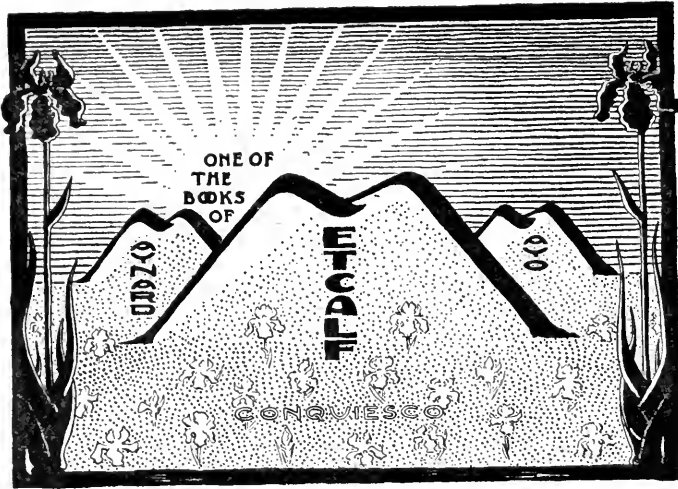


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THE LIVING
PLANT

WILLIAM R. GANONG

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American Nature Series
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THE LIVING PLANT

A DESCRIPTION AND INTERPRETATION OF ITS
FUNCTIONS AND STRUCTURE

BY
WILLIAM F. GANONG, PH. D.
PROFESSOR OF BOTANY IN SMITH COLLEGE



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1913

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Of the scholars of Salomon's House,—“lastly, we have three that raise the former discoveries by experiments, into greater observations, axioms, and aphorisms. These we call Interpreters of Nature.”

FRANCIS BACON, *The New Atlantis*

PREFACE

The very first words I would write in this book are addressed to my botanical colleagues, whom I wish to inform that the work is not intended for them. In this statement I am by no means invoking immunity from scientific criticism, but emphasizing the aim of the book. It is not designed as a digest of our present scientific knowledge of plant physiology for the use of experts in that subject, but, in conformity with the aim of the series of which it is a part, it seeks to present to all who have interest to learn an accurate and vivid conception of the principal things in plant life. I was once myself such a learner, and I have tried to write such a book as I would then have delighted to read. It is, in a word, an attempt at that literature of interpretation which was foreshadowed by Francis Bacon in the fine passage that stands on its dedicatory page.

This aim will explain peculiarities of the work not otherwise obvious. Thus, I have been at more pains to be clear than to be brief, assuming on the part of my reader no great knowledge of the subject, but a large willingness to take trouble to learn; and as I have tried to discuss every process with fulness enough to elucidate its nature, my book has wandered through a leisurely course to a length quite shockingly great. But I comfort myself with the reflection that the plan and the subject hardly permit other treatment; for a royal road to a real understanding of plant phenomena does neither exist nor can it be built. Perhaps, indeed, the very portliness of the volume will act as a deterrent to any attempt at a desultory reading in the hammock, and will rather suggest the study table, and the principal feature of an evening's business,

and sternly-preserved leisure for reflective concentration on the matters it considers. At least, any value it may have for the reader will be realized best through this mode of approach.

As to the method of treatment in particular, I have sought especially to interpret those phenomena of plant life which come within ordinary observation and experience, penetrating just deeply enough into each to make clear the principle of its operation,—“the theory of the thing” in popular phrase;—and sometimes that has taken me far and sometimes it has not. Thus is explained the absence of some matters of high technical interest, which lie, however, outside the experience of the general observer. Where explanations are concerned, I have given the known ones when there are any, and when these are lacking I have not hesitated to supply suggestions of my own, though in a way designed to show their hypothetical character. As to statements of fact, I have meant to present only those which have acquired the impersonal validity of science, for which reason I have omitted a good many of the newest ideas, even at the risk of seeming not to know them; for I have noticed that he who is too closely up to date in science has later a good deal to unlearn.

This deliberate conservatism is not, however, the inspiration of my advocacy of Darwinian adaptation, for that is based upon conviction as to its essential correctness. I am very well aware that some eminently respectable people now consider adaptation, except as an accident, an antiquated idea. I have myself experienced periods of this belief, but have always found myself back to causative adaptation as the most rational explanation we possess of the relations of living beings to their environment. But while holding to the reality of adaptation as an historical and causative process, I do not by any means suppose that all plant phenomena are explainable on this basis; and in this book I have tried to sort out the numerous influences at work, and to show which phenomena are best explained by adaptation, which by mechanical causation, and which by others of the possible forma-

tive influences. But adaptation seems to me to guide the course of a mightier current upon which mechanical causation and other influences are ripples or eddies, or at least no more than the waves whose only lasting influence is occasionally to open new directions for the current to move in. With this belief in adaptation, I have naturally not hesitated to use the corresponding language of purpose,—not a mystical, supernatural, forethoughtful purpose, but a physical, natural, experiential purpose, which does not presuppose any forethought, but only the preservation and accumulation of the results of past experiences wherein each step in advance was purely chanceful, and survived only because it happened to fit.

There is one other matter of this kind I would mention, and that will be all. Throughout the book I have made great use of diagrams, generalizations, and conventionalizations; and this may seem inconsistent with the vitalistic rather than mechanistic tone of the work. The scientific and educational status of this practice are sufficiently explained in Chapter I, but I would like also to say that I think our advance in plant physiology is measured exactly by our ability to represent each detail in a mechanical diagram, a physical formula, or a chemical equation. For the evidence certainly indicates that every individual process of plants is purely mechanical, physical, or chemical. What cannot thus be explained, and what we have made as yet little progress towards explaining, is the nature of the influence which establishes and holds these processes in orderly sequences repeated in wonderfully complicated cycles generation after generation. When we have explained the operation of each gun, and dynamo, and powder-hoist on a battleship, have we thereby explained the rationale of the operation of a battleship? Here is where the real difference lies today between mechanism and vitalism. And this is the vitalism of this book,—not a supernatural vitalism of the theological type, and certainly not designed for theological needs, but a perfectly natural vitalism based on the superior interpretive

power of an hypothesis assuming the existence in Nature of an X-entity, additional to matter and energy but of the same cosmic rank as they, and manifesting itself to our senses only through its power to keep a certain quantity of matter and energy in the continuous orderly ferment we call life. If those complicated and regularly-recurring cycles of material and energy changes which constitute the visible phenomena of life were mechanistically self-originating, self-controlling, and self-surviving, then Nature should be full of scattered fragments of such cycles, whereas she is not. For everything in Nature has either all of the characteristics of life, or else it has none of them; it is either alive, or it is not. And there you have the chief argument of vitalism against mechanism.

Having thus explained, the best that I can, the spirit and scope of this book, I turn to make my grateful acknowledgement to those who have rendered kind aid in its preparation. For the illustrations, in particular, I am indebted to many persons. For the privilege of using the two dozen or more fine pictures from Gray's *Structural Botany* and the Chicago *Textbook*, as acknowledged with the cuts, I am indebted to the publishers of those works, the American Book Company; and I have also been permitted by the Doubleday Page Company to use figure 8, and by the Bullard Company to use figure 15, from publications of theirs. Further, a ready consent has been given by Professor G. F. Atkinson to my use of figure 118, and by Dr. C. C. Curtis, to my use of figures 67 and 73, from books of theirs published by Messrs. Henry Holt and Company. In addition, I have copied a number of figures from various foreign works, notably those of Sachs, Kerner, Strasburger and Kny, taking pains, however, to acknowledge the sources with the cuts themselves. Further, I have made use without special acknowledgement of a good many pictures which have been copied so often as to have become a kind of common property (viz., figures 17, 35, 94, 147, 149 to 161, 164, 166-7, 169-171), although these, together with certain others

whose source is acknowledged (viz., figures 81, 85, 107, 168, 175), have been re-drawn for this work by one of my students, Miss Bertha Bodwell, now Mrs. Richard Potter. The remainder of the pictures, somewhat over one-half of those in the book, are new. Several have been made by students of mine:—figures 18 to 23, with 76 and 84 by Miss Bodwell: figures 27, 56, 57, 132, illustrating physiological apparatus, with 126–7–8, showing phases of growth, by Miss Margaret Sargent: figures 103, 104, parts of a series representing the development of representative plants, by Miss Ruth Huntington, now Mrs. Max Brödel: figure 87 by Miss Stella Streeter: figure 133 by Miss Hope Sherman: while the fine graphs of figures 70 and 123 were worked out from the original materials as well as drawn by Miss Marion Pleasants. The photograph of figure 26 was given me by another student, Miss Anne Barrows, now Mrs. Walter Seelye. The elaborate and exact drawing of root tissues forming figure 53 was made by my colleague, Dr. F. Grace Smith, Associate Professor of Botany in Smith College, while the markedly original and very satisfactory series of generalized drawings in illustration of the principal physiological processes, embodied on the colored Plate I, and in the multiple figures 54, 66, 139, together with the figures 30 and 99, were specially drawn for this book by another of my associates, Miss Helen A. Choate, Instructor in Botany in Smith College. To all of these willing and efficient collaborators I desire here to express my indebtedness, and my grateful thanks. The remainder of the illustrations, including the new photographs and diagrams, are productions of my own.

But the greatest of my obligations is to Miss Choate, who has read both manuscript and proofs in a critical spirit no less militant because friendly. She has not been concerned so much with the scientific aspects of the chapters as with their exposition, representing in this the rights of the reader, for whose benefit she has curbed much exuberance of expression, and eliminated many an obscurity and inconsistency. That some of these faults re-

main is not to be laid to her, since I have sometimes leaned back on superior official authority and had my own way.

In the first announcement of the book it was said that keys, similar in principle to those used in works on classification, would be appended as aids to the reader in finding the explanations of phenomena. These keys, however, have assumed such proportions that it seems best to transfer them to a separate work. They are now in process of elaboration in detail by another of my associates, Miss Julia Paton, Fellow in Botany in Smith College, and will presently appear as a synoptical handbook.

Finally, I recall that in advising the reader to try as many experiments as possible for himself, I said that practical guides to experimentation would be suggested in the Preface. Unfortunately the one of these I consider the best, I am forbidden by modesty to name, excepting that I may mention, as our friend Mr. Dooley would put it in similar case, that it is entitled *A Laboratory Course in Plant Physiology*, is published by Messrs. Henry Holt and Company, and is written by myself.

THE AUTHOR.

Smith College,

March 15, 1913.

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The nature and properties of living substance, called Protoplasm, of plants, which, however, can be understood better after some study of the physiological processes, and hence is discussed in Chapter 6. Protoplasm.

The physiological processes of plants, concerned with,—

The methods by which plants become altered in structure, habits, and identity, including,—

Maintenance of the Individual, dependent on,—

Preservation of the Race, dependent on,—

The methods of alteration

The results attained, considered

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LAY THE PLAN OF THIS BOOK

		<i>Chapters</i>
		1. Methods of Study
he pro- r daily needs,	The acquisition of food, which is constructed by plants inside their own tissues, as described in Chapter	2. Photosynthesis
	The development of photosynthetic structures, to which is devoted Chapter	3. Leaves and Stems
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THE LIVING PLANT

CHAPTER I

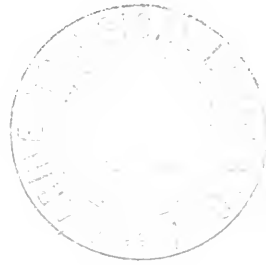
THE VARIOUS WAYS IN WHICH PLANTS APPEAL TO THE INTERESTS AND MIND OF MAN

Methods of Study in the Science of Botany



AND he spake of trees, from the cedar tree that is in Lebanon even unto the hyssop that springeth out of the wall." Thus runs the record of the first botanical teacher, reputed also the wisest of men, as writ in the greatest of books. And from the days of King Solomon down to our own, men never have ceased to speak and learn of plants, until now the circle of knowledge has long been too vast for any one mind to encompass. To us, plants embrace not alone the cedar and the hyssop, but the fern, the moss, the lichen, the seaweed, the mushroom, the mold, the blight, the yeast, and the germ of disease within the body of man. And it is not alone their forms, their uses, and their habits which concern us, but as well the minutest details of their internal construction: the meanings of their resemblances and their differences: the ways of their nutrition, increase, and adjustment to their surroundings: the possibilities of their development to greater and yet undiscovered utilities: and in truth no less than every fact which the intellect of man can discover about them.

The field of botanical study is therefore not simply vast, it is practically limitless,—in this respect transcending the natural powers of man, which are small. Therefore, while every school-



boy can grasp the salient facts in that organized knowledge of plants which we call the Science of Botany, no one person can actually master any more than a limited portion thereof, especially if he have the ambition to know it sufficiently well to aid in expanding the bounds of our knowledge. For the purpose of specialized study, accordingly, there have been developed within the science a number of divisions which are dependent on the nature of the problems presented, and therefore on the methods employed in their study. The divisions are these. First is *Classification* (called also *Systematic Botany*, or *Taxonomy*), the oldest and most fundamental of all, and doubtless the theme of King Solomon's discourse. It establishes the relationships of plants to one another, and arranges them accordingly, while describing and naming them. It is studied through exact observation and comparison of the external parts of plants, which can be kept preserved in a pressed and dried condition in collections called Herbaria, while its results are embodied not only in great monographs, but in handbooks, or Manuals, so arranged as to enable any person to identify plants for himself. Second is *Morphology*, which deals with the parts, or structures, of plants, and establishes their relationships to one another while describing and naming them. Morphology is very much the same to the parts of plants that classification is to plants as a whole. The name in the past has been associated most closely with the comparative study of the large external structures,—roots, stems, leaves, flowers, and fruits,—and their transformations into tendrils, spines, pitchers and the like, but is nowadays given a far wider extension; while special names describe the phases concerned with minute or internal parts, and needing the use of such exact and delicate instruments as the microscope and microtome,—*Embryology* or “life-history,” for the development of the structures in the individual plant, *Anatomy*, for the cellular construction, and *Cytology* for the internal structure of the cells themselves. Third is *Physiology*, a word which

has precisely the same meaning with plants as with animals, comprehending the study of those functions or processes by which they secure the maintenance of their daily lives and the perpetuation of their kinds. It is studied chiefly through experiment by aid of the exact methods and instruments of physics and chemistry, though it reaches into realms which those sciences do not touch. Fourth is *Ecology*, youngest of the divisions of the science, and greater as yet in promise than performance, but nevertheless of the very first interest to a great many people. It explains the adaptations of plants and their parts, that is, the ways in which these are adjusted to the conditions of the world around, involving the meanings of their forms, sizes, colors and the like. This division has sometimes been called, and still is by some Germans, *Biology*; but that word should be kept for its legitimate use as meaning the study of life comprehensively, and therefore equivalent to Zoology and Botany together. Fifth is *Plant Industry* (called also *Economic Botany*), which is the study of the ways in which plants may be made to yield the greatest service to man. The older phases thereof, *Agriculture*, *Horticulture*, *Pharmacology*, and *Forestry*, originally purely practical, are now scientifically studied, and to their very great profit; while strictly scientific from their foundation have been the newer phases of *Pathology*, or the study of diseases, *Bacteriology*, or the study of germs and their effects, and *Plant-breeding*, or the systematic development of better kinds of plants. And to these divisions there is every promise that the near future will add yet a sixth, *Botanical Education*, which will attempt not only to train students much better in the science, but also to interpret botanical progress to the world at large. An important phase of this division will be the production of works, on the *Natural History of Plants*, which will set forth, with a combination of scientific accuracy and literary charm, not only the technical and economic aspects of plant life, but also those historical, legendary, and imaginative aspects which give to a study its

widest human interest. Indeed, the production of such works may be viewed as the logical aim of all botanical study.

Such are the principal divisions of botanical science as we know them at present. This book, concerned as it is with the life of plants, deals chiefly with Physiology, but the divisions are interlocked inextricably, and I must perforce make many an excursion into the others. This science, and all science, is a unit, and subdivisions thereof are nothing other than a concession to the limitations of the powers of man.

As the reader reflects on this matter of the various divisions of botanical science, he cannot but notice how unequal they are in apparent utility to man, and he may even inquire why we should study at all the ones that seem useless. Two reasons at least exist why we should, and do. First, some people take pleasure therein, precisely as do others in art, music, and literature. Nobody thinks of asking what use these latter may be, the value of pure pleasure being obvious enough; but the world has mostly yet to learn to extend the same approbation to the seemingly useless sciences. Second, the history of human progress has shown that the greatest applications of science to the useful arts have sprung from purely scientific investigations of a non-useful type. Nothing, doubtless, could have seemed more useless to cotemporary critics than the studies of those early naturalists who delighted to apply the new-made microscope to the investigation of the living atoms which swarm in slime; and yet from these very studies has come our knowledge of Bacteria, and our power to control the deadliest diseases that scourge mankind. Likewise photography, all the applications of electricity, a vast range of chemical arts, and indeed most others of the wonderful applications of science to utility, have developed incidentally from purely abstract scientific researches made without any regard to useful applications. Furthermore, it is quite impossible to predict at what point upon the general surface of expanding knowledge the next useful discovery will spring forth. In fact there is no natural

boundary between useful and useless knowledge; they are one and indivisible, and such boundary as may seem to exist is simply a shadow that shifts over the surface, changing with times and our customs. Accordingly, the only possible way in which humanity can obtain useful results from science, lies through the encouragement of the development of all of its phases; and this may be done with the assurance that now and then some useful applications will somewhere appear, and pay manifold for it all. And this is precisely the reason, moreover, why no good system of education can confine itself to teaching useful knowledge alone. It is unfortunately still true, as it was when Stephen Hales, the founder of Plant Physiology, wrote nearly two centuries ago, that pure science needs protection "from the reproaches that the ignorant are apt unreasonably to cast on researches of this kind, notwithstanding that they are the only solid and rational means whereby we may ever hope to make any real advance in the knowledge of Nature." When, therefore, the reader hears anyone asking what is the use of this or that phase of knowledge, or when he sees practical men showing impatience with the impracticability of great scholars and contempt for the uselessness of their knowledge, he may well state these facts by way of courteous reproof. And he may even add, as to such knowledge, that those who pursue it, in the absence of the material rewards reaped in full measure by practical men, deserve no less tribute of respect and approbation than is accorded by common consent to those whose efforts bring them personal wealth. Both in fact, though in different ways, are contributing to the welfare and progress of humanity.

I have spoken, just now, of the pleasures of the study of Botany, and over this theme I would linger a little. It is true of all science that the pleasures of its study lie deep, and one must reach far before he can grasp them. It is not as with literature, for example, which makes appeal to the feelings, that lie near the surface and are easy to touch; for science appeals chiefly to reason, which

lies deeper and is slower of action. This is why literature is enjoyed by nearly all people and science by only a few, and why literary reputations can be made in youth while those of science are mostly attained much later in life. Yet, when grasped, the pleasures of science are no less keen than those derived from any other field of intellectual endeavor, and I have even fancied that they yield an especially deep and lasting satisfaction, though in this perhaps I am wrong. There can be, I believe, no pleasure in life any greater than that which comes to the scientific man with the moment in which some truth heretofore not known to mankind first dawns upon him; and it is in the hope of such moments of exaltation that he is willing to undergo toil, poverty, hardship, and even peril of life itself. The charm that there is in this pursuit of truth receives many illustrations from the biographies of eminent scientific investigators, and especially from their familiar letters, in which can be seen more clearly than elsewhere the actual workings of the scientific spirit.* But though felt to the

* A characteristic example is furnished by the following letter written by Charles Darwin to Asa Gray,—the eminent American Botanist.

Down, August 9 [1862].

My dear Gray,—It is late at night, and I am going to write briefly, and of course to beg a favour.

The *Mitchella* very good, but pollen apparently equal-sized. I have just examined *Hottonia*, grand difference in pollen. *Echium vulgare*, a humbug, merely a case like *Thymus*. But I am almost stark staring mad over *Lythrum*; if I can prove what I fully believe; it is a grand case of TRIMORPHISM, with three different pollens and three stigmas; I have castrated and fertilized above ninety flowers, trying all the eighteen distinct crosses which are possible within the limits of this one species! I cannot explain, but I feel sure you would think it a grand case. I have been writing to Botanists to see if I can possibly get *L. hyssopifolia*, and it has just flashed on me that you might have *Lythrum* in North America, and I have looked to your Manual. For the love of heaven have a look at some of your species, and if you can get me seed, do; I want much to try species with few stamens, if they are dimorphic; *Nesaea verticillata* I should expect to be trimorphic. Seed! Seed! Seed! I should rather like seed of *Mitchella*. But oh, *Lythrum*!

Your utterly mad friend,

C. DARWIN.

fullest only by those who fare the farthest, the pleasures of science are by no means unknown even to youthful students; and I have myself experienced in the past and have since noticed in others, a keen enjoyment in the use of exact scientific methods and tools, a great satisfaction in the acquisition of knowledge that one feels to be solidly grounded, and a lasting pleasure in an understanding of the workings of the greater natural phenomena. But while the personal and æsthetic elements are certainly by no means absent from scientific study, as indeed the accompanying picture will bear witness, the student must realize that the deepest pleasures of science are of stern and spartan sort, somewhat like those felt by the strong man when he rejoiceth to run a race.

We must return for a moment to the matter of the unity of botanical science in order to consider yet another concession, besides its artificial divisions, to human limitations. This unity of the science is of course but a reflection of the unity of Nature, where all of the vast number of facts and phenomena intergrade and interlock without any real boundaries. Yet the mind of man is so made that it can grasp only definite conceptions, and not many of these; and it can no more form a definite image of the infinite intergradation of phenomena than it can of the infinite largeness of space or the infinite smallness of the sub-constitution of matter. Hence it is necessary, for purposes of education and exposition, to create definite images out of indefinite material. Take, as an example, the subject of leaves. Leaves are so many, so diverse, so intergradient, that no learner can grasp any considerable proportion of the facts about leaves as they actually are. The substitute therefor, to which every teacher and author is obliged to resort, is a subjective conception of a generalized or average leaf, built up for the learner from observation of a number of actual leaves; or, better, it is a composite conception of a leaf built up in the receptive mind of the learner from many observations of actual leaves, much as composite photographs



FIG. 1. View in an experiment greenhouse in which studies on Plant Physiology are made by college students.

of human faces are built up from exposures of many actual faces upon the sensitive photographic plate. This is precisely what our Text-books are doing when they devote chapters to "The Leaf," "The Stem," and the like. These titles do not represent things, but ideas; there are *leaves* in Nature but no such thing as *the leaf*. But the analogy of these composite conceptions to composite photographs goes yet a step farther, for, just as a real face is occasionally seen which resembles the composite face of the photograph, so an actual structure or phenomenon is sometimes found which is like our mental composite of its kind. Such a real thing is then said to be *typical*, and that is what is actually meant by this word in science. When, however, no typical representative of the composite is available, we are still not without resources; for it is possible to give exact and clear definition to the dim and elusive outlines of the composite itself by drawing firm sweeping lines through its more prominent places,—a process which constitutes *generalization*, or *conventionalization*. When the data concerned are expressed in figures, then the result is a round-number average, or *conventional constant*; when they are expressed in pictures, the results are *generalized drawings*, or, if simplified to mere structural aids to the imagination, *diagrams*; when they are expressed in words, the results are generalizations, or *verities*, the "aphorisms" of Bacon. Throughout this book, in accordance with its aim to interpret plant life in the large, I have made great use of composite conceptions, typical things, conventional constants, generalized drawings, diagrams and verities,—to a degree which will meet with much disapprobation from my scientific colleagues. But I maintain that such generalized knowledge of plants is not only infinitely better than no knowledge at all, but is actually the most useful kind, as it is the only practicable kind, for the non-technical learner, whose knowledge in other departments of learning,—in geography, history, and so forth,—is largely of this character. And I further maintain that if only we would make greater use of it, along with its logically-correlated methods,

in our educational system, we should have less cause to complain of the comparatively empty condition of our elective science classrooms. It is not of course representative of the methods whereby scientific investigation is successfully pursued; but where else in human affairs do we insist upon teaching all people the technical methods or none? In large measure, Science, in order to be advanced, must be dehumanized; but in order to be used, it must be humanized.

The fact is, the human mind is a very poor instrument for scientific research, for which it was never developed. Unless all of our knowledge is at fault, the mind of man was evolved under stress of use as his chief weapon in the struggle for physical existence; naturally, therefore, all of its stronger traits are fitted to that very concrete activity rather than to uses of an abstract intellectual sort. Its power of concentration upon a single aim, with determination to achieve it by any means: its instinctive and partizan exaltation of its own case and minimization of its opponent's: its tendency to warp all testimony to its own credit: its quick defense of its own caste or clan, right or wrong, with its ready submission to the conventions thereof and contempt for everything outside: its preference for keeping to beaten and safe paths and for shunning the unknown, which it peoples with mysteries and evil designs: its liking for following the most assertive leaders and for leaning back upon their authority;—all of these are invaluable traits in the struggle of the individuals of a social community for existence, but they form a very bad basis for scientific investigation, which requires the opposite qualities of disinterestedness, impartiality, and the judicial weighing of evidence for the determination of the exact truth without any regard to its effects upon persons, interests or dogmas. All men have the primitive self-centering qualities highly developed; and the scientific research of mankind is done upon a small residue of the opposite qualities which a few of them happen to possess, and which even in them are not so much natural as assiduously

cultivated. Is it any wonder, then, that scientific progress is so slow, so laborious, and so expensive?

There remains one other phase of the relation existing between Science and the mind of Man, which is so fundamental to the subject of this book that we must give it some special attention. It concerns the apparent purposefulness of many biological phenomena, as expressed especially in adaptation. What, then, is this adaptation, with which the writings of Darwin have made us so familiar? It is any feature, whether of structure or action, which brings a life process into harmonious relation with the external conditions that affect it. The flatness of a leaf is an adaptation to the need for a very wide spread of green tissue to light, as is to be fully explained in the following chapter. The colors, shapes, sizes and peculiarities of form in flowers are chiefly adaptations to the utilization of insects in the transfer of pollen, which is an indispensable prerequisite to cross fertilization, as will also be demonstrated in the suitable place. And other cases are known without number, involving not only single features, but often the coöperation of several. Now the question is this,—in what way has this remarkable fitness of form to function, of structure to use, of parts to environments arisen? It was formerly supposed that these adaptations were the direct work of the Creator,—the ETERNAL, IMMEASURABLE, OMNISCIENT, and OMNIPOTENT,—as Linnæus grandly characterizes him in the *Systema Naturæ*. But Darwin gave evidence, in *The Origin of Species*, greatest of all secular books, tending to show that they arose by a gradual process of evolution, developing in causative touch at every step with the conditions which they fit; and this view has long appealed as satisfactory to most biologists. But in our own day it is becoming somewhat customary to attribute adaptations rather to various adventitious origins, and to explain their persistence merely by the negative supposition that they are not out of harmony with the conditions concerned. In a book of this kind it is needful to take a definite position on this subject,

if for no other reason than this,—that the language one may use is concerned. My position in general is the Darwinian one,—that adaptation in the main has arisen as a gradual causative accompaniment of evolution. Indeed, such a causative, or historical development of adaptation appears to me an inseparable corollary of the very idea of evolution, and wholly independent of its method,—whether it proceed by many imperceptibly small steps as Darwin believed, or by fewer and perceptible ones, as newer evidence seems to be showing. And the point about use of language is this, that if adaptation is a causative process,—the feature developing in causal touch with the conditions concerned,—then it is quite suitable and correct to say that the adaptation exists for such-and-such a purpose; and I do not hesitate to use such expressions in this book. In so doing I am in the very best of company, for Darwin himself continually uses the language of purpose, or teleology; and both Huxley and Asa Gray, Darwin's devoted friends and co-believers, point out in their writings that evolution on the basis of Natural Selection places teleology on a scientific basis.* This fact is overlooked in our day by many, who think it scientific to avoid teleological or purposeful language as though it were a plague. Science, indeed, hath her fashions and her dogmas no less than other fields of human endeavor.

A chief reason for the occasional denials of the causative origin of adaptation arises from reaction against the over-importance, and over-perfection, so often attributed to it. Adaptation has often been claimed on the scantiest evidence without any attempt at proof. At its best, however, adaptation can never be perfect, but is rather a general or generic affair, very much like our own adaptations to the trades or professions we follow. This is because no feature of structure or function is free to respond to one adaptive need alone, but has to compromise with other consider-

* An example of Darwin's teleological language is found in the passage from one of his books cited on page 234 of this volume. As to his establishment of teleology as a scientific principle, compare his *Life and Letters*, New York, 1888, II, 430.

ations which often have more influence than adaptation itself. Thus, in addition to the principal adaptation, (such for example as the flatness of a leaf in adaptation to the need for spreading much surface to the light), there are secondary adaptive needs, such as for protection against dryness or other hostile influences. Further, a prominent feature may not be adaptive, but incidental to some other process, as in autumn coloration of foliage, or the mathematically-arranged origins of leaves: or it may be merely a mechanical effect, like the drooping of old branches of evergreen trees: or it may represent an individual adjustment to one feature of the surroundings, like the bent-over leaf-stalks of house plants in windows: or it may be inherited from the past without present significance, as in the compound early leaves of the Boston Ivy: or it may represent a spontaneous new variation, or mutation, or sport, such as originate new garden varieties of flowers, leaves, or fruits; or it may have yet other meanings of minor sort. These cases and illustrations will all be further explained in the following pages, and I merely cite them to show that not all features of plants are adaptations, while all adaptations are interwoven more or less with these other considerations, the actual structure being the resultant of the interaction of them all. The matter can be expressed in this way, that adaptation can never fit a condition as an old glove fits the hand, but rather as a cloak fits the body. One should therefore neither expect too much of it on the one hand, nor reject it altogether on the other. The real problem is not so much to find adaptations as to separate out and define the various factors that enter into the combinations of which adaptation is only a part.

One other important phase of the relations existing between the human mind and the workings of organic nature, concerns the question as to whether there is anything in living beings except physics and chemistry,—in other words whether they are mechanism only, or whether the mechanism is inspired by vitalism. The evidence seems to be showing clearly enough that all of the in-

dividual processes of plants and animals are purely physical or chemical, with no trace of a vital force in the old sense. Furthermore, the orderly sequence and coöperation of these processes is largely explained by their linking up through the medium of stimuli, as will later be explained in the suitable places in this book. But it does not seem to me probable that the processes only happen to be thus linked up, or that these particular linkings are merely the accidental survivors of innumerable ones that happened in the past. Indeed, the most reasonable explanation of the phenomena of organic nature in the large seems to me this, that all of the life processes are subordinate to some influence which is using living matter as a seat for its operations. Thus there would exist in nature not two, but three working entities, matter, energy, and this X-influence. Perhaps the living matter is the home which the principle of intelligence in Nature has built for its residence. This is something more than vitalism, or even the neo-vitalism of some philosophers; it is a super-vitalism. But its acceptance harmonizes some of the greatest difficulties in the interpretation of Nature, as the following pages will illustrate in the suitable places.

Finally there remains one matter which I wish to add at this place. It may seem to the reader, as it will to some of my colleagues, that in laying so much stress as I do upon causative adaptation, and a number of things of that sort, I am reading into Nature a principle closely akin to intelligence. If I seem to do this it is because that is my intention. I believe that the evidence now accumulating is sufficient to show that the same principle which actuates intelligence also actuates all the workings of Nature; or, as I have expressed the matter on a later page of this book, all living matter thinks, though only the portion thereof which enters into the brain of man is aware that it thinks. Our intelligence is a kind of epitomized expression of the principles underlying the operations of nature, very much as mathematics is an epitomized expression of the relations of number,

or as the daily newspaper is an epitomized expression of the doings of civilization. And this I mean not as a metaphor, but as a serious scientific hypothesis.

This discussion of adaptation and kindred matters, and perhaps some others of the matters contained in this chapter, will have little meaning, I know, to the reader who may be making his first acquaintance with plant life through this book. But I venture to hope that the case will be different after he has made some study of the pages which follow. Perhaps I should earlier have advised him to read this chapter the last; and at least I do now suggest that he read it again after he has finished the rest of the book.



