, and honey locust are commonly the dominant species of the bottomland forest in this region and such a forest may become well established on stripland in twenty-five to fifty years after stripping (Fig. 102).

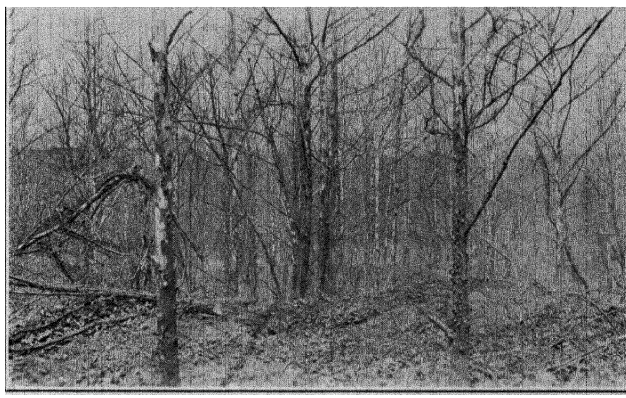


FIG. 102.—Sycamore consocies on stripland, twenty-five years after stripping.

A sere on an upland clay-gravel area in this same general region would start in much the same way as the xerarch succession on striplands, the pioneer plants being xeric annual and perennial herbs. These would be followed by a xeric shrub community dominated by such shrubs as the smooth sumac (*Rhus glabra*), the hazel (*Corylus americana*), and blackberries (*Rubus sp.*). The shrub stages would be followed by a xeric tree community in which the dominant species would be the black and the white oaks and the shagbark and the pignut hickories (*Carya ovata* and *C. cordiformis*).

In the tall grass prairie region, which includes a large part of Illinois and several states west of the Mississippi River, one of the dominant species of the climax community is the tall blue-stem grass (*Andropogon furcatus*). The xerarch succession here starts much the same as in the forest region, but the pioneer herbs are followed by the short blue-stem grass (*Andropogon scoparius*) and this in turn by the climax tall blue- stem association.

The hydrarch succession may be traced as it occurs in a slough. Here the bulrush (*Scirpus fluviatilis*) is at first the most abundant plant, though it may be accompanied by many other kinds of water plants. The bulrushes begin to die as the slough becomes drier through filling and are replaced by sedges (*Carex sp.*) which dominate the second stage. The sedges are followed by slough grass (*Spartina michauxiana*). Sometimes

the slough grass follows the bulrush directly without an intervening sedge stage. The slough grass is followed by blue joint-grass (*Calamagrostis canadensis*) and tall panicum (*Panicum virgatum*), or by panicum alone, which, in turn, is finally replaced by tall blue-stem.

138. **Successions on Rock.**—Areas of bare rock are relatively infrequent and of limited extent. They are for the most part rocks that have been exposed through erosion by water or by glaciers. Rocks vary greatly in hardness and this factor is very important in determining the rapidity with which the earlier stages of plant succession may take place. Rocks are classified as igneous, sedimentary, and metamorphic. Igneous rocks are those which were melted and have solidified by cooling. They are glassy or crystalline in character and are usually very hard. Granite is a familiar example. Sedimentary rocks are those which have been laid down under water by mechanical, chemical, and biotic processes. They are composed of more or less rounded and worn fragments, are seldom crystalline, and frequently are quite soft. The common sandstones, limestones and shales are sedimentary rocks. Metamorphic rocks are those which have been changed from igneous or sedimentary rocks, usually by heat and pressure. They are usually harder than the rocks from which they are formed. Marble, for example, is metamorphosed limestone and slate is formed from shale.

An area of very hard rock affords no available water for plants except from dew and rain. Soft and porous rocks, however, contain varying amounts of water and this may be a factor of considerable importance. The presence or absence of cracks and crevices also are important in their influence on the rate of weathering and on the establishment of certain kinds of plants. The slope of rock surfaces may vary all the way from horizontal to vertical and this leads to great variations in exposure to climatic factors. A south-facing cliff is extremely xeric while a north-facing slope, because of its protection from heat and evaporation, may be almost mesic.

It was formerly believed by all ecologists that crustose lichens were practically always the pioneer plants that initiated successions on bare rocks. Studies in recent years, however, have shown that, although crustose lichens are often the first plants to appear on rock surfaces, they have little if any influence on succession. The pioneer plants that actually initiate the succession on bare rocks are little mat-forming mosses such as *Grimmia laevigata*, *Hedwigia ciliata*, and certain species of *Rhacomitrium*. These xeric mosses are able to form colonies on rock surfaces regardless of whether they have been preceded by lichens. After the moss plants have become established they begin to accumulate wind-blown and water-borne materials and they probably accelerate the disintegration of the rock surface somewhat, and so they start the building of a soil. The resulting moss mat spreads radially and may become an inch or more in thickness. This mat is usually invaded, sooner or later, by foliose lichens, especially species of *Cladonia*, or by larger mosses, especially species of *Polytrichum*, or by both, and the pioneer mosses then gradually disappear. As more soil accumulates xeric grasses and some other herbaceous seed plants appear. The species of seed plants that come in as pioneers depend upon the nature of the feeder vegetation, that is, the surrounding communities from which migrations may take place. If the rock surface is somewhere is the north-

eastern quarter of the United States they are likely to be such plants as golden-rod (*Solidago*), cinquefoil (*Pontentilla*), chickweed (*Cerastium*), harebell (*Campanula americana*), etc. The accumulation of soil will now go on more rapidly and such xeric shrubs as blackberries (*Rubus*), smooth sumac (*Rhus glabra*), and sassafras (*Sassfras variifolium*) begin to appear. By this time the rock will be completely covered with soil containing a supply of humus, and trees gradually enter. The first trees are likely to be xeric oaks and hickories accompanied by various other species and these are followed in order by the climax mesic trees, hard maple and beech, accompanied by red oak (*Quercus borealis*), basswood (*Tilia americana*), etc. (Fig 103).

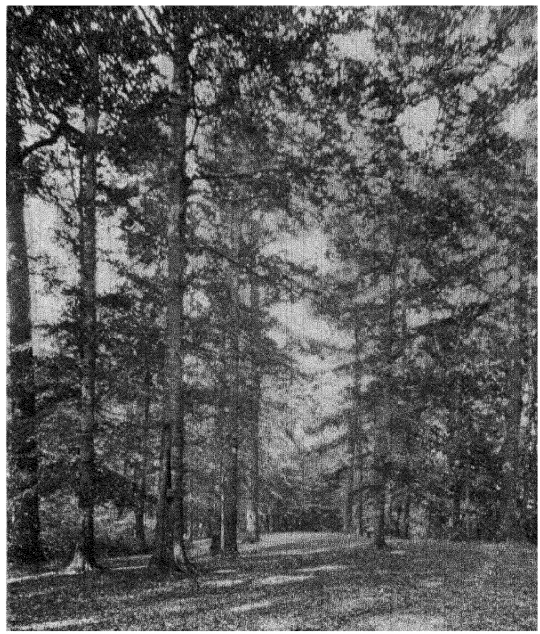


FIG. 103.—Remnant of a climax beech-maple forest. (Photograph by A. G. Eldredge)

The rock succession discussed above is outlined as it would normally occur on an area that was essentially horizontal. In the case of a vertical cliff the conditions are even more severe and succession is usually much retarded. The accumulation of humus is impossible and the pioneer stage is likely to persist until physiographic changes have brought about more favorable conditions. This unually begins with a collection of soil at the base of the cliff. As this soil increases in amount the plants of later stages climb higher and higher and at the same time plants from the surrounding upland descend as the ledges near the top of the cliff become covered with soil. Eventually, of course, the whole rock surface will be covered with soil and plants, but this takes a very long time.

A rock canyon usually presents very complex and interesting ecological

conditions. The head of a canyon is constantly eating its way back into the upland and so is always young, while farther down it is middle-aged, and at the mouth may be relatively mature. The pioneers in the young canyon are likely to be liverworts instead of mosses or lichens because of protection from the sun and the constant presence of moisture. Where the rocks are exposed to the sun, however, xeric mosses and lichens are the pioneers. In general, the succession is more or less comparable to that on a vertical cliff as the canyon broadens out and conditions become less severe. Successions in rock canyons have not been sufficiently studied to enable us to know accurately just what does happen. Such canyons, therefore, offer a fertile field for investigation.

139. **Successions in Water.**—Successions may take place either in standing water or in running water. The successions in standing water have been more thoroughly studied than any others, due to the fact that often all stages can be found forming distinct zones around a single body of water.

In the normal succession in a depression that is not entirely unprovided with drainage, the pioneer plants are floating or submersed aquatics that grow in water 5 to 10 feet in depth. Characteristic plants are many kinds of algæ, the duckweeds (*Lemna*), the pond weeds (*Potamogeton*), etc. As the depression becomes filled and the water more shallow, 2 to 5 feet deep, plants of the second stage, which root at the bottom but have shoots which extend nearly to the top of the water, or float, in part, upon its surface, come in. This stage is characterized by water lilies (*Nymphea*) and such plants as the water crowfoot (*Ranunculus aquatilis*) and the water smartweed (*Polygonum amphibium*). In still shallower water, up to 2 feet, we find the bulrush-cat-tail stage characterized by such plants as the bulrush (*Scirpus*), the cat-tail (*Typha latifolia*), the pickerel weed (*Pontederia cordata*), the arrowleaf (*Sagittaria latifolia*), etc., whose shoots extend well above the water.

After the depression has filled to such an extent that the water table is just at the surface there appears a stage which is characterized by various species of sedges and grasses and such flowering herbs as wild iris (*Iris versicolor*), skull-cap (*Scutellaria*), water horehound (*Lycopus*), and several kinds of gentians (*Gentiana*). This stage is followed by the shrub stage in which the dominant plants are likely to be willows (*Salix*), alders (*Alnus*), button-bush (*Cephalanthus occidentalis*, and dogwoods (*Cornus*). The first trees to follow the shrubs are likely to be ashes, soft maples and elms. These are replaced later, as the substratum becomes drier, by the trees of the climax forest.

When the depression is poorly, or not at all, drained the normal aquatic succession is modified into a bog succession. In this the first three stages are like those of the normal succession but in the fourth stage a quaking bog is formed. This consists of a floating mat of vegetation which is held together by a network of roots and rhizomes of sedges and other plants and may extend out over the surface of the water for some distance. The mat appears like solid ground but walking upon it is like walking upon India rubber for it is depressed at each step and then springs up again so that one actually walks in several inches or more of water. Upon this floating mat are found many of the typical bog plants such as *Sphagnum* moss, cranberry (*Vaccinium*), the pitcher plant (*Sarracenia*), the sundew (*Drosera*),

etc. As the mat becomes more stable and somewhat drier through the accumulation of dead organic matter the shrub stage appears. The first shrubs are usually the dwarf birch (*Betula pumila*), the leather-leaf (*Chamædaphne calyculata*), the bog rosemary (*Andromeda polifolia*), and the swamp blueberry (*Vaccinium corymbosum*), and they are followed later by such taller shrubs as the winterberry (*Ilex verticillata*) and the poison sumac (*Toxicodendron vernix*). The first tree to appear on the bog is usually the tamarack (*Larix laricina*) which is followed later by spruces at the north, or deciduous trees at the south, and finally by the climax trees of the region.

The swiftly-running water of a young stream presents conditions that are unfavorable to most plants and the succession does not progress beyond two or three stages until the stream becomes more mature and the water more sluggish. Some of the plants that are found in the young stream are *Cladophora* and some other algæ, mosses of the genus *Fontinalis*, and some species of pondweeds and saxifrages. The later stages which finally take place in an old stream are very similar to the later stages in standing water.

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CHAPTER XX

PHENOLOGY

PHENOLOGY, the word being a shortened form of phenomenology, is a branch of ecology that deals with the seasonal occurence of the various vital phenomena of plants, such as leafing, blooming, fruiting, falling of leaves, etc. The time at which the various phenomena occur in any particular species of plants may vary from year to year because of varying climatic conditions but there is sufficient regularity so that in periodic climates, such as are found throughout the United States, rather definite seasonal aspects can be recognized in most plant communities. In some species the vital phenomena are so strictly controlled by the length of the days that they take place at about the same time each year regardless of climatic conditions but in other species the phenomena are greatly influenced by temperature and moisture as well as by length of day and so may vary much more.



FIG. 104.—*Sanguinaria canadensis*. A prevernal flower.

140. **Seasonal Succession in a Deciduous Forest.**—Considering a deciduous forest in the east-central United States at about 40° north latitude as an example, six seasons can be quite readily recognized. These are as follows:

A. *Winter Season.*—During the winter the trees are essentially inactive and have dropped their leaves as a means of conserving the water supply during a season when absorption is difficult or impossible. Most other plants are also in a dormant condition either as rhizomes, corms, bulbs, tubers, wintergreen rosettes, or seeds. There are a few algæ and fungi, and perhaps a few mosses, that are more or less active all winter but in general the forest is in an inactive condition.

B. *Prevernal Season.*—The prevernal season begins with the first activity of the plants, usually late in March or early in April, and lasts until the leaves of the trees are out, usually in early May. Many trees bloom during this season as do also the early spring flowers. These early spring flowers, such as hepatica, bloodroot (*Sanguinaria canadensis*) (Fig. 104), spring beauty (*Claytonia virginica*), dutchman's breeches (*Dicentra cucularia*), etc., all take advantage of the short period when the forest is warm and sunny, before the trees have leaved. They are active only about three months and dormant during the remainder of the year. They are northern plants and perhaps are relicts of the glacial period and have developed the three-month habit during that period.

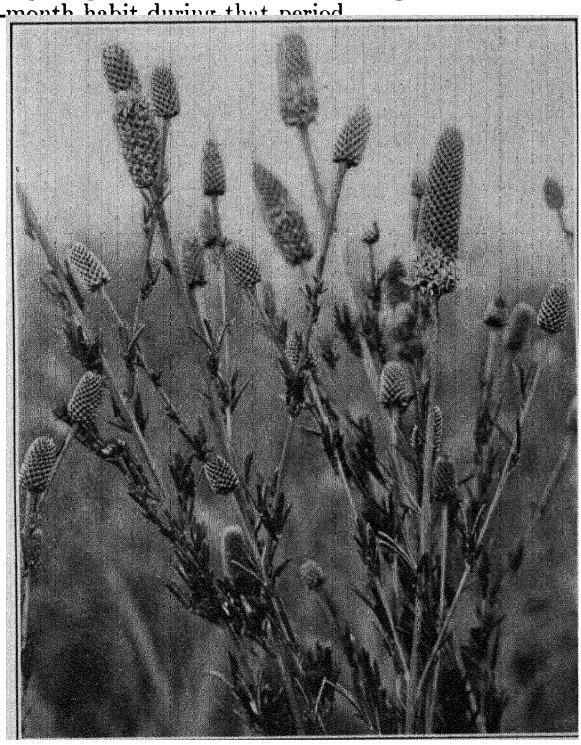


FIG. 105.—Prairie clover (*Petalostemum*), a flower of the æstival season. (Photograph by A. G. Eldredge.)

The seedlings of many later blooming plants appear during the prevernal season.

C. *Vernal Season.*—The vernal season begins with the opening of the forest tree leaves and lasts until near the middle of June. This is the season of the later spring flowers, such as the Virginia cowslip (*Mertensia virginica*), the May apple (*Podophyllum peltatum*), the wild geranium (*Geranium maculatum*), the Solomon's seal (*Polygonatum biflorum*), the wild spikenard (*Smilicina racemosa*), the wild strawberry (*Fragaria virginiana*), and many others. The most of these bloom during the month

of May and by the first of June there begins to be a scarcity of wild flowers.

D. *The Aestival Season.*—The æstival season begins about the middle of June and lasts until about the middle of August. At the beginning of this season an entirely new crop of wild flowers appears, but they are found in open places along forest margins, in meadows, and along streams rather than in the shade of the forest. Many of the legumes, mints, figworts, roses, etc., bloom during this season (Fig. 105). The winter buds of the forest trees develop at this time.

E. *Serotinal Season.*—This season lasts from the middle of August until late in September and is characterized by the blooming of many tall coarse plants largely of the composite family. The harebell (*Campanula americana*) is also characteristic of this season. By this time forest tree activity has practically ceased above ground.

F. *Autumnal Season.*—The autumnal season usually begins late in September and extends to the beginning of winter in the middle or latter part of November. It is characterized by the blooming of such plants as the goldenrods and asters, and by the falling of leaves and the ripening of fruits.

141. **Seasonal Succession in a Desert Community.**—The desert vegetation in the vicinity of Tucson, Arizona, has been more carefully studied than has that of any other place in the world. Here four seasons are recognized and these will be discussed in the following paragraphs.

A. *Winter Wet Season.*—The secondary maximum of precipitation for the year occurs in December and January and amounts to 2 or 3 inches of rainfall. The vegetation begins to awaken in January and a large number of plants begin blooming early in February and mature their fruits in March and April when there is a decrease in the rainfall. The plants that bloom during the winter season may be classed into two groups, namely, winter perennials and winter annuals. The factor which usually checks the awakening of these plants in the early part of the winter is the low night temperature which often is several degrees below freezing. Sometimes, however, a few warm days in December will bring forth a crop of low annual herbs which may almost reach the blooming stage only to be blighted by a frost early in January. The most outstanding characteristic of these winter annuals which adapts them for desert conditions is the remarkable power of resistance of the seeds. These seeds are ripened and thrown onto the ground during March and April. The surface layers of the soil reach temperatures above 100°F. during the summer months. The summer rains soak both the soil and the seeds but still no activity is shown. The summer cools into a rainless autumn and finally the cooler nights are followed by the winter rains of December and not until then do the seeds show signs of life.

Many of the winter perennials lose their leaves with the approach of the high temperatures of April and May and the stems, bulbs, or root-stalks go into a resting condition from which they do not awaken until the following December or January, eight or nine months later, the entire period of activity being limited to about one hundred days. Some, however, such as the creosote bush (*Larrea divaricata*), which has varnished leaves, and a few others with protective coatings of cutin or hairs, retain their leaves during the greater part of the year. No plants without protected surfaces can do this because during the summer the relative humidity is between 30 and 40 per cent and evaporation is, therefore, very rapid.

B. *The Dry Fore-summer.*—The winter season may be said to end about April 1st and is followed by the dry fore-summer which comprises April, May, and June with a total average precipitation of less than 1 inch and maximum temperatures of 95° to 112° F. The evaporation exceeds the precipitation in an enormous ratio but these severe conditions bring into activity the spiny, succulent xerophytes. These succulents are of two general types; the one represented by the cacti with storage stems and the other by the yuccas and agaves with succulent leaves. Both of these types of plants bloom in great profusion during the dry fore-summer.

C *The Humid Mid-summer.*—This season begins about July 1st and extends nearly to the end of September. The temperature is exceedingly high but the greatest precipitation of the year is during July and August. Millions of seedlings spring up when the rains come and forty-eight hours may change the entire appearance of the landscape. Some perennials, such as the great barrel cactus, bloom at this time and there are many annuals among which are a number of spurges (*Euphorbia*) and several parasitic dodders (*Cuscuta*) which make a very rapid growth.