CHAPTER II

THE PREVALENCE OF GREEN COLOR IN PLANTS, AND THE REASON WHY IT EXISTS

Chlorophyll and Photosynthesis



SO manifold are the works displayed in the world of living plants, that to one who seeks some tie to bind them all into a single natural group they seem at first to present only an endless diversity. They do in fact exhibit every possible gradation and variation; in *size*, from the stately Sequoia of the Sierras, or the giant Eucalyptus of Australia, towering high above all other living things and mighty in girth, down to the humblest weed of the wayside; in *form*, from the graceful tree with its spray of twigs and myriad leaves to the simplest sea-born plant whose life is wholly encompassed within a miniature globe: in *color*, from the quiet green of the forest to the brilliant hues of flowers, sea-mosses, or mushrooms: in *texture*, from the ivory-hard seeds of palms to the jelly-soft fronds of some seaweeds; in *habit*, from the independent life of the mightiest trees in the woods to the parasitic existence of a deadly germ of disease within the body of man. Nowhere among these features, nor yet among any others that we know, can we find a single one which applies to all plants. What is it then which binds all of this heterogeneous assemblage into a single natural group?

Failing to find any one feature common to all kinds of plants, a scientifically-minded inquirer would next turn to ask what feature prevails most widely among them. If one marshals before his mental vision all of the great groups, from the flowering trees to the microscopical germs, and centers observation upon

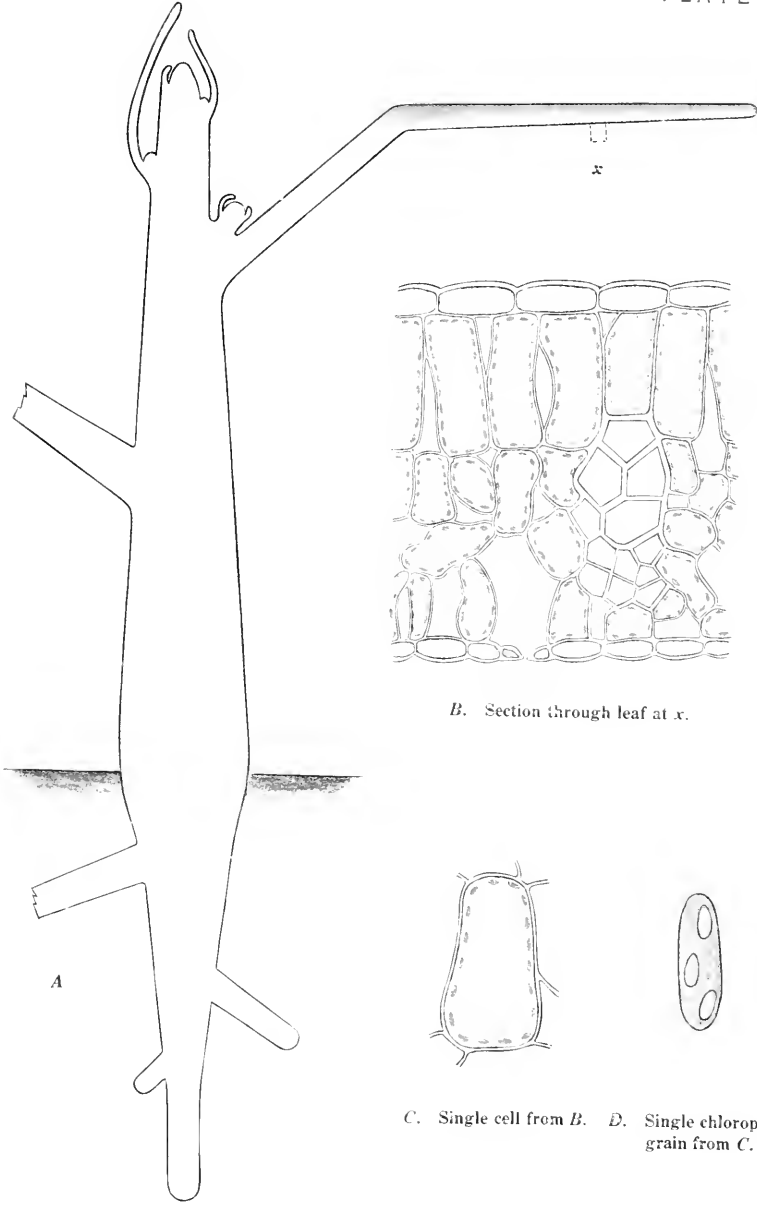
one after another, it gradually becomes plain that one feature, and only one, does prevail very widely,—and that is *the possession of green color*. Moreover, a deeper study by aid of microscope and experiment shows that this truth is more nearly universal than appears at first sight, for a good many plants that display other colors,—e. g., the red foliage plants of the gardens and the brown and red seaweeds,—prove to be green in reality, though that color is masked by the presence of the others.

But although the green color, which is that of a definite substance called *chlorophyll*, is thus very wide spread among plants, there are some, nevertheless, which really do not have it. Such are the mushrooms, molds, mildews, yeasts and germs, as likewise the Ghost Plant (or Indian Pipe), of the woods, the twining Dodder of the fields, and a few others. These plants are mostly white to brown, though they often exhibit very brilliant hues of red, yellow, and even a kind of a green, which, however, is very different in shade and nature from chlorophyll. All of these brighter colors are easily removable by chemical means; and when that is done, the tissues are left either white or brown, with never a trace of the chlorophyll.

There are, accordingly, plants which really are green and plants which really are not. And the reader's first natural thought, that so striking a difference in one feature is probably linked with differences in others, is correct. In the first place, observation at once shows a very fundamental difference between the two kinds in habit, for all of those lacking the chlorophyll are dependent for their food upon other beings, either upon living plants or animals, (in which case they are called *parasites*), or else upon their decaying remains, (when they are called *saprophytes*). In sharp contradistinction stand the green plants, practically all of which subsist without aid from other living things, thriving upon materials which they take from the air, the soil and the waters. A second great difference consists in this, that all of the non-green plants are small and of humble

habit, as the list above given will testify, contenting themselves with the odd and obscure places of nature, while the green plants grow grandly in stature and number, possessing the earth. And still a third difference exists, less likely to be thought of but no less important for our present inquiry, namely, the study of classification has shown that the non-green plants, for the most part at least, are descended in the course of a long evolution from green ancestors, and therefore have been green in the past. Hence we are brought to a generalization of the greatest importance, the first indeed of the great botanical verities,—*the possession of chlorophyll is a well-nigh universal characteristic of plants, and their most distinctive feature.*

Such is the notable fact concerning the occurrence of chlorophyll in nature. Obviously so wide-spread a substance must play some very great part in the life processes of plants, and it is our manifest duty to determine what it is. In any such study the first resort of the biologist,—his first aid, as it were, to his ignorance,—is observation, exact and interrogative observation, of so much as the eye can discover. If, now, the reader will look over, from this point of view, any collection of plants in garden or greenhouse, drawing meanwhile on his memory for additional facts from his own experience, he will find these things to be true;—that chlorophyll is not omnipresent in those plants which possess it, being absent from their roots and interior parts not reached by the light: that even in lighted parts it is not uniformly distributed, being denser in the better-lighted places, as well exemplified in the deeper green of the upper as contrasted with the lower faces of leaves: that it does not develop at all in leaves which are grown out of the light, as witness the colorless sprouts of potatoes started in the darkness of cellars, or the grass of lawns accidentally left covered in spring: that it vanishes from green parts kept away some time from the light, as shown in the blanching of celery when banked up with earth: and that most green parts turn over towards light when this comes rather strongly



B. Section through leaf at *x*.

C. Single cell from *B.* *D.* Single chlorophyll grain from *C.*

from one side, as all plants kept in house windows attest. All of these facts unite to imply an extremely close relation between the meaning of chlorophyll to the plant and the action of light, even suggesting, indeed, that the chlorophyll is inserted, as it were, between the light and the use thereof by the plant. To this subject we shall later return, for we are dealing at present with the distribution of chlorophyll in the individual plant, a matter which can further be illustrated, in purely diagrammatic or conventional fashion, by the picture which forms figure A of Plate I of this book.*

So important is chlorophyll, that the reader ought really to make its closer acquaintance through actual experiment; for here, as everywhere else in science, an actual personal contact with facts or phenomena makes all the difference in the world in the clearness of one's understanding of them. It is possible to extract the chlorophyll very easily from leaves. If one takes two or three soft thin green leaves, places them in any glass dish which is uninjured by heat, covers them with alcohol (of any of the common kinds), and lowers the dish into hot water, then the chlorophyll will come out into the alcohol before one's very eyes. Its most striking characteristic is the beautiful green color of the clear solution, together with a remarkable and beautiful red fluorescence which appears when the solution is held in some lights, and especially when sunlight is focussed upon it with a lens. And the

* This picture is meant to represent that which one would see on a surface exposed by a lengthwise cut through the center of such a reduced conventionalized plant. Such sections, called *optical sections*, are very much used in biological works. Thus, on the very same plate, (Plate I), appear optical sections of a piece of a leaf, a single cell, and a chlorophyll grain; and a good many others occur elsewhere in this book. In every case an optical section is supposed to be typical, that is, taken through the part most illustrative of the structure in question; and, where only one section of an object is given, it means that the object is substantially alike all around the axis that is represented. Such sections, therefore, always stand for solid objects, and the reader should learn, as quickly as possible, to construct the solid in his mind from the section on the paper. This intellectual visualization, of course, requires imagination, but that is a quality which, despite the popular belief to the contrary, is highly essential to success in science.

reader should experiment also upon its instability in sunlight, a fact of importance as will later be proven; this he may do by dividing his solution into two portions, of which he puts one in bright sunlight and awaits its changes of color, while he places the other in darkness for comparison. Incidentally, too, this experiment will show an important fact about the color of leaves apart from their coloring matters, for, when the action of the alcohol is complete, the leaves appear a soft creamy white. This, in fact, is the natural color of all living plant tissues when no special coloring material is present.

We must, however, pursue a bit farther the study of the chlorophyll substance, partly because of its importance, and partly because the study will lead the reader to an acquaintance with other matters which he should learn very early in his botanical studies. To the naked eye alone, no matter how closely applied, the chlorophyll seems to color uniformly the whole of the leaf, which, except for the veins, looks homogeneous in texture. But if we call to aid that wonderful instrument by which the range of the eye into the minute is increased a full thousandfold,—that first and greatest tool of the biologist, the microscope,—and place under its lenses a very thin section or slice cut right through some green leaf from surface to surface, then a very different idea of leaf structure is presented to the observer, as the accompanying picture attests (figure 2). And with this picture of an actual leaf, the reader should compare the generalized or conventionalized section represented in figure *B* on Plate I. Clearly, the interior of the leaf is not homogenous, but partitioned into a great many little compartments, with empty spaces here and there interspersed. These compartments are called *cells*, a word of vast importance in Biology, because not only the leaf, but all parts of all plants, and all parts of all animals, are composed of them. These cells differ greatly in details of structure according to their function, but are always compartments of some sort; and the reader should as promptly as possible incorporate this idea of

universal cellular structure into his visual conception of plants. In our picture (figure 2), carefully drawn from an actual leaf, and as well in the conventionalized leaf (*B* on Plate I), the reader can see for himself the cells of the upper and lower skin (or epidermis), those of the vein (the clearer mass lacking chlorophyll), and finally those of the green tissue, distinguished by the large black or green spots which represent the chlorophyll grains. For the

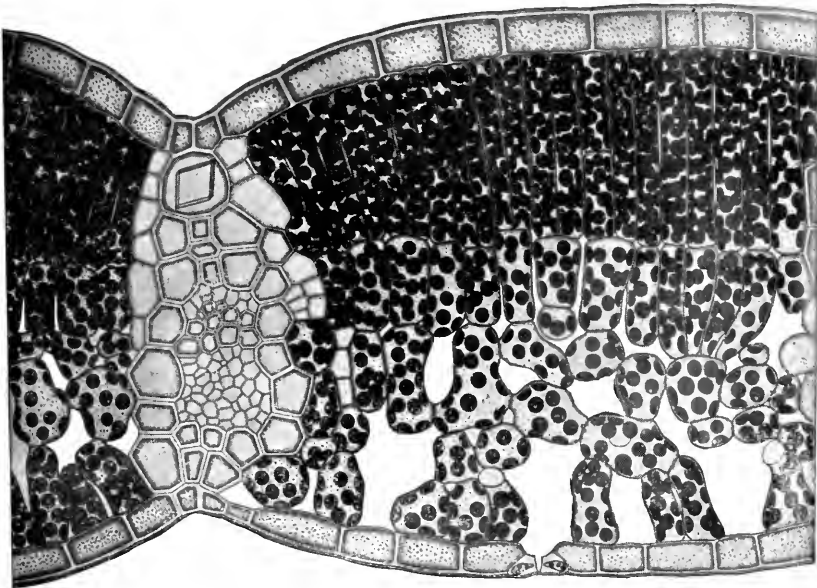


FIG. 2. A thin slice, or section, cut across a typical leaf (the European Beech), and highly magnified. From a wall-chart by L. Kny. In the original, the numerous black discs are green, as in the living leaf.

chlorophyll really is contained in definite grains, and is not a dye spread all through the leaf. These cells are roughly spherical, cylindrical, or polygonal in shape, though the open clear air-spaces between them are most irregular in form. Each cell has its outer thin transparent wall (little more than a line in figure 2), within which comes a complete lining of a thin gelatinous substance (shown in Plate I, *B*, by the faint grayish or dotted

shading), so nearly transparent as to be almost invisible. But though so insignificant in appearance, this grayish material is nevertheless the most important of all substances, for it is Protoplasm, the exclusive seat and sole physical basis of all the phenomena of life, as I shall show in a later chapter devoted to that subject. Within this living substance, close up to the wall, lie the chlorophyll grains, each of which has a definite shape, something like that of a disc or a lens, and consists of denser protoplasm deeply stained by a green liquid which is the chlorophyll substance proper. Finally, it should be added, in order to complete the reader's conception of the cell, that all of the remainder of its interior is filled with the sap, which is simply water containing many kinds of substances in solution. As to the spaces between the cells, they contain as a rule nothing but air, which is in connection with the atmosphere outside of the plant through tiny little openings, called *stomata*, between the cells of the epidermis. We shall return, and that often, to this subject of cellular structure, and the reader will then recognize the advantage of having thus made some preliminary acquaintance therewith.

We must now return to the problem involved in the observation that a close connection exists between the distribution of chlorophyll and the presence of light. Observation alone, however, cannot lead any farther, and we must resort to the second of the biologist's methods,—experiment. In such a situation the scientific mind would reason somewhat like this,—if, as seems implied by the facts, the chlorophyll has in the plant a function dependent on the action of light, then some difference should develop between leaves kept for a time in darkness and others kept equally long in light. Accordingly the experimenter would darken certain leaves on a plant, in a way that would not injure their health, and then, after a day or two, would examine a darkened and lighted leaf side by side. The result is always disappointing to the naked eye, by which no differences at all

are discernible, but a very different story is told by the microscope. That indispensable instrument shows in the lighted leaves the presence of tiny white grains (figure *D*, Plate I), which are absent from the leaves that were darkened, while chemical tests prove these grains to consist of a definite and familiar chemical substance,—*starch*.

This fact that starch makes appearance in ordinary green leaves when exposed to the light but not in those kept in the dark, is so important in plant physiology that the reader should make some further and practical acquaintance with the matter. If he selects some one of the commoner house plants, (e. g., Fuchsia, Garden Nasturtium, Horseshoe Geranium), covers some of the leaves from the light by a box, exposes the plant for a day or two to light, removes the darkened and lighted leaves at the close of the second day, dips them for a moment into boiling water, blanches them of chlorophyll by aid of warm alcohol, immerses them in water a minute to neutralize the brittleness the alcohol causes, spreads them out in a white saucer, and covers them with a solution of iodine diluted from the tincture he may buy from a druggist, he will be rewarded by seeing a very remarkable difference develop between the lighted and darkened leaves, for immediately the former will all turn a very dark blue, while the latter will remain of their natural cream color. Now iodine, as anyone may prove by a touch to some part of his starched linen, though brown of itself turns starch a dark blue; and thus our experiment proves that the leaves form starch in the light but not in the dark. So exact, indeed, is this relation that if a familiar sharp pattern be cut in opaque material and applied during the experiment to the upper face of a leaf, that pattern is found reproduced in equivalent sharpness when the iodine test is applied; and not only this, but if a photographic negative be used instead of the pattern, the picture will be printed very accurately in starch in the leaf, and may be “developed” in remarkable fashion by the addition of iodine. For full success in these two

latter experiments, however, special appliances and methods are necessary; and these are fully described in the various works devoted to experimental plant physiology, and mentioned in the preface to this book.

If the reader should experiment at all widely upon this matter of starch formation in leaves, he will sooner or later come upon kinds which exhibit no starch whatsoever, even under perfect conditions of light. Chemical analysis, however, always shows this fact,—that such leaves contain an equivalent amount of some sugar. Moreover, and this is a matter of consequence, analysis shows also that even the starch-forming leaves contain a sugar, and that, furthermore, it is from this same sugar the starch is made. We come therefore to a generalization of the greatest physiological consequence, the second, in fact, of the great botanical verities, and one which the reader should fix deep in his memory and incorporate with his visualized image of the working green plant, that *plants containing chlorophyll make in the light a sugar which is commonly transformed into starch*. The process being one of formation, or synthesis, under action of light, is called scientifically *photosynthesis*, while the substance made is the *photosynthate*.

It will sooner or later occur to the reader to ask, especially if he has tried these experiments for himself, whether this photosynthetic sugar is simply a transformation of something already existent in the plant, or a new substance that has been added thereto. This can be settled by the conclusive test of comparative weights; for, obviously, if it is a transformation, photosynthesis would not be accompanied by increase in weight while if a new substance it would. It is with difficulty that I resist the temptation to describe to the reader the simple but highly satisfactory methods and instruments by which this important matter is experimentally determined; but my book has limits, and besides I am well aware that any attempt to exhaust my subject is likely to produce a similar effect on my reader. So I must

simply state that the result of the test is perfectly conclusive,—it shows that leaves, apart from varying amounts of water they contain, always gain weight in the light but not in the dark. They are always heavier in the evening than they were in the morning. As to what becomes of the starch and sugar which disappear

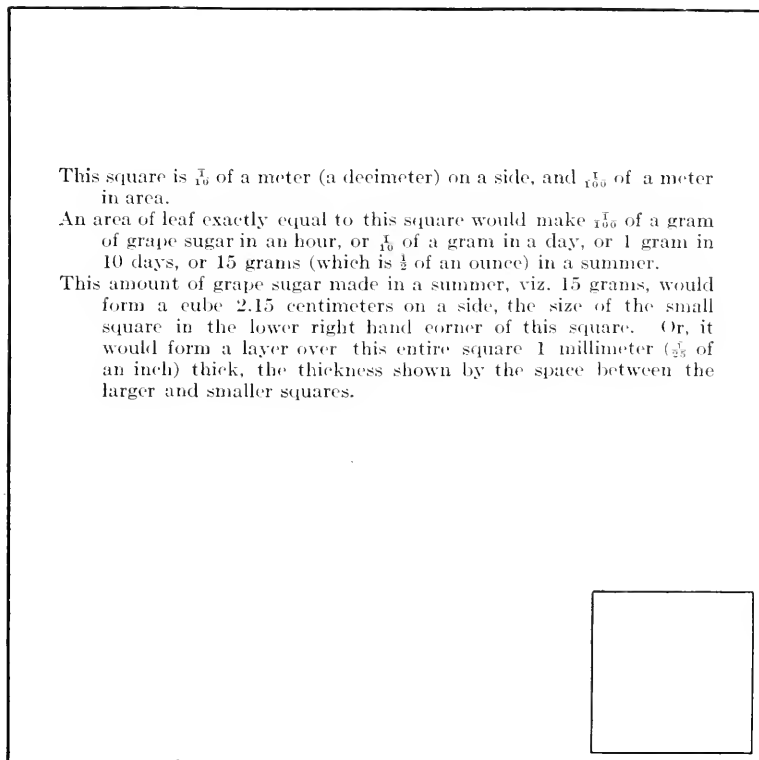


FIG. 3.—Diagram to illustrate the quantity of photosynthate made per unit area of leaf.

from the leaf, that will later be shown, though we may here note in passing that there is a continuous movement of the sugar from the leaves into the stem. Furthermore, this same method enables us to establish the amount of the increase in weight. This varies greatly, of course, with different plants and under different

conditions of light; but calculations have shown that for many plants collectively out of doors it approximates under average summer conditions to one gram for each square meter of leaf area per hour (scientifically expressed $1 \text{ gm}^2\text{h}$), or one twenty-fifth of an ounce per square yard per hour, and is about half that

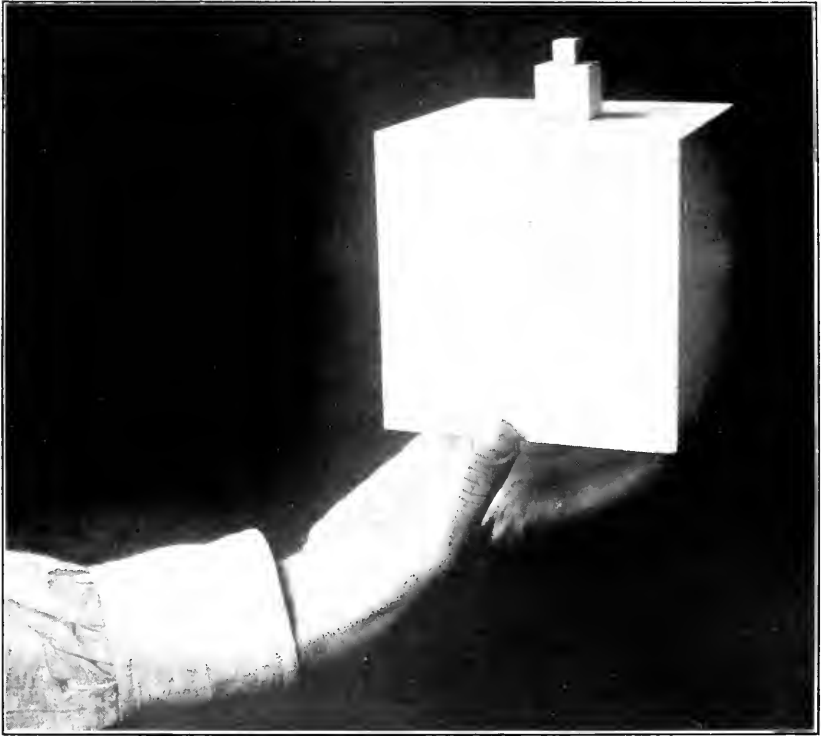
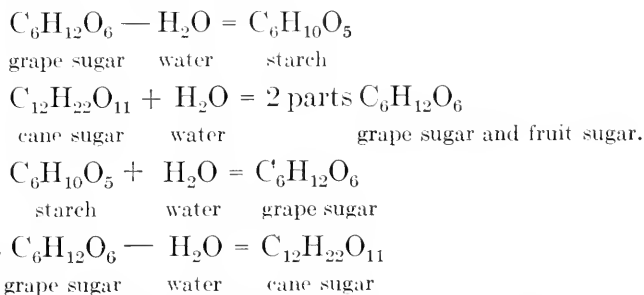


FIG. 4.—These cubes, which are two-fifths the original size, show the amount of solid crystalline grape sugar made by a square meter (or yard) of leaf in an hour, a day, and a summer.

amount in greenhouse plants in the winter. This figure constitutes one of those useful conventional constants which the reader should store in his mind, and keep ready for use. Expressed in a different way, a leaf forms in a summer enough photosynthetic sugar to cover itself with a solid layer a millimeter

(one twenty-fifth of an inch) thick. The same quantities are also expressed in a graphic way in the accompanying figure 3, and still more expressively, perhaps, in figure 4.

We must now examine more closely the photosynthetic sugar and starch which appear in lighted green leaves. The microscope does not show much about them, for the sugar is always dissolved in the sap of the cells, and the starch, although solid, is in grains too small to be seen very clearly. Their chemistry, however, is well-known and important. The sugar is of more than one kind, but the commonest is that known as grape sugar, or dextrose, which has the chemical composition, $C_6H_{12}O_6$, and which is intermixed with some fruit sugar or fructose having an identical formula. This formula, I need hardly say to the reader of this book, means that this sugar is composed of 6 parts of carbon, 12 of hydrogen and 6 of oxygen, though why this particular combination of these three diverse elements should give a substance with the properties distinctive of grape sugar, nobody yet knows. Much less abundant in leaves is cane sugar, which has the composition $C_{12}H_{22}O_{11}$. Starch has for its formula $(O_6H_{10}O_5)n$, the n meaning a multiple, though for our purposes we may treat it simply as $C_6H_{10}O_5$. Now it is immediately obvious that these three substances, so closely associated in the leaves of plants, are also very closely related in their chemical composition, for they differ from one another only in their relative proportions of hydrogen and oxygen. Thus,—



These three important substances thus differ, so far as their

composition is concerned, simply in the proportions of the incorporated water, though this tells by no means all of the story; but it helps to explain why they are so easily transformable by the plant one into the other. Taken together the facts suggest the probability that one of the three is a first-formed or basal substance from which the others are transformed. In a general way chemical research sustains this hypothesis, and points to grape sugar as the usual basal substance first formed in the light in green leaves. For all of our purposes, therefore, we may accept grape sugar as the conventional basal photosynthate, and its formula ($C_6 H_{12} O_6$) should be fixed by the reader in his memory as another of the valuable conventional constants.

It may seem to the reader just here that in treating this sugar so fully, I dwell overlong on a point of only subordinate value. But in this my critic would err, for, as a later chapter on the subject will show in detail, this photosynthetic grape sugar is the material from which, with certain transformations and some additions, plants make all of their substance and special materials, including their protoplasm, and derive all of their energy for work; in other words, it is their food. And since animals all take their sustenance, whether directly or indirectly, from plants, it is the basis of their food also. These facts may conveniently be brought together, even though somewhat in advance of all of the evidence, in this generalization, which constitutes another of the great botanical verities,—that *the photosynthetic grape sugar formed in green leaves in the light is the basal food of both plants and animals*. This sugar is therefore one of the three most important substances in organic nature, chlorophyll and protoplasm being the other two.

Our next task is sufficiently obvious; we must find the source of supply of the materials entering into the composition of the sugar, which, the reader will remember, is an addition to the plant. Now a scrutiny, from this point of view, of its formula, viz., $C_6H_{12}O_6$, at once reveals the suggestive fact that the H and the O

are present in exactly the proportions they exhibit in water, (H_2O); this suggests that they may be derived from the water which, absorbed from the soil, always saturates the tissues of the living plant, and this hypothesis is confirmed by experiment. As to the carbon, a supply thereof exists both in mineral compounds in the soil, and also in the carbon dioxide, commonly called carbonic acid gas, in the atmosphere. But experiment easily decides between these two sources, for when plants are grown in a soil or in water from which every trace of carbon is excluded, the plants make their photosynthate as readily as ever, thus apparently proving that the carbon must come from the air. At first sight it may seem an objection that this gas exists in the atmosphere in such an extreme of dilution, for it comprises only 3 parts in 10,000, that is .03 (or $\frac{3}{100}$) of 1 per cent. This amount is very small, it is true, though we must remember that the bulk of the whole atmosphere is vast in proportion to the bulk of all plants. However, suppositions cut small figure in comparison with facts; and it is easy to prove by simple experiments that leaves, or even small parts thereof, exposed to an atmosphere from which the carbon dioxide has been removed, can make no starch at all, although neighboring leaves or parts, exposed in the ordinary atmosphere, form it abundantly. Indeed, innumerable facts unite to prove that the carbon used by leaves in the making of sugar is derived from the carbon dioxide (the carbonic acid gas), of the atmosphere. This, as the reader well knows, is the very same gas which is poured out by animals in breathing, by organic substances in decaying, and by fires in burning. The fact that leaves absorb this gas in making their sugar explains in part the scientific basis of a widely known and very important phenomenon,—that plants purify the air which is vitiated by animals.

All chemical processes can be expressed in equations of the formulæ of the substances concerned, and therefore we proceed to set down together the formulæ of the carbon dioxide (viz.,

(CO₂), and water, with the formula of the grape sugar they form, thus,—

In photosynthesis CO₂ and H₂O form C₆H₁₂O₆
 carbon dioxide water grape sugar

Obviously now the proportions of the two former must be increased in order to yield the latter, thus,—

6 CO₂ + 6 H₂O are needed to form C₆H₁₂O₆

But a chemical equation must balance exactly on the two sides, and this in the present case can occur only thus,—



But such a balance of the equation implies that, in the making of sugar from carbon dioxide and water, oxygen is set free, and not only so, but in a volume exactly equal to that of the carbon dioxide absorbed. So striking a conclusion based upon purely theoretical evidence demands rigid test through observation or experiment. That a gas of some kind is released from green plants in the light is easily seen in submerged water plants which, if kept in an aquarium, give off tiny bubbles when lighted, though not in the dark; and everybody has seen those large gas bubbles which are caught in the felted green scum-plants floating on ponds. Analysis shows that the bubbles, in both cases, consist mainly of oxygen. But the matter can be tested much better by experiments. In a word, it is only necessary to place a green plant or a leaf in a suitable tight glass chamber, give it a known quantity of carbon dioxide (it has plenty of water), expose it for some time to the light, and then make a chemical analysis of the air in the chamber. The experiment yields an invariable result. A certain amount of the carbon dioxide has disappeared, and in its place there is present an exactly equivalent amount of pure oxygen. As to the significance thereof, it seems plain that the oxygen is a by-product formed incidentally in the chemical transformations, and useless in the main process.

Thus is our equation triumphantly vindicated, and we shall know it henceforth as the *photosynthetic equation*. Its importance and meaning may thus be expressed as another of our botanical verities,—that *the photosynthetic sugar made in green leaves in light is constructed from water drawn from the soil, and carbon dioxide derived from the atmosphere, with an incidental release of pure oxygen, according to the photosynthetic equation* $6\text{CO}_2 + 6\text{H}_2\text{O} = \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$.

It may interest the reader now to know what quantities of these gases are necessary in the making of the sugar. For one gram thereof there are required 750 cubic centimeters (about $\frac{3}{4}$ of a quart) of pure carbon dioxide, which is all that is contained in 2 cubic meters of atmosphere, and there is released the same quantity of pure oxygen. This, therefore, is the amount of those gases absorbed and released by a square meter (or yard) of green leaf each hour on a bright summer day. This release of oxygen, by the way, explains the remainder of the fact earlier mentioned, that plants purify the air which animals vitiate, for the plants not only remove the poisonous carbon dioxide from the air, but replace it by pure oxygen. And it may interest the reader to know how this balance of purification and vitiation works out between green leaves and men. Calculations have shown, in brief, that about 25 square meters (or yards) of green leaf are required to balance the respiration of a man on an ordinary summer day. But as the release of oxygen stops at night, it takes about 60 square meters of leaf working for a day to balance the man's respiration for 24 hours, and about 150 square meters working through the summer to balance his respiration for a year.