D. *The Dry After-summer.*—The dry after-summer extends through October and November which are rainless months. The grasses which started late in the humid mid-summer ripen their seeds and remain as dry tufts. Some other plants ripen their seeds during the early part of this season but in general there is an almost total cessation of vegetative activity.

142. **Phenology of the Pine-barren Region.**—Harshberger has studied the phenology of the pine-barren vegetation of New Jersey and the information here presented is taken from his book which is cited at the end of this chapter. His study included 548 pine-barren plants which is only 7 less than the total number of native species of the region.

The period of activity of the pine-barren vegetation extends through the seven months from the beginning of April to the end of October, leaving five months when the vegetation is practically dormant. There is very little activity in April, however, and in fact the active period for the majority of the plants, so far as flowering and fruiting is concerned, is in July, August and September, the culmination being reached in August. The opening of the leaves of the deciduous trees takes place largely in May and the leaves fall in October. The period of photosynthetic acitvity of the mature leaves is about four and a half months. The length of the flowering period varies greatly with different plants, from fifteen days for some trees, such as some of the willows and oaks, to one hundred and fifteen days for the forget-me-not (*Myosotis laxa*) and one hundred and thirty-five days for the water lily (*Nymphæa variegata*). Two hundred and sixty-three of the 548 species are in bloom during August although only 106 begin blooming in that month. Although the largest numbers of flowers are in bloom during the middle of the summer, the region is practically never without some plant in bloom from the middle of March to the end of October.

143. **Phenology in East Central Texas.**—In Brazos County, Texas, where the average annual temperature is about 68° F., there are some plants in bloom in each of the four seasons. There are, however, seven distinct "waves" of flowering periods, one in winter, three during spring, two during summer, and one in autumn. The differences in blooming time of the plants representing these seven "waves" are due to different responses to

relative length of day and night, temperature, and other variable factors of the environment and, while many species of one group may overlap into the blooming period of the next group, the year is divided up among the numerous native species in such a way that there is much less competition between species than there would be if all had their period of blooming activity at the same time of year. A knowledge of such phenological data is of great practical importance in connection with the matter of honey plants for domestic bees and of food plants for quail and other wild animal species.

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CHAPTER XXI

THE DISTRIBUTION OF PLANT COMMUNITIES IN THE UNITED STATES

THE present and past distribution of plants over the surface of the earth and the causes thereof constitute the science of phytogeography or plant geography This is a science that is closely related to plant ecology and it is, therefore, important that a student of ecology should know something of it. It is a large subject in itself, however, and space does not permit us to treat it fully here. All that will be attempted in this chapter, therefore, is a brief and necessarily incomplete account of the present distribution of of plant communities in the continental United States.

144. **Deciduous Forest Communities.**—The deciduous forests of the north temperate zone occur in regions where the annual rainfall is between 25 and 60 inches with more than half of it falling during the warm months. In the United States the deciduous forest communities of varying floristic composition occupy nearly all of the area east of the Mississippi River, with the exception of the northern part of Maine, the higher parts of New York, New Hampshire and Vermont, the northern parts of Michigan and Wisconsin, the central part of Illinois and a rather narrow belt along the coast from Louisiana to North Carolina. West of the Mississippi these forests occupy most of southeastern Missouri, nearly all of Arkansas and much of the eastern parts of Oklahoma and Texas. Long tongues of deciduous forests also extend along all of the tributaries of the Mississippi that flow from the west and northwest.

All of the deciduous forests are considered as belonging to the same formation but there are at least three types of climax associations due to the differences in climate in different parts of the area occupied by the formation. The beech-maple forest is typical of much of central Wisconsin and Michigan, northern Pennsylvania, central and southern New York and central and southern New England. The southern boundary of the area occupied by this association is rather closely correlated with the southern limit of the Wisconsin glaciation. The two most important dominants are the hard maple, *Acer saccharum*, and the beech, *Fagus grandifolia*. These two trees are the most tolerant of shade of all deciduous trees of this formation. The yellow birch, *Betula lutea*, and the linden, *Tilia americana*, are also important dominants in this association. The hemlock, *Tsuga canadensis*, the environmental requirements of which are much the same as those of beech and maple, is often present and appears like a dominant but is usually considered a relict of a former time when the pine-hemlock coniferous forest is believed to have extended farther south. Several other species of trees, including several oaks, which are more important in other associations also occur in the beech-maple forest.

The beech-maple forest is a magnificent and extremely interesting vegetation type and contains a very large number of species, not only of trees but also of shrubs and herbs. No other forest can boast of a more attractive succession of seasonal societies. The spring flower societies are especially attractive but the autumnal societies, composed mostly of composites, are fully as striking.

The oak-chestnut-tuliptree forest occupies the area south of the beech-maple forest (Fig. 106). It is the climax association throughout most of the southeast, extending westward to include eastern Ohio and most of Kentucky, Tennessee and Mississippi as well as the other southeastern states although much of the southern part of this area is actually occupied by the southeastern coniferous forest. Characteristic dominants are the tuliptree (*Liriodendron tulipifera*), the chestnut oak (*Quercus montana*), in the northern part of the area, and southern red oak (*Q. falcata*) farther south. The chestnut (*Castanea dentata*) was formerly a very important

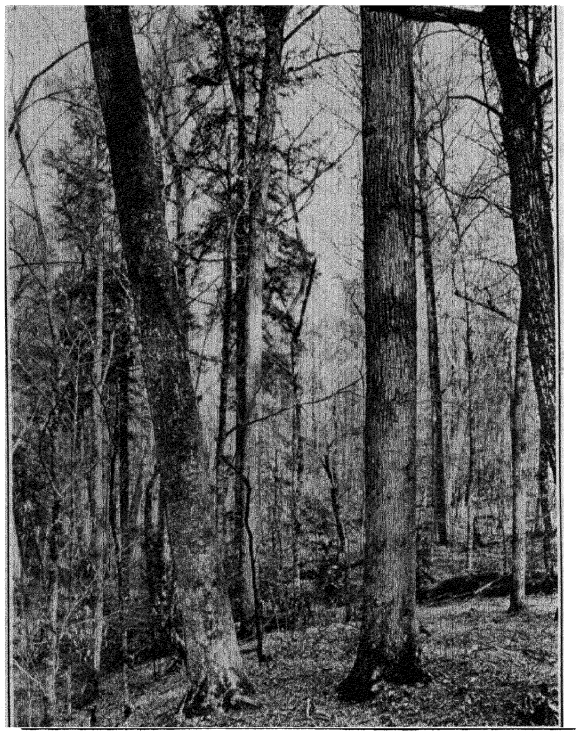


FIG. 106.—A deciduous forest of tuliptree and chestnut. North Carolina. (Photograph by F. G. Plummer. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

dominant in this association but in the early part of the present century nearly all of the chestnut was killed by the chestnut bark disease so that this species is no longer an important constituent of the forest. The number of species of trees associated with the dominants in this forest is greater than in any other in the United States and formerly some of the most luxuriant deciduous forests in the world were found in the Ohio Valley.

The oak-hickory forest is found between the other two types of deciduous forest and the prairie. It extends from south central Texas through Oklahoma, Missouri, southern Illinois, Indiana, western Ohio, southern

Michigan and Wisconsin, and a rather narrow band through south central Minnesota. This is also the type of forest that extends into the prairie along streams. The principal dominants are the red oak (*Quercus borealis*), black oak (*Q. velutina*), white oak (*Q. alba*), bur oak (*Q. macrocarpa*), shellbark hickory (*Carya ovata*), mockernut (*C. alba*), and, in the southern part, pecan (*C. pecan*). However, there are several other species of oaks and hickories that are nearly as important as those named. In the forested parts of Oklahoma and Texas there are considerable areas that are occupied by a rather open forest dominated by post oak (*Q. stellata*) and blackjack



FIG. 107.—Southeastern coniferous forest of long-leaf pine, loblolly pine, and short-leaf pine. (Photograph by E. Black. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

(*Q. marilandica*). These have usually been considered as part of the oak-hickory forest but some ecologists prefer to consider them as postclimax rather than true climax. This is because the climate is really a prairie climate and these oaks are believed to be relicts of a former moister climate.

145. **Coniferous Forest Communities.**—Coniferous forests are found for the most part, where the seasonal distribution of the rain is similar to that in the deciduous forest region but where the annual precipitation and the temperatures are too low to support deciduous forests. An exception to this statement is found, however, in the southeastern part of the United

States where the greater part of the coastal plain south of New Jersey and east of Texas, with the exception of the southern end of Florida, is occupied by coniferous forests although the rainfall is 50 inches or more throughout (Fig. 107). The limiting factors here are primarily, the high evaporation rate, the sandy soil which is relatively infertile, and the recurring fires. The dominant trees in these forests are pines but there are also many cypress swamps along the Alantic Coast and in the valley of the Mississippi River.

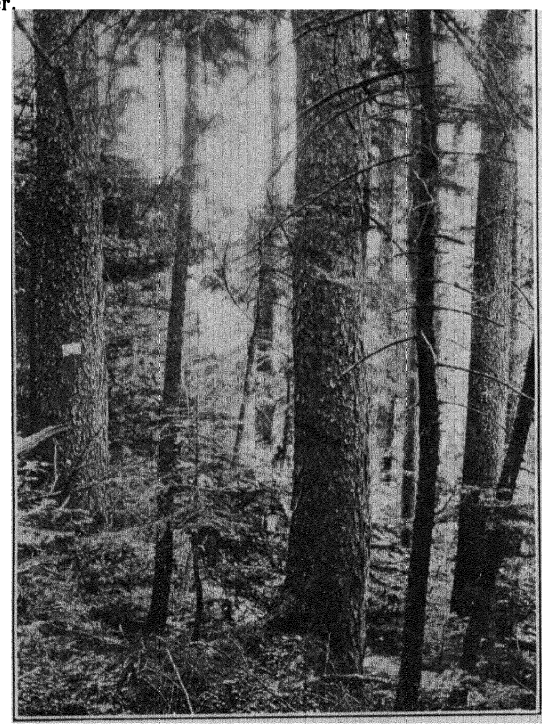


FIG. 108.—Mature spruce forest. Adirondack Mountains, New York. (Photograph by A. Gaskill. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

Elsewhere in the United States coniferous forests are found in the greater part of Maine, the Green Mountains of Vermont, the Adirondack Mountains of New York (Fig. 108) and the highest parts of the Appalachian Mountains farther south. They are also found in the northern portions of Michigan, Wisconsin and Minnesota, and throughout the mountainous portions of the western states (Fig. 109).

The southeastern pine forest is composed of several species of pine ranging from the Virginia pine (*Pinus virginiana*) and pitch pine (*P. rigida*) in the north to long-leaved pine (*P. palustris*) and loblolly pine (*P. taeda*) in the south. The slash pine (*P. caribaea*) occurs mostly along the coast from South Carolina southward and the short-leaf pine (*P. echinata*) occurs throughout but is most abundant in the western part of

the range. This forest is subclimax in nature. It is the result of past fires and is maintained by recurrent fires. Wherever fires are prevented over a long period of time the pine forest is replaced by a deciduous forest climax.

The northeastern coniferous forest is dominated by red pine (*Pinus resinosa*), white pine (*P. strobus*), and hemlock (*Tsuga canadensis*). Frequent also in certain parts of the forest are the jack pine (*P. banksiana*), the red spruce (*Picea rubra*), and the balsam fir (*Abies balsamea*). This forest has been so depleted and modified by lumbering and fires that its true nature is difficult to recognize in most places.



FIG. 109.—Engleman spruce forest. Subalpine park in foreground. Uinta Mountains, Utah. (Photograph by Edward J. Ludkin. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

The Rocky Mountain coniferous forests, which extend from Montana and Idaho to New Mexico and Arizona on the mountains, are of two main types. The higher parts of the mountains are occupied by a spruce-fir forest in which the dominant trees are Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*). This forest extends from the upper tree limit downward for 2000 to 3000 feet in most places. From central Colorado northward there are extensive areas of lodgepole pine (*P. murrayana*) forest in pure stand. These, it is believed, have been caused by past fires and will, in a natural course of events, be gradually replaced by the spruce-fir climax. Below the spruce-fir forest is the yellow pine (*P. ponderosa*) Douglas-fir (*Pseudotsuga taxifolia*) forest. The yellow pine and Douglas fir are often accompanied by lodgepole pine, limber pine (*P. flexilis*), and white-bark pine (*P. albicaulis*). The yellow pine usually extends somewhat lower than the other species and is often observed in pure stands.

The forests of the Sierra Nevada and Cascade Ranges are similar to those of the Rocky Mountains but possess larger numbers of dominant species. The uppermost forest which corresponds to the spruce-fir forest in the Rocky Mountains may be called the sierran subalpine forest and is characterized by mountain hemlock (*Tsuga mertensiana*), scrub pine (*P. contorta*), foxtail pine (*P. balfouriana*), western larch (*Larix lyallii*), and red fir (*Abies magnifica*). In addition to these the dominant species of the Rocky Mountain spruce-fir forest occur as secondary species. The lower forest of these mountains, which corresponds to the yellow pine-Douglas fir forest of the Rocky Mountains, may be called the yellow pine-sugar pine forest. It is characterized by the sugar pine (*P. lambertiana*), yellow pine (*P. ponderosa*), Douglas fir (*Pseudotsuga taxifolia*), white fir (*Abies concolor*), and incense cedar (*Librocedrus decurrens*). The big tree (*Sequoia gigantia*) is found only in this forest but is localized in limited areas in the central Sierras. This forest is much more characteristic of the Sierras than of the Cascades. On the east slope of the Cascades it is replaced by a larch-pine forest characterized by the larch (*Larix occidentalis*) and western white pine (*P. monticola*).

The west coastal coniferous forest occupies the western parts of Washington and Oregon from the western slopes of the Cascades to the coast and extends into California along the coast as far as San Francisco Bay with some islands still farther south. In Washington and Oregon there are large areas that are occupied by Douglas fir in almost pure stand. Associated with this species, however, are the western hemlock (*Tsuga heterophylla*) and white cedar (*Thuja plicata*). These two species were formerly much more abundant. The sitka spruce (*Picea sitchensis*) is an important constituent near the seacoast and in northern California occurs the famous redwood (*Sequoia sempervirens*) which is confined largely to the fog belt along the coast. It may well be claimed that the coastal forest is the most magnificent coniferous forest in the world. Because of the moderate temperatures, excessive rainfall which ranges from 50 to 120 inches, and frequent fogs, growth is very luxuriant and mature trees reach heights of 200 to 300 feet and trunk diameters of 15 to 20 feet.

146. **Chaparral Communities.**—Chaparral communities are dominated by shrubs (Fig. 110). They are more xeric than forests but somewhat less xeric than most grasslands and much less xeric than desert scrub communities which also have shrubs as dominants. Most chaparral communities occur where the rainfall is between 10 and 20 inches and especially where a large percentage of the rain falls in winter. There are two general types of chaparral, deciduous and sclerophyllous or evergreen.

The deciduous chaparral association is at its best in Colorado, eastern Utah and northern New Mexico where, for the most part, it occupies an intermediate position between forest and grassland. Perhaps the most characteristic dominant is Gambel oak (*Quercus utahensis*). Almost equally important are the mountain mahogany (*Cercocarpus parvifolius*), the squawbush (*Rhus trilobata*), the western chokeberry (*Prunus demissa*), and the western serviceberry (*Amelanchier alnifolia*). Outlying islands of this community are found in all directions from the main area as outlined.

The evergreen chaparral association is characteristic of the southern half of California, especially near the coast, but it may be found as far north as southern Oregon. There is only one important deciduous dom-

inant in this association. This is the scrub oak (*Quercus dumosa*). The characteristic evergreen dominants are chamiso (*Adenostoma fasciculatum*), several species of buckthorne (*Ceanothus*), manzanita (*Arctostaphylos pungens* and *A. tomentosa*), and holly-leaved cherry (*Prunus ilicifolia*). This community is much subject to fires and when burned the shrubs are not killed below ground and usually make a rapid recovery with several new stems for each one that burned. This results in a growth that is so dense that it is practically impenetrable to man and other large animals.

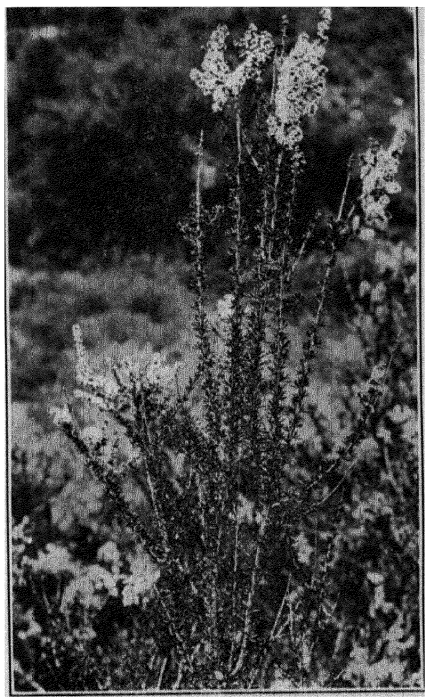


FIG. 110.—*Adenostoma fasciculatum*. A common plant of the chaparral of Southern California. (Photograph by W. S. Cooper.)

147. **Woodland Communities.**—The woodland formation, like the chaparral, is intermediate between forest and grassland or, in some places, between forest and desert. In some places, especially in north central Arizona, it has encroached upon former xeric grasslands where the grasses have been depleted by overgrazing. The woodland is typically southwestern in its distribution. It is found on the lower slopes of the Chisos, Davis, and Guadalupe Mountains of southwestern Texas and covers extensive areas in New Mexico, Colorado, Utah (Fig. 111), Arizona, Nevada, and California. It consists of small trees, usually between 10 and 40 feet high, belonging to the genera, *Pinus*, *Juniperus*, and *Quercus*. In California the digger pine (*P. sabiniana*) is important but elsewhere the pine that is concerned is the pinyon pine (*P. cembroides* and its varieties). In

the northern part of the range the juniper that is most important is *J. utahensis* while farther south it is *J. monosperma* and in some places *J. pachyphloea*. In the Chisos Mountains of Texas the drooping juniper (*J. flaccida*) is an added constituent while in northern New Mexico and Colorado *J. scopulorum* is frequent, and in California *J. californica* is important.

The oaks are more important in the southern part of the range and are mostly evergreen oaks such as *Quercus reticulata* and *Q. hypoleuca* and, in California, *Q. douglasii* and *Q. wislizeni*. In some places the oaks are present to the exclusion of one of the other genera, thus making an oak-juniper or a pine-oak community, but the most typical community is a pinyon pine-juniper association.



FIG. 111.—A very sparse pinyon-juniper woodland, Capitol Reef National Monument, Utah.

148. **Grassland Communities.**—The grassland formation is the most extensive type of vegetation in the United States. It occupies nearly all of the central portion of the country from the deciduous forests of the east to the foothills of the Rocky Mountains on the west, extending northward into Canada and southward into Mexico. It also occurs, intermittently and in various modifications, westward to the Pacific coast.