In composing the foregoing paragraphs I have given much care to the form of their presentation, for the reason that this particular topic illustrates exceptionally well the principal method of scientific procedure in the acquisition of new knowledge. First, in the given problem, to observe all the facts that the militant eye can discover: next to compare and marshal the data thus won

with a view to finding an explanatory principle: then to express the most probable conclusion in tentative form as an hypothesis: and finally to devise experiments whereby the truth or falsity of the hypothesis may be tested; these are the constituents of that scientific method through which all of our great scientific triumphs have been won. Hypothesis is a kind of a scout which Science sends on ahead to spy out the way for a further advance.*

For the completion of our subject of photosynthesis, there remains but one matter of consequence, and that is the explanation of the association of light and chlorophyll with the process. We have seen earlier that the chlorophyll occupies a position between the light and the new-made starch or sugar, which fact implies that it forms a necessary link between the two. This in turn would suggest that the chlorophyll perhaps acts on the light in a way to make it available for the photosynthetic process. Taking this hypothesis for guidance, we turn to investigate the effect that chlorophyll exerts upon the light which penetrates into it. Now the sunlight, as everybody knows, is a composite mixture of vari-colored lights, which, taken together, give the impression of whiteness. If this sunlight, however, be passed through chlorophyll, whether a living leaf or a solution in alcohol, there issues, as the reader will recall, only a clear green, or yellowish-green, light; and this fact seems to imply that all of the colors

* That this is in practice, as it is in theory, the method of scientific men in their researches is illustrated by the following passage from the writings of the great German physiologist, Sachs. In connection with this very subject of starch formation, he tells of his preliminary observations, on the basis of which, he says,—“I came to the conclusion in 1862 that the enclosed starch, which had already been observed in the chlorophyll-corpuseles by Naegeli and Mohl, is to be regarded as the first evident product of assimilation [i. e., photosynthesis] formed by the decomposition of carbon dioxide. I said to myself, if this view is right, the formation of starch in the chlorophyll-corpuseles must cease on the exclusion of light, since the decomposition of carbon dioxide can then no longer take place; and that in like manner renewed access of light to the chlorophyll-corpuseles must also bring about a renewal of the formation of starch in them. These and similar deductions were confirmed by appropriate investigations.” (*Lectures on the Physiology of Plants*, Oxford, 1887, p. 307.)

in sunlight have been stopped by the chlorophyll excepting only the green. But the human eye is far too crude an analyzer of color to be scientifically trustworthy, and we turn for aid to an instrument which science has devised for the exact analysis of light,—the spectroscope. I confess, it is only with reluctance that I refrain from explaining to the reader the principle of this beauti-

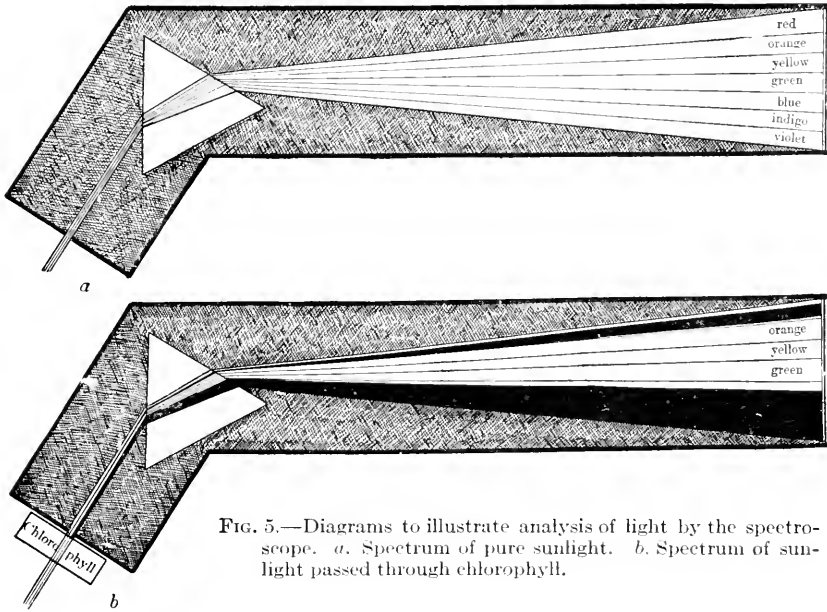


FIG. 5.—Diagrams to illustrate analysis of light by the spectroscope. *a*. Spectrum of pure sunlight. *b*. Spectrum of sunlight passed through chlorophyll.

ful instrument, one of the most delicate and exact, but withal one of the simplest in theory, of all that have yet been evolved in the progress of science. It must suffice to say that the spectroscope takes any mixture of colored lights, no matter in what complication, and, through the mediation of a prism, spreads them out in a band (called a spectrum), each color by itself. So, when a ray of white sunlight is sent into this instrument, it is made to fringe out into its red, orange, yellow, green, blue, indigo and violet constituents, all beautifully clear and distinct, as shown diagrammatically in our accompanying figure 5, *a*. Now

if, while one is observing this spectrum, a solution of chlorophyll is inserted into the path of the light, a remarkable phenomenon follows, for the green liquid blots out from the spectrum most of the red and nearly all of the blue-indigo-violet, making those parts of the spectrum quite black, while all of the rest of the colors are left practically unaffected, as represented in our diagram (figure 5, *b*). Chlorophyll, therefore, has power to absorb red and blue rays out of the sunlight, ignoring the others,—in observing which fact the active scientific mind would jump straight to the conclusion that these red and blue rays are probably the ones which are useful in photosynthesis. This hypothesis also is easily tested by experiment, for, obviously, if the red and blue rays really are those used in photosynthesis, while the others are not, then starch ought to be made under red light and blue light, but not under any others of the colors of the spectrum. It is possible to supply the different colored lights singly to the green leaf, either by use of colored glasses or liquids or by throwing a solar spectrum directly upon a leaf. The result of the experiment is conclusive; a leaf can form starch very readily under red light or blue light; but it can form none at all under the yellow, orange, or green. It seems a safe inference, therefore, that chlorophyll is a substance which picks out of white sunlight and applies to photosynthetic work, just those rays which can be utilized in the photosynthetic process, while rejecting the others; and all evidence attests the correctness of this conclusion.

This conclusion, however, raises a correlated question, which is this,—for what particular purpose is light needed in photosynthesis? Light, of course, is a form of energy, like heat and electricity; and energy is the source of power which underlies every kind of work. Light, so physicists teach, consists of wave-motions in a space-pervading medium called the luminiferous ether; and the motion of these ether waves forms a source of power that can accomplish work, just as surely as can the billows of the ocean. Our problem, then, resolves itself into this,—is

there in photosynthesis any step requiring the doing of work, and therefore the expenditure of energy? Our photosynthetic equation supplies the answer, for it shows that the oxygen set free has to be torn away from either the carbon or the hydrogen of the carbon dioxide or water, as a necessary preliminary to the union of the carbon with the remaining elements to form sugar; and other evidence shows that the carbon dioxide at least is thus dissociated. Now carbon dioxide is among the most stable of natural compounds, which means that its constituent atoms have an extremely strong affinity for one another, which means in turn that ample power must be exerted to tear them apart. Most people know that in our laboratories water can be separated into its constituent hydrogen and oxygen only through action of an electric current (electrolysis), or of intense heat; but carbon dioxide is even more difficult of dissociation. Here then, in the preliminary dissociation of this very refractory substance is that need for energy which we seek; and all the results of research confirm this conclusion. Why it should be the red and blue rays and no others which can do this work, we do not yet know, nor yet precisely the way in which the chlorophyll applies them to the task; but there is no question as to the facts. That is, chlorophyll is a transformer of light energy into photosynthetic work; and there you have the explanation of its function in plants, and the reason for its overwhelming prevalence in vegetation.

We can now summarize this part of our subject as another of our botanical verities,—*the formation of photosynthetic sugar in leaves requires first the dissociation of the refractory carbon dioxide, which is effected by the energy of the red and blue rays of the sunlight, applied to that work by the chlorophyll.*

It will perhaps contribute further to clearness if we summarize the whole process of photosynthesis from another, and very human point of view. The formation of the photosynthetic sugar, the end of the whole process, is, after all, a manufacturing process

comparable directly with those carried on by men, as the following table well shows.

The Factory	The Leaf, or other green structure.
Rooms therein	The cells.
The power	Sunlight, the red and blue rays.
The machinery	Chlorophyll.
The raw materials	Carbon dioxide and water.
The manufactured product	Grape Sugar.
By-products	Oxygen.

The photosynthetic machinery can not only be apprehended, but also represented in a mechanical plan, as our accompanying diagram illustrates (figure 6). It represents the parts concerned in the process, (shown simplified in figure *B* on Plate I,) reduced each to a single one, and given a regular shape, though otherwise constructed and related as in the plant. Later we shall consider exactly the forces which keep the gases and liquids in motion in the suitable directions.

The reader should now be able to visualize, or see vividly in imagination, this process in progress. Streaming in through the stomata and along the air passages is a steady current of the tiny particles, or molecules, of carbon dioxide, which reach the cell walls, pass in solution through these and the protoplasm into the chlorophyll grains, where they meet with water supplied in a continuous stream by the ducts. Here in the grain the chlorophyll is stopping the red and blue light, and turning their vibrating waves against the molecules of the carbon dioxide in a way to shatter that substance into its constituent atoms. The carbon thus forced apart from its own oxygen is uniting with the elements of the water into sugar, which is streaming into the sap cavity and then away through the sieve tubes, while the discarded oxygen is passing out from the grains through protoplasm and wall to the air space, along which it is streaming to the stomata and the outside world. And this is what is occurring inside of all leaves through all the bright days of the summer.

So striking and far-reaching are the conclusions already reached in this chapter that anything added thereto must come as a kind of anti-climax; and therefore I wish we could stop just here. Moreover the chapter is already over-long, though no longer, I maintain, than the relative importance of its subject sufficiently justifies, especially as it seemed to me best to make this first treatment of very important topics illustrate the methods through which our scientific knowledge has been gained. Yet several closely related matters, especially concerning the colors of plants, should have our attention before we depart from this subject, though I venture to suggest to the reader that he should not attempt to read all of this chapter at one sitting, but reserve the following part for a time by itself.

One of these matters may be dismissed very briefly. Is it quite clear to the reader why chlorophyll looks green to the eye? This, indeed, is told very plainly by the spectroscope, when it shows that chlorophyll, in stopping the useful red and blue rays from the light of the sun, allows the other and useless rays to

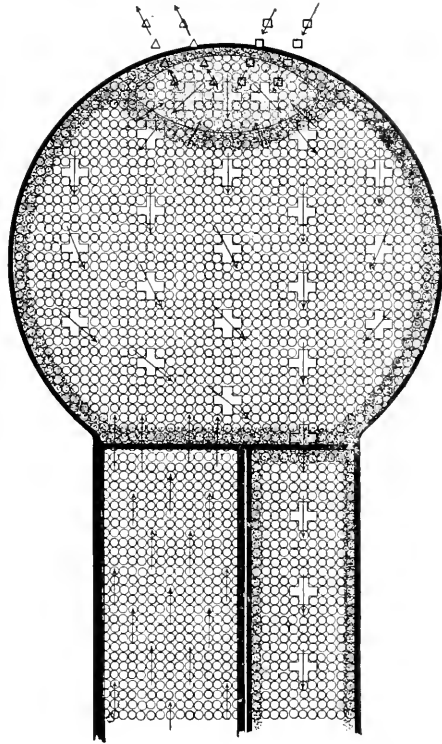


FIG. 6.—A diagram of the photosynthetic machinery, showing the parts reduced to the lowest possible terms, viz., a single living cell, with a single chlorophyll grain, a water-carrying duct (on the left) and a sugar-carrying sieve-tube (on the right); shading is protoplasm. The circles are water; the squares are carbon dioxide; the triangles are oxygen; the crosses are grape sugar; the arrows show the directions of movement. Cells magnified about 200 and molecules about six million times.

pass through as waste; and these of course are the ones which come to our eyes. Now these waste rays include the entire green light, which gives the principal color, together with all of the yellow, which, mixing with the green, gives thereto the characteristic yellowish tinge which chlorophyll always shows. As to the remaining rays, they happen to form complementary pairs; thus the bit of red and bit of green-blue form one pair, while the orange and unabsorbed blue form another; and as complementary colors (with lights) always give white or gray, these minor rays thus neutralize one another so far as color is concerned, and do not at all affect the positive yellow-green. If it had happened that, instead of red and blue, the red and green had been the useful rays, then chlorophyll, and all vegetation, would have looked blue; and had green and blue been the useful kinds, then all vegetation would have looked red. The greenness of vegetation is simply the wastage of that part of the white light of the sun which is not needed in photosynthesis.

In the early part of this chapter it was mentioned that many leaves of a red color really possess chlorophyll, which becomes visible when the red is removed by suitable solvents. This is true of the seaweeds, the red and brown colors of which are due to special pigments in the same grains with the chlorophyll; and there is good reason for believing that these colors bear a relation to the light conditions under which those seaweeds live, aiding the chlorophyll to utilize the sunlight as altered by its filtration through water. The case in the more familiar red plants of garden and field, however, is different. The colors in the foliage plants (Coleus, Copper Beeches, Japanese Maples) as well as in some vegetables (Beet, Red Cabbage), is a product of enormous intensification under cultivation; but in all cases the wild ancestors of these plants possessed some red color to begin with. This red, indeed, is fairly common in wild plants, where it shows especially in veins, petioles, nodes, or the under sides of leaves, and in the stigmas of many wind-pollinated flowers. It reaches, however,

its most striking, though a temporary, development in the young shoots of a good many plants (e. g., Maples, Oaks, and many herbs), which it flushes with translucent rose red as they push from the buds in the spring, though later it fades away with the increasing rapidity and vigor of growth. In all of these cases the color resides in a particular substance, named *erythrophyll* (or anthocyan), dissolved in the sap of the cells, from which it can usually be extracted by hot water. It is typically a beautiful deep rose red material, varying much, however, in tint according to the conditions surrounding its formation, and the substances with which it is associated. Its identity, therefore, is plain enough, but concerning its significance to the plant there is very much doubt. One explanation argues thus; erythrophyll, as its color implies, permits the red rays of sunlight to pass unaltered, but cuts off, or at least weakens, the blue-violet ones. Now it is known that the red rays, while the most useful in photosynthesis, are harmless to the living protoplasm, but the blue-violet rays, though also useful in photosynthesis, are injurious, when untempered, to the living protoplasm and detrimental to some of the physiological processes; therefore (runs the argument), the erythrophyll probably acts as a protective screen, especially in the case of the early spring vegetation, admitting the beneficial red rays and tempering the noxious blue-violet rays until the formation of the chlorophyll, which, while developed for a different purpose, incidentally acts as a protection to the protoplasm,—a subject to which, by the way, we shall return for fuller discussion in the later chapter on Protection. A second explanation is based upon the fact that erythrophyll has been found to possess a notable power of transforming light into heat; it must therefore serve, this argument holds, to warm the tissues which possess it, and thus, during the bright but cool days of the spring, must facilitate those processes, such as nutrition, translocation of food, and growth, which are promoted by warmth. More recently a third explanation has been offered, based upon the fact that when-

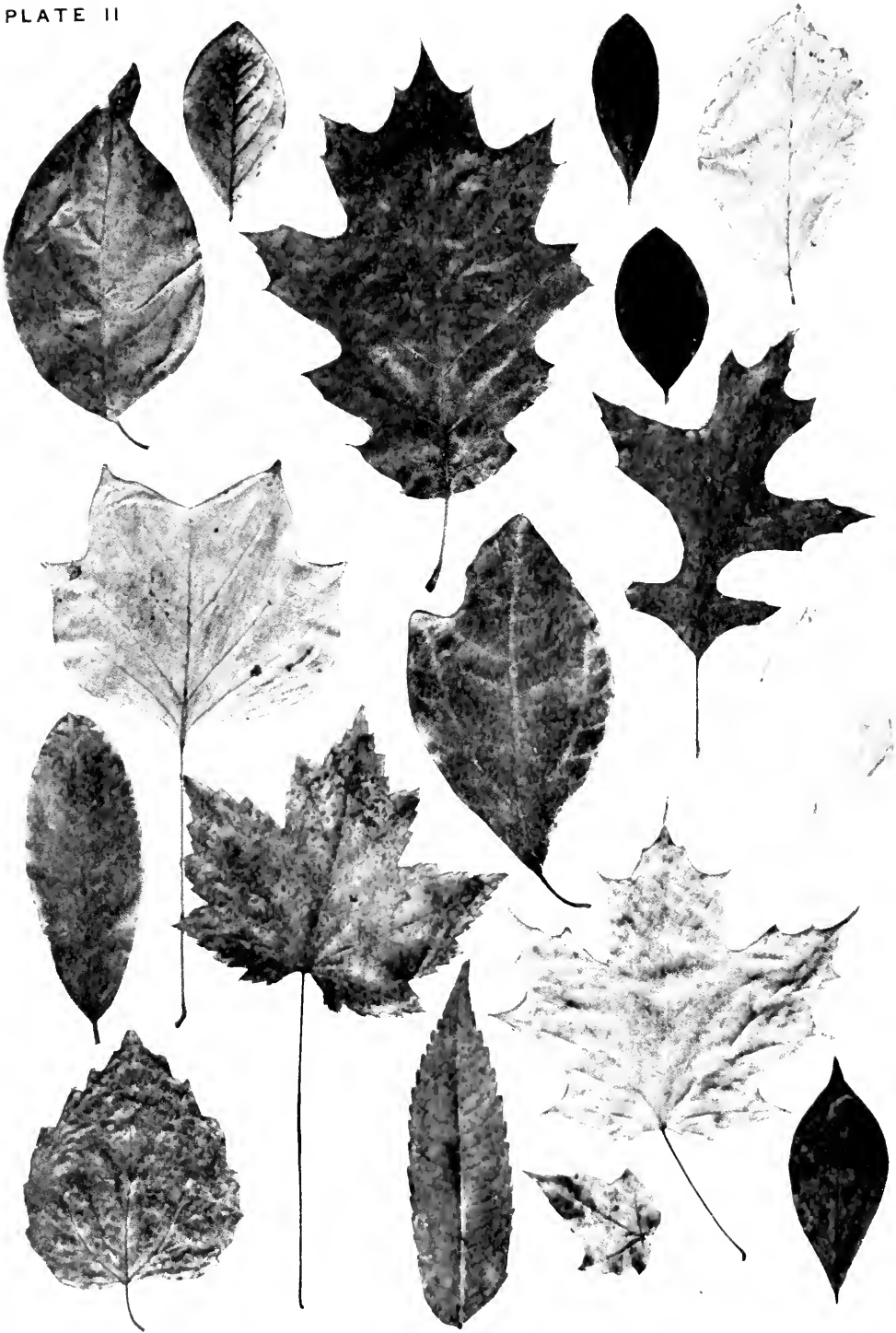
ever bright light, a relatively low temperature, much sugar, and some tannin happen to come together in a living cell, then the substance erythrophyll, of which the composition-color happens to be red, is formed incidentally as a purely passive chemical result. On this view the red color may be purely accidental, and may have no utility whatever to the plants which possess it, though the possibility is not thereby excluded that the plant may bring those conditions together, adaptively, in a cell where it has need for the red color to appear. The substance of the whole matter in reality is this,—that we do not yet know surely the significance of erythrophyll in the plant; and herein lies another of the problems which make science so ever alluring.

Connected with chlorophyll in a different way is one of the most striking and beautiful of all the phenomena of nature, the transition in the foliage each season from the uniform green of summer to the brilliant colors of autumn. Strangely enough, for a subject so important, our knowledge thereof is still very imperfect, and there is even a difference of opinion as to the very significance of the colors to the plant. A basal fact, however, upon which there is agreement, is this,—that the autumn coloration results from changes connected with the death and fall of the leaf. We know that in late summer our trees are preparing for the annual leaf fall, in anticipation of which they are gradually bringing the activities of the leaves to a close, ceasing to make new chlorophyll, withdrawing certain precious materials into the stem, and building right across the bases of the leaves those corky layers which both cut them away from the stem, and also heal in advance the wound that is thus to be made. Now chlorophyll, as the reader's own experiments will have shown, is soon destroyed by bright light; this destruction, indeed, is continually in progress throughout the summer in the living green leaves, where the color is maintained only through virtue of its constant renewal. It was formerly believed (and I mention the matter because the statement persists even yet in some writings), that this chloro-

phyll left in the leaf when the new supply ceases to form, breaks down in the light to other substances, which either themselves are highly colored, especially red, or else unite chemically with other materials in the cells to form colored compounds, the autumn colors being supposed, on this view, to be simply an incidental product of chlorophyll decay. But later research has shown this supposition to be wrong, for chlorophyll, in breaking down, does not form colors, but fades away to transparency in the leaf precisely as it does in the alcoholic solution which the reader has placed in the sun. Now, sooner or later in the autumn the waning activity of the leaf reaches a point where no more chlorophyll is made, after which all of that substance already present fades away, with this notable result,—that its disappearance renders visible any other colors which may have been present in the leaf, but masked by the greater brilliance of the green; and this fact constitutes the basal step in the explanation of autumn coloration. As a matter of fact leaves do contain other coloring matters, especially a bright yellow material, called xanthophyll, occurring in tiny grains associated with the chlorophyll. It is the exposure of this xanthophyll by the fading away of the chlorophyll which gives the yellow, most common of the autumn colors, to autumn leaves. If the reader desires, he can himself extract this xanthophyll, and very easily, in a beautiful clear yellow solution, by treating yellow autumn leaves precisely as he did the green leaves for extraction of chlorophyll, but using much leaf in proportion to the quantity of alcohol. Indeed the reader has seen the xanthophyll already, for, as he will recall, when he placed his solution of chlorophyll in the sun it faded away not to a transparent whiteness but to a clear yellow; this was xanthophyll, which itself fades away extremely slowly to whiteness. The whole situation must now be quite clear. Chlorophyll and xanthophyll exist together in leaves, from which indeed they can be extracted and separated in beautiful solutions well known to all students in physiological laboratories; but xanthophyll is

ordinarily completely masked by the far greater brightness of the chlorophyll, though it has influence enough to give the living leaf its yellow-green rather than a pure-green color. But xanthophyll is vastly more resistant to the action of light than is chlorophyll, which explains its persistence in both leaves and solutions. The precise function of the xanthophyll, by the way, is not known, although it seems probable that this is to be found in some incidental chemical connection with the chlorophyll, in which case its persistence in autumn leaves is purely incidental and of no service to them.

Second in abundance, though first in brilliance, among autumn colors is red, which has a very different origin. It is due to the presence of that same erythrophyll which we have already considered in connection with foliage plants and the spring coloration. This erythrophyll, also, the reader can extract for study in a beautiful clear rose-red solution by aid of the method he used for the chlorophyll, excepting that water must be used instead of alcohol, and the material should be abundant and consist of the very brightest red leaves he can find. Unlike the xanthophyll the erythrophyll is not present in the leaves before the chlorophyll fades away, at least not in appreciable amount; but it forms as the disappearance of the chlorophyll admits the light to the interior of the leaf cells. That the presence of bright light is essential to its formation is easily proven by experiment, and by the readily observable fact that in cases where one red autumn leaf overlaps another closely enough to shield it largely from light, the darkened portion is yellow not red; and this same fact further proves that red autumn leaves are actually yellow underneath the red. The brilliancy of the red, indeed, is proportional in general to the brightness of the light. But light alone is not sufficient to produce a formation of erythrophyll without the presence of the chemical substances requisite to its formation, which include certainly sugar and probably tannin; and it is only those leaves which happen to contain a sufficiency of these materials that can





turn red at all, the others being restricted to yellow. The Maples and the Oaks are trees well-known for their richness in sugar or tannin, which helps to explain why those particular trees are more brilliantly red than most others. It happens, furthermore, that erythrophyll formation, contrary to the usual rule with chemical processes, is promoted by lower temperature; and this explains why it is that a cool season promotes the brilliance of color, which indeed reaches its highest perfection in seasons or places where the skies are very bright and the frosts come early.

Thus much for the facts as to the yellow and red autumn coloration. We have now to take notice that two conflicting views exist as to its significance to plants. Many botanists believe that since erythrophyll seems to have definite functions in spring vegetation (as we have seen a few pages earlier), it has also an identical function in the leaves of the autumn, acting usefully as a selective light screen. The argument runs thus:—chlorophyll fades away in the leaf before the protoplasm has wholly ceased its activity: full exposure to bright sunlight, especially the untempered blue-violet rays, would injure this protoplasm, and act unfavorably on the translocation of the valuable materials from the leaf into the stem: an erythrophyll screen must temper the blue-violet rays while permitting the passage of the red rays which are not simply harmless but, being warm rays, would actually aid the final vital processes of the leaf during the cooling days of autumn. And those who hold this view assume that xanthophyll must have something of the same action, though inferior in degree to erythrophyll. On this view autumn colors are believed to be useful if not indispensable to the plants which possess them, and inferentially, have been developed adaptively to such use.

Sharply contrasting, however, with this utility explanation of autumn coloration is the view that it is merely incidental. While the utility theory has certainly some facts in its favor, the most of the evidence seems to me heavily against it. Thus the utility

theory, that of the protective and heating screen, requires in autumn leaves certain features which the spring coloration does in fact to some extent exhibit,—viz., a prevalence of red rather than yellow, a fairly uniform coloration over all the parts to be protected or warmed, an especially deep coloration in the conducting parts, and a fairly constant development of the color year after year without much regard to the details of the weather. As a matter of fact the phenomena of autumn coloration are different at almost every point—red is less common than yellow; the colors are very uneven in distribution, forming spots, blotches, and streaks; the color shows no particular tendency to cover the conducting veins: and its intensity varies greatly in different years, even almost to suppression of red in certain kinds of leaves in some seasons. The utility theory of autumn coloration receives, therefore, no support from comparison with spring coloration, even granting, as is not at all certain, that the latter is useful. The facts, therefore, taken all together seem to favor the incidental theory, which may thus be expressed;—that autumn coloration, for the most part at least, is a purely incidental result of the chemical and physical conditions which happen to prevail in ripening leaves and around them, and has in it no more element of utility than has the red of a sunset or the blue of the firmament.

The yellow and red in the autumn coloration are so much more common and striking than any other colors that they naturally attract the most of our attention. Yet other colors occur, as everybody knows well, and as appears very clearly on the accompanying plates (Plates II, III), which represent a selection from New England autumn vegetation, photographed in the natural colors. In fact, however, the great variegation thus displayed results from permutations and combinations of a very few colors. In addition to the red and yellow, there is only one other pigment at all common in autumn leaves, and that is an occasional brown, the mode of formation of which is uncertain. Most of the brown color in such leaves, however, belongs to the cell-walls, which are

white-transparent when alive, but turn brown on their death and decay. In fact the conditions prevailing in the ripening and dying leaf are most complex, for not only are different chemical substances and physical forces interacting in large number, but their interrelations are constantly changing as the death of the protoplasm weakens its regulatory control upon them. This combination of complexity and changeability produces a state of unstable equilibrium, which permits even very minor external influences to exert relatively great effects,—and thus is explained the differences in the coloration of the same plants in different seasons or different places. In general, however, the effects of the weather upon the intensity of coloration are clear. Thus a bright autumn (and, equally, a sunny climate) intensifies the coloration, at least for the red, while dull weather is accompanied by dull coloration. Early frost helps somewhat to intensify color, partly by hastening the death of the leaf, and partly by aiding the chemical formation of the erythrophyll; though frost is not, as many suppose, a cause of the coloration itself. Furthermore, the coloration can be brought on much earlier in the season than usual by any injury,—a break in the bark, a split in the trunk, some damage to the roots,—which weakens the vitality of the tree and hence promotes the waning of life in the leaves; and this is the explanation of the occasional reddening of a single branch, or even whole tree, which one finds turning sometime ahead of its neighbors.

The reader will feel, I am sure, that this is an unsatisfying answer to his natural wish for a definite knowledge of the causes of autumn coloration, but it is all that the present state of our knowledge permits. The subject has been studied heretofore by botanists from their side, and by chemists from theirs; but its problems will not be solved until some competent investigator takes autumn coloration as his unit, and attacks it by any and all methods,—chemical, physical, physiological, observational, experimental, or any others essential for attaining his ends.

Some day this will be done, and then we shall know the meaning of autumn coloration just as surely as we now know the causes of the colors of chlorophyll, of fruits, and of flowers. Meantime, it is not the least of the pleasures of science that everywhere about us lie problems of moment, whose progress towards solution we may constantly watch, and the triumph of whose conquest we may perhaps even share.

CHAPTER III

THE PROFOUND EFFECT ON THE STRUCTURE OF PLANTS PRODUCED BY THE NEED FOR EXPOSURE TO LIGHT

Morphology and Ecology of Leaves and Stems



N the foregoing chapter we have considered photosynthesis solely as a physiological process operating within the body of the plant, and have taken no thought for any relations it may have with the world outside.

Yet the internal process is dependent on the external world in this very fundamental particular, that the supply of the indispensable light, carbon dioxide and water has to come from outside. Furthermore, and this is a point of importance, the environment rarely offers these essentials in precisely the right quantities, but sometimes too abundantly, oftener too sparsely, and sometimes in ways involving grave dangers. Their photosynthetic needs plants cannot help, and their environmental conditions they cannot change, but there is one thing that is alterable, and that is their own structure, with its large potentialities of adaptive development. Accordingly, in the course of long ages of slow evolution, plants have become so molded in form and in structure as to bring the photosynthetic process into advantageous or adaptive relation with the conditions of supply of the photosynthetic essentials outside, and in such manner, moreover, as to permit of particular adjustment to special peculiarities of the surroundings. Plants are like housekeepers who possess certain needs, and a desire for having the best, but who have no control over the purse-strings; under the circumstances there is nothing for them to do but adjust the scale and style of

the establishment to the exigencies of a fixed income. This is the real meaning of the photosynthetic adaptations, which it is now our business to consider. Each one of the physiological processes of plants produces, of course, in like manner its effect upon their structure; but the one process of photosynthesis far surpasses all others, indeed all others put together, in the profundity of its influence in making plants what they actually are. The evidence thereof will appear in the following pages.

The photosynthetic essentials for which plants are dependent upon the environment are in reality four, because, in addition to light, carbon dioxide, and water, plants need also, for reasons that will later appear, certain minerals, which are, however, for the most part very widely distributed in soils. Now in showing the way in which these four are supplied by the environment to plants, I must recall to the reader some very familiar and commonplace facts. But I remind him that there is nothing in the world so difficult to see in its real significance as the commonplace; moreover let him remember the truth expressed by a brilliant writer in the saying that little minds are interested in the extraordinary, but great minds in the commonplace.

The crucial facts about the mode of supply of the four photosynthetic essentials are these.

First. *They all exist widely even if not abundantly distributed in nature, and moreover are incessantly in movement or circulation,—* the light with the swing of the sun through the heavens, the carbon dioxide with every breeze that stirs the still air, the water in the form of the mists and the rain, and the minerals in solution in the water which soaks and drains through the soil. Therefore plants have no need to go in search of these essentials, as animals must for their food, but are able to stay fixed in one place and allow the essentials to be brought them by the general circulation of nature. This method renders needless any self-motive power, with the accompanying muscular system and jointed skele-

tion such as animals must have, and permits a simply continuous structure. *This is why plants are sedentary beings, rooted for life in one spot.*

Second. *The four essentials circulate in no definite paths or directions, but come to the plant from every point of the compass.* This is true even of sunlight, despite the regular path of the sun through the heavens, for so uniform is the diffusion of the light through the sky that plants really receive it from every direction. And as to the wind, does it not blow where it listeth, and the waters, do they not cover the earth? Therefore plants have no need to face their parts in any particular direction, as animals must do in connection with their movements in search of their food, but face evenly outward in every direction, thus requiring a symmetrical distribution of their parts around a central vertical axis. *This is why plants are radially built, presenting the same face to all points of the compass.*

Third. *The four essentials are not evenly commingled, but segregated into two strata,—the light and carbon dioxide in the atmosphere above, and the water and minerals in the soil underneath.* Therefore plants must needs have two parts to their structure adapted to life in these two very different situations. *This is why plants exhibit their primary division of structure into the green shoot (leaf and stem), and colorless root.*

Fourth. *The four essentials exist rarely in abundance and then never for much of the time,* and most commonly are sparser than plants can make use of. Frequently the light, always the carbon dioxide, often the water, and sometimes the minerals are accessible only in dilution. Therefore the plant must needs reach out extensively to come into contact with a sufficiency,—a condition in great contrast to that prevailing in animals with their concentrated food and consequent compactness of body. *This is why plants are branched so profusely and slenderly.*

Fifth. *One of the four essentials,—viz., light, is of such nature that it cannot be transmitted far into the plant, and therefore must be*

used at the surface. Hence plants have had to distribute the green tissues of the shoot in a manner ensuring the exposure of a great spread of surface to light, and this involves a flattening of most of the tissues of the shoot to the thinnest practicable structures. *This is why leaves exist, and why the green plant consists of them so largely.*

Sixth. *One of the essentials, the sunlight, falls upon plants from every direction in the aërial hemisphere.* Not only does it come from a source which forever is changing its position in the skies, but, furthermore, this light is so strongly diffused through the atmosphere that it falls upon plants from every direction in an intensity which for most of the time is as great as leaves can make use of; for it is a physiological fact that plants cannot use all the energy contained in full sunlight, and strong diffused light is enough for their needs. Hence it comes to pass that plants receive light in amount and direction sufficient to illuminate a great many leaves if only these are carried to various heights and spaced well apart, in a general distribution answering to that of the incident light. This necessitates the specialization of a part of the shoot for carrying the leaves upwards and outwards. *This is the reason why stems exist and branch in such manner as typically to carry the leaves to a hemisphere of foliage.*

Thus it is evident that the most distinctive features of structure and form displayed by plants of the highest development, the features indeed which are most closely associated with our very idea of plants,—the sedentary habit, the radial symmetry, the diffuse-slender branching, the primary division into shoot and root, and of the shoot into flat leaves and supporting stems,—all exist as adaptations which adjust the photosynthetic process to the conditions under which the photosynthetic essentials are supplied by the external world. It is therefore a fact that the photosynthetic process determines the ground form and primary structure of plants just as truly as it determines their ground color.