Most of the grassland occurs where the rainfall is somewhere between 25 and 35 inches with nearly three-fourths of it falling in the warmer half of the year. However, grasslands occur under a very wide range of conditions. Some are found where the rainfall is only 10 inches or less and some where no more than 10 per cent of the rain falls in the summer season. The range of temperature is also very great in different parts of the grassland formation. In the north it is subject to winter temperatures far below zero while in the south there are places in which the freezing point is seldom if ever reached. The essential requirement seems to be merely that there shall be sufficiently frequent rains during the growing season to enable grasses to bloom and produce seeds.

The tall grass prairie formerly formed a belt along the western edge of

the deciduous forest formation and occurred as islands within the forest. It also occurs in sandy areas farther west, especially in the sand-hill area of Nebraska. These sand-hill areas are the best places to see tall grass prairie at the present time since elsewhere it has practically all been destroyed in order to utilize the land for agricultural purposes. The most important dominants of the tall-grass prairie are the beard grasses (*Andropogon furcatus* and *A. scoparius*) and Indian grass (*Sorghastrum nutans*). These are tall, sod-forming grasses that grow 5 to 8 feet tall. Associated with them are many other grasses and many herbs which form seasonal societies at blooming time.

The true prairie, like the tall-grass prairie, has been largely destroyed by cultivation. Originally it is believed to have formed a quite distinct belt between the tall-grass prairie on the east and the mixed prairie or short-grass plains on the west. The true prairie is composed largely of grasses that are intermediate in height. The most characteristic dominants are species of *Stipa* and *Sporobolus* which are bunch grasses but some of the sod-forming genera are also represented. Since the change of climate from east to west is gradual the lines of separation between the true prairie and the tall-grass prairie on the one hand and between true prairie and mixed prairie on the other, as might be expected, are not lines that can be drawn accurately on a map but are broad belts or ecotones where the species of neighboring types of grassland are mixed. The true prairie probably contains a larger number of aspect societies, composed of beautiful flowering herbs, than any other type of grassland. The sequence of spring, summer, and fall societies produces an ever changing aspect in addition to that which is due to the prairie grasses themselves.

From the western edge of the true prairie to the foothills of the Rocky Mountains is the great expanse of grassland that has commonly been called the short-grass plains. Studies during the past quarter of a century or so have shown rather conclusively that the climax over this vast area is a mixed prairie in which short grasses and medium grasses are about equally important. The familiar short-grass plains, in which the medium grasses are nearly or entirely absent, are due to overgrazing, formerly, in some places, by buffalo and in more recent times by domestic cattle. The short-grass plains are often a continuous and unbroken sod of grama grass (*Bouteloua*) and buffalo grass (*Buchloe*), sometimes with the addition of the low sedge (*Carex filifolia*), but in the climax mixed prairie there are in addition to these several other short grasses, such medium grasses as *Stipa comata, Sporobolus cryptandrus, Agropyron smithii, Koeperia cristata,* and several others. The societies in the mixed prairie are similar to those in the true prairie but, because of the more xeric climate, the number of species concerned is much smaller.

In the southern part of the great central grassland, near the Gulf of Mexico, is the gulf coast prairie which resembles the mixed prairie in having both short grasses and medium grasses as dominants but differs from it in having a larger number of dominants, some of which, notably *Stipa leucotricha,* are not found outside of this community. Here, again, the societies are similar to those of the true prairie but many of the species concerned are of southern origin and are not found farther north.

The desert grassland extends from southwestern Texas through southern New Mexico and Arizona, mostly between the 3000 and 4500 foot contours.

Its dominants are almost entirely short grasses, species of grama grass (*Bouteloua*), wire grass (*Aristida*), and mesquite grass (*Hilaria*). For this reason it very closely resembles the short-grass plains except that it is usually dotted with such shrubs as creosote bush (*Larrea*), mesquite (*Prosopis*), catclaw (*Acacia*), *Yucca*, cholla (*Opuntia*), bisnaga (*Ferocactus*), desert hackberry (*Celtis*), Morman tea (*Ephedra*), etc. Over much of the area, however, overgrazing by domestic animals has destroyed most of the grasses and brought about a very great increase in the numbers of shrubs so that the community has been transformed from desert grassland to desert scrub. Societies of flowering herbs are in evidence both after the summer rains and after the winter rains. They are especially attractive after the January and February rains, making this community one of the most colorful in all America during March and early April.

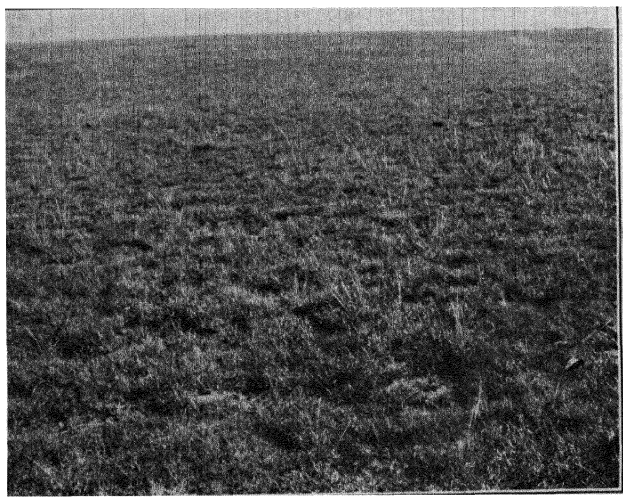


FIG. 112.—Short-grass plains vegetation. Montana. (Photograph by H. L. Shantz. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

The Pacific prairie, or California bunch grass prairie, has been so completely destroyed by overgrazing and fire that it is now difficult to find even small remnants that are typical. Formerly it occupied much of the Great Valley of California as well as many of the valleys and foothills of most of the mountains of the state. In its typical form it had much the same general appearance as the true prairie. Its most important dominant was the needle grass (*Stipa pulchra*) which, however, was accompanied by several other medium sized bunch grasses, but these native grasses have been very largely replaced by exotic annual grasses introduced from Europe.

A bunch grass association also occurs in eastern Washington and Oregon, southern Idaho, and northern Utah which is sometimes called the Palouse prairie. This resembles the California bunch grass association but its major dominants are different. Like the California bunch grass it has been largely destroyed by overgrazing and fire and has been replaced partly by exotic annual grasses and partly by sagebrush.

149. **Desert Communities.**—Deserts are found where the annual rainfall is uniformly low, usually below 15 inches, and the evaporation rate is high. Because of these environmental conditions the vegetation is very xeric.

In the United States two general types of desert vegetation may be recognized. The first is the sagebrush (*Artemisia*) type which occupies the northern part of the desert region where the rainfall is fairly well distributed throughout the year (Fig. 113). This type of desert occurs extensively in Wyoming, western Colorado, northern Arizona, Utah, Nevada, southern Idaho, southeastern Oregon, central Washington, and in central and southern California. Its most typical development is in the central portion of the Great Basin where the most characteristic dominant is *Artemisia tridentata* accompanied by other species of *Artemisia*,

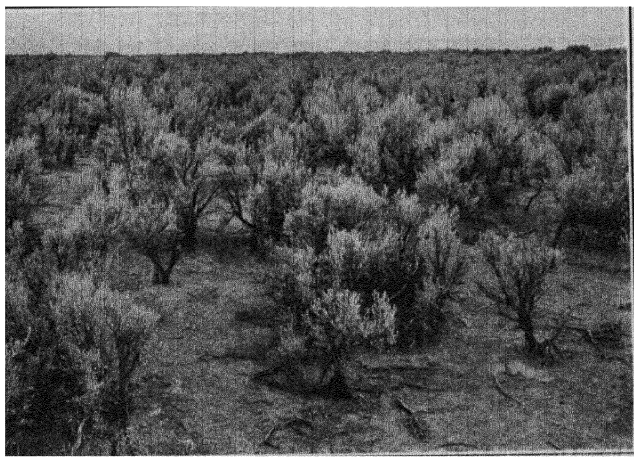


FIG. 113.—Sagebrush desert. Utah. (Photograph by H. L. Shantz. Courtesy of H. L. Shantz and the U. S. Department of Agriculture.)

rabbitbrush (*Chrysothamnus*) and other xeric shrubs. The California sagebrush is very similar in appearance to that in the Great Basin but its dominants are different. The most important sagebrush there is *Artemisia californica* and this is accompanied by shrubby species of sage (*Salvia*), buckwheat (*Eriogonum*), beardtongue (*Penstemon*), sumac (*Rhus*), and various others. Cacti are not characteristic of this type of desert.

The southern part of the desert region is occupied by the creosote bush-bursage-cactus desert (Fig. 114). The climate is characterized by two rainy seasons, one in winter and one is summer, and by high temperatures and high evaporation rates. This type of desert is found in southern Nevada, southern and western Arizona, and in the Death Valley, Mohave, and Colorado Desert areas of southern California, and extends southward into Mexico. This is the most xeric type of vegetation in the United States. For the most part the average annual rainfall is between 3 and 6 inches but sometimes an entire year may pass with no rain at all and sometimes the rain for the entire year may all come in a single downpour.

Universally characteristic dominants of this desert are the creosote bush (*Larrea divaricata*) and the bursage (*Franseria dumosa*), but there is great variation from place to place. In parts of northwestern Arizona and southern California the joshua tree (*Yucca brevifolia*) is by far the most conspicuous plant while in southern Arizona, especially in the Organ Pipe Cactus National Monument, there are extensive areas where the aspect is dominated by large cacti such as the saguaro (*Carnegia gigantea*), the Organ Pipe Cactus (*Lemaireocereus thurberi*), senita (*Lophocereus shottii*), and cholla (*Opuntia*). Along with these cacti may be found the unique ocotillo (*Fouquieria splendens*), the palo verde (*Parkinsonia*), and many others. If the winter rains come on schedule and bring all of these plants into bloom in early spring along with innumerable winter annuals it makes a floral display that beggars description.