It is worth while to try to express the sum of these features in diagrammatic form, and my suggestion thereof is contained in figure 7. The purely photosynthetic plant would exhibit a system of equal rigid branches springing as radii from a central trunk, and forking regularly outward to a vast number of young twigs which would turn up near the tips to spread the leaves horizontally in a hollow hemisphere of foliage. This theoretical form, of course, is modified in practice by other considerations, especially the exigencies of mechanical support, as we shall later consider;

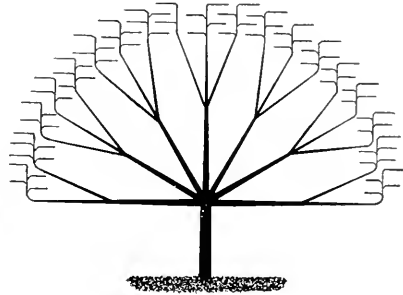


FIG. 7.—The form, as seen in vertical section, which a plant would display (theoretically) if free to adapt itself to photosynthesis alone. Further particulars in the text.

but nevertheless it comes appreciably close to realization in the most typical of the great trees, when these are free to develop without interference, as was the case with the Oak of the accompanying picture (figure 8).

We turn now to a particular study of those two most distinctive plant structures, the leaf and the stem. A first view over leaves in general gives only the impression of bewildering multiformity; but continued observation gradually sorts out the important from the trivial, and builds one of those visualized composites of which I have spoken in the first chapter. As the reader should review and confirm for himself by inspection of a number of kinds brought together for the purpose, the principal part of an ordinary leaf is the spreading thin blade, which exhibits two constituents,—first, the soft, seemingly-homogeneous, chlorophyllous tissue, denser in green on the uppermost surface, and seat of the food-making process, and second, the slender white veins, springing out from the leaf-stalk and variously branching and interlacing while ever attenuizing towards the margin and tip of the

blade. The tiniest veins are embedded within the green tissue, where they end in polygonal areas, as one can see with a lens in some leaves by holding them up to the light (for example in Rose, Cabbage, and Wild Ginger), and as shown in the accompanying cut (figure 9); but the larger veins stand out from the surface, though always from the undermost side where they are out of the way of the light. The veins have a double function,—the conduction of water from the stem to the green tissue, and the



FIG. 8.—An oak tree, showing an approximation to the theoretical form of figure 7. (Copied from Blanchan's *American Garden*.)

conduction of the photosynthetic sugar back to the stem; and they have also a secondary use in helping a little to support the soft tissue, though the rigid but elastic stiffness of the healthy green leaf is due for the most part to osmotic turgescence, of which I shall speak in the suitable place. In addition to the blade, most leaves possess a leaf-stalk, or *petiole*, stem-like in appearance and function and varied in length, which carries the blade out into the light and aids to adjust it therein, as we shall later

consider more fully under light-adjustment, or phototropism. Finally, some leaves exhibit, just where the petiole joins the stem, a pair of little leaf-like bodies called *stipules*, whose most remarkable feature is the diversity of their somewhat insignificant functions and forms. All of the parts of a typical leaf,—blade, petiole and stipules,—are well shown and in typical form, in the accompanying picture (figure 10).

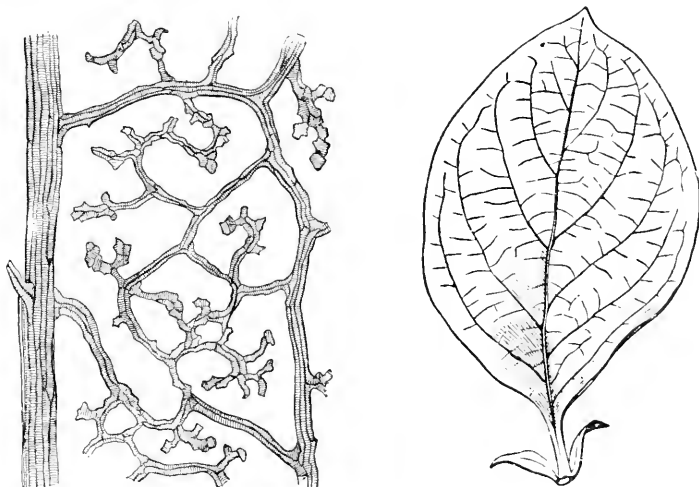


FIG. 9.—A fragment of the vein system of a leaf, highly magnified, showing the typical mode of ultimate branching and ending of the veinlets. (From Sachs' *Lectures*, reduced.)

FIG. 10.—A typical leaf,—the Quince. (From Gray's Text-books).

The most striking of the features of leaves is perhaps the remarkable variety of their shapes, which seem in their multiformity to defy explanation or classification. Yet in reality the matter is simple, for there exist only three primary forms of which all the others are modifications and combinations, as the following analysis will show.

First, the ideal condition for the best working of a leaf is obviously that in which it can have full exposure to all the light that

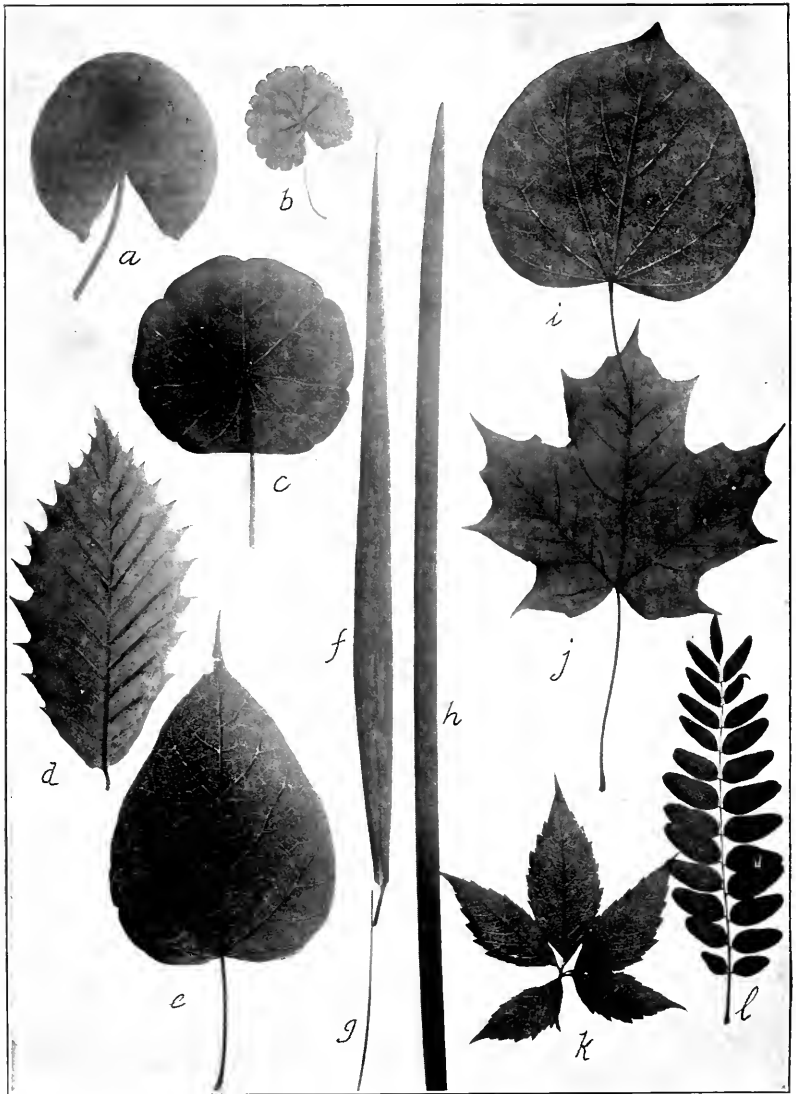


FIG. 11.—Leaves selected to illustrate the typical shapes; a photograph of living specimens, one-third the natural size.

there is, without any shading by its neighbors. This ideal exposure allows the development of the ideal type of construction, i. e., the shape that encompasses the most green tissue within the least outline, and a venation ensuring the shortest paths for conduction of water and the photosynthate. Such a leaf must be round, with its veins radiating from a central petiole. It is well-nigh realized in the leaf of the Common Garden Nasturtium (figure 11, *c*), a low-stemmed plant whose long petioles permit a full exposure of each leaf to light (figure 12); and it is shown conventionalized in figure 13, *a*. Furthermore, this association of round-radiate (or, in the current terminology, *round-palmate*), shape with full exposure to light is actually found in most plants which grow in such manner that their leaves do not shade one another, as for example in the floating leaves of Water Lilies (figure 11, *a*), Ground Ivy (figure 11, *b*), Wild Ginger, and others which trail or creep on the ground, and in low-growing long-petioled herbs like Geranium, Cyclamen, and Pelargonium, and partially in Ivies. Most of these leaves show a slit from the petiole to margin, but that does not alter the principle of the central-standing petiole, for the slit is merely a relic of the evolution of these leaves from kinds in which the petiole stood on the margin; indeed all intermediate gradations exist in heart-shaped, arrow-shaped, and "auriculate" leaves, where a part of the blade bulges backward on each side of the petiole.

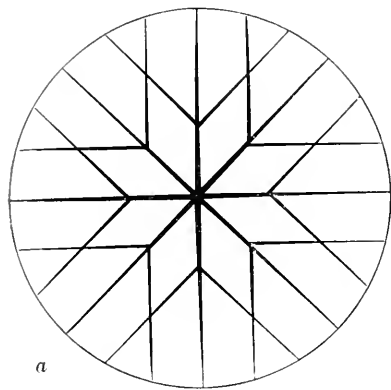
Second, the opposite extreme of habit is found where leaves are compelled to grow crowded together, as they are in most plants living in especially dry or light places. In this case the best shape and arrangement would be necessarily the exact opposite of those found in the round type, that is, the leaves would be slender or *linear*, without distinction of petiole and blade, and with the veins running parallel; while they would take such positions as would admit the light most deeply and evenly among them,—viz., they would point at the light and therefore stand parallel or radiating with respect to one another. Such a position for the leaves is in

fact not at all bad for illumination, since diffused light can penetrate rather deeply among them, while the sun, in its daily swing through the heavens, slants its beams at times to the innermost parts of them all. The typical linear shape is actually realized in a great many leaves, of which our figure 11 shows a few (*f, g, h*); and it is shown conventionalized in figure 13, *b*. The association of linear shape with a crowding of leaves into dense-radiating heads is found typically developed in a good many plants, such as



FIG. 12.—The three types of plant form with which are associated the three fundamental types of leaf shape. On the left is the trailing Garden Nasturtium, in the middle, the half-desert Cordyline, on the right the typical woods-plant *Ficus religiosa*.

Spanish Bayonets, and the remarkable Tree Yucca of the deserts, in Century Plants, the ornamental Cordylines (figure 12), and some of the Bunch Grasses. The association of the linear form with parallel-standing leaves is realized in the Flags and Cat-tails of stream margins, and especially in the Grasses of the meadows, which thus crowd a vast number of leaves into a limited area. And another phase of the very same thing is presented by some of our evergreen trees, with their linear or needle-shaped



leaves. These symmetrical cone-shaped trees may be viewed, indeed, as a series of superposed meadows, spaced well apart in stories so arranged that each is smaller than the one next beneath it, thus avoiding injurious shading thereof, while the leaves point outward as well as upward towards the strongest light. This condition is represented diagrammatically in figure 14, and it comes very close to actual realization in some of our Spruces and Firs when these are free to develop as they will (figure 15). - This is the principal factor, I believe, in the explanation of the conical form of the evergreens.



Third, the conditions to which are adjusted the round and the linear shapes of leaves are uncommon in comparison with that in which numerous leaves are spaced at different heights along ascending stems,—for this latter is the prevailing mode in vegetation, (figure 12, right). Since this condition is intermediate between the other two, we anticipate an intermediate shape of leaf, which would therefore be elliptical in out-

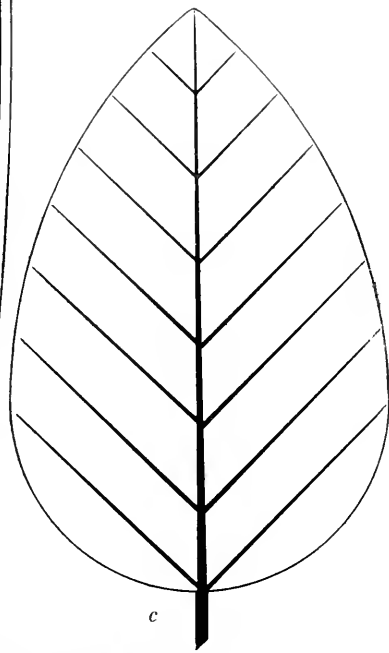


FIG. 13.—Conventionalizations of the three fundamental types of leaf form.

line with the petiole at one end and the veins branching off pinnately from an axial mid-rib. This shape and venation are actually realized in the leaves of some trees, very typically in Chestnut (figure 11, *d*), Elm, Rubber-plant, and Banana. Much

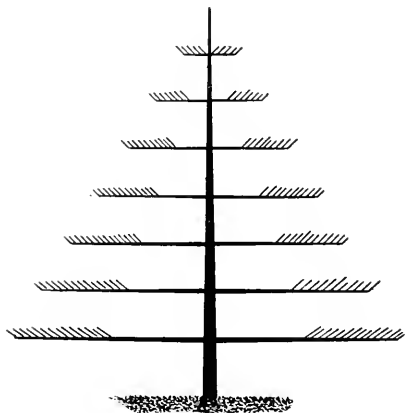


FIG. 14.—The theoretical form, seen in vertical section, of an evergreen tree. Further particulars in the text.

oftener, however, this outline is modified by a condensation of the green tissue towards the base of the leaf, which ensures a shorter path of conduction for water and the photosynthate, while lessening simultaneously the weight and leverage on the petiole. Such leaves are necessarily of ovate outline, and these *ovate-pinnate* leaves are very common in nature. The shape is well typified in the Catalpa, for example, (figure 11, *e*), and is represented in conventionalized form in our figure 13, *c*. In some plants the condensation goes so far as to make the leaf almost round, as for example in the Red-bud (figure 11, *i*), when the venation makes some approach to the palmate type and the petiole is apt to be notably long. Such leaves often show a bulge of the tissue downward each side of the petiole, thus displaying a transition to the typical round shape with which we began.

It is thus evident that three fundamentally-distinct conditions of leaf exposure exist, with three corresponding types of leaf shape,—the *round-radiate*, the *linear-parallel*, and the *ovate-pinnate*. But innumerable intermediate conditions of leaf-habit exist, and therefore innumerable intermediate leaf shapes occur. These shapes have a large practical importance in the classification and description of plants, and accordingly have been named for this purpose with very great accuracy; and it is inter-

esting to note that while some of the shapes have been named for their resemblance to familiar mathematical forms or common objects (e. g., ovate, lanceolate), the majority have to be designated by combinations of these terms (as ovate-lanceolate, etc.).

For completion of our subject of leaf shape, one matter of importance remains, and that concerns the curious emarginations, lobings, and compoundings which so many of the kinds exhibit. The margin of a leaf is typically smooth or entire, and many leaves actually exhibit this character; but others again are more or less waved, toothed, or incised, through the sagging, as it were, of the green tissue between the ends of the veins, or, occasionally, its swelling out beyond them. When this lobing becomes deep, it influences greatly the form of the leaf, especially as it follows the type of the veining. Thus, a deep lobing between palmate veins results in a shape like that of the Ivies, and the Maples



FIG. 15.—Engelmann's Spruce, showing an approximation to the theoretical form of figure 14. (Copied from Kirkegaard's *Practical Handbook of Trees*, etc.)

(figure 11, *j*), while if it goes clear down to the leaf-stalk (in which case the separated segments usually develop little stalks of their own), it results in a leaf that is palmately compound, like the Woodbine (figure 11, *k*). A similar deep lobing in pinnately-veined leaves leads through forms like those of the Oaks to pinnately-compound leaves, like those of the Locust (figure 11, *l*) and many Ferns, which latter, indeed, are often again lobed and compounded, and re-compounded again. In a general way,

as will later appear, there is a probable adaptational advantage in the compounding of leaves, since it aids them to resist the tearing action of strong winds, and there is a possible adaptive explanation of the deep lobing of leaves like Ivies and Maples in the opportunity thus afforded for an interlocking of the leaves and consequent utilization of every ray of the incident light. But nobody, so far as I can find, has yet been able to give a reasonable explanation of the significance of the emarginations of leaves, for the suggestion that the points thus resulting serve to collect atmospheric electricity for some use by the leaf can hardly be seriously entertained. Emargination, lobing and compounding are evidently three degrees of the same thing, but it is by no means necessary to believe that because compounding is adaptively useful, therefore emargination must be useful likewise. On the contrary, it is not only possible that the emargination of leaves originates non-adaptively in some manner purely incidental or accidental, and is later intensified adaptively to lobing and compounding, but the method embodied in this supposition affords the most reasonable explanation we yet possess of the origin of adaptations.

While adaptation to the mode of exposure to light is the chief factor in determining the shape of the leaf, other adaptations and influences, very different in different cases, exert also their effects, making the shape of any given leaf a resultant of the coöperation of many influences. This fact the reader must remember when he tries to apply the principles of the preceding pages to the explanation of leaf shapes he may find in his walks abroad in the country. At first he will find so many exceptions and contradictions that he may incline to dismiss my explanations as groundless; but if he will continue his observations with patience, he will gradually find the exceptions disappearing and the essentials standing out in those composite conceptions of which I have spoken in the first chapter; and then, I believe, he will agree with the conclusions here expressed.

From the leaf we turn to the associated and well-nigh equally distinctive part, the stem, of which, however, the structure is comparatively simple and uniform. Since its principal function consists in raising and spreading a great many leaves to the light, it must of course be adapted to provide a firm mechanical support in conjunction with much branching; and in fact it consists of a cylindrical-tapering, rigid-continuous, regularly-ramifying structure familiar in the stems of the majority of plants. Although older stems become strongly thickened and woody, and protectively enwrapped in layers of bark, the young growth is soft and green like the leaf, and likewise consists of veins and soft tissue, though the relative importance of the two is reversed in the stem as compared with the leaf. The veins can be seen by the eye in young stems that are translucent (e. g., Balsam), when these are held to the light; and they can also be made visible through the tissue in some others if these are stood with their cut ends in a deeply-colored liquid. And they can always be seen in thin sections cut crosswise of the stem, as well illustrated in some later figures (73, 139, *B*) which accompany a fuller discussion of the stem in another connection. The veins form a ring in most kinds of young stems, though in some they are scattered about; and wherever they branch to run out to the leaves the stem is commonly swollen a little, and oftentimes lighter in color, giving origin to the so-called *nodes* separated by spaces called *internodes*, which are by no means "joints," as sometimes described. Outside the ring of the veins, as the later figures 73 and 141 show very clearly, the soft tissue holds chlorophyll, and thus aids the leaves in their photosynthetic function. The amount of such work that stems can do must in fact be little; but the plant takes advantage, as it were, of every bit of its surface exposed to the light and not needed for other uses, even including such parts as the stamens and pistil of the flower, to spread out additional chlorophyll for the invaluable photosynthesis.

Stems, as a rule, grow continuously from buds at their tips,

and new branches from buds in the angles between stems and leaves,—a position which has the advantage of nearness to the manufactories of food. This brings us to consider the causes which determine the arrangement of leaves on the stem, a curious matter, scientifically called *phyllotaxy*, and once discussed more commonly than now in botanical books. Leaves do not originate on the stem at hap-hazard, as may seem the case on some slender branches, but in quite definite and even mathematical order, as rosette-like plants, cones, and some other very compact structures suggest. Two primary systems of leaf-arrangement are possible, and occur. The simplest is the *opposite* (or *whorled*) system, in which two leaves stand at the same node exactly opposite one another, as occurs for example in the Mints, (figure 16, *A*), in which case the next pairs above and below stand at right angles and thus cover the space left by the first set, producing four vertical rows often in remarkable symmetry, as our common cultivated *Coleus* illustrates. This, with the other arrangements, is shown diagrammatically in figure 16, where the reader is supposed to look down from above on the stem, which is imagined to be telescoped, so to speak, chinese lantern fashion, to a single flat plane, as indeed the stems actually are in the buds. In some kinds, three instead of two leaves stand at a node, or four or five, or more, producing a regular whorl, but in all such cases, illustrated for instance by large Lilies (figure 16, *B*), the leaves in a whorl are evenly spaced and cover the breaks in the whorls above and below. This is the system prevalent in flowers, for, as everyone will recall, the whorl of sepals covers the breaks in the whorl of petals, with a similar arrangement in stamens and carpels. Thus much for the opposite or whorled system; the other is the *spiral*, in which only one leaf ever stands at a node, while the one on the node next above or below stands part way around the stem, the successive leaves falling always into a regularly-ascending spiral. Now this space around the stem from one leaf to another is a definite fraction of the circumference;—in some plants it is $\frac{1}{2}$,

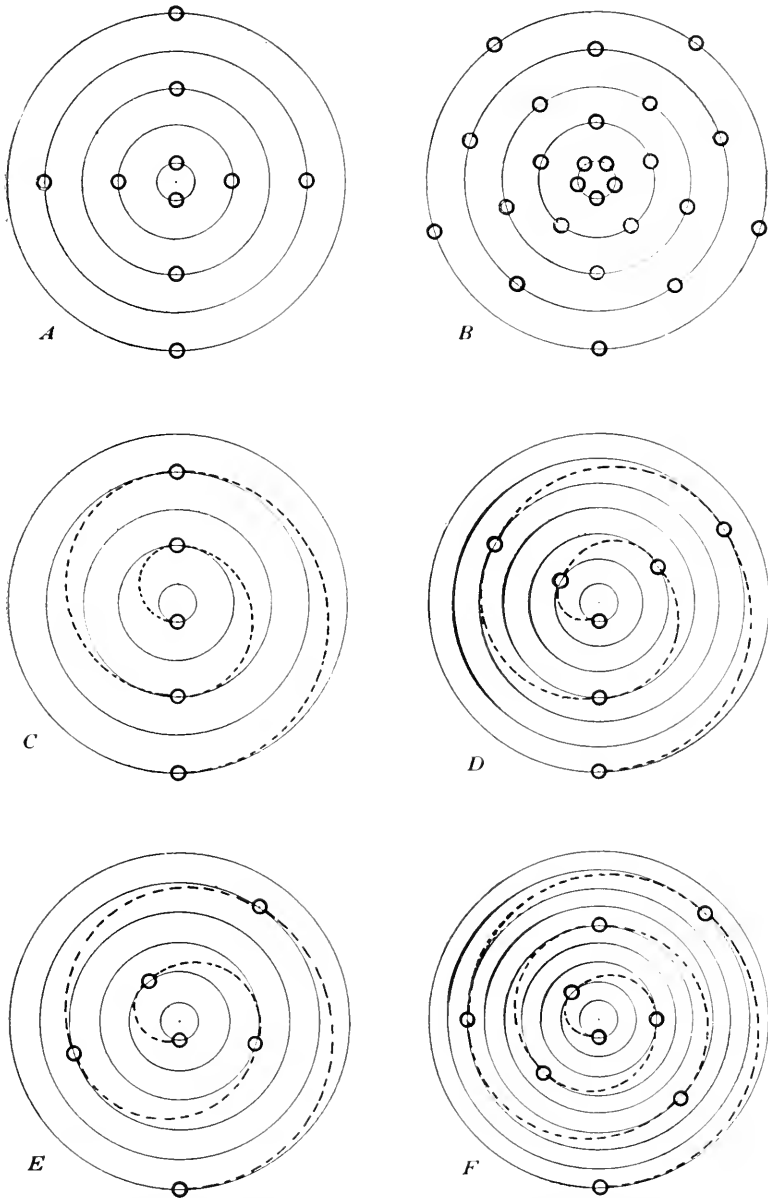


FIG. 16.—Diagrams to illustrate the principal systems of leaf-arrangement, as they would appear from above if the stems were telescoped to one plane. The rings are nodes, and the small heavy circles are leaf bases. Further particulars in the text.

as in the Elm and Grasses, in which case one must pass once round the stem and cover two spaces to reach a leaf over the first (figure 16, *C*). In others, (e. g., the Sedges), the fraction is $\frac{1}{3}$, and a spiral drawn through the bases of the leaves passes once round the stem and across three spaces to reach a leaf over the first (figure 16, *D*). In others, (e. g., the Apple) it is $\frac{2}{5}$, when the spiral must pass twice around the stem and cross five spaces to come to a leaf over the first (figure 16, *E*), an arrangement which is, perhaps, the commonest of all. In others the fraction is $\frac{3}{8}$ (in Holly and Plantain figure 16, *F*), or $\frac{5}{13}$, as in cones of White Pine, while $\frac{8}{21}$, $\frac{13}{34}$, and even some higher fractions are said to have been traced in special places where the leaves are greatly condensed together in rosettes. And a curious thing is this, that while these fractions occur, the various possible intermediate ones do not. In these fractions, which primarily express the amount of circumference between two successive leaves, the numerator also expresses the number of turns that must be made around the stem to reach a leaf over the first, while the denominator expresses the number of spaces that must be passed over for this purpose, and also the number of vertical ranks into which the leaves fall. Moreover, these fractions bear to one another a very curious relationship, for when they are arranged in a series,—viz.,

$$\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}$$

it is found that each numerator is the sum of the two numerators preceding, and each denominator likewise the sum of its two predecessors, and moreover each numerator is the same as the denominator next before the preceding. This curious series, known in mathematics as the Fibonacci series, is said to find expression in other phenomena of nature, including the arrangement of the planets, and is therefore not peculiar to the phyllotaxy of plants. The question of present importance, however, is this,—what is its meaning in connection with leaf-arrangement? Of course one's first natural thought is,—*adaptation*, which appears reasonable enough with the opposite system and the whorls, and even with

the lower fractions of the spiral system, where one can see the advantage of a spacing which may give to the leaves the best aggregate exposure to light. But this interpretation meets increasing difficulties with the higher fractions, and even has trouble with the lower when one notices how freely the leaf-blades, the very parts which need the exposure to light, are swung by their slender petioles into positions of advantageous individual exposure in callous disregard of the orderly arrangement in which they start from the stem. There is, however, another and very different explanation of the systems of phyllotaxy advanced by some investigators, viz., that they are wholly determined by the positions in which the young leaves originate inside of the growing bud, which positions in turn are determined by mechanical principles connected with the easiest mode of origin of new swelling parts in buds of a certain size and shape. In other words the fractions of phyllotaxy are merely an incidental result of mechanical conditions present in growing buds, and have only a secondary, if any, reference to adaptation. This explanation I believe to be substantially correct. It is of course not an explanation of phyllotaxy, but merely a transference of the problem into another field, as most of our explanations are. But I dwell upon the subject at this length because phyllotaxy seems to me to offer a fairly clear case in which a conspicuous feature of plant structure has merely an incidental and not an adaptive origin.

There is one other feature of leaf and stem structure to which I have not yet made any particular reference, and that concerns their sizes, which are wonderfully diverse in different plants. Leaves are measured in terms of feet in Bananas and Palms, but need the assistance of lenses to show them at all in some of the kinds that grow in the deserts; they are merely of tissue thinness in some kinds of Ferns, but cylindrically-thick and stem-like in Aloes and Century Plants. Stems display a thousand feet of length in the Rattan Palm, but are invisible supports to tufts of leaves in the Houseleek; nearly as thin as a hair in some Ferns,

but quite as thick as a house in the larger species of Redwood; branched to a spray in a Mango Tree, but an unbranched shaft in the Royal Palm. Thus it is evident that leaves and stems exhibit well-nigh as remarkable a diversity in size as in shape, and we must conceive of our generalized or composite leaf and stem as well-nigh indefinitely modifiable, possessing, as it were, a kind of a super-elasticity in both of these features. As to the causes determining size in these parts, that is reserved for discussion in the chapter on Protection, where it will be shown that the size actually displayed by any leaf or stem represents in the main a compromise or truce between the conflicting tendencies of the plant to make its leaves larger for photosynthetic advantage on the one hand, and smaller for better resistance to hostile external conditions on the other.

In this chapter thus far but little has been said concerning the root. This is because the consideration of that organ is more convenient and natural in the chapter that deals with its function of Absorption; and there its description will be found in detail. It is enough for our immediate purpose to say that roots, the principal organs for the absorption of water and minerals, and the third of the primary plant parts, grow out from stems, which they closely resemble in structure, having much the same internal cellular construction as well as the same long-tapering, freely-branching forms. Though not without diversity in form, size, and structure, they are yet far less varied in these respects than are leaves and stems, and for a sufficient and obvious reason,—namely, they grow under far more uniform conditions; for life in the soil is much the same thing all the world over, however varied it may be upon the surface.

Thus far we have considered only those diversities which leaves and stems exhibit while still retaining their typical function of photosynthesis. But their remarkable plasticity does not exhaust itself here, for these parts can even perform entirely different functions, becoming adaptively modified therefor to such a de-

gree that their original nature would hardly be suspected were it not for the existence of intermediate stages. And not only that, but conversely, substantially all of the structures performing remarkable or unusual functions and displaying remarkable forms, are simply transformations of the three primary parts, leaf, stem and root. This subject of the formation of all the special organs of plants out of leaf, stem, and root, (a typical example, by the way, of morphological study,) we must now proceed to consider.

The particular structures performing definite functions in typical plants, other than ordinary leaf, stem, and root, are the following:

Bud coverings, or scales, give needed protection to living buds over winter. Adaptively to this function, they are small, concaved, thick, corky, brown, and often resinous, as the large winter buds of any common trees will illustrate.

Bud scales are transformed leaves, usually leaf-blades, but in some plants (e. g., the Horse Chestnut) are petioles, the blades being suppressed, while in others they are stipules, as shows very beautifully in the Tulip Tree (figure 17.)

Tendrils, or similar parts, enable slender plants to cling to a support and thus mount upward towards the light. Adaptively to this function they are slender, tough, cylindrical, or cord-like structures, endowed with remarkable powers (to be later considered in the chapter on Irritability), of reaching out for a support, taking a firm hold thereon, and subsequently shortening and toughening their structure (figure 85). The best tendrils, like those of the Passion Vine or the Grape, are transformed stems, issuing from buds precisely as branches do. Others are transformed leaf-blades, as in the curious *Lathyrus Aphaca* (figure 18), or a part thereof, as in *Vetches,* or *Bignonia*; or are stipules, as in the *Wild Smilax,* or merely the petiole



FIG. 17.—The stipular bud coverings of the Tulip Tree; one-third natural size.

which makes a turn around some object, as in the Clematis, or a cylindrical part between two portions of blades as in those Pitcher plants called *Nepenthes* (figure 20). In some tropical plants, e. g., climbing Aroids, the aerial roots clasp horizontally around a support. In some others, and notably those having the habit of the Ivies, and growing against stonework, the tips of the tendrils do not twine around a support, but end in discs which are firmly appressed to the stones, as in the Woodbine, though more commonly the disc-holding structures are aerial roots, as the English Ivy illustrates.



FIG. 18.—Tendrils transformed from leaf-blades, with stipular foliage, of *Lathyrus Aphaca*; one-half natural size.

Spines project repellingly from some kinds of plants as if they might form a protection against the attacks of large plant-eating beasts. They possess a stiff, hard, conical structure, and a firm attachment to the skeleton, consistent with that use. In some plants they are no more than prickles, erupted, so to speak, from the surface, as in the Rose; in other cases they are the sharpened ends of the veins, as in the Holly; in others they are the leaf-blades, as in the Barberry and the Cactus; in others they are stipules as in the most spiny of the Euphorbias (figure 19), though in some other kinds the spines are the persistent and indurated floral branches; in others, such as the Locusts, they are transformed branches coming from ordinary axillary buds; in some Palms they are roots; and cases are known where they are petioles.

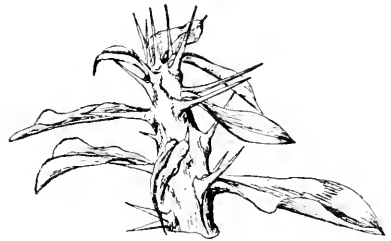


FIG. 19.—The stipular spines of *Euphorbia splendens*; one-half natural size.

Food Reservoirs store up for later use the food-material made

in the leaves of herbaceous perennial plants, and, adaptively to this function, are greatly-swollen, soft-bodied, large-cellular structures. They are leaves in the bulb scales of Lilies and Hyacinths, stems in the common Potato (the eyes being axillary buds), and roots in the Sweet Potato.

Insect Traps effect the capture and digestion of insects, and thus enable some plants to augment the scanty supply of nitrogenous compounds available where they grow. Adaptively thereto these traps have highly special forms and accessory features contributing to the attraction and capture of insects, as will later be noted in a particular description of these plants. The trap is a pitcher formed by a special cup-like-upgrowth of the leaf-blade, as in the various Pitcher Plants (figure 20), or else a hinged or inrolling blade, as in the Venus Fly-trap and Sundew.

Flower parts contribute in various ways to the efficiency of reproduction, as will later appear in a discussion of that subject. The parts are transformed leaves, and display features adaptive to their functions,—the green leaf-like sepals which protect the other parts while in bud, the brightly-colored petals which exhibit the position of the flower to the visiting insect, and (though with a reservation) the stamens and pistil concerned with the actual pollination. In some kinds of flowers the petals are missing, but their function is performed by brilliantly-colored leaves close under the flowers, as shown so strikingly in the Poinsettia.

Miscellaneous. There are, furthermore, a great many special

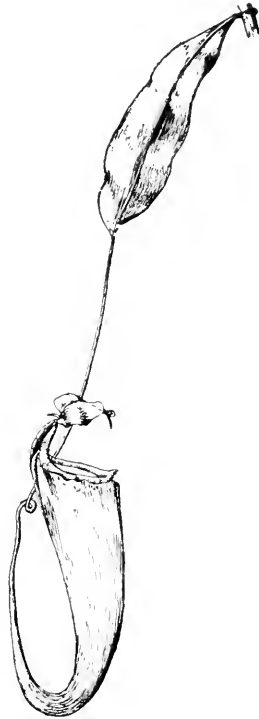


FIG. 20.—An insect-trapping pitcher, formed by a cup-like extension of the leaf tip in *Nepenthes*; one-third natural size.

structures with particular functions not belonging in any of the definite categories above mentioned. Thus, the bladdery air-filled floats which keep the Water Hyacinth resting so lightly on the water are petioles; the wing which ensures the carriage of the Linden seeds is a leaf-blade (figure 157); the indurated hooks by which some tropical vines do their climbing are stipules; while the reduced or rudimentary leaves which we call bracts often also possess functions of a minor sort.

Substitution foliage. Finally, we must take notice of another curious transformation in function and structure found in all parts



FIG. 21.—A flattened petiole serving as foliage (the blades being insignificant), in an Australian Acacia; one-half natural size.

other than the leaf-blade, namely, they may become transformed into foliage, either in aid of the blade, or its replacement. Thus, in some kinds, the blade is greatly reduced or missing, and the petiole is flattened and thin and acts as the foliage, e. g. in the Australian Acacias (figure 21), and some kinds of Oxalis. In a good many plants the stipules are sufficiently big to render appreciable aid to the leaf-blade. In *Lathyrus Aphaca* (figure 18) they form all of the foliage there is, while in the common Bedstraw or *Galium*, they are as large as the leaves and so like them as commonly to be thought additional leaves helping to make up a whorl. In a great many plants, and especially those found in dry places, the leaves become very small or are absent, and the function of foliage is performed by the stem, which either remains smooth and round, or becomes fluted by the presence of vertical green ribs, or becomes flattened in various degrees, all three conditions of which are found in the family of Cactuses. In some cases the stem is flattened as thin as a leaf, while still displaying the nodes distinctive of the stem, as in the *Muehlenbeckia* of our greenhouses (figure 22); but in other cases no nodes appear, and the stem assumes a form and general aspect so leaf-like that

the botanical teacher has often much ado to convince his students that it is anything else, even when he shows them the actual leaves, reduced to scaly bracts, out of whose axils the leaf-like branches clearly spring. Such is the case with the Butcher's Broom of Europe, (figure 23), our common *Asparagus*, and the cultivated *Smilax* of the florists. Finally there is even a case



FIG. 22.—The leaf-like stem, with some small leaves, of *Muehlenbeckia*; one-half natural size.

FIG. 23.—The leaf-like branches of *Butcher's Broom*; one-half natural size.

in a tropical Orchid, *Taeniophyllum* by name, where the roots serve as foliage, becoming suitably flattened and otherwise appropriately constructed.

We cannot take space to follow any farther this most interesting subject, but if the reader desires another and much fuller discussion thereof, he will find it in the appropriate places in *Asa Gray's Structural Botany*, where it is treated in a manner that in my opinion cannot be surpassed. The subject, moreover, is one which offers attractive opportunity for concentrated field study

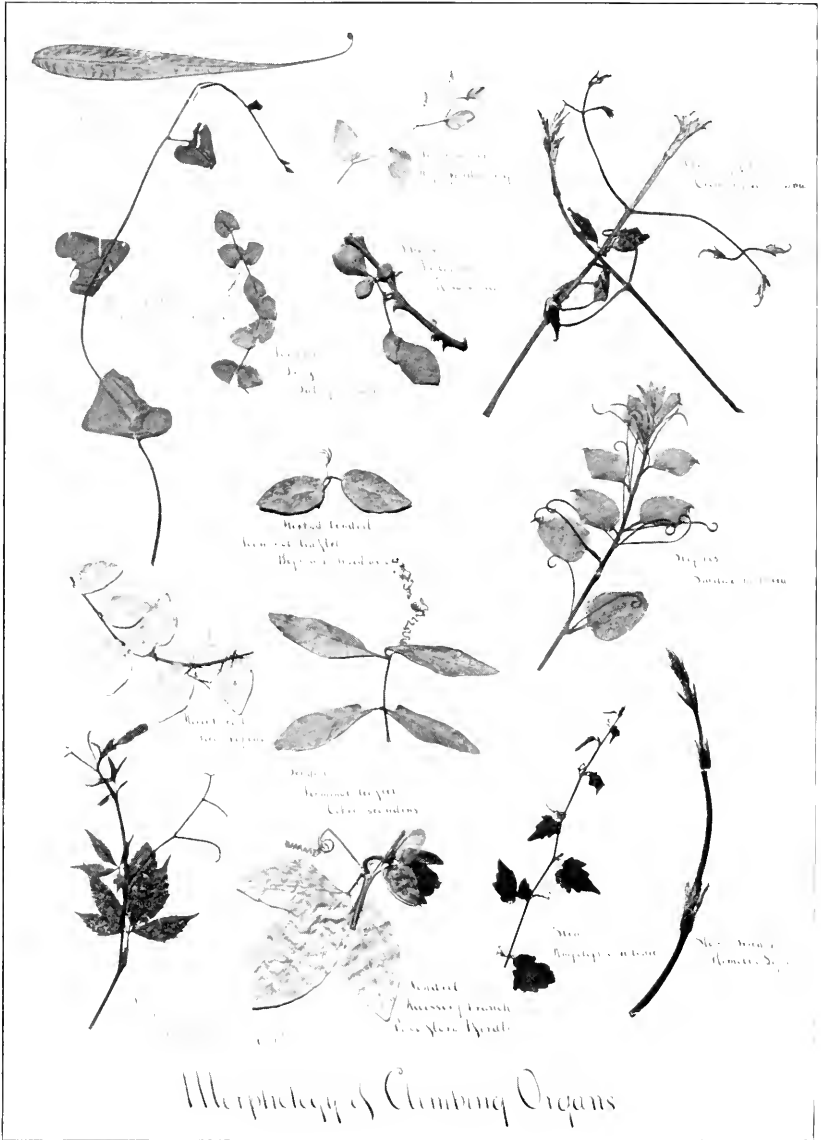


FIG. 24.—A collection of specimens, pressed and dried, and arranged to illustrate a morphological topic; photographed one-third the original size.

in the discovery, identification, collection and arrangement of the various special structures of plants, which can then be preserved in some such manner as our picture illustrates (figure 24).

Thus it is evident that, on the one hand, the three primary plant parts,—leaf, stem and root,—though developed with a structure adaptive to the very particular function of photosynthesis or food-making, have in many cases become transformed into other parts of very different ecological significance and structure; while, on the other hand, and correlatively, all of the great number of highly specialized parts performing other functions can be traced back to an origin morphologically in the three primary plant parts. This interlocking relationship of morphological origin with ecological meaning,—of morphology with ecology,—can perhaps be made clearer by use of a diagram such as is given herewith (figure 25).

Although I ought now to end this long chapter, I will continue far enough to answer two questions which I am sure have arisen in the mind of the reader. Thus, he will surely be wondering why it is that some plants make their tendrils, for instance, from leaf-blades, others from petioles, others from stipules, others from stems, and others even from roots. The most reasonable answer appears to be this, that when a plant, owing to a change of habit forced on it by a change of environment, develops a need for a new organ, that organ is made by a transformation of the part which happens to be most available for the purpose, often some part which the change of habit has happened to set free from its former use; and sometimes that most available part will be one thing and sometimes another. In the second place the reader will wonder why some plants should abandon their leaf-blades as foliage, and then proceed to replace them by petioles, stipules, stems, or even roots, which are for the purpose converted physiologically and structurally into leaves. In answer it may be said that the abandonment of the leaf-blade, as will be shown in the chapter on Protection, usually accompanies exposure to very dry

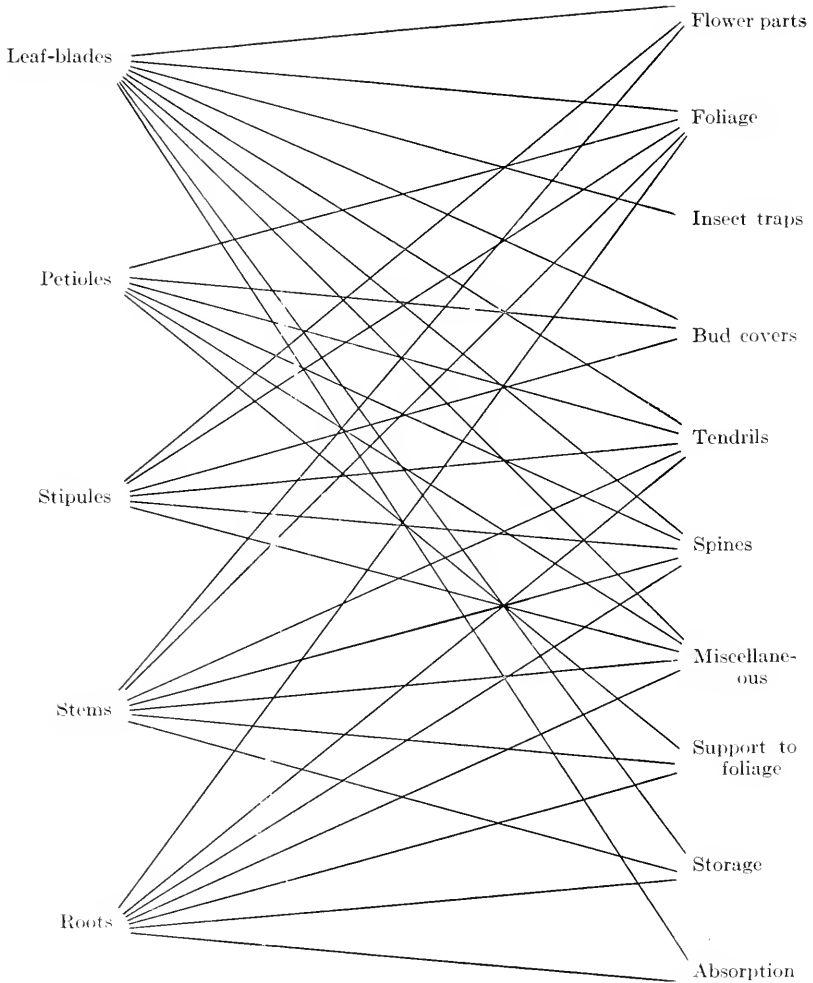


FIG. 25.—Diagram to illustrate the interrelations of morphological origins with ecological uses in the parts of the higher plants.

climate, in which case the function of foliage is taken over by some other part, usually the stem. Now it is conceivable that when, by another change of habit, the plant finds itself in need of a much larger spread of chlorophyll surface, this may be more easily obtained by further enlarging and flattening the already

leaf-like stem than by re-developing the lost leaves. It is probable that some peculiarity of this kind in the past history of the plant will explain in each case such curious features, the course of development being always that which offers the least resistance at the moment.

The reader will now be prepared, I think, to admit that of all the influences concerned in the determination of plant form,—indeed in making plants what they are,—the most important by far is the physiological process of food-making, or photosynthesis, and that the feature of this process having the most profound effect is the need for exposure to light.



CHAPTER IV

THE KINDS OF WORK THAT ARE DONE BY PLANTS, AND THE SOURCE OF THEIR POWER TO DO IT

Respiration



WHEN first I had written this chapter, and made it the best that I could, it assumed that the fact of plant work was already well-known to the reader. A later experience, however, made me see very clearly that most people do not know that plants work at all. Accordingly I shall make it my first endeavor to show beyond question that plants do work; then we can pass with better understanding to the study of the very remarkable source from which they derive their power to do it.

The principal reason why the majority of people do not associate with plants the idea of work is found in the slowness of most plant actions. Our conception of work is almost entirely subjective, and because plants are placid of mien, and do not hurry and fret and strain, we think they are doing no work. When the Master said of the Lilies, that they toil not neither do they spin, his words expressed the popular fancy but not the physical fact. Work is none the less real because it is slow, and the matter of slowness is entirely relative and subjective. Even the very swiftest actions performed by any of us must seem slowness personified to the lightning, or to a dynamite charge which can finish its work before you can think, or to the forces of collision which reduce a railway train to a heap of tangled scraps within the space of an instant. Probably the lightning, the dynamite, or the collision forces, if interviewed on the subject, would say that

mankind does not work. But if plant actions could be magnified immensely in speed they would impress one very differently in this particular. For then the observer would see the tip of every growing plant-structure nodding and moving energetically about, so that a meadow, a copse, or a forest would seem all of a vigorous tremble as if straining at some hidden leash: he would see the buds of some flowers open and close with a straining yawn or a sudden snap, and others burst into bloom like a rocket when it breaks to a spray of mani-colored lights: roots in their efforts to penetrate the earth turning and twisting like angleworms impaled on the fisherman's hook: seedlings in their struggle to break through the ground heaving and straining at their burden of superincumbent soil, like a powerful man at some load which has fallen upon him: seed pods pushing into the earth on a twisting or hard-thrust stalk: tendrils swooping in curves through the air, gripping the first thing they meet, and jerking their plants towards the support. As matter of fact, there does exist a way in which we can readily behold these actions thus magnified, for if the structure in question be photographed at regular intervals, say of fifteen minutes to half an hour, and then these photographs are run at high speed through a moving-picture machine,—the thing is done. Such studies have actually been made in the case of twisting roots, moving fruits, and opening flowers; and all of those who have seen them agree in the impression of vigorous work thus presented.

Furthermore, if we could magnify in like manner the interior parts of the plant we should witness as remarkable actions proceeding with equivalent vigor. In some plants the living protoplasm would be seen flowing in thick turbid streams round and round within the encasing cell-wall; in certain cells those remarkable structures called chromosomes would be seen performing their curious manœuvres,—arranging themselves into groups, collecting in pairs, passing backward and forward in a manner suggestive of the measures of the dancers in a quadrille; else-

where new cells would be seen in process of birth, and engaged in forcing the older apart to make room for themselves; while minor actions without number, mechanical, physical, and chemical, would appear in vigorous progress in various parts of the organism. Truly if one could see these actions under the conditions here imagined, he would have no trouble at all in connecting with plants the idea of real work.

We are not, however, dependent solely on imagination, or the moving-picture machine, for a conception of the reality of plant work. The rapid closing of the leaf of a Venus Fly-trap upon a captured insect, or the sudden collapse of the Sensitive Plant when touched, suggest some such idea. Everybody has noticed that the great granite curbstones along streets where shade trees are grown, become heaved from the regular lines in which they are laid, while the pavements themselves are oftentimes thrown into irregular swells; this is all brought about by the growth of the roots of the trees, which thus exhibit a work as real as that of a jack-screw or derrick. If the reader has not already observed these phenomena, let him do so when next he walks through a shaded street. In a similar manner young roots, insinuated between the stones of buildings, tombs, or walls, force the masonry apart in their growth, and finally accomplish the destruction of the edifice. Occasionally asphalt pavements are burst upwards by the growth of some kinds of plants, including even soft-bodied Fungi, as the accompanying photograph well proves (figure 26). And the technical literature of plant physiology tells of the thousands of pounds pressure exerted by large gourds, like Squash, when suitably harnessed to recording machinery. And, finally, experiment proves that every operation of plant life, even the least of them all, involves some movement, and therefore real work; so that animals and plants are working, and often right hard from the physical point of view, when they merely are keeping alive,—a conclusion from which the reader is welcome to draw any comfort that he can.

At this point, perhaps, some one will rise and declare I am wrong in my statement that work is as real when slow as when swift. But note that I say as *real*, not as *hard*. When a weight of a ton is lifted a foot, no matter by what means, the work is the same whether done in a day or a minute, although it is over a thousand times harder to do, (to be exact, the power required, is 1440 times greater) in the latter case than the former. But the fact of im-



FIG. 26.—An asphalt pavement burst upward by the growth of soft-bodied mushrooms, whose conical heads are visible over the wreckage.

mediate importance is this, that the work is as real in one case as the other.

We come now to the bond of connection between this matter of plant work and the principal theme of this chapter, viz.,—it is a fact of physics, which the reader must long since have learned, that every bit of work of every kind done anywhere whatsoever in nature, whether in a plant, or an engine, or the skies, or the thinking brain of a man, requires for its accomplishment the presence and expenditure of *energy*, which is the source of all power. The reader, of course, knows what energy is,—the entity in Nature, and the only one, that produces motion by which

work is accomplished. Energy is most familiar as heat or electricity, though manifest also in light and in chemical reactions. Without energy there is no motion, no power, no work; and without it a plant or an animal stops as dead as an engine when no fire burns under its boiler. Plant work, therefore, requires and implies a supply of energy. And with this conclusion it will be well to gather the foregoing matters into a generalization, another of our botanical verities;—*all plants, like all animals, are incessantly at work while alive, as truly as any moving machine, not only in the performance of their active and visible movements, but also in the bare maintenance of their existence; and this work requires a proportional supply of energy.*

It is now our business to find the source of the energy by which plants do their work. We know the source of the energy in the work of the engine just mentioned; it is the heat released from the burning of coal in a grate. But what is the source of the energy in the work of the plant, which has neither grates, nor boilers, nor flaming of fuel?

When the student of science is faced by a problem like this, his first resource is to look around for suggestions from some analogous process. In this instance he would turn naturally to animals, and his earlier studies on the physiology of man would have taught him that the power of animals to do work is connected in some way with their *respiration*,—that process in which they give forth the gases carbon dioxide and water vapor to the air, while absorbing the gas oxygen into their bodies. How intimately this process is connected with work is easily realized when we recall the familiar fact that respiration increases in proportion as work becomes harder. Is it possible, then, that plants also respire? That is, do plants in their work release carbon dioxide, and absorb oxygen? Obviously this matter is determinable by experiment, and the following is a very good method. In a bottle arranged as shown by the picture (figure 27), we place some plant parts which are actively working with-

out the complications introduced by photosynthesis (e. g., germinating seeds, such as Oats), then close the bottle air-tight by means of the stoppers and clamp provided for the purpose, and stand it for some hours in a warm and dark place where growth can take place. Obviously, any carbon dioxide released by the seeds must collect in the bottle, where its presence may be detected by its well-known property of turning clear lime-water milky. If, accordingly, clear limewater is poured into the tall vessel into which the delivery tube leads, the clamp is loosened, and water is poured down the thistle tube, then the gas will be forced from the bottle and sent bubbling up through the limewater. The result is always decisive. The limewater turns white-milky proving the presence of carbon dioxide in abundance. And if a bright person should here rise to remark that the carbon dioxide always present in air is sufficient to explain the result, it is easy to prove it is not; for, if an equal quantity of air

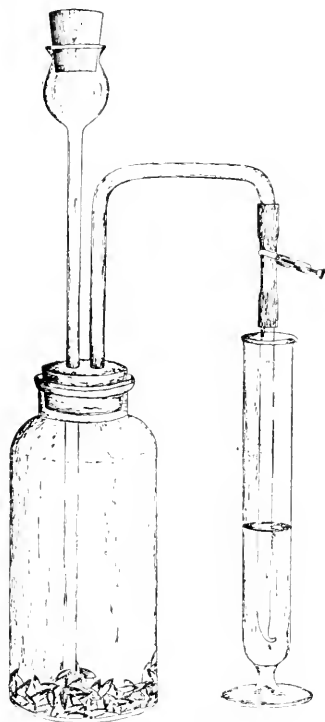


FIG. 27.—A Respiroscope, or arrangement for demonstrating that plants respire. Its operation is explained in the text.

be forced from an empty bottle through limewater no milkiness appears. And if, in the bottle, we place buds, or roots, or colorless plants like Mushrooms, or even green leaves (in the dark), the result is always the same. Furthermore, it is also the same whether the working parts are kept in the light or the dark, and it is still the same, as the reader may be confounded to learn, even with green leaves when kept in the light, though here the process is obscured by the absorption of that gas in photosynthesis, as can

be proven by experiments, too elaborate, however, for description at this place. Furthermore, as we may conveniently note here, all of these same working parts are simultaneously releasing water as well. It is therefore true, as a general principle, that all working

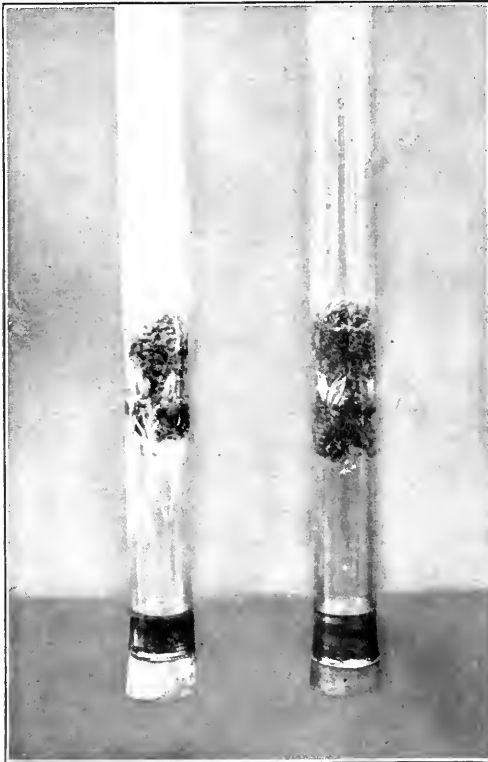


FIG. 28.—Two similar tube-chambers in which were placed similar sets of germinating oats kept wet and in place by wads of moss, and treated precisely alike except that those on the right were deprived of oxygen.

parts of all plants are giving off carbon dioxide as well as water, precisely as animals are doing.

But do plants exhibit the other phenomenon of animal respiration,—absorption of oxygen? It is very easy to prove that plants must have oxygen in order to live and work, precisely as animals must; for if two sets of the same seeds are placed in two similar closed chambers, and then the oxygen is removed from one chamber by a chemical absorbent while it is left untouched in the other, the seeds in the oxygenless chamber will not germinate at all and will soon die, while in

the other they will grow normally for a considerable time (figure 28). Furthermore, if the air of a closed chamber in which seeds have been growing for some days be subjected to chemical analysis, it is found that most of the oxygen has disappeared from the chamber, and must therefore have been absorbed by

the seeds. And the same thing is true no matter what structures we place in the chamber (saving only an apparent exception, soon to be noted, in the case of lighted green leaves), and no matter whether the chamber is exposed to the light or kept in the dark. It is evident, therefore, that all parts of working, (and that is to say, of living) plants, absorb oxygen and release carbon dioxide precisely as animals do.

There is no one, I think, who can grasp fully the bearings of a complicated subject after only a single presentation, no matter how clear this may be. It is therefore quite likely that some reader ere this has experienced a feeling of dazement, and been led to exclaim, along with the much-puzzled German, "Jemand ist verrückt, aber wer?"; and he may even incline to imagine that I am the "wer." For have not I shown, in an earlier elaborate chapter, that plants absorb carbon dioxide and release oxygen, while now I have proven by evidence quite as conclusive that they do exactly the opposite? But there is, nevertheless, no inconsistency. For the reader will recall that it is only the green tissues which absorb carbon dioxide and release oxygen, and then only in light, and then only from the tiny little chlorophyll grains embedded inside of the protoplasm. There should therefore be no trouble in understanding how the protoplasm in which those grains are embedded, like all other living parts of the plant, can be respiring, while the chlorophyll grains alone are engaged in the photosynthetic process. The case of the chlorophyll grains, however, is not so simple as my statement implies, because, since they are living protoplasm, there is every reason to think that they also respire even in light, and that in them,—and in them alone,—the two processes go on together. If, now, photosynthesis and respiration, with their exactly opposite gas exchanges, proceed together in leaves, why do they not neutralize one another's results? The answer is easy. Experiment shows that on the average the photosynthesis in green leaves in the light is over twelve times as active as respiration (and it may rise

very much higher), a preponderance that is obviously so great as to over-balance not only the respiration of the leaves, but of all the remainder of the plant besides, and not for daytime alone, but also for night. Therefore, day and night together, the green plant absorbs much more carbon dioxide than it releases and releases much more oxygen than it absorbs. It vitiates the air by its respiration, but in the long run purifies it still more by its photosynthesis.

Before leaving this part of our subject, we should look a little more closely into the relations of the two processes within the

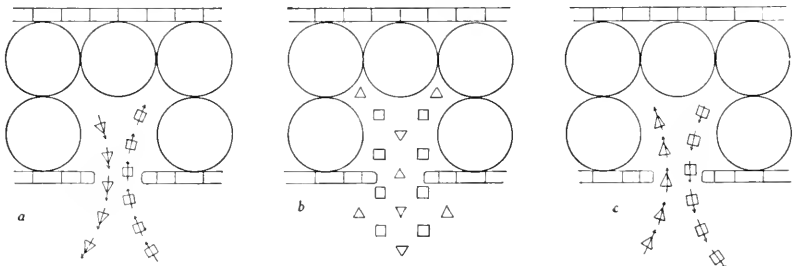


FIG. 29.—Diagrammatic sections across leaves, to illustrate the movements of gases in and out of the same during,—*a*, light, *c*, darkness, and *b*, the balance period between. The squares are carbon dioxide, the triangles are oxygen, and the arrows show the direction of movement.

lighted green leaf,—a subject diagrammatically illustrated by the accompanying figures (figure 29). At night all of the carbon dioxide given off by the respiration of the living cells into the air passages, makes its way along these and through the stomata to the atmosphere outside, (figure 29, *c*). In the daytime any carbon dioxide given off by the respiration of the protoplasm is absorbed by the chlorophyll grains in the same cells, but as this supply is wholly insufficient, a constant stream of that gas passes in from the atmosphere through the stomata and along the passages to the different cells, where it is absorbed by the chlorophyll grains; simultaneously a part of the oxygen given off by the chlorophyll grains is absorbed by the protoplasm of the same cells for their respiration, while the very large surplus is sent into the

air passages and along them and through the stomata to the atmosphere; and the reader should thus visualize these matters in his imagination (figure 29, *a*). But here comes an interesting point. Since photosynthesis is dependent upon light while respiration is not, there must evidently exist a certain intensity of light at which the two processes in a leaf exactly balance. At such times the processes use one another's gases, and there is no movement of carbon dioxide or of oxygen either into or out of the leaf (figure 29, *b*). Such a balance period must occur every day just after sunrise and before sunset, and on some very dark days it probably lasts for considerable periods. It is of course by virtue of approximation to such a balance that some kinds of plants such as Ferns, if not given too much light, can thrive so well for long periods of time in tightly-closed cases, or masses of red-berried vines (Partridge-berry) can exist all winter in little closed globes on dining-room tables.

We may now express the important facts of the past few pages in another of our botanical verities, to this effect,—that *plants, like animals, respire, and in identical manner, absorbing oxygen and releasing carbon dioxide, throughout all of their living parts.*

In the preceding paragraph I have said that the gases enter through stomata and pass along air passages, but I have given no hint of the forces which impel them. This matter will be taken up fully in the chapter on Absorption, where it will be shown that the gases move along diffusively under action of forces internal to themselves. We need only note here that plants have no system at all for absorbing and expelling large masses of air as animals do by the use of their chest-muscles and lungs,—an operation that is always called breathing. Accordingly, the matter can be stated in this way,—that plants respire, but do not breathe.

It will be well, at this point, to turn aside for a moment from our main subject to consider some phases of plant respiration which have economic importance. The first is concerned with aëration of soils. Roots, like all other living parts, must respire

in order to grow, and, with the exception of a few which possess long air passages connecting with the leaves, they take the indispensable oxygen from air in the soil, by a method to be later explained. A soil in the best condition for the respiration of roots has the structure represented, under large magnification, in the accompanying picture (figure 30). Soil is formed of particles

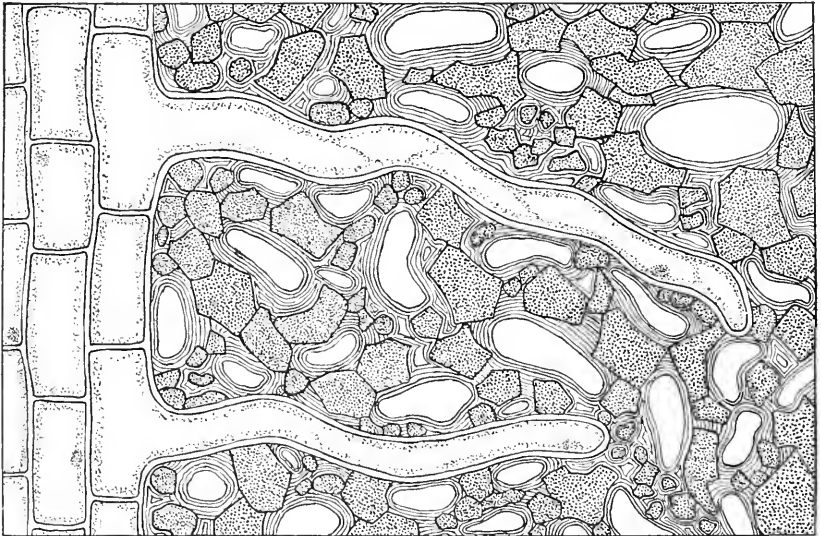


FIG. 30.—A generalized drawing of a section, highly magnified, through a well-conditioned soil and a fragment of root. The soil particles are dotted, the water is concentrically-lined, the air spaces are left blank; into the soil project the root-hairs from the root on the left. (Improved from a picture in Sachs' *Lectures*.)

of rock, irregular in size and form. Around these particles and in the angles between them is water, held in the capillary state, while bubbles of air exist in the larger of the spaces among the soil particles. When more water is added, then the air, being lighter, is driven upwards and comes bubbling out of the ground; but it returns again as the surplus water drains or evaporates away. It is from this air in the soil that roots take their oxygen, and if the air is kept out of the soil by excess of water, then the roots are suffocated and die, precisely as air-breathing animals do when they

are kept under water. Roots, in fact, drown as truly and in exactly the same physiological way as do animals, and with only this difference, that roots can stand immersion for hours or days, while animals can endure it only for minutes. This explains the need for drainage of wet soils; it is not that these have too much water, but too little air. It explains also why the soil of flower pots needs to be carefully drained, and the cause of the failure of so many persons in the care of their house plants, which most people keep too constantly wet. The very best treatment for most potted plants is to give to the soil an occasional soaking, and allow it to dry out pretty well in between times; the roots do not mind the absence of air for some of the time if they can have a sufficiency at other times. Moreover this method of watering has another great advantage over that of adding a little water more frequently, in the far greater effectiveness with which it drives out the foul air and ensures a fresh supply.