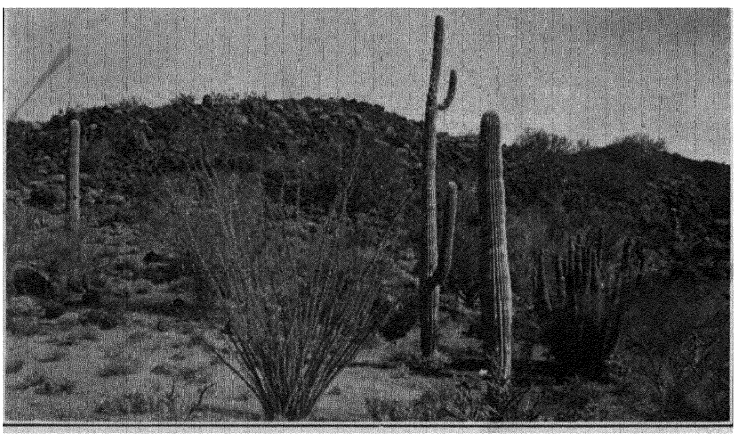


FIG. 114.—Creosote bush-bursage-cactus desert, Southern Arizona.

150. **Alpine Communities.**—Alpine vegetation is found near the tops of the higher mountains all over the world. In going up the side of a high mountain one encounters variations in climate comparable to those encountered in going north or south from the equator and these variations in climate lead to a recognition of more or less definite belts of vegetation. Usually four of these belts or zones of vegetation can be recognized, the lowermost being called basal, the second montane, the third subalpine, and the fourth, or uppermost, alpine. The basal zone consists of vegetation that is similar to that of the adjacent plain or valley. The montane zone is usually more luxuriant than the basal and ordinarily consists of forest communities, either deciduous or coniferous. The subalpine zone is more xeric. It consists largely of coniferous forest, but the trees are dwarf and at the timber line form the characteristic "elfin timber" (Fig. 115). There are also frequent open spaces which are occupied by grasses and flowering plants. Above the tree line is found the true Alpine meadow which becomes more and more dwarf as it ascends the mountain. The brilliance and profusion of bloom encountered in the Alpine meadows cannot be matched anywhere else. If the mountain is not too high the Alpine

meadow may cover the top but the highest mountains are covered by perpetual snow and so are destitute of vegetation while some others have only lichens and a few xeric mosses at their summits.

None of the mountains in the eastern part of the United States are high enough to support typical alpine vegetation but in the west there are many mountains that extend beyond the tree line and there alpine communities are encountered.

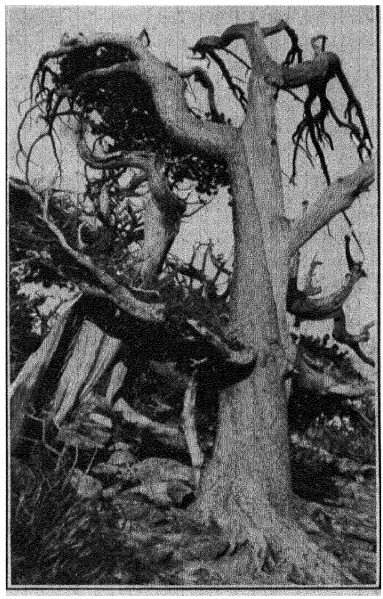


FIG. 115.—*Pinus flexilis* at timber line on Long's Peak, Colorado. (Photograph by Raymond J. Pool.)

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CHAPTER XXII

APPLIED ECOLOGY

PLANT ecology is the most intensely practical of the plant sciences. In all branches of applied botany man is necessarily concerned with the interrelations between plants and their environments. Therefore all branches of applied botany are necessarily based upon ecological principles. If we were to take ecology out of botany, or any of its subdivisions, there would be very little left that would have any practical application to the economic affairs of man. For this reason it is essential that anyone preparing to pursue any branch of economic biology be trained in ecology.

Obviously it would require volumes to deal in a comprehensive way with the entire field of applied ecology. In this chapter, therefore, we shall discuss briefly some of the most common applications, primarily for the purpose of making clear the fact that ecology is a very practical science.

151. **Forest Ecology.**—Forestry, wherever it is successfully practised, is based entirely upon ecological principles. Practical foresters are realizing this more and more and are coming to recognize the need of training in plant ecology for anyone who is preparing for any phase of forestry as a life work. The forester should be perfectly familiar with the life cycles and the phenology of the trees under his care. He should understand such physiological processes as respiration, absorption, and transpiration and should know how these and other activities of the plant are affected by such environmental factors as heat, light, moisture, soil variations, etc. It is necessary also that he understand the methods of reproduction of each species, whether by seeds or by vegetative shoots, and the most favorable conditions for reproduction. He should know what species of trees are ecologically suited to the conditions in his forest, both of native and foreign species, and whether they will grow best in pure stands or in mixed stands. The purpose for which trees are grown, whether for lumber, fence posts, railroad ties, etc., or whether they are being grown as a windbreak or to prevent erosion, influences the choice of species and makes it necessary to understand the characteristics and habits of growth of the various kinds. In order to properly care for and protect the forest it is necessary that the forester understand the dangers from tree diseases, insects, fire, and storms, and the effects of over-grazing and over-cutting. Since animals form an important part of the environment of the forest trees it is essential that the forester have an intimate knowledge of the ecological relations of the animal life as well as the plant life of his forest. Extremely important also, of course, is a knowledge of dominance and of plant succession in relation to natural reproduction in the forest.

Much of the information that is so essential to a forester can at present be taught in courses in plant ecology and in technical forestry. There is a very large number of pressing problems in forest ecology, however, that are waiting solution and there is urgent need for an increased number of trained workers in this line of research.

152. **Grazing Problems.**—Millions of acres of grazing lands in the western part of the United States have been injured to a greater or less degree by over-grazing so that the number of head of stock that might otherwise be

pastured on them is materially decreased. Until ecological methods were applied there was no reliable means of recognizing over-grazing in its early stages. The usual methods of estimating the condition of the range was based on observations on the general abundance and luxuriance of the forage supply and the condition of the stock being grazed. These general observations do not enable one to recognize over-grazing until large numbers of the most valuable plants have been destroyed. It is not the total amount of green herbage on an area but the kinds of plants present and their relative numbers that tell the ecologist whether an area has been over-grazed.

By applying the principles of plant succession to the problem of over-grazing it is possible to overcome many of the difficulties. Taking the ranges in centeral Utah as an example four major plant communities are recognized. In the order of their position in the successional series these are the ruderal weed community, the foxglove-sweet sage-yarrow community, the porcupine grass-yellow brush community, and the wheat-grass community. The wheat-grass community is the most permanent and will endure over-grazing longer than any other type and it makes very efficient pasture for cattle and horses but is not quite so good for sheep. The porcupine grass-yellow brush community contains a larger number of palatable species and will probably support more stock than any other type. The other two communities are due to excessive over-grazing and do not furnish valuable pasturage.

Any area on this range which is ungrazed or only moderately grazed develops eventually into the wheat-grass community while more intense grazing causes the wheat-grass to be replaced by the porcupine grass-yellow brush community and excessive over-grazing brings about the appearance of the earlier stages of the succession. Since the porcupine grass-yellow brush community is the most valuable of all, the most successful scheme of management is to graze just heavily enough to prevent the development of wheat-grass but not heavily enough to destroy the porcupine grass-yellow brush community. Thus by staking out permanent areas on the range and making observations from time to time for the appearance of species belonging to the preceding or following stages of the succession it is possible to increase or decrease the number of head of stock grazed before any appreciable damage has been done.

153. **Indicator Vegetation.**—We have shown in the preceding paragraph how plants characteristic of certain stages of a sere may be used as indicators of grazing conditions. There are many other practical uses that may be made of native plants as indicators of present conditions and often of past or future conditions as well. Every plant is a measure of the conditions under which it grows and therefore it indicates how other plants may behave in the same habitat. The only thing that limits our use of native plants as indicators of environmental conditions is our lack of accurate knowledge concerning so many of the ecological relations of plants.

Either single plants or plant communities may be used as indicators, the communities being somewhat more significant than single plants or single species. The most important species in the community are the dominants and they may indicate past and future as well as present conditions. The native communities may be used to indicate the kind of practice that will prove most successful, that is, whether agriculture, grazing, or forestry should be practiced. They may indicate whether ordinary humid farming,

dry farming, or irrigation farming should be used. For example, a tall-grass community indicates humid farming conditions while a short-grass community indicates dry farming and a sage-brush community indicates irrigation farming. Even the kind of crops that are best suited to a region may be indicated by the native vegetation. Thus the areas of maximum production of corn and of winter wheat correspond to areas where the native grass communities are dominated by species of *Andropogon* while spring wheat and durum wheat reach their best development where *Stipa spartea* and *Agropyrum glaucum* are dominant. It is undoubtedly true that a land classification based on a thorough study of the indicator value of the native vegetation would be much more valuable than a classification made on any other basis.

Plant successions, especially where they bring about a shifting of an ecotone between two types of vegetation, may be used as indicators of climatic changes. For example, studies extended over many years have shown that timber lines in certain places in Alaska are advancing while those in the central Rocky Mountains are remaining essentially static and those on Mt. Washington in the White Mountains of New Hampshire are receding. This probably means that the climate in northwestern North America is at the present time becoming milder while that in the northeastern part of the continent is becoming more severe and that in the central Rocky Mountain region is remaining unchanged.

154. **Crop Production.**—The entire problem of crop production is an ecological problem since it is concerned solely with the relation of crop plants to the environment. Before planting the seeds of a crop plant it is necessary to select a place that is ecologically suitable in its climatic and soil factors, and to prepare the seed-bed in the way demanded by the ecological adaptations of the plant concerned. After the seeds have germinated it is necessary to know what methods of cultivation will make the habitat most favorable for development of the plant. The problems of soil fertility are ecological problems. Crop rotations are based upon the ecological relations of the crop plants concerned. Thus it is readily seen that the art or vocation of crop production is solely applied ecology. Crop ecology is, therefore, an all-important part of agronomy and is based, of course, upon general plant ecology.

155. **Symbiotic Phenomena.**—The practical applications of studies in symbiosis are many and varied. We have already pointed out some of the applications of studies of plant communities, which represent social disjunctive symbiosis, and the grazing problems that we have discussed fall under antagonistic nutritive disjunctive symbiosis. Pollination studies are extremely important from an economic point of view. The business of honey production is based entirely, of course, upon the symbiotic relation between bees and flowers. The commercial production of figs in America was entirely impossible until the symbiotic relation of the fig tree to a pollinating insect had been studied. The successful production of vegetables and fruits in greenhouses has depended in some cases upon pollination studies. The symbiotic relations between crop and ornamental plants and disease-producing organisms are, of course, of vast importance to man. In fact the science of plant pathology deals almost solely with symbiotic phenomena. The importance of the symbiotic relation between legume plants and nitrogen-fixing bacteria can scarcely be overestimated. The

successful cultivation and propagation of orchids has until recently depended upon a knowledge of their symbiotic relation with endotrophic mycorrhizal fungi, and this is more or less true also of the cultivation of blueberries and other members of the heath family such as *Rhododendrons* and mountain laurel (*Kalmia*). The exact relationship between ectotrophic mycorrhizal fungi and their host plants, especially in the case of forest trees, is still a somewhat unsettled question and much work must yet be done before these symbiotic structures will be fully understood. It is urgently important to the practice of forestry to know whether these mycorrhizas are of vital importance to forest trees or not.

156. **Phenology.**—Phenological data are often very valuable in enabling one to know when certain correlated phenomena may be expected to take place. For example, a wildlife manager by watching for easily observable plant phenomena, such as the blooming of flowers, may know when to expect less easily observed activities of animals, such as the first laying of eggs, the first birth of young, the first appearance from hibernation, etc. It has been found that the first appearance of the larvæ of malaria-producing mosquitoes in ponds and reservoirs is closely correlated with easily observed plant phenomena. Therefore, by observing the plants, the proper time for initiating measures for controlling the larvæ can readily be determined.

It is, of course, exceedingly important for bee-keepers to know the blooming time of the flowers from which their bees obtain nectar for making honey. In the western part of the United States it is a common practice to move bees regularly from one "pasture" to another, usually from south to north, as the blooming season progresses.

157. **Landscape Gardening.**—Ecology is as fundamental to landscape gardening as to forestry and crop production. It is as essential for the landscape gardener as for anyone else concerned with the growing of plants to know the general ecological relations of each species of plants with which he deals. Furthermore, it is essential that he have a thorough training in the structure and development of plant communities in order that he may make naturalistic plantings intelligently. He should understand the significance of ecological equivalents in order that he may vary the floristic composition of his plantings without sacrificing the optimum habitat conditions for the plants. The symbiotic relations between ornamental plants when planted in groups or in extensive communities is a field about which we know surprisingly little. It is well known that plants do influence one another, that some species get along well in the same planting and others do not, but these facts have never been organized or classified and the reasons for them are very obscure. This is, therefore, another very fertile field for future investigation. This is especially true of symbiotic relations below the surface of the soil, that is, the interrelations of the root systems of ornamental plants.

158. **Ecology and Conservation.**—Conservation may be defined as the prevention of waste and it usually refers to preventage of wastage of such natural resourses as minerals, soil, water, and plants and animals including man. The word conservation implies neither use nor lack of use but it permits use so long as there is no wastage.

Plant ecology is not concerned with the conservation of minerals but it is intimately concerned with the conservation of soil, water, and living

things. The conservation of both soil and water is based largely on the maintenance of a proper plant cover and it is necessary, therefore, for the conservationist in these fields to have intimate knowledge of the ecology of the plants concerned. The planting of shelter belts and other windbreaks for the prevention of soil erosion by wind also depends for its success upon a knowledge of the ecological requirements of the plants that are to be used.

The conservation of wildlife has received an increasing amount of attention during the past few years. Wildlife includes all native species of both plants and animals. The conservation of wildlife, therefore, includes the conservation of wild flowers as well as of forests and grasslands and the conservation of non-game animals, including predators, as well as of game animals. Before white men came to America the native plants and animals were getting along together very nicely. There was a nice balance between the plants and the animals that fed upon them, between hosts and parasites, between predators and those preyed upon, which has been called the balance of nature. It is known, however, that the balance of nature is never a static thing but is always fluctuating. For each species of animal there seem to be natural cycles involving maximum and minimum numbers in any particular community. These cycles may or may not coincide with climatic cycles. Their causes are not fully understood and they offer a fertile field of investigation for the wildlife conservationist.

The purpose of wildlife conservation may differ in different biotic communities. On farms the object may be to maintain a proper cover and food supply to support normal numbers of the smaller game animals. In larger communities, such as some of the national forests, the object may be to produce maximum numbers of the larger game animals primarily for the sport of hunting as well as maximum production of timber and other forest products. In addition to these and other purposes, it is necessary that some chunks of wilderness areas be preserved in an unmodified condition in order that the ecological relations of the plants and animals may be studied in wholly natural habitats and that the millions of nature lovers of the country may be able to enjoy unspoiled biotic communities. Such areas are provided for in the national parks and monuments where all species of native plants and animals are given full and impartial protection. In all cases, however, success in the conservation of wildlife can come only if those charged with administering it have an adequate knowledge of the ecological relations of both plants and animals.

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APPENDIX

(FOR THE TEACHER)

SUGGESTIONS CONCERNING LABORATORY AND FIELD WORK

NEARLY every teacher of any branch of biology finds it necessary to work out his own laboratory and field exercises for the reason that it is impossible for anyone to make a manual, or set of exercises, that will fit all localities and all working conditions. It is believed, however, that the following suggestions will prove helpful as a working basis, especially for teachers who are offering a course in plant ecology for the first time or who are unfamiliar with methods of carrying on field work. They are intended only as suggestions and should be modified to meet the varying needs of individual classes of students.

The Scientific Method.—Every course in any science should have as one of its chief aims the teaching of the inductive method which is the method of science. In the practical use of this method one first accumulates as many data as possible on the questions involved. He then classifies and evaluates the data and frames hypotheses to explain them. Finally he compares these hypotheses with known facts in every possible way and draws definite conclusions as to the truth or falsity of each. To train students in this orderly method of thinking is the greatest and most valuable thing that any teacher can do. It is true that the students must be expected to acquire a certain amount of information, but the mere acquisition of information is the easiest part of scientific training. The information can practically all be found in books and the simplest and quickest way to get it is to go to the books for it. In the laboratory and field work the chief concern of both teacher and student should be with mental development; with growth in ability to acquire data and to make use of these data in arriving at conclusions through scientific thinking. This mental growth is more likely than anything else to lead the students to an enthusiastic love of the subject being pursued for nearly everyone gets pleasure from doing things that lead to personal accomplishment and that is what the scientific method enables us to do. The problem method is the accepted method for teaching scientific thinking and certain problems will be suggested in some of the following paragraphs.

Laboratory versus Field Work.—Plant ecology is preëminently a field subject. Most phases of it can be studied successfully only in the field. Students of ecology should, therefore, spend just as much time as possible in the field where the plants are at home. There are some phases of ecology, however, such as ecological anatomy, that can best be studied in the laboratory and this should be done when the weather is too inclement for field work. Except during the severest part of the winter the weather is seldom so inclement that field work cannot be done. It is good practice to tell students at the beginning of the course that all field trips will be taken as planned regardless of the weather. This is the only way to avoid complaints and absences on account of the weather for the weather is seldom

exactly right and if one waits to take his field trips on days when the climatic conditions are satisfactory to everyone he is not likely to do much field work.

Field Work in Winter.—No great amount of work can be accomplished on a field trip unless the students are reasonably comfortable, but if they can be induced to dress in such a way as to remain comfortable much profitable field work can be done during the winter months. Most students are surprised to find that there are many plants in addition to evergreen trees that remain green all winter and one or more trips may be made to find rosette plants and others that are "winter greens." A good trip can be planned for the study of the growth habits of stems, especially if a visit to a greenhouse may be included. The greenhouse will also offer opportunity for studying variations in size, form, and arrangement of leaves. Profitable trips may also be made, out of doors, to study the dormant condition of various kinds of plants with special reference to protection against loss of water, and to study such symbiotic phenomena as are evident in winter.

Suggested problems

1. To discover what kinds of plants remain green during the winter season.
2. To discover whether "winter greens" are more abundant on uplands or on lowlands.
3. To find how many variations in stem habits there are on the campus and in the greenhouses.
4. To find how many variations in size, shape, and arrangement of leaves there are in the greenhouses and to explain their ecological significance.
5. To discover how many kinds of symbiotic phenomena are in evidence in a wood-lot during winter.

Ecological Anatomy.—Studies in ecological anatomy must be carried on largely in the laboratory. Since leaves are much more plastic than roots and stems more time is devoted to them. The few problems stated below will serve to suggest others.

Suggested Problems

1. To make a comparison between the stem and root of a mesic plant as to internal structure, and to explain the ecological significance of the differences.
2. To make a comparison between a rhizome and a root as to internal structure and to explain the ecological signficance of the similarities as well as the differences.
3. To discover which of the leaves provided is mesic, which xeric, and which hydric. (Students should cut their own sections if possible, but if time or facilities do not permit this, prepared slides may be used.)
4. To discover which of the leaves provided is a sun leaf and which a shade leaf. (Sun and shade leaves of sugar maple make good material for this.)
5. To classify each of the leaves studied as diphotophyll, diplophyll, staurophyll, or spongophyll.