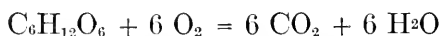
Another economic phase of respiration is involved in the popular belief that it is unhealthful to keep house plants in sleeping rooms. It will now be plain to the reader that this belief is correct. But in fact the danger is slight. The amount of carbon dioxide given off in respiration by a square meter of leaf is only about the three-hundredth part of that given off in the same time by a person, and although buds and roots respire more actively, it is likely that a whole window-full of plants does not give off one fiftieth of the amount that one person does. Or, it has been stated thus, that all of the plants which could be crowded into the windows of any ordinary sleeping room give off less carbon dioxide to the air than would a tiny light kept burning over night; and nobody would consider this quantity injurious, especially if the room were ventilated as it should be. Indeed, were the respiration of the plants in a room not negligibly small, it would obviously be unsafe for any person to camp out in a forest in summer!

We must now come back to the more technical aspects of res-

piration, and examine more closely the chemical and physical aspects thereof. Since the plant, in this process, absorbs oxygen only, but releases carbon dioxide, a question is raised as to the source of the carbon. This must come, of course, from some of the innumerable carbon-holding compounds inside of the plant, but, for our present purpose it does not much matter from which, since they all are derived by transformation from the basal grape sugar manufactured in the leaves. This grape sugar, accordingly, is the ultimate, even though not the immediate source of the respiratory carbon. Therefore we can state the end products of respiration in this wise:—

In respiration $C_6H_{12}O_6$ and O_2 form CO_2 and H_2O
 grape sugar oxygen carbon dioxide water

This general statement can be given a definite chemical form by making the two sides sum up alike, which requires these proportions:—



Now although this equation is rarely if ever actually realized in any particular case, (respiration being never so simple, but a process highly complicated in its details), it does represent the facts as to the ultimate materials and products, the two extremes of the process; and accordingly we may place it in our series of conventional constants as the *respiratory equation*. And its relations to the photosynthetic equation will not escape the notice of the observant reader. The two are the exact reciprocals of one another, which fact is one of the most consequential in all nature, as will presently appear.

And now we come to a matter which I wish to impress, the strongest I can, on the mind of the reader. The phenomena we have thus far considered, including the one which stands for most people as the very embodiment of the process, viz.,—the remarkable exchange of the gases,—are by no means the ones of greatest importance in respiration, but are secondary and incidental to the central and crucial object of the process, which

is this,—*the release of energy*. This release takes place in a single perfectly definite way, namely, as the result of the invariable physical fact of Nature that at the instant carbon unites chemically with oxygen, it matters not in what place or under what circumstances, energy is released. It is for the release of this energy that the process of respiration exists; and the plant no more respire for the purpose of absorbing oxygen and releasing carbon dioxide than we kindle a fire in the grate in order to make oxygen rush into the furnace or carbon dioxide pour out of the chimney. The object of respiration and of building the fire (i. e., of combustion), are one and the same,—namely, to secure that energy which is always released at the moment of chemical union of carbon with oxygen. Respiration and combustion are strictly homologous terms, applying to phenomena which are also homologous. In the combustion of coal, which is carbon, in a grate, the energy is released chiefly as heat (with some light); and by causing that release to occur underneath a suitable arrangement of boilers, pistons and wheels, the energy can be made to produce motion and thus do work, as every steam engine is a visible witness. In the explosion (which is merely a rapid combustion), of gasolene and oxygen inside the cylinder of an automobile engine, we have exactly the same thing with a very much simpler machinery. In respiration within the cells of an animal or a plant, the machinery is simpler still, but the principle remains the same; the energy is released at the moment of oxidation under such conditions that it acts on the simple protoplasmic machinery provided by the plant in a way to secure transformation into motion and work. The source of the energy of the work done by the engine and plant is identically the same; it is only the intermediate machinery which is different. The nature of this machinery, it is true, is not at all understood in the plant, but we know that something of the kind must exist. The machinery must also differ somewhat for the different kinds of work that plants and animals do; but in all cases it is driven by one and the

same power, which depends on the energy released by the oxidation of carbonaceous food. And it may interest the reader having a turn for figures to know that the energy released by the respiration of sugar is just about half of that released by the combustion of an equal weight of the best coal.

These matters though clear on reflection, are hard to grasp in a first presentation; and I suggest that we rest a little by considering an incidental matter of interest. In the foregoing paragraph I implied that the energy of respiration is not released as heat, and thus differs from combustion. But the implication is not strictly correct, as is easily proven. If one takes two handfuls of seeds, soaks them, and starts them growing and therefore respiring, kills one set by hot water, places them both in good non-conducting chambers provided with thermometers, and leaves them some hours, he will notice a remarkable result. The thermometer in the living and respiring seeds will soon read several degrees above that in the others, which are obviously similar in all ways except that they cannot respire. And further experiment shows that this release of heat by these respiring seeds is representative of all respiring parts, and that the release of heat is a constant accompaniment of respiration. Although usually small in amount this heat sometimes becomes readily recognizable. Thus the rapidly-opening flowers of Aroids (our Jack-in-the-Pulpit and its relatives) often show by the thermometer a temperature several degrees above that of the air; some alpine flowers can melt their way up, by aid of this heat, through the snow; grain germinating or fermenting in large masses becomes often noticeably warm; the warmth of hot beds derived from fermenting manures has the same origin, though here the respiration is that of bacteria or molds; and various cases of spontaneous combustion, where correctly reported, must have the same origin. It does not appear that this heat, in plants at least, secures any physiological advantage but is rather an incidental result of the physical forces at work, very much as incandescent electric lamps made

primarily to give only light incidentally give much heat as well. But it is this very same heat developed and kept in regulation which is the basis of the uniform warmth of the animal body.

A few pages earlier it was shown that the carbon in the carbon dioxide released in respiration comes from inside the plant. This being so, respiration ought always to entail a loss of weight in



FIG. 31.—Plants of Buckwheat grown from the same number and weight of seed in light and darkness respectively. The plants are in porous saucers supplied with water and minerals from below.

respiring plants or animals; which in fact is found by experiment to be true. The loss must be compensated by new supplies of food, else the phenomena of starvation, including emaciation, ensue. The emaciation of a starved animal, indeed, is due much more to the loss of substance through respiration than through the ordinary excretions. In plants, however, it often happens that those which have lost much weight by respiration without opportunity to make it up by photosynthesis, look larger than

others which have done the normal photosynthetic work, the extra bulk being nothing but water. Thus, the two sets of plants in the accompanying picture (figure 31), were started by the water-culture method, (later to be explained), from two sets of seeds of exactly the same weight. But one set (that on the left) was grown in the light and was able, therefore, to make up its loss by photosynthesis, while the other was grown in the dark and could not. Yet the latter, owing to the habit of plants to spindle out greatly in length in darkness, actually look larger than the former. When, however, I weighed these two sets after all of the water has been dried out, leaving only dry substance behind, the smaller lighted plants weighed a good deal more than the larger ones from the dark. It can always be accepted as true that respiration entails loss of weight through the loss of carbon from the plant.

We can now gather up the facts set forth in the preceding pages in another of our generalizations, or verities,—*the energy indispensable to the work of plants is principally provided by the oxidation of carbonaceous food, and this is the essential feature of respiration.*

In the statement of the foregoing verity the reader will notice that I have used the word “principally,” thus implying that some other source of energy is available. In fact, while respiration supplies by far the larger part of the energy used by organisms, and especially by animals, they do derive some small part from other sources, notably the heat of the surroundings. But this part of the subject will all be elucidated later in this book.

We are now face to face with a question of a very fundamental sort,—namely, what is the source of that energy which is thus released from food in respiration? For everybody knows that energy is not created upon the spot, but originates only by transformation of pre-existing energy. In all science there is no principle better established, or more important, than that of the conservation of energy and matter, which teaches that the sum total of both energy and matter in nature is constant, and that

none of either is ever created anew or obliterated, though they may change their forms multifariously. Where, then, and in what form was the energy in food before it was released by respiration? The answer is easy, though its comprehension is not. It was where the energy was in the coal before it was released as heat in combustion: where the energy was in the storage battery before it turned the wheels of the electric automobile: where the energy was in the coiled spring or the wound-up weight of the clock before it turned the wheels to move the hands: where the energy was in the full millpond before it drove the looms of the water-power mill: where the energy was in the gunpowder before it started the flying bullet. The fact of the matter is this,—that energy exists in Nature in two different forms, not only in the familiar active or kinetic form which produces motion and does work, but also in a resting, latent, or potential form, when its power to produce motion is held in suspension. Whenever, in Nature, kinetic energy is exerted to force apart bodies whose attractions, whether through gravitation, magnetism, cohesion, or chemical affinity, tend to bring them together, the energy goes into the potential form for so long as those bodies are kept apart, and it becomes again manifest in kinetic form when the bodies are allowed to re-unite. All unsatisfied attractions in Nature are latent energy. When a small boy draws back the powerful elastic of his favorite sling-shot, he is exerting kinetic energy against the tension of the elastic; while he holds the elastic stretched to take aim, that energy is latent as energy of tension; and when he lets go of the string the energy becomes kinetic again as it drives the stone in delightful swiftness of flight. So, kinetic energy can raise a weight, go into the latent form as energy of position while it is suspended, and come out again in kinetic form, as it does when it turns the wheels of an old-fashioned clock. Kinetic energy can charge a storage battery, become latent for a time, and come out once more as kinetic energy driving an electric automobile. The storage battery, indeed, is typical of all cases

where energy is potential in the form of unsatisfied chemical affinity. The electric current forces apart the tightly-cohering atoms of certain very stable chemical compounds; but these atoms nevertheless retain all their old attraction for one another, and it is in the form of this unsatisfied attraction that the energy is latent; and this energy is given out again in kinetic form at the moment when the atoms are allowed once more to unite. Now the very same thing is true of carbon dioxide, which is a very stable substance of tightly-cohering atoms. To force apart carbon dioxide into its constituents requires kinetic energy, which then remains in the latent form, as energy of unsatisfied chemical affinity, so long as the carbon and oxygen are held apart, but becomes kinetic again when the carbon and oxygen are allowed to reunite to carbon dioxide. Does the reader see the application? Surely he must. The kinetic energy of the sunlight splits apart carbon dioxide in the green leaf, the oxygen going out to the air and the carbon combining with the elements of water into grape sugar; so long as this carbon and oxygen are kept apart, that energy is latent in the form of unsatisfied chemical affinity; and when the carbon of the sugar (or of any other substance into which the sugar is transformed) is allowed to unite with the oxygen of the air, as it is in the process of respiration, then kinetic energy is again given out and can be used for the work of the plant. Such is the source of the energy of respiration,—it is energy released from the latent state in food, where it was placed (or “stored”) by the kinetic energy of the sunlight. Food, therefore, is a storage battery charged by the sun, and discharged by respiration.

The principal function of food must now be quite plain. As a storage battery it has advantage over any that man has yet made in the fact that it can be reduced to very small fragments, or even to solution (by digestion), and thus transported to all parts of plants and throughout the bodies of animals. Then, at the spot where work needs to be done, just at the right instant,

under the suitable machinery, the carbon of the food is allowed to unite with oxygen, and the energy is released to do the needful work. And that is the way in which plants and animals accomplish their work; and the power to do this,—to absorb stored energy, transfer it to all of their parts, hold it ready for use, and release it when needed,—is the most distinctive feature of living beings.

The reason is now evident also for the reciprocal character of the photosynthetic and respiratory equations. In photosynthesis carbon dioxide and water are made into sugar and oxygen with storage of energy; the sugar is transported by plants or by animals to places of need, undergoing chemical changes on the way but ever retaining the store of unsatisfied carbon; then in respiration oxygen is allowed to come into chemical contact with the sugar, and the two are changed back to carbon dioxide and water with release of energy. It is because substances exist which thus permit of such storage and transportation of energy that organisms as we know them are possible.

It may aid still more to a clear understanding of these two most fundamental and important of all physiological processes if we set their chief features in contrast in form of a table;—

<i>Photosynthesis</i>	<i>Respiration</i>
Occurs only in plants	Occurs equally in plants and animals
Occurs only in chlorophyll grains	Occurs in all living protoplasm
Occurs only in light	Occurs equally in light and darkness
Manufactures food	Destroys food
Increases weight	Lessens weight
Absorbs carbon dioxide	Releases carbon dioxide
Releases oxygen	Absorbs oxygen
Forms $C_6H_{12}O_6$ from CO_2 and H_2O	Reduces $C_6H_{12}O_6$ to CO_2 and H_2O
Stores energy	Releases energy

We can now gather up these latter facts in another of our verities thus,—*the energy released in respiration was previously latent in the unsatisfied affinity of the carbon in the food for the*

oxygen outside, those two elements having originally been separated by the kinetic energy of the sunlight in photosynthesis and kept separate through all the subsequent transformations and transportations of the food through the bodies of plants and animals; the original source of respiratory energy is therefore the sunlight, and food is primarily a storage battery, charged by the sun in green leaves and discharged by respiration at the places of need.

It will doubtless ere this have occurred to some philosophic reader to ask whether carbon dioxide and water are the sole substances by which organisms can thus store and transport energy, and whether, accordingly, life is dependent solely upon them. There is, however, no chemical reason why organisms might not use in the same way any other decomposable and oxidizable substances, and indeed even in our common plants some small quantity of energy is no doubt derived from the oxidation of other elements, while certain Bacteria exist which can use the energy derived from the oxidation of sulphur compounds. Plants probably use carbon in photosynthesis and respiration chiefly because its chemical transformations, which are very susceptible to temperature, happen to be easily under control at the temperatures now prevailing on the earth's surface. Under markedly higher or lower temperatures carbon would be unavailable for this purpose, but it is conceivable that life might still exist by the similar use of other substances whose combinations would be under control at those temperatures. It is only a step farther to assume that life might even exist in this way in the flames of a nebula, or the awful cold of interplanetary space, and hence that its origin may be contemporaneous not only with the origin of the earth, but even with the origin of matter itself. It is not at all likely that life is something which results incidentally from the properties of carbon; it is far more probable that it is something which uses the properties of carbon as the most convenient tools for its own ends. This is a phase of the super-vitalism of which I have spoken in the first chapter.

This chapter has already attained to a length so great that I wish it were possible to end it right here. But certain additional matters are connected with respiration so closely, and are besides in themselves so important, that we must really keep on to include them, though perhaps the reader will find it best to defer a reading thereof for another occasion. These matters are fermentation, decay, and disease.

Fermentation is a phenomenon familiar to all, and best known, perhaps, in the "working" of preserves, which become "strong" i. e. alcoholic, while giving off tiny bubbles of gas. The most typical kind of fermentation is that caused by Yeast. Yeast, I venture to remind the reader, is a very tiny non-green plant which lives as a saprophyte in sweet liquids. Magnified to a high degree by the microscope it looks much like our picture (figure 32), though whiter. A Yeast plant is a single ovoid cell which buds out into others,



FIG. 32.—Yeast plants, each a single cell which buds out from a parent cell; very highly magnified.

and these into others, in loose chains which fall easily apart,—and so on, as long as the food supply lasts. And that is all, except that when the liquid dries up, the cells produce very thick-walled spores which float around in the air with the dust, to start once more when they happen to fall into another sweet liquid. It is by the growth of these cells that a sweet liquid is "fermented" with a formation of alcohol and carbon dioxide. This can be demonstrated very easily and clearly to the eye by an interesting experiment. If one puts together in a glass flask a solution of sugar and a cake of compressed (not dried) yeast, and stands it in a warmish place, then within a very few minutes tiny bubbles of gas begin to rise through the liquid, producing a froth on its surface. If, now, the stopper of the flask

be provided with an outlet tube bent over to end at the bottom of a vessel of clear limewater, the gas will come bubbling up, and will soon turn the limewater milky, thus proving its identity. And when the fermentation is ended the liquid left in the flask has always that "sourish" smell distinctive of the presence of alcohol, which, indeed, can be separated for testing by distilling the liquid. As to its quantity, however, it is important to know that even when all the conditions for fermentation are most favorable and the sugar is present in plenty, the Yeast nevertheless does not form more than a limited quantity of alcohol,—(about ten per cent of the liquid in round numbers), for then the plant is rendered inactive and may finally be killed by the very alcohol which it has produced.

Such is the process of fermentation, which, as everybody knows, is vastly important in the arts. Sometimes it is used for the sake of its carbon dioxide and sometimes for the sake of its alcohol. The conspicuous case of the former is found in the making of bread, where the carbon dioxide released from the growth of the yeast cells throughout the mass of the dough, forms the cavities by which it is lightened and raised. When everything goes as it should, the alcohol evaporates in the baking, but sometimes it does not, and then the bread goes "sour." Of course other methods of raising bread are in use, notably by aid of gases released in the dough from chemical action between the constituents of suitable "baking powders," or other substances, and also by use of air blown into the dough; but yeast fermentation is much the most used of the methods. But far more extensive is the employment of fermentation for the making of the various kinds of alcoholic liquids. When the sweet juice of the grape is allowed to ferment (by action of yeast blown as spores through the air to the fruits), the carbon dioxide escapes to the air, and the remaining admixture of alcohol, water, and flavors we call wine. When the sweet pulp of the germinating grains of barley is allowed to ferment (by Yeast which is added for the purpose),

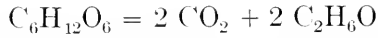
we give the name beer, "lager beer," to the liquid resulting. And innumerable other sweet juices and saps are fermentable, with resulting formation of alcoholic beverages, which are so many and diverse in kind that most nations have each some favorite one of its own, the differences between them being due in the main to various flavoring materials originally present with the sugar. None of these fermented liquids, however, are ever stronger in alcohol than the ten per cent, or thereabouts, which the Yeast can yield before it is killed. The stronger liquors are obtained by an additional and very different kind of operation, depending on the fact that alcohol boils at a much lower temperature than water (78°C , or 172°F as compared with 100°C or 212°F). For this reason a fermented liquid, if heated above 78° but under 100° , gives off its alcohol (though also with some water) as vapor, which can be conducted away, cooled and collected as a strongly alcoholic liquid. The process is called distillation, and in this way are made the stronger alcoholic drinks,—brandy, whisky, rum, gin, and all the remainder of this precious rogue's gallery,—their peculiar flavors and colors being due to particular substances, sometimes naturally present and sometimes purposely added, in the juices from which the alcohol is fermented. It is by repeated distillation of the fermented juice of germinating corn that the strong alcohol of commerce is made, and this when mixed with a little of the poisonous wood alcohol to make it undrinkable becomes the "denatured alcohol" of the household and the chafing dish.

We turn now to the chemistry of fermentation, which is simple. It is grape sugar which is fermented, for other sugars or starches are first changed to that form or its equivalent. Therefore we have this expression,

In fermentation $\text{C}_6\text{H}_{12}\text{O}_6$ forms CO_2 and $\text{C}_2\text{H}_6\text{O}$
 grape sugar carbon dioxide alcohol

This statement can be given an exact chemical form in this way,—





And this equation expresses exactly the known facts of the process.

What now is the meaning of fermentation, and why does the Yeast do it? Nowhere in Nature, so far as I can find, excepting in the case of humanity, is there even the least evidence that any kind of organism ever does anything whatever for the sake of service to any other kind. We should not expect to find, accordingly, that the Yeast makes the carbon dioxide and alcohol for any disinterested or philanthropic purposes,—not for providing thrifty housewives with light bread or their shiftless husbands with strong drink,—and we turn to seek some desirable object of its own to which the use by mankind is purely incidental. But of course, the reader has inferred the explanation before this,—fermentation is simply the Yeast's respiration, the source of its power for growth and other work that it does. And the explanation of so peculiar a form of respiration is well known. Living immersed in a liquid, the Yeast cannot obtain respiratory oxygen from the air, and must take it from some other source. Only one source is available. Locked up in the molecule of sugar is some oxygen brought into it with the hydrogen, which holds it away from the carbon, as the formula $\text{C}_6\text{H}_{12}\text{O}_6$ suggests. But the Yeast plant, absorbing the sugar into its body, shatters the molecules (by means of a peculiar agency called an enzyme soon to be described), and allows the carbon and oxygen in the fragments to unite with one another; this produces the usual result,—a copious release of energy which the Yeast at once utilizes for its growth, while of course the resulting carbon dioxide is thrown off into the liquid. This is the object, or meaning, of fermentation;—to secure a union of carbon and oxygen for the sake of the energy which is always thus released. As to the alcohol, that is simply the remains of the shattered molecule; it is a chemical fact that the number of atoms of carbon, hydrogen and oxygen which happen to be left after the carbon dioxide is formed, fall naturally

into alcohol, and the Yeast plant cannot help it. That is why the Yeast produces the poisonous alcohol, despite the suicidal character of the proceeding. The Yeast, however, can respire in no other way, and with commendable philosophy, prefers a short life, even at the risk of an alcoholic grave, to no life at all. Yet in fact the case is not really so bad, for the alcohol is very volatile, and in Nature commonly evaporates as rapidly as formed; and even when not, the drying up of the liquid and spore-formation allow the yeast to escape and renew its activity at another time and place. If the Yeast plant had nothing to do but respire, the sugar would all be converted to carbon dioxide and alcohol, which are probably the sole products of its respiration. But the Yeast must also make new substance, protoplasm and walls, for which purpose it uses some of the sugar in a different way, along with other substances, and thereby develops incidentally a small percentage of by-products,—glycerin, acids, etc., the pursuit and capture of which affords a fine joy to the special student of chemistry, especially if some student of biology has previously told him that carbon dioxide and water are the “products of fermentation.”

Alcoholic fermentation caused by Yeast is the most typical and familiar kind, but other sorts occur, caused by germs (Bacteria), or Molds. Thus the souring of milk, the rancification of butter, the genesis of vinegar, and even the development of distinctive flavors in ripening cheese, are products of fermentations, caused in their respiration by various organisms. As these cases illustrate, the secondary products need by no means consist only of alcohol, but can include substances of the most diverse chemical natures. All that is requisite is that carbon and oxygen shall be allowed to unite; the matter of the particular compounds is secondary.

If any doubt could exist that fermentation is simply the respiration of the Yeast plant, it would vanish before the remarkable fact that an exactly intermediate step is known between the

respiration of the higher plants and typical fermentation. Ideally, in the respiration of the higher plants, the oxygen absorbed and carbon dioxide released are equal in volume, but often they are not. Thus, some kinds of seeds, like Peas, if shut away from oxygen, can release plenty of carbon dioxide without absorbing any oxygen at all; and analysis of the seeds then shows the presence of alcohol. In other words, these Peas, like the Yeast plant, can cause fermentation (though in limited degree) of some of their own substance; and there is no doubt that it represents the form of respiration to which the seeds resort when no oxygen from the air is available. This form of fermentation is called in the Peas, and the other plants which make use of it, *anaerobic*, or *intramolecular*, respiration.

There remain two other forms of fermentation so important as to require a separate treatment. One is decay, or putrefaction, which is really the fermentation of dead plant and animal substances by Bacteria, or germs. Bacteria are plants even smaller and simpler than Yeasts. The products of their respiration and growth are most diverse, including not only carbon dioxide and water but various other gases, some of which possess those very vile odors distinctive of rotting organic matter. When the decaying substances are complex, e. g., flesh or other proteins, certain Bacteria ferment them to simpler sorts, other kinds to simpler still, and so on, until they are finally reduced, as in ordinary respiration, to carbon dioxide and water, and such other elemental substances, (e. g., nitrogen) as may also have entered into their composition. All decay is simply a form of fermentation, that is respiration, by Bacteria, or, in some cases, by simple Molds.

Another phase of the same phenomenon is involved in those deadly diseases which are caused by Bacteria,—Asiatic Cholera, Tuberculosis, Diphtheria, Typhoid, Lockjaw, and a number of others. It is a popular belief that Bacteria produce their effect in disease by destroying the tissues, or, as a plain-spoken student of mine once expressed it, they “chew you all up inside.” That

belief is far from the truth, for what happens is this. The Bacteria, in order to obtain energy and material for their own processes, act on the tissues or the blood in just the same way that Yeast acts on the sugar, likewise forming incidentally in the act various accessory substances. Now some of these substances, bearing much the same relation to the Bacteria that alcohol does to the Yeast, are those alkaloids or ptomaines which happen to be violently poisonous to man, and it is these poisons, and not the Bacteria directly, which are the cause of his death. At least they are the cause of his death if they are formed more rapidly than his system can antagonize them, for the body has a wonderful power of forming antagonistic chemical substances, or antibodies, which neutralize these poisons,—which antibodies, by the way, can be made to form in the body, or even can be injected as antitoxins, ensuring immunity against some diseases. These deadly diseases are therefore an incidental result of the respiration and growth of Bacteria which are leading their own lives in their own way, as oblivious to any harm they may do as is the Yeast to the benefit it confers.

It is not only true that fermentation, decay, and some disease, are caused by the activity of Yeasts, Molds, and Bacteria, but the converse is equally well-known,—that those processes occur through no other agency and can be prevented entirely by killing these organisms. This can be done by heat, poisons, certain strong solutions, or even, in some cases, bright light; and such is the basis of the various sterilizing and antiseptic processes so familiar in the household, the arts, and in medicine.

We can now express these later facts in another of our verities as follows;—*all fermentation and decay, and some phases of disease, are forms of the respiration of simple organisms which thereby destroy organic matter by reduction back to the carbon dioxide, water, and other elements, from which it was originally built up.*

It is thus evident that all of the carbon dioxide and water built into plant substance by photosynthesis, are ultimately re-

leased again by respiration or decay. A quantity, rather small, of the earth's supply of carbon dioxide and water is therefore always locked up in plant and animal substance; but though the quantity is approximately constant the precise molecules are constantly changing, and with the changes go those transformations of energy which are the principal manifestation of life. And if the question be asked, why are not more of the carbon dioxide and water of nature locked up in plant and animal substance, that is, why are there not more and larger plants and animals on earth, I think the answer is easy. There do already exist upon the earth all of the plants and animals, and as big ones, as the physical conditions permit. As to plants, every spot on the earth that can maintain plant life at all is bearing all the plants it can support, and these plants are just as big as the physical conditions permit them to grow. As to animals, they are dependent upon plants for their food, and it is evident that there is available for their use only the surplus of food produced by plants over that which these need for themselves,—and animals are just as abundant and big as that surplus can support.

Thus, these apparently very complicated processes of photosynthesis and respiration, like many another and probably like all of the physiological processes in plants and in animals, can be reduced to a basis of pure physics and chemistry. And we shall learn later, in our chapters on Irritability and on Growth, that we have a good explanation of the orderly sequence and regular connection of the processes in their linking up together through their interactions as stimuli. Is there then, nothing in the plant except the interactions of chemistry and physics? Let the remaining pages of this book give their testimony before we attempt the answer.

CHAPTER V

THE VARIOUS SUBSTANCES MADE BY PLANTS, AND THE USES THEREOF TO THEM AND TO US

Metabolism



N chapter two of this book it was shown that plants manufacture grape sugar in their lighted green leaves; and I said it would later be proven that this sugar represents a basal food substance out of which, with sundry minor additions, plants build all of their other materials. The time has now come for this demonstration, to which, as a subject possessing perhaps more importance than interest, I bespeak the reader's somewhat spartan attention. Since all of the substances constructed by plants have a meaning in their vital economy, I might also have entitled this chapter "on the various uses that plants make of their food," in which case I should have to commence with a review of respiration, for that is the most important of the uses of food. The others here follow in an order determined chiefly by the chemical nature of the substances concerned.

The number of substances constructed by plants is verily legion, for the vast variety of foods and fabrics, drugs and dyes, and other materials yielded by them to us is only a small portion of those which they actually make. Fortunately, however, for our limited comprehensions, those which are really important are few, and moreover, they fall into somewhat definite classes. Since the subject is new to most persons, I will give these classes in synopsis as a kind of table of contents to this chapter. They are these:—

- Class I. The **BASAL FOOD**, or **PHOTOSYNTHETIC SUGAR**; the substance first formed in lighted green leaves; composition $C_6H_{12}O_6$.
- Class II. The **FOODS**, active and reserve, and the **SKELETON**; chemically called **CARBOHYDRATES**, with a composition identical with or readily transformable from that of the photosynthate, viz., $C_6H_{12}O_6$, or $C_{12}H_{22}O_{11}$, or $(C_6H_{10}O_5)_n$.
- Class III. The **SECRETIONS**; various non-nitrogenous substances, mostly of special ecological functions, **DERIVATIVES OF CARBOHYDRATES** and containing the same elements, but in markedly different proportions, and hence collectively expressible only in the form $C_nH_nO_n$.
- Class IV. The **NITROGEN-ASSIMILATES**, chemically called **AMIDES**; inconspicuous but important substances containing the elements of the photosynthate with the addition of nitrogen, and forming the transition from Class I to Class VI; collectively expressible only as $C_nH_nO_nN_n$.
- Class V. The **PRINCIPAL POISONS**, chemically called **ALKALOIDS**; containing (as a rule) the elements of the Amides but in different proportions, substances of uncertain meaning, and collectively expressible as $C_nH_n(O_n)N_n$.
- Class VI. The **FLESH-FORMERS**, chemically called **PROTEINS**, contributing to the formation of protoplasm and consisting of the elements of the Amides with the addition of sulphur and phosphorus, and collectively expressible only as $C_nH_nO_nN_nS_n(P_n)$.
- Class VII. The **REGULATORS OF METABOLISM**, called **ENZYMES**, substances of unknown composition, but supposed to be proteins, possessing remarkable properties of causing chemical transformations in other substances.
- Class VIII. **LIVING PROTOPLASM**.

Class I. The Basal Food, or Photosynthetic Sugar

This substance needs no introduction to the reader of the earlier parts of this book; but for others it may be characterized as a sugar made abundantly in the lighted green leaves of plants from carbon dioxide and water, and forming the foundation of all organic substances. It belongs in a class by itself only because of its unique mode of formation and function, for chemically it belongs in the second class, being nothing other than a mixture of the grape and fruit sugars next to be described.

Class II. The Food and Skeletal Substances, or Carbohydrates

Grape Sugar. This substance is formed abundantly in green leaves as the photosynthate, and is common in nearly all parts of all plants. It is, however, much less known than its importance would imply, because it has no prominent economic uses, and exists in the plant only in solution in the sap of the cells, which therefore display through its presence no more striking appearance than that represented in the accompanying example (figure 33). However, it sometimes accumulates considerably in fruits, which it helps to make nutritious and attractive to animals in connection with dissemination, a subject to be later discussed in a special chapter devoted to that subject; and in grapes, especially, it is so plenty that it crystallizes out when they are dried, forming the soft sugar abundant on some kinds of raisins.

Its many and easy transformations into other substances will be traced in the following pages. It has, however, a second origin and significance in the plant, for it is that into which many other

substances are converted in digestion, as we shall presently learn, and is the commonest form in which substances are translocated through the plant. It is white in mass, looks amorphous and not crystalline to the eye, is sweet to the taste, though much less sweet than cane sugar, and is the easiest of all sugars for Yeast to ferment. It is interesting to know that it has been made artificially in the chemical laboratory. Chemically its correct name is dextrose, though often also called glucose, and its formula is $C_6H_{12}O_6$.

Fruit Sugar. This substance is extremely like grape sugar, with which until lately it was more or less confounded, and with which

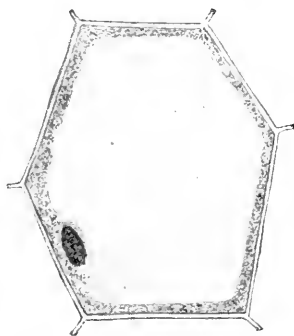


FIG. 33.—Appearance in optical section, highly magnified, of a cell in which sugar is stored in the sap.