Symbiotic Phenomena.—The studies that may be made of symbiotic phenomena are almost unlimited. It is well to advise students to be on the look-out for symbiotic relations on all field trips made in addition to making some trips especially for these studies. Numerous structures resulting from symbiosis make good material for laboratory work.

Suggested Problems

1. To discover how a dodder plant obtains food from its host.
2. To discover what kinds of trees in a wood-lot have ectotrophic mycorrhizas.
3. To compare the mycorrhizas of a hickory tree with those of an orchid.
4. To make a list of the lianas in a wood-lot and discover which ones twine in a clockwise and which in a counterclockwise direction.

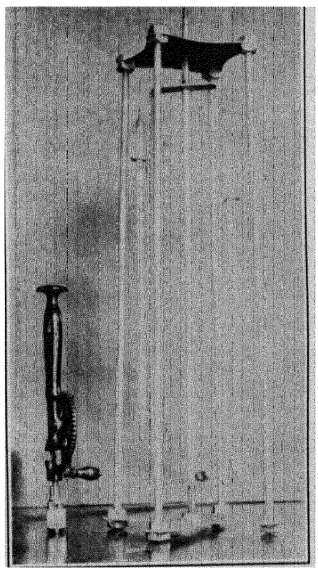


Fig. 116.—A cog psychrometer.

5. To investigate the internal structure of a lichen and explain the ecological significance of the various component parts.
6. To discover how certain kinds of flowers are pollinated.
7. To find as many kinds of insect galls as possible and decide whether any of them are ecologically important in the lives of the host plants.

Instrumental Methods.—It is not essential that a beginning class in ecology be provided with expensive equipment. The use of instruments for the measurement of physical factors is so important, however, that, if they can be provided, students should have an opportunity to do at least some work with them, and in almost every case at least some instruments can be provided. In order to obtain accurate and valuable data on most of the physical factors it is necessary to take long series of measurements.

This is usually impossible for a beginning class. Two methods have been used with classes at two universities for teaching the use of instruments and the significance of instrumental measurements. By one of these methods five diverse habitats were selected and the class was divided into five groups, one for each habitat. Each group was provided with a photometer for taking light readings, an anemometer for measuring wind velocity, a psychrometer for measuring relative humidity (Fig. 116), a stop-watch, a soil thermometer, and a soil can for taking a sample for determination of soil-water content. Each group worked upon a time-schedule previously agreed upon so that each kind of measurement was made simultaneously in all five habitats. The groups then exchanged data and were asked to explain the differences in vegetation in the five habitats on the basis of the physical factors. The second method used was similar to the first except that instead of working on a time-schedule each group of students was given

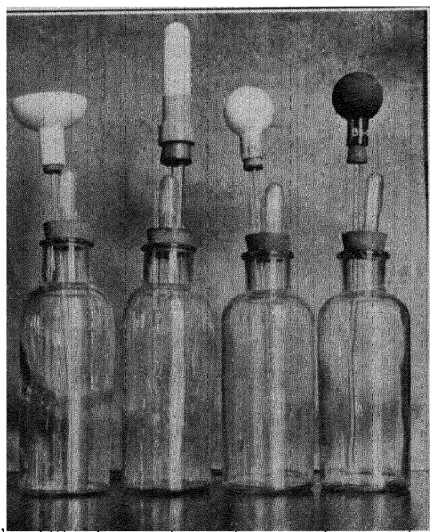


FIG. 117. — Various types of porous clay-cup atmometers.

a set of instruments and told to devise methods of making a thorough investigation of one of the five habitats. While this method gave less accurate data than the former it had the advantage of placing the students more upon their own responsibilities with fewer specific directions to follow.

SUGGESTED PROBLEMS

1. To learn to use common instruments for making measurements of the physical factors of the invironment.
2. To make a thorough investigation of the physical environment of a single plant.
3. To make a comparison of five habitats as to the physical factors of the environment.

4. To discover reasons for differences in vegetation in five dissimilar habitats.

5. To compare the evaporation rates in five dissimilar habitats. (Porous clay-cup atmometers are useful for this) (Fig. 117).

Quadrat Methods.—A quadrat is a square area used for making studies of vegetation (Fig. 118). A quadrat may be of any convenient size such as 1 meter square or 10 feet square or 100 feet square. Quadrats are used in various ways and are designated accordingly. A list quadrat is one in which the plants are counted and a list is made of the species with the number of each. A chart quadrat is one which is charted on paper and the position of each plant in the quadrat is shown. A denuded quadrat is one from which the vegetation has been removed, while a permanent quadrat is one that is staked out so that observations may be made on it from year to year. Sometimes in studying vegetation a transect is found to be more useful than quadrats. A transect is a line drawn through a plant community and usually the plants along one side or along both sides of the line are listed.

One way of using the quadrat method in class work is as follows: 6 or 8 100-foot steel surveyor's tapes and about the same number of 10-foot tapes are provided, the number depending upon the size of the class. When a place for mapping has been selected 4 of the long tapes are used to lay out

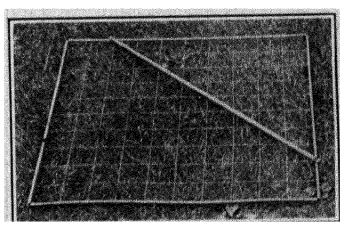


FIG. 118.—A portable folding quadrat divided into decimeter squares by means of cords.

a quadrat 100 feet square, steel tentpins being used to hold the tapes. A fifth tape is now stretched 10 feet from one side of the quadrat in such a way as to lay off a 10-foot strip. The short tapes are used to subdivide this strip into 10-foot quadrats. A party of about three students works on each 10-foot quadrat, two counting the plants and the third serving as recorder. Quadrat paper, ruled into 100 squares, each square representing a 10-foot quadrat, is used for the record. A combination of the chart and list quadrat is made. A symbol, usually an initial letter, is used for each species and a list of the species with their symbols is placed on the margin of the quadrat paper. The symbol of each species, with the number of individuals representing it, is placed within the quadrat space in which it occurs. Thus when the entire 100-foot quadrat is finished the record contains a list of all species found, the number of individuals of each species, and the position of each plant within 10 feet of its actual occurence. From such a study students may readily determine the dominant species, the subdominant species of societies, and other structural characteristics of the community.

The quadrat method may also be used for determining the frequency of occurrence of the various species of a community. This may be done by

using a folding meter quadrat, though some workers prefer a smaller size and some prefer a circle instead of a quadrat. This quadrat is placed in the vegetation and the species occuring in it are listed, the process being repeated at more or less regular intervals throughout the community. The result is that lists are obtained for a large number of small quadrats scattered through the community, the number depending upon the size of the community and the character of the vegetation. The next step is to determine in how many quadrats each species occurs. The dominant species may occur in all of them but most of the secondary species will not. The percentage of the total number of quadrats used in which a given species occurs is taken as the frequency index of that species. For example, if the total number of quadrats is 200 and a given species is found to occur in 72 of them, the frequency index of this species is 0.36.

Suggested Problems

1. To make a map of the vegetation of a limited area.
2. To compare a climax association with a seral community as to number of species and number of individual plants.
3. To discover which species occur most frequently in a given plant community.
4. To study the revegetation of a denuded quadrat.

The Structure and Local Distribution of Plant Communities.—The quadrat method may be used for studying the structure of plant communities but a great deal may also be done by observation alone. In most localities a considerable amount of time can be given to this phase of the work. In this as in all ecological work it is necessary for the students to know the names of the plants concerned and there is always a question as to how much time should be devoted to systematic or taxonomic studies. The amount varies with the total amount of time available for class use but as a rule the ability to use keys for plant determination should be acquired in other courses rather than in ecology. At any rate it is much better to simply tell the students what the plants are than to sacrifice real ecological studies to the work of identification.

Suggested Problems

1. To discover how many layers of vegetation may be found in a forest and to determine the subdominant species of each.
2. To discover what plant societies are present in certain local associations.
3. To describe in detail the structure of a given association.
4. To compare "uplands" and "bottomlands" as to characteristic tree species.
5. To discover whether there is any correlation between soil types and the local distribution of vegetation.

Plant Succession.—The studies that may be made on plant succession will vary greatly with local conditions. Usually some early stages can be found on rock outcrops or on areas that have been denuded by erosion or by man, perhaps in the construction of a drainage ditch, or some other agency. Even an ant-hill or the soil thrown out around a woodchuck hole

may be made to serve a valuable purpose. Usually also some examples of "zonation" may be found, each zone of vegetation representing a stage in a sere. This is especially well shown around ponds or lakes but may frequently be found also along streams. If coal-mining striplands, or sand-dune areas, or rock ravines, are available the class will be unusually fortunate.

Suggested Problems

1. To work out the hydrosere of an inland lake.
2. To discover what plants are the pioneer species on bare rock.
3. To outline the succession that takes place on an area denuded by the activity of man.
4. To compare a psammosere with a lithosere in the same climatic region.
5. To determine the successional significance of zonation.

Phenology.—As a rule phenological studies are not well adapted for single field exercises but they furnish an abundance of excellent problems for individual students or groups of students to carry on throughout a field season.

Suggested Problems

1. To make a study of the seasonal succession of flowers in a local plant community.
2. To make a comparative phenological record of all species of maple (or some other genus) that are available.
3. To make a comparative study of the time of leaf development on the various species of trees on the campus or in a local wood-lot.
4. To make a comparative study of the time of leaf fall on the above trees.
5. To make a comparative study of the time of ripening of fruits on the plants of a local plant community.

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