Inside the wall is a lining of living protoplasm which encloses the large sap cavity wherein is water containing the dissolved sugar.

it occurs in the various roles above mentioned for grape sugar. It is sweeter than grape sugar but ferments less easily. Chemically it is called fructose, and has the formula $C_6H_{12}O_6$, differing from grape sugar not in the kind or number of atoms entering into its composition, but in the arrangement of these within the molecule, as best demonstrated by physical tests with polarized light.

Cane Sugar. This substance is perfectly familiar to everybody, for it is the granulated sugar of the table. It is widely spread through plants dissolved in the sap, and accumulates in some kinds so abundantly as to form a reserve supply of food for them, and a store upon which animals, inclusive of man, are accustomed to draw for their needs. This accumulation occurs conspicuously in the Sugar Cane and the Sugar Beet (both of which plants have had their percentage of sugar immensely increased by cultivation), in the Maple tree, and in a few other less conspicuous plants, while it is common as well in ripening fruits. Chemically cane sugar is called sucrose, and has the formula $C_{12}H_{22}O_{11}$. It is built up by living protoplasm from photosynthetic sugar through this simple step, $2 C_6H_{12}O_6 - H_2O$ (water) = $C_{12}H_{22}O_{11}$; and it falls back by a reverse process to a molecule of grape sugar and one of fruit sugar. This latter step actually occurs in the ripening of fruits, in cooking, and in digestion; and it is, therefore, as grape sugar or fruit sugar that cane sugar is finally incorporated into both the plant and the animal body.

In addition to these sugars, there are others of rarer sort described in the technical books,—all closely related and more or less intertransformable into those we have mentioned. Such are, for example, maltose, mannose, galactose, arabinose, xylose, fucose. I am very well aware that these names will have no great attraction for the reader, but I take somewhat the same satisfaction in their recital that Homer derived from the roll of his heroes, whom also he mentions but once.

Starch. This substance is perfectly familiar to everyone as common laundry starch, and especially as flour, which is mostly

composed of it. Occurring as a rule in tiny white grains scattered widely through all kinds of tissues, it collects in some organs, which swell very greatly for its reception. Such is the Potato, which is simply a starch-storing underground stem: the Sweet Potato, a starch-storing root: bulbs, which are masses of starch-filled leaves: and most seeds, including all of the grains, which contain copious starch either inside or around the embryo. In all of these cases, starch presents a characteristic homogeneous firm whitish appearance, contrasting markedly with the soft translucent aspect of structures in which the food is stored up as sugar, e. g., the Sugar Beet, Sugar Corn. It happens, however, that its presence can be detected in a very conclusive way, namely by the deep blue color it assumes when touched by a solution of iodine, as the reader already has learned, and as he can easily prove for himself by applying a little of the tincture of iodine to a lump of starch from the laundry box, or to a disused cuff, or to water in which some starch has been scraped,—and heated until it forms a fine paste. The test is one of the most satisfactory and important in all organic chemistry, and so delicate that, by its use with the aid of the microscope, one can detect even the minutest quantities of starch in the tissues of a plant, where it is sometimes distributed with a curious and beautiful geometrical exactness. It is necessary to warn the experimenter, that in living tissues, however, the test often works rather badly, because iodine penetrates active protoplasm very slowly.

Starch, when it accumulates in the plant, serves as a store of reserve food upon which the plant can draw when it starts new growth; and starch is by far the most common and abundant of plant foods. Moreover, it serves equally well as a food for animals, which, accordingly, rob the plants; and these are therefore obliged as a whole to make a huge surplus in order to keep any at all for themselves. The importance of starch as food for man is evident when one recalls that Wheat, Corn, Rice, Barley, Rye,—grains, which constitute the principal food of the great

majority of the human race, are composed almost wholly of starch.

Chemically, starch has the formula $(C_6H_{10}O_5)_n$. It is formed apparently thus,—from dextrose, $C_6H_{12}O_6$, water, H_2O , is withdrawn, leaving $C_6H_{10}O_5$; this substance does not occur in this form in the plant, but the molecules immediately aggregate themselves (chemically, polymerize), to a considerable but unknown number, expressed by the letter n , into compound molecules. Starch is made up in this way from dextrose, and it is of interest to note that a corresponding substance made from fructose occurs as a reserve food dissolved in the sap of the swollen roots of some Composite plants, where it is called inulin. The formation of starch has never been effected artificially outside of plants, and in them it takes place only inside of those living protoplasmic bodies called plastids, which include chlorophyll grains and which are to be described more fully in the next chapter. The re-conversion of starch to dextrose is effected through the action of diastase,—one of those remarkable chemical agents called enzymes, which we are presently to study; and this is exactly what happens in the digestion of starch in both the plant and animal body. Indeed, this digestion can be carried on experimentally and very easily in a test-tube by action of diastase bought from any chemical supply company, the disappearance of the starch being proven by use of the iodine.

A fact of another kind about starch should be noticed at this place. Even to the unaided eye it looks granular in texture, while the microscope shows that it really is composed of definite grains, which, moreover, display a remarkable structure. If a section be cut from the interior of a potato, for instance, and magnified, the cells are found to present an aspect well shown in the typical example here pictured, (figure 34). Within each cell are numerous solid grains, various in details of their shapes, but all possessing in common a focal spot near the smaller end, around which are excentrically-arranged layers (figures 34 and 35). Starches from

other plants are of different aspect, as our plate so clearly illustrates (figure 35); but each kind exhibits characteristics peculiar to itself, and in general it is true that no two species of plants have grains exactly alike, while each species has a kind distinctive of itself. This fact has a practical value, because experts with the microscope can thus learn to recognize the starches of different plants at sight, and by this means can detect adulterations in starchy foods or drugs. Biologically, also, this individuality of the starches is of very great interest, for it gives us a clear case in which a well-developed specific character exists without any regard to utility; for even the most radical adaptationist would

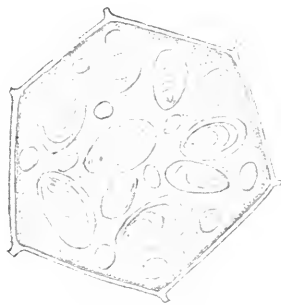


FIG. 34.—A cell, highly magnified, from a Potato, showing the concentrically-lined starch grains embedded in living protoplasm.

hardly consider the forms of the deeply-buried and invisible starch grains as useful in adapting the species to its environment. And if an internal specific character can be useless, what need to try to explain every external specific character as necessarily useful? I am very well aware that this little digression will seem without point to most of my readers, but I pray them to have patience a little, for I have a good object. I am calling their attention when I can to certain data which will later be useful when we come to consider the subject of evolution.

Cellulose. This substance is vastly abundant and prominent in plants, for it is the material out of which they construct the walls of their cells and therefore their entire firm skeletons. The reader can obtain a good idea of pure cellulose by recalling the fibers of cotton, the pith of woody stems, or some of the purest unstarched paper, such as the filter-paper of the laboratories,—all of which exhibit the distinctive cellulose qualities of toughness, elasticity and transparency. In some plants also, it is stored up as a reserve food in the seed, when it appears as an im-

mense thickening of the cell-wall (figure 36). A conspicuous case is the Ivory Palm, which has seeds so hard as to constitute a substitute for ivory in the making of buttons and other bijouterie, while the seed of the Date owes likewise its stony hardness to the same material. Though so hard, this cellulose is easily digested to sugars by the action of suitable enzymes, and the pro-

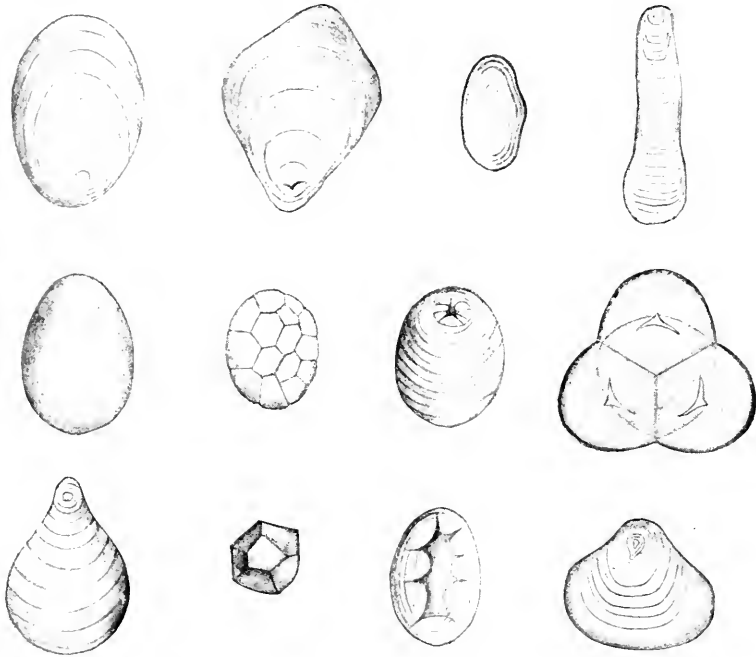


FIG. 35.—Typical grains of a dozen different kinds of starches, highly magnified. The kinds, in order of arrangement in this picture are;—

Potato	Maranta	Pea	Hyacinth
Wheat	Oats	Sago	Smilax
Canna	Corn	Bean	Oxalis

cess is applied commercially to ordinary wood in the manufacture of wood alcohol. Naturally, the very cells which make cellulose have the power to digest it away once more where needful; and this is why cell-walls, even when well grown, can become perforated, absorbed, split, or even re-adjusted in such a way that they seem to have slid upon one another.

Chemically, cellulose is related to grape sugar and formed therefrom in much the same way that starch is, its formula being the same as that of starch, $(C_6H_{10}O_5)_n$, with the n , however, representing a different but unknown value.

Although cell-walls when young consist only of cellulose, in some structures they become penetrated later by other materials which are probably formed by alteration of the cellulose itself, and which give new properties to the walls. Thus, it is a stiffening substance called lignin, added to cellulose walls, which converts them into wood, and also forms other hard tissues, such as the shells of nuts; while a very different substance, cutin or suberin, makes the walls thoroughly waterproof, as they are in all cork, and in the thin waterproof epidermis which ensheaths the entire plant. An alteration of the cellulose of another kind produces the mucilaginous material displayed when some seeds (e. g., those of the Flax), are placed in water, or when fallen leaves turn gummy on sidewalks in wet, warm, autumn weather; and such also is the origin of the mucilage or slime found in desert plants on the one hand and water plants on the other, with peculiar functions in those plants to be later considered.

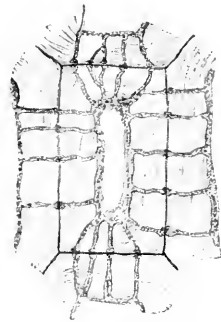


FIG. 36.—A cell with parts of four others, from the interior of the nut of Ivory Palm, showing the walls immensely thickened by deposition of layers of cellulose, through which run canals permitting a continuity of protoplasm from one cell cavity to another.

There are highly consequential facts of another kind about cellulose whether lignified or not. It burns readily in presence of oxygen, being converted back in the process to carbon dioxide and water, the very substances from which it was originally made. When, however, it is subjected for a long period of time to pressure and heat, gradually it undergoes definite chemical changes through which its hydrogen and oxygen are removed, leaving behind the solid and non-volatile carbon. This is exactly what has happened in the case of the plants which grew of old time in

the swamps of the Coal Period; their walls, losing the oxygen and hydrogen, have become proportionally richer in carbon and incidentally darker in color, passing gradually through stages represented by peat, lignite, soft coal and anthracite, which latter is almost entirely carbon. It is thus that our beds of coal have been formed. Somewhat the same thing occurs, through the action of heat, in the charring of wood, and a similar process produces the black humus of good soils from roots and the like. When the carbon of coal remains yet longer exposed to suitable conditions, it becomes graphite or black lead, while if crystallized it forms diamond, the end of the series. And it is interesting to note in this connection that we do not yet know any natural way by which pure carbon can be isolated from oxygen without photosynthesis constituting a step in the process. If one were to burn the diamond, he would form carbon dioxide again, and thus close the chain of transformations through which the carbon has gone since it was absorbed from the air by a living green plant long ages ago. And as to this burning, it is interesting to reflect that the heat and light released in the combustion of coal is energy that was rendered latent by the photosynthetic dissociation of carbon dioxide when the coal was first formed as a photosynthate; it has been kept stored all this time in the unsatisfied affinity of its carbon for oxygen; and when released in our midwinter fires, it is really the heat and the light of the ancient carboniferous sun that is warming and cheering us.

Gums. These are solid but very elastic sweet substances, of which gum arabic, used in gumdrops and on postage stamps, is the most familiar example; the gum of cherry trees is another, and the substance of marsh mallows another, though the spruce gum, of the woods and the schoolroom, is quite different as will be noted below under resins. These gums are accumulated in rifts of the tissues of some trees, but it is not at all clear why the plant should make them, though apparently they serve at times as reserve food. Chemically they have the formula $(C_6H_{10}O_5)_n$,

the same as that for cellulose and starch, but with n meaning another figure; and they are formed no doubt from grape sugar, (probably viâ the mucilaginous modification of cellulose mentioned in the preceding paragraph), to which they are readily digested back by both plants and animals.

Fruit-Jellies. These substances are familiar to all housekeepers as the jelly which forms when fruits or vegetables are cooked (e. g., grape jelly, orange marmalade, pumpkin preserves), though it must be remembered that gelatine, from which the jellies of the tea-table are made, is an animal product. In the living plant they are solid, being insoluble in cold water; but they are dissolved by hot water, which explains why they appear after cooking. They represent, it is believed, another form of reserve food. Chemically they are known as pectins, and they have also the same general formula as starch $(C_6H_{10}O_5)_n$. They are formed without doubt from grape sugar to which they are easily digested back.

In reading this account of these various carbohydrates, two questions will inevitably arise in the mind of the reader. First, he will ask how it is possible that substances with properties so different as those of starch, cellulose, gums and jellies can have the same chemical composition. The answer is this, that on the one hand the letter n in these formulæ represents without doubt a different number in each case, and hence the composition is not really identical, while on the other, even an identical formula can be associated with very different properties, because the properties depend not only on the elements present, but upon the way these elements are arranged in the molecule; and they can be arranged in very different ways. The differences between grape sugar and fruit sugar are wholly of this latter kind. The second question the reader will wish answered is this,—why do some plants store up their reserve food in the form of sugar, some as starch, others as cellulose, and others as oil, soon to be mentioned. This question we cannot yet answer with certainty, but probably the general explanation offered in Chapter III for the

diverse ways in which plants develop the same organs, applies to the present matter, also,—namely, the plant makes the form of food easiest chemically for it to construct, provided of course there is no ecological reason for making one kind rather than another.

Class III. The Secretions, or Derivatives of Carbohydrates

So heterogeneous are these substances in composition, properties, and uses, that they are held in one class by hardly any stronger bond than that, while including the elements of Class II, they do not belong therein. Nor is the name which I give them a good one, for they include some things which are not truly secretions, while not all of the secretions are included in this class; but I can think of no better general designation. The principal members are the following.

Plant Oils. These are of two distinct kinds. First, are the fixed oils, which are properly plant fats, familiar to us in the various oils used in food or in medicine, notably olive oil, castor oil, cotton seed oil. They occur rather widely scattered in plants, as tiny isolated drops, scattered through the protoplasm; but they accumulate in quantity in many kinds of seeds, including nuts, to which they give a distinctive oily luster, and in which they act very obviously as a reserve food for the use of the embryo in germination. A reason why oil is stored in seeds more frequently than elsewhere has been found in a linking of two facts;—first, food value for food value, oil is a much lighter substance than any other kind of food stored by plants; and second, the seeds storing it are mostly disseminated by the wind and hence need to be kept just as light in weight as possible. And with these oils as with other substances, good food for plants is good food for animals also, the food needs of both being closely alike. Chemically these fats are rather complex, a typical formula being $C_{57}H_{110}O_6$, which shows that they are markedly poor in oxygen; and herein lies the reason why plenty of fresh air is needed for their assimila-

tion by man. They are formed in living cells from starch, and therefore ultimately from grape sugar, to which they can be changed back in germination and digestion by the action of suitable enzymes.

Related to the fats in some respects, though to the later-described proteins in others, are the *lecithins*, widely distributed in plants, and possessing a considerable interest as the probable basis for the formation of the vastly-important and complicated substance chlorophyll, the composition of which, aside from the presence of carbon, hydrogen, oxygen and phosphorus, is still rather uncertain.

The other kind of oils,—the ethereal, essential, or volatile oils, are very different in composition and meaning. They are familiar to us chiefly in the fragrant oil of lemon and oil of cloves, and are the causes also of the odors, sometimes fragrant and sometimes acrid, of many kinds of leaves (e. g., Lemon Geranium) when cut or crushed; and they cause likewise the fragrance of flowers and fruits. Camphor, and some other aromatic materials are related substances. They are not food products, as the fats are, but serve mostly ecological uses, either in connection with the protection of plants against insects or Fungi, or for the attraction of animals in connection with dissemination of seeds and cross pollination of flowers, as we shall later consider in detail along with those respective subjects. They are stored as a rule in special receptacles or glands, often of considerable size (figure 37). Chemically they are most diverse, some of them consisting only of carbon and hydrogen, approaching near to the formula $C_{10}H_{16}$. Little is known as to their exact mode of formation.

It is a non-volatile oil (called toxicodendrol), which is the poisonous substance in the Poison Ivy; and the fact that it is a non-evaporating oil explains why it is so very difficult to remove from the skin, and why it persists in plants which are long dead and dried.

Plant Acids. These are agreeably familiar to us as the sub-

stances which give the pleasant acid taste to fruits. Thus, malic acid gives the tart taste to apples and currants, citric acid to lemons and oranges, tartaric acid (from which cream of tartar is made) to grapes. In all of these

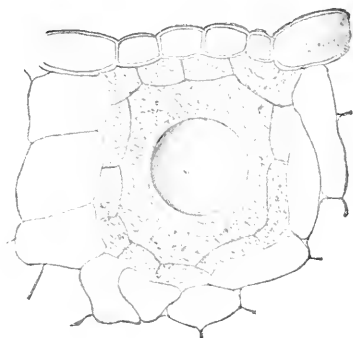


FIG. 37.—A gland, highly magnified, formed by a fusion of several cells, containing a large drop of an ethereal oil, as seen in a cross-section of a leaf of *Dictamnus Fraxinella*.

cases there is a reason, as our chapter on Dissemination will show, why these fruits should be eaten by animals, to which the acids certainly serve to render the fruits more attractive. On the other hand tannic acid, which occurs in the bark of many plants, (and from which man extracts it for tanning leather), has an astringent taste unpleasant to animals, against which, accordingly, its presence has some tendency to

protect the plant tissues. These acids, which all occur in solution in the sap, have a comparatively simple composition, the formula of malic acid, for example, being $C_4H_6O_5$. Their mode of formation is not entirely understood.

Plant Waxes. These occur chiefly on the surface of plants, where they constitute the bloom, commonly of bluish color, which is familiar upon plums and some leaves. On the dry berries of the Bayberry, a common plant of the coast, a wax accumulates in such quantity that in early days it was gathered and used for the making of candles. In general the waxes seem to render plants immune against wetting, after the manner of the oil on the back of the proverbial duck,—the disadvantage of the wetting being this, that the water would clog the stomata, and hence prevent the passage of gases that are needed in photosynthesis. If, now, the reader should ask me why, when the wax is thus of advantage, so many plants do not have it, I would answer by asking in turn why it is, that, if riches are such an advantage (or

at least are commonly thus reckoned), so few men possess them. The reason I take to be fundamentally the same in both cases;—some kinds never get the right start towards constructing them, or else have not the capacity to manufacture them. Chemically the waxes are very closely related to the oils, and no doubt are built up in the same general way.

Resins. Under this name falls a variety of substances of which typical examples are familiar in the balsam of the Fir and the Pine; in spruce gum; and in rosin; myrrh and frankincense are others; and much of the milky juice (or latex) of plants, from which the rubber of commerce is made, is composed of resins or closely related substances. Chemically the resins are most diverse, and their mode of origin is as little understood as is their function in the plant. They are usually accumulated in special passages, from which they sometimes flow out at a break (e. g., in Pines), in a way to suggest that they serve as a temporary salve,—a kind of first aid to an injury. At times they appear to be utilized as food, which is likely enough, since there is every reason to suppose that plants, precisely like animals, when driven by hunger, will resort to the use of materials which they would otherwise reject with disdain.

Glucosides. These substances are more interesting than conspicuous, the most familiar being that called amygdalin, which gives the bitter taste to seeds of almonds and apples; while the peppery taste, so common in plants of the mustard family, is also due to a glucoside. Their meaning in the plants is not known, although they may find some incidental service in protecting against animals the parts which possess them. With the glucosides belong also some of the brightest coloring matters produced by plants, including the red dye madder and the blue dye indigo. Here also comes erythrophyll (called also anthocyan), that red color with which we have made pleasant acquaintance already as giving brilliant hues to ripened fruits, and the glory to the foliage of autumn. Chemically the glucosides owe their name to

the fact that they are compounds of glucose with some one or more definite substances, into which they can again be broken up. Some of them contain nitrogen, as for instance the amygdalin above mentioned (its formula is $C_{20}H_{27}O_{11}N$), which allies them in some measure with the nitrogen-containing substances next to be considered, especially the alkaloids.

Class IV. The Nitrogen-Assimilates, or Amides

These substances, dissolved in the sap of plants and having no particular uses to us, are not commonly known; but they are vastly important nevertheless, inasmuch as they constitute the connecting step between the carbohydrates and the indispensable proteins, soon to be considered. The commonest is asparagin, dissolved in the sap of young asparagus plants, from which it can easily be crystallized out. Its formula, typical of the group, is $C_4H_8O_3N_2$, which shows the presence of the nitrogen along with the elements of carbohydrates; and there is no doubt that the ultimate source of the materials is the photosynthetic grape sugar together with nitrogen from compounds absorbed with water by the roots. The amides are not known to perform any special function of their own in the plant, and probably find their significance simply as a necessary chemical step in the formation of proteins.

The incorporation of nitrogen with the elements of the carbohydrates is a step of the first biological magnitude, since the nitrogen is the most essential and distinctive additional constituent of the most important of all biological substances,—living protoplasm. We have already considered, (in Chapter II), the source of the plant's supply of carbon, oxygen, and hydrogen, and must now turn aside from our main theme to examine the source of the nitrogen supply, a subject all the more important because of the fundamental economic bearings it has. Nitrogen, it should be needless to recall to the reader, is the colorless gas which makes up very nearly four-fifths of the atmosphere; and from such an abundance plants ought apparently to have no

difficulty in drawing all that they need. As a matter of fact, however, the typical plants take no nitrogen at all from the air, even starving to death for want of a little while bathed in this lavish abundance; and the reason they do not is that they cannot. The most prominent characteristic of nitrogen is its chemical inertness, or reluctance to enter into combination with any other substances,—a circumstance, indeed, to which its abundance in the atmosphere is due; and its union with oxygen or other substances can be effected only by the agency of electric sparking machines, or other methods involving the expenditure of high tension energy. Now our typical large plants have not in their structure any equivalent for sparking machines or other arrangements releasing suitable energy, although, as will presently appear, the lowly Bacteria seem better provided in this particular. Since they cannot make use of the free nitrogen of the air, plants have had to resort to the only other possible source of supply, viz., substances in the soil containing it already combined, which substances, moreover, must be soluble in water to admit of their absorption by the roots. The compounds called nitrates best meet these conditions, and they, accordingly, are the source of most of the nitrogen which, with appropriate intermediate chemical steps, is combined with the elements of the carbohydrates to form amides.

If nitrates were as plenty in soils as plants could make use of, then our digression in pursuit of this substance could end right here. But in fact the nitrates in most soils are so scant that the majority of plants live all the time in touch with nitrogen scarcity, and this is one of the chief of the factors which limit the luxuriance of their growth and expansion. It is, perhaps, worth noting in passing, that especial scarcity of nitrogen in some situations is correlated with an insectivorous habit in plants which reside there,—the advantage of this habit consisting in the abundance of combined nitrogen obtainable by digestion from the bodies of insects. A chief reason for the scarcity of nitrates in the soil lies

in that very solubility which renders them absorbable by plants, for it leads to their constant drainage away with the superfluous water; and were it not for a constant renewal of the nitrate supply plant life would soon be starved to extinction. This renewal, known as the nitrification of soils, is a matter of such biological and economic consequence that we must now consider it with some care.

The natural nitrification of soils takes place in four ways. First, there is a constant return of combined nitrogen to the soil from the excretions of animals, and the decay of plant and animal bodies. Second, a small amount of combined nitrogen is added to the soil with the rain which falls during thunder showers, for the lightning acts as a kind of gigantic natural sparking machine which forces the nitrogen and oxygen of the air into combination; thus is formed the soluble nitrous acid, which is caught and taken into the soil by the rain. Third, nitrates are constantly though slowly added to the soil by the natural decay of the rocks which contain them. In moist climates they must drain away about as fast as they are formed, but in dry climates the drainage is slower than their formation and they accumulate in the soil. This is a reason for the richness of the finer soils of the deserts, which blossom as the rose when water is added by aid of irrigation. Fourth (and far the most important) of the natural methods of soil nitrification is bacterial activity. Everybody knows that a soil in order to be rich must contain a proportion of humus, the material which is dark in color and supplies the open character. This humus consists chiefly of decaying vegetable matter, which provides both the home and the nourishment for countless numbers of tiny organisms, chiefly Molds and Bacteria. These Bacteria, popularly known as Germs, are of several kinds, of which some, in the course of their own processes, incidentally work over the less valuable nitrogen compounds of the soil to more valuable ones, while still others, and these the most important, actually force the nitrogen and oxygen of the air to unite

into the simple compounds which later are worked up to nitrates by the others. It is not yet known how these Bacteria accomplish this crucial first step of nitrification, but the source of the energy is plain; it is supplied by their intense respiratory power, in which they surpass some hundred-fold the larger plants. This fact of the nitrification of soils through the activity of Bacteria is one of the most important in nature.

It may here occur to the practically-minded reader to ask whether this power of Bacteria to add nitrogen compounds to soils cannot be utilized artificially for the enrichment of poor soils. It can be, and to some extent, has been; and living Bacteria of the suitable sorts have actually been multiplied and distributed for trial by our own Department of Agriculture, and have been offered for sale to farmers both in Europe and America, though the process is not as yet a commercial success. However, in the utilization of the nitrifying Bacteria man was long anticipated by at least one great group of Plants, the Pea Family, or Leguminosæ, the members of which have actually colonized the nitrifying Bacteria upon their own roots, thus making sure that the entire product of the Bacteria shall be available to themselves without any loss through drainage or use by other plants. Most people have seen upon the roots of Peas, Beans, and others of this family, the wart-like or pea-like swellings, whose appearance is well shown in the accompanying photograph, (figure 38). These nodules are residences inside the plants occupied by the Bacteria. The connection is mutually beneficial, for the Bacteria receive carbohydrates from the green plants which receive nitrogenous compounds from them. It is because of the efficiency of this arrangement that the seeds of plants in the Pea Family are richer in nitrogenous food substances than any others; and this latter fact in its turn explains why Peas and Beans are the best of all plant substitutes for meat, which is mostly protein. This relative richness of Leguminosæ in nitrogenous compounds explains also the reason underlying the ancient farming practice

of green-manuring, that is, plowing in Clover and other leguminous crops to enrich the soil. It is from these same nodules, also, that the Bacteria have been taken and grown for the commercial enrichment of the soil, as mentioned on the preceding page.

In our consideration of these four natural methods of soil

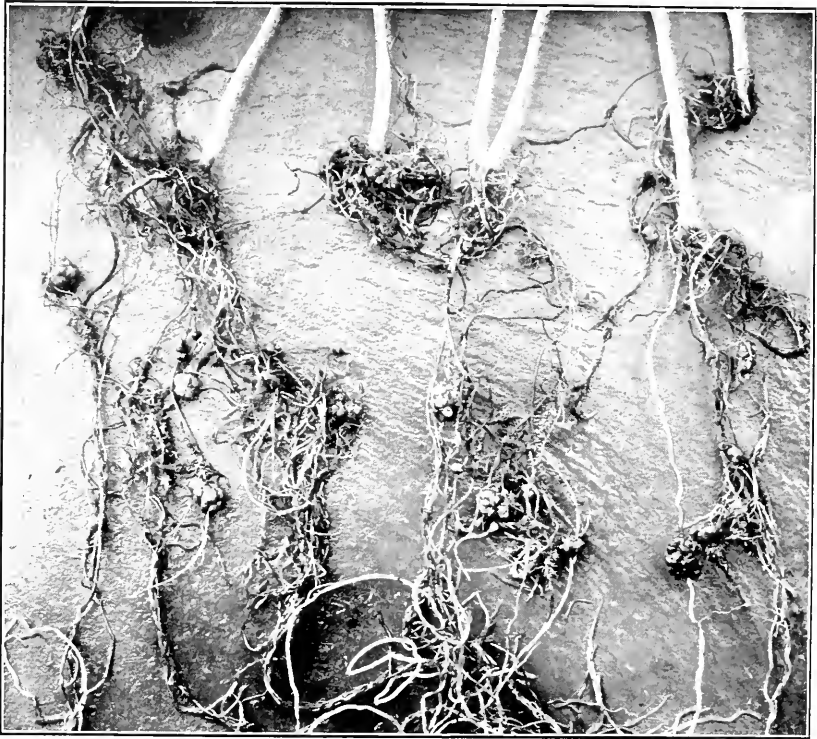


FIG. 38.—The roots of several Bean plants, photographed about half the natural size, showing the collections of wart-like nodules which contain the nitrifying Bacteria.

nitrification we must not forget the artificial aid of man, who, for his own purposes, adds to the soil both chemical fertilizers and barnyard manures, with their rich supplies of nitrogenous and other compounds.

Finally it is important to note that the plants, for their part, have a way of meeting the nitrogen scarcity of soils,—viz., they

waste none. To this end they even go so far as to remove from their leaves, before these are dropped, such of the nitrogenous and other compounds as can be used economically again. Unlike animals, they excrete no nitrogen, or extremely little, in either solid, liquid, or gaseous form, but conserve it with care and use it over and over again; so that it is only released in the end by their decay after death.

Class V. The Principal Poisons, or Alkaloids

These substances are notorious as including the most violent plant poisons. Thus *strychnine* (from the *Strychnos* bean), *nicotine* (from the Tobacco leaves), *morphine* (from the milky juice of Poppies) are alkaloids, as is the poison, *muscarine*, of the deadliest Mushrooms. Some alkaloids, while not poisonous, have strong properties in other respects, such as *quinine*, obtained from the bark of the *Cinchona* tree and efficacious in breaking up fevers; *caffeine*, the stimulating substance in Tea leaves and Coffee berries; *cocaine* from Cocoa seeds, the well known local anæsthetic and fatally-alluring drug. Their meaning in the plant is uncertain, and all the more puzzling since they mostly are poisonous to the very plants which produce them if injected into other parts of their tissues. Nor is it certain just how they produce their poisonous effects. Alkaloids occur also in animal tissues as a product of the processes of fermentation and decay; they are called ptomaines, and are very deadly, being the real cause of death in bacterial diseases. Chemically the alkaloids are related to the amides, from which they are no doubt formed, not at all as a step in the formation of proteins, but as a side group. A typical formula is that of caffeine, $C_8H_{10}O_2N_4$.

It has recently been discovered that the roots of our common field crops appear to excrete into the soil minute quantities of substances poisonous to the plants which produce them; and it is probable that the presence of such substances, and not the exhaustion of the necessary mineral matters, is the real cause of

the sterility of some soils, which are therefore "poisoned" rather than "exhausted." The composition of these substances is not known, except that they are complicated and perhaps nitrogenous, in which case they may be found to belong with this group of the alkaloids.

The reader will recall that the active properties of the alkaloids were somewhat foreshadowed in the nitrogenous glucosides, and later he will also make acquaintance with remarkably active properties of another kind which characterize not only the proteins entering into living protoplasm, but also the enzymes, with their very striking chemical powers. The common feature which distinguishes all of these substances in contrast with the more passive groups is the possession of nitrogen, which seems therefore to be associated with the most active properties in plant substances. This fact is sufficiently curious in face of the chemical inertness of nitrogen, and one can fancy this element as reluctant to enter into combinations, restless, so to speak, while in them, and making disturbance in its efforts to escape to its original freedom.

Class VI. The Flesh-Formers, or Proteins

These are the most important substances made by plants, entering as they do into the composition of living protoplasm. They are more familiar in animals than in plants, for flesh is made up of them; but they are distributed throughout the living parts of all plants, either in the active protoplasm or stored as reserve food, especially in seeds. They are vast in number, elaborate in composition, and only imperfectly known. Chemically they are distinguished from all of the preceding groups by containing not only the elements of the latter, but also sulphur, while some of them possess phosphorus too, so that their composition may thus be expressed $C_n H_n O_n N_n S_n (P_n)$. Some of their molecules are of very great complexity; thus, there is an albumin with the formula $C_{720} H_{1134} N_{218} O_{248} S_5$; and there are other proteins

in which the elements, or atoms, of the molecule, must sum up to more than 15,000, or even, in some cases, more than 30,000. Many of these substances differ little from one another in properties, and moreover are readily convertible one into another; and the facts seem to indicate that these elaborate forms are really multiples (or polymers) of some simple protein molecule, built up in the same manner as are starch and cellulose from a simple carbohydrate molecule. Nor is it to be supposed that all of these substances have each a separate meaning in the plant, though they may have; but many of them no doubt are simply manifestations of chemical individuality in the plant, as the forms of starch grains are manifestations of physical individuality.

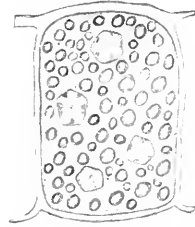


FIG. 39.—A cell, highly magnified, from the proteinaceous layer just under the husk of Corn, showing numerous protein grains interspersed with a few starch (larger) grains, all embedded in living protoplasm.

Several different groups of Proteins are recognized by chemists, of which I shall here mention, even though in little more than the

Homeric fashion, the more important. They are,—*Albumins*, substances like white of egg, thinly spread through many plants: *Globulins*, which form definite grains in some seeds like Corn (figure 39), and beautiful crystals in Castor Bean, Potato and some other plants (figure 40): *Glutelins*, typified by the familiar gluten of flour which gives the agglutinosity to dough: *Prolamins* especially distinctive of the seeds of grains: *Nucleo-proteins*, containing phosphorus, and forming the chromosome substance of the nucleus of cells: *Phosphoproteins* (called also albuminates) cheese-like materials found in some seeds: *Proteoses and Peptones*, very important because they are the soluble and diffusible proteins into which the insoluble kinds are converted in digestion by the

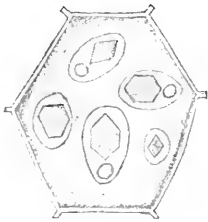


FIG. 40.—A cell, highly magnified, from the interior of a Castor Bean, showing the crystalline protein grains, (their structure rendered somewhat clearer by treatment with reagents), embedded in living protoplasm.

action of peptonizing enzymes: and there are others likewise of rarer sort and lesser consequence.

The mention of the presence of sulphur and phosphorus in proteins will lead the reader to inquire for the source of supply of those elements. The answer is ready. They are derived from soluble sulphates and phosphates absorbed from the soil by the roots, and are incorporated, through chemical reactions still imperfectly known, with the elements contained in the amides. All soils contain all of the sulphates that plants need, and usually all of the phosphates, though at times the latter are insufficient, and must be added as fertilizers to ensure good crops.

Class VII. The Regulators of Metabolism, or Enzymes

It is safe to say that the enzymes (called also ferments) are the most remarkable and least known, although among the most important, of all substances produced by plants,—or by animals, either. They are characterized by this remarkable power,—viz., they can cause chemical changes, each of one definite kind, in other substances, without themselves entering into the reaction or suffering any appreciable alteration. Because of this mode of action very small quantities of enzymes can alter chemically great quantities of material. Thus the enzyme *diastase*, which occurs both in the saliva of man and also in the starch-storing organs of plants, can convert (chemically, hydrolyze) great quantities of the insoluble starch by two or three steps into grape sugar, a soluble diffusible material; likewise the enzyme *protease* (pepsin) occurring in both plants and animals, hydrolyzes insoluble indiffusible proteins into soluble diffusible peptones; also the enzyme *lipase* converts insoluble fats into soluble fatty acids and glycerine: *cytase* converts cellulose of Ivory palm and Date into soluble sugars; and there are many others of lesser prominence. It is these changes which constitute digestion, whether in plants or in animals. By aid of the enzymes the plant

can not only produce and control chemical changes within its own body, but, by pouring them out in suitable places, can dissolve extraneous materials and later absorb these again for its own use. It is thus that insectivorous plants can digest the insects they capture; parasites can penetrate into the tissues of a host; and pollen tubes can digest their way down the solid tissues of the style, absorbing the digested materials for use in their own growth. But there are many other phases of enzyme action also; thus the unfermentable cane sugar is hydrolyzed (or inverted) to fermentable grape sugar by *invertase*, and grape sugar is fermented to alcohol and carbon dioxide by *zymase*, produced by the Yeast plant. And there are other cases innumerable which we cannot take space to consider.

Chemically and physically we know very little about the enzymes, because it has not yet been found possible to extract them from the protoplasm in a pure state; and even their very existence would not be recognized at all were it not for their effects. It is not even certain that they are related to the Proteins, although there is indirect evidence pointing that way; nor are we sure that they are liquids thinly saturating the protoplasm, though this seems probable. Still less is it known how they produce their remarkable effects, although a homologous power exists in those inorganic substances called catalyzers. Each kind can produce only one chemical change, and that as a rule but a slight one, but the coöperation of several can cause a series of changes large in the end; and it may be true that they cause most, if not indeed all, of the chemical processes which the living protoplasm carries on. They are the tools, so to speak, with which the protoplasm effects the chemical results it requires. Indeed to some investigators it has seemed likely that the enzymes are the principal material bases of heredity, and that the chromosomes of the nuclei, known to be conveyors of heredity, consist chiefly of collections of enzymes. Truly the importance of the enzymes is great, and their further study in the near future is likely to throw

much light upon some of the most fundamental problems of Biology.

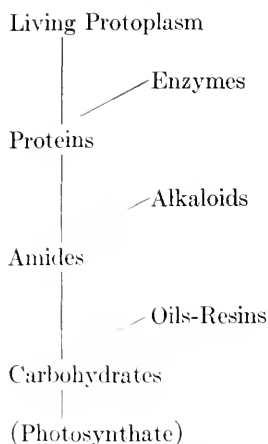
Class VIII. Living Protoplasm

This substance is of such importance and complexity as to require for its treatment, a separate chapter, which follows. It need only be said in this connection that so far as chemical analysis has been able to penetrate into the mysteries of living protoplasm, it appears to be merely a very complicated mixture of proteins with many simpler substances. Here for example is a list of the substances which have been recognized in a chemical analysis of the protoplasm of one of the lower plants;—

Water, Pepsin and Myosin, Vitellin, Plastin, Guanin, Xanthin, Sarkin, Ammonic carbonate, Asparagin and other amides, Pepton and Peptonoid, Lecithin, Glycogen, Aethalium sugar, Calcic compounds of higher fatty acids, Calcic formate, Calcic acetate, Calcic carbonate, Sodid chloride, Hydropotassic phosphate, Iron phosphate, Ammonio-magnestic phosphate, Tricalcic phosphate, Calcic oxalate, Cholesterin, Fatty acids extracted by ether, Resinous matter, Glycerin, coloring matter, etc., Undetermined matters.

In this list, which I give in order to illustrate the chemical complexity of protoplasm, all of the constituents are well-known substances, no one of which has any of the properties of life, unless such a substance lies hidden in the trifling amount of “Undetermined matters”; nor has any chemist yet been able to identify any distinctive living substance,—any of that protoplasm *par excellence* which we are logically bound to believe must exist. But the further consideration of this subject belongs with the next chapter.

Such are the groups of substances which plants build upon the foundation laid by the photosynthate. We may summarize their relationship in a diagrammatic manner, after the analogy of a tree of ascent, as shown herewith.



It may perhaps have occurred to the reader ere this to inquire what proportion of the original basal photosynthate is used in the construction of each of these classes of substances. The question is a fair one but difficult to answer, partly because the proportions would be so different with the various kinds of plants, and partly because we have so few data for making calculations. However, it is possible to make a generalization for plants as a whole, and this has been done in the table below, which, although little more than a guess, has yet some value. For simplicity I have reduced the table to the kinds of known and visible substances, grouping together the others as "special substances"; and incidentally I have added the ultimate fate of the various groups.

A Table to Illustrate the Uses Made of Photosynthetic Sugar, with its Origin
and Ultimate Fate.

$\left. \begin{array}{l} \text{CO}_2 \\ + \\ \text{H}_2\text{O} \\ 100\% \end{array} \right\} \text{form}$	$\left. \begin{array}{l} \text{Photosyn-} \\ \text{thetic} \\ \text{Sugar} \\ 100\% \end{array} \right\} \text{which}$	$\left. \begin{array}{l} \text{Foods} \\ \text{Skeleton} \\ \text{Protoplasm} \\ \text{Special subs.} \\ \text{Respiration} \end{array} \right\} 50\%$	$\left. \begin{array}{l} 25\% \text{ new plant} \\ \text{growth;} \\ 25\% \text{ eaten by} \\ \text{animals;} \end{array} \right\}$	$\left. \begin{array}{l} \text{is respired or decays to CO}_2 + \text{H}_2\text{O, } 25\% \\ \text{is respired or decays to CO}_2 + \text{H}_2\text{O, } 25\% \\ \text{burns or decays to CO}_2 + \text{H}_2\text{O, } 25\% \\ \text{decay to CO}_2 + \text{H}_2\text{O, } 10\% \\ \text{is respired to CO}_2 + \text{H}_2\text{O, } 15\% \end{array} \right\}$
100%	100%	100%		CO ₂ + H ₂ O, 100%

This table brings out clearly once more that most fundamental of facts about the physical constitution of living things, that their substance is all derived originally from carbon dioxide and water, with a few minor additions, and is all returned in the end back to the same source, undergoing en route transformations of substance and energy which constitute the principal visible phenomena of life. The organism is made up of a little of those substances temporarily withdrawn from the general circulation of nature and interacting vigorously with one another under the stimulus of external forces,—principally the sun. Organisms are, as it were, little whirlpools in the general circulation of matter and energy. And I cannot forbear to attempt to illuminate this matter somewhat further by aid of one of my favorite diagrams, which is presented herewith (figure 42).

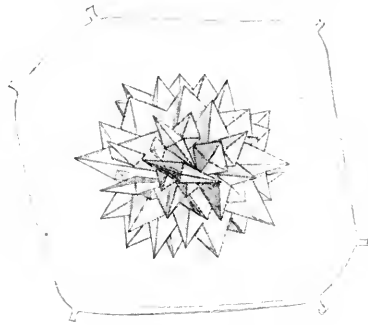


FIG. 41.—A cell, highly magnified, from a Begonia, showing a mass of crystals composed of calcic oxalate, lying within the cell-cavity around which can be seen the living protoplasm. (Copied from a wall-chart by L. Kny).

There is yet one other group of substances made by plants, very different, however, in kind from those already described. In the tissues of all plants the microscope reveals mineral matters, sometimes in great abundance and crystallized in very beautiful forms, of which our illustration (figure 41) gives some, though an inadequate idea. A few are probably useless minerals absorbed by the roots along with the useful kinds presently to be noted, but the great majority are by-products of useful chemical reactions. Thus, the commonest of the crystals is oxalate of lime, which is formed from oxalic acid, probably a by-product in the manufacture of proteins. These crystalline matters are obviously of no use, but are waste materials. In the absence of a regular excretory system such as animals possess, the plant has no resource except to store

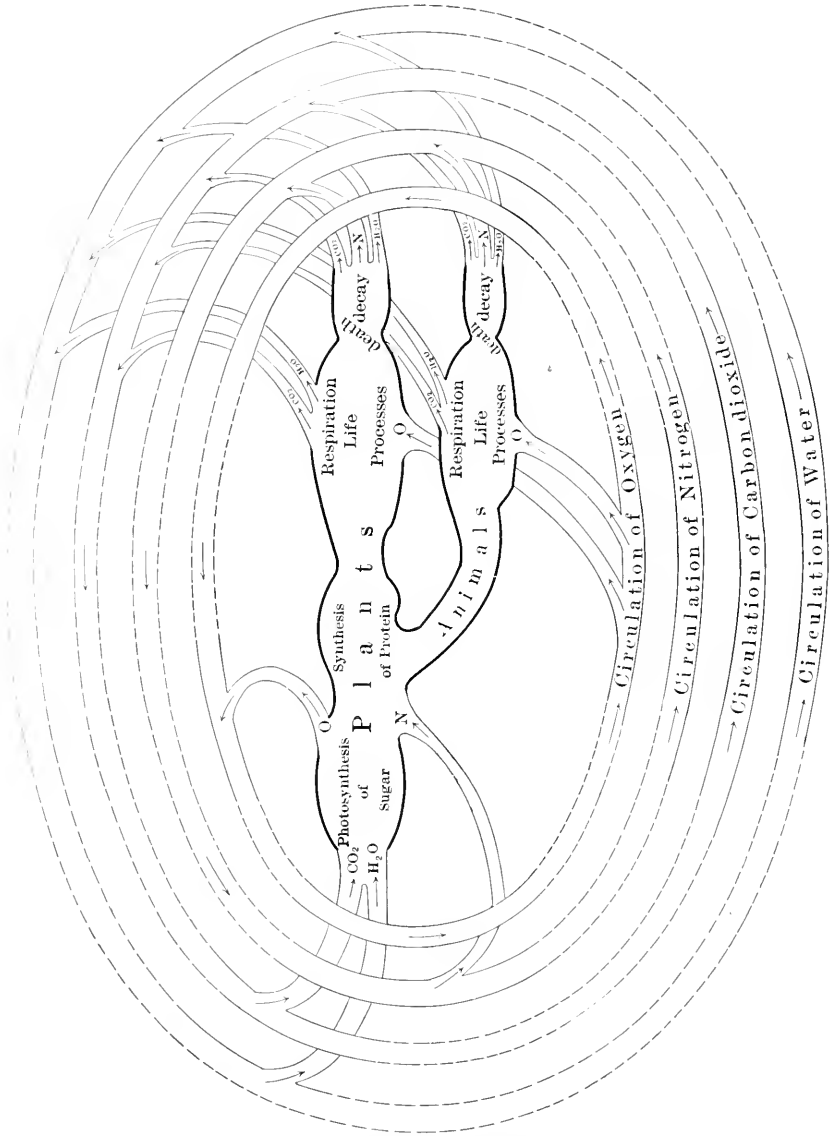


FIG. 42.—A diagram illustrative of the relation of plant and animal life to the circulation of the principal substances of nature.

them up in out of the way places, though they may ultimately be partially removed by the fall of the leaves and the bark.

There remains one other important phase of our subject. It concerns the indispensability of certain elements for healthy metabolism, although they do not enter into the composition of any of the substance manufactured. Everybody knows that



Lacks,—all potas- cal- nitro- phos- mag- iron nothing
 sium cium gen phorus nesium

FIG. 43.—Illustration of the method and results of water culture. The plants are Corn, all started at the same time. (Copied from a wall-chart by Errera and Laurent.)

potash (potassium) is thus indispensable, to such a degree that it must often be added as a fertilizer to soils; but its symbol (K) is not found in any of the formulæ cited in this chapter. The same is true of the elements calcium, magnesium and iron, and probably sodium and chlorine, all of which are indispensable to the healthy growth of most or all plants, but none of which enter into the composition of the most important plant substances. Naturally a

great many attempts have been made to determine the exact function of each substance, and why it is essential. The reader will be interested in the principal method used to this end. It depends on the fact that there are plants, and many, which will



FIG. 44.—Corn plants growing by water culture in a common tumbler. The screen is ruled in centimeters.

grow through their whole cycle from seed to seed in water, without any contact with soil, if only the needful minerals be contained in the water. This method is called water culture, and the practical arrangements therefor are well shown in the accompanying figure (figure 43), while a product of the method, produced in my own laboratory, is shown by figure 44. Now, by growing one plant in water containing all of the necessary minerals except one, side by side with another plant grown in water containing all of the needful minerals, it is possible to observe what effect the absence of this one substance produces, and hence to infer what its use to the plant must be.

The general results of an experiment of this kind are well shown in figure 43. In this way we have found that potassium is necessary to the formation of the photosynthate, calcium to its transfer through the plant, and iron to the formation of chlorophyll (into the composition of which, however, it possibly enters); but further than this, and as to the other materials, our knowledge is most vague and unsatisfac-

tory. It seems quite plain, however, that the rôle of these elements lies in services incidentally necessary to the greater processes,—such as aiding in chemical steps, neutralizing poisonous excretions, and so forth. They are like the servants at a party; they are indispensable to its success, but their names do not appear in the list of those present. But our ignorance on these matters, and upon so many other phases of our subject of metabolism, is only acting as a spur to the efforts of many devoted workers, who, in laboratories all over the world, are attacking these problems with the full determination to solve them. The methods of science are slow, but they are irresistible; and the solution of the problems is only a matter of time.

CHAPTER VI

THE SUBSTANCE WHICH IS ALIVE IN PLANTS, AND ITS MANY REMARKABLE QUALITIES

Protoplasm



ALREADY more than once in this book the reader has met with a mention of protoplasm,—the living substance of plants. Besides, almost everyone has some knowledge about it, or thinks that he has, though much of the current information is a very long way from the truth. There are even some persons who believe that protoplasm is an abstract conception evolved by the mind of man to help explain phenomena otherwise incomprehensible; while a few seem to cherish the idea that it is one of the many inventions sought out by science for undermining the faith. Yet protoplasm is not any of these notions, but a real material which can be seen, handled, and subjected to experiment. The reader will wish to know the facts about this most important of substances, and here is the suitable place to consider them.

It is nowadays an educational axiom that a good understanding of any scientific subject is possible only through personal contact and experience with the matter in question. A great many people do not comprehend this necessity, and believe that well-written and fully-illustrated books are a sufficient, if not actually a superior, substitute for the laborious and time-consuming methods of the field or the laboratory. When the reader meets with this error he can refute it effectually by asking the objector whether he considers that guide-books, even the best written and most

profusely illustrated, are a satisfactory substitute for foreign travel. The case is still stronger with scientific facts and phenomena, for these are mostly of a sort even more foreign to the student's previous experience than are the sights and impressions of distant lands. All this is quite true of the subject before us, and if the reader would really understand the substance Protoplasm he must take steps to see it for himself, even if he has to trouble some friend, his physician, or the nearest botanical expert, for the use of a microscope.

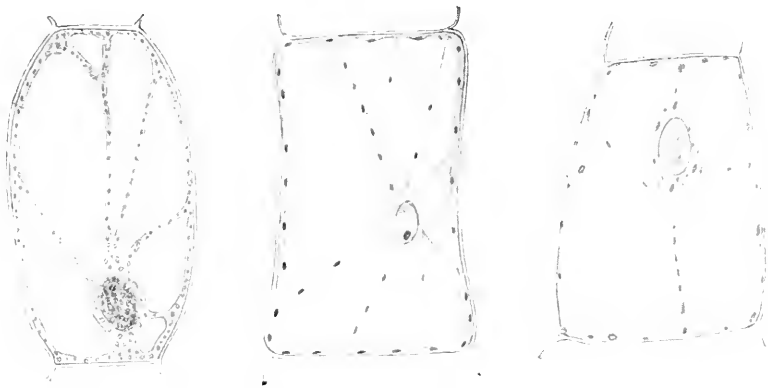


FIG. 45.—Typical cells, in optical section highly magnified, of hairs from Spiderwort, Gloxinia, and Squash, respectively, showing as accurately as the author can represent it by pencil, the appearance of their gray-granular threads and lining of living protoplasm.

If, now, the reader will carefully remove some of the younger of the hairs which are so prominent in the flowers of the common Spiderwort of the gardens, (or the closely-related Wandering Jew of greenhouses), or some of the hairs on the young leaves or stems of Squash, or Gloxinia, (or even of "Geranium"), will place them on a glass slide in a drop of water, cover them with a thin glass, and then examine them with the microscope, he will see before him living protoplasm, the most remarkable of all natural substances. These particular objects display an appearance represented in the accompanying pictures, (figure 45); and they have an advantage

over others which might be chosen in this, that while comparatively easy to obtain, their protoplasm exhibits a streaming motion, which, though often slow and difficult at first to detect, nevertheless when seen forms a valuable proof of its living condition. The rather inconspicuous grayish-granular, translucent, semi-fluid appearance here presented inside of the cells is representative of the aspect of protoplasm in general. The granular look is due largely to the presence of food granules, which in some cases are absent, leaving the protoplasm so nearly transparent that it can hardly be seen at all unless stained by some dye, while in other cases the granules are so plenty as to give the protoplasm an appearance of solidity. Moreover, as these granules consist largely of protein which has a slight yellowish color, they give to protoplasm in dense masses a distinctly yellowish or brownish-yellow tinge; and this is the cause of the yellow color which shows so plainly through the tips of white roots, and of the brownish-yellow of the interior of young ovules. In the hairs supposed to be lying before the reader, the protoplasm is obviously soft enough to flow freely, though it is not wholly a fluid; and it is known to possess about the consistency of a soft jelly. Indeed, if one were to imagine an uncolored jelly, somewhat too soft to retain the form of its mold and all clouded instead of quite clear,—in other words just the kind of jelly that the thrifty house-keeper doth most despise, he would have a very good idea of the protoplasm of these hairs. In some plant tissues the substance is still softer and almost a liquid; in others it is firmer, to such a degree that in seeds it becomes tough and hard as horn, though never approaching the hardness of ivory, as a prominent dictionary says that it does. The visible streaming of the protoplasm in these hairs, however, is not typical, for while in some kinds the streaming is even more active, generally it is very much slower, and commonly is imperceptible; so that the reader must not allow the motion to become too prominent a feature of his visualization of plant protoplasm. A white-granular, slow-moving

jelly;—that is what protoplasm looks like, and that is precisely what it is.*

While protoplasm for the most part can be observed in plants only by aid of the microscope, there are cases in which it occurs in masses sufficiently large to be studied by the unaided eye, and to be taken in the hand. Everybody has seen those soft, whitish, slimy masses which are flattened against decaying wood in damp dark places, such as the rotten underpinning of old buildings, in cellars and dark greenhouses, or on old shaded tan-bark,—whence they are known as “Flowers of Tan.” These are called, scientifically, Slime-molds, and they are practically pure naked protoplasm, the accessibility of which has made these low plants very favorite objects for protoplasmic studies.

Such is the appearance of living plant protoplasm as seen by the eye or through an ordinary microscope; and try as one will, he can see little more. The supreme importance of protoplasm among earthly substances has of course acted as a stimulus to the most thorough researches into its structure; and all the highest powers of the microscope, and all the most refined devices and methods known to microscopical science, have been brought to bear upon it. Yet these efforts have yielded little additional knowledge, and even that little has been left involved in uncertainty and controversy. We do not even know what texture the protoplasmic substance possesses. Some investigators have concluded that such protoplasm as the reader has seen streaming in plant-hairs is a loose network of fine elastic fibers,

* The streaming of Protoplasma is thus vividly visualized, though with some exaggeration natural at that time, by Huxley,—“Currents similar to those of the hairs of the nettle have been observed in a great multitude of very different plants, and weighty authorities have suggested that they probably occur, in more or less perfection, in all young vegetable cells. If such be the case, the wonderful noonday silence of a tropical forest is, after all, due only to the dulness of our hearing; and could our ears catch the murmur of these tiny Maelstroms, as they whirl in the innumerable myriads of living cells which constitute each tree, we should be stunned, as with the roar of a great city.” *The Physical Basis of Life* in his *Collected Essays*, New York, I, 136.

holding liquids in its meshes as a sponge might do,—a view more prevalent formerly than now, even though it is sustained by the appearance of the substance when killed and colored by dyes. Others consider that protoplasm, aside from certain solid granules, is chiefly an emulsion of various liquids, which rest suspended as tiny globes in a matrix of fluid ground substance, very much as the tiny globules of oils remain suspended in water after violent shaking of a mixture. And the advocates of this view, now in the ascendant, have supported it by constructing, out of ordinary chemicals, certain emulsions or foams, which show striking similarities to living protoplasm not only in appearance, but in movements, though they are, however, far enough removed from protoplasm in all other respects. And a third view tries to harmonize the two others by supposing that some protoplasm has one structure and some the other. In one part only does protoplasm display a definite structure, and that is in the nucleus during reproduction, a matter we shall presently consider.

It may seem to the reader remarkable that I do not attempt to illustrate so important a subject more fully by pictures. But protoplasm in fact, because of the lack of clear definition in its structure, is most difficult to represent well in any kind of picture. Indeed, hardly any two persons represent it alike, as follows naturally enough from the fact that hardly any two persons see it alike. In various figures in this book, however, I have tried incidentally to give some, even though rather a conventional, idea of its appearance, and to these figures (figures 33, 34, 39, 40, 41, 45) the reader will now find it worth while to refer. And I shall at this point, add one more, and one of the best, in which the great botanist Sachs has tried to represent it as if projected against a black background, (figure 46).

We come now to the important matter of the chemical composition of protoplasm, from which, in view of its many remarkable powers, we naturally anticipate something of very unusual interest. The most striking of the chemical facts about it, as the

chapter on Metabolism further illustrates, is this,—that protoplasm, despite its aspect of simplicity, is not a single substance, but a very heterogeneous mixture of many different substances of diverse grades of complexity, from the simplest of mineral salts up to the most complicated of proteins. None of these substances, however, are of themselves alive, nor has chemical analysis yet succeeded in locating any distinctively living constituent,—any protoplasm *par excellence*, although we are logically bound to believe that some such substance must exist as a seat for the distinctive properties of life. Protoplasm, therefore, is probably composed chemically of two classes of materials;—first, a very small amount of a distinctively living constituent, not yet identified, but consisting, in the fibers, or else the ground substance of its physical texture; and second, a very large amount of various non-living substances, nutritive and other, which are under the control of the living constituent.

There are, however, some further chemical facts about protoplasm which go a little way towards explaining its various powers. Thus, a part of its constituents (in general the most complicated)

are very unstable, or, chemically stated, labile, and change their composition under slight provocation whether from without or within. Such changes are accompanied, like all others of a chemical nature, by transformations of energy, either release or absorption. And these in turn cause other changes,



FIG. 46.—The protoplasm of a hair cell of a Gourd, projected against a black background. (Reduced from Sachs' Lectures.)

and these yet others, in an almost endless succession. Thus living protoplasm, complex and unstable in its constituents, and acted upon constantly by diverse forces both from without and within, is a constantly seething mass of energy-and-material changes;—and it is such changes which constitute the visible phenomena of life. But,—and here is the crux of the matter,—these changes are not hap-hazard and aimless, but on the contrary proceed in a definite and orderly sequence, resulting in the formation of definite structures and the performance of definite actions time after time and generation after generation; and it is this orderliness, this definite procession of physical and chemical processes, rather than anything in the processes themselves, which is the most distinctive characteristic of life. The failure of the regulatory power breaks the circuit of the processes, and leaves the protoplasm a helpless mass of matter all ready for decay; and this failure we name death. Life thus consists of two elements, first, material and energy changes, that is, purely physical and chemical processes, whose general nature we can understand, and which are seated in the various substances that chemists have identified in the protoplasm, and second, a regulatory power which directs and makes use of those processes but whose nature and location is still quite unknown. Perhaps the nature of this regulatory power is incomprehensible, or unknowable, in our present philosophies, though as to that, science never admits that anything is unknowable, but works ever under the assumption that everything can be known if we but refine sufficiently our methods of investigation.

There is one other feature of the chemistry of protoplasm which may have some importance in explaining its powers. In a general way it seems true that the protoplasm of the higher and more elaborate plants and animals is more complicated chemically, or at all events produces a greater number of complicated substances (proteins especially), than the lower. This suggests that each of the special physiological features successively ac-

quired by plants and animals in the course of their evolution has its seat in a special chemical constituent of the protoplasm. On this view, evolution, physiologically considered, depends upon chemical experimentation, so to speak, in the protoplasm, and follows step by step on the successful formation of new chemical compounds. But let the reader beware of accepting this suggestion as knowledge; it is merely a speculation, but one of those which, in science, it is legitimate to throw out ahead as a temporary guide to further investigation.

In common with all other substances in Nature, protoplasm thus possesses its physical and chemical properties. But in addition it possesses another set not found in other substance; and thereupon depend its powers to do the remarkable things that it does. These may be termed its physiological or vital properties, which are as follows;—the property of *metabolism*, or power of causing orderly chemical changes within itself, including photosynthesis and respiration, and the other changes recorded in our chapter devoted to that particular subject: the property of *conduction*, or power to transport substances in definite paths through itself, including absorption, transfer, and excretion: the property of *growth*, or power to incorporate new material and to increase in size at special places: the property of *division*, or power to separate portions of its own substance, the basis of reproduction: the property of *mobility*, or power to cause definite movements of its own substance, the basis of protoplasmic streaming and locomotion: the property of *irritability* (sensitivity), or power to respond advantageously to various stimuli. This enumeration of the physiological properties of protoplasm reads like the table of contents of a book on physiology,—and it ought to, because physiology is nothing else than a study of the properties of protoplasm. And here is a point of importance. Just as the physical properties of any substance are believed to reside in certain ultimate structural units, which are the smallest portions into which that substance can be divided and still retain those properties,

and which units in this case are the molecules, and just as the chemical properties are supposed to reside in their ultimate units, in this case the atoms,—so the vital properties must be supposed to reside in some kind of units distinctively their own. These units, obviously, must be larger than the molecules and made up of organized aggregates thereof. They have been called by various names, notably plasomen, (in the singular, plasom), and are probably identical with the micellæ of which we shall have much to say in the chapter on Absorption. All substances are made up of atoms and molecules; protoplasm alone is made up of atoms, molecules and plasomen. And the reader will observe, by the way, that the very conception of the plasom involves the idea of a distinctive protoplasmic main substance, and constitutes indeed, an additional reason for believing in the existence thereof.

As one views the various physical features of protoplasm, and thinks of the remarkable things it can do, he cannot but wonder at the discrepancy between its aspect and its accomplishments. For protoplasm is one of the most insignificant in appearance of all substances, yet secures the most wonderful of all results. For has it not built the whole plant and animal world, culminating in man with his powers of thought? Yet this discrepancy between promise and performance is not without parallel in our human experience. If some stranger from far away space, where all things are differently done, were to visit this earth and be shown the multifarious works of man's hands, and were afterwards to have man pointed out as their maker, he would doubtless exclaim in astonishment;—"How can a creature so small build these cloud-cleaving towers a hundred times loftier than himself, or these huge leviathans of steamships ten thousand times bigger than he: or how can a thing so weak raise pyramids so ponderously colossal: or one so slow of foot drive such fleet-flying engines: or one with hands so soft bore tunnels through miles of solid rock?" Man gives no suggestion in his appearance of the nature of the power whereby he does these things, for that lies not in

his visible body but his invisible mind, which enables him to plan and make use of tools, and harness the restless forces of nature. So, we can only suppose that the physically-insignificant protoplasm accomplishes its results by some analogous power. Indeed, I venture for my part to believe that all protoplasm can think,—not mind-thought it is true, for that appears to belong only to man, but body-thought of which the mind is unconscious. Or the matter may better be stated in this way, that man's thought is but the conscious form of a principle which exists unconsciously through all living substance. All protoplasm thinks, but only the portion thereof in man's brain is aware that it thinks. However this may be, there is one thing that is plain;—man's is not the only protoplasm which makes use of tools, and compels the forces of nature to do its work, in evidence whereof let the reader observe, for example, what is said in this book about enzymes, and the dissemination of seeds.

We must here turn back for a moment to the chemistry of protoplasm in order to notice a matter important to an understanding of the relations of the substance to the external world. The chemical complexity and instability of protoplasm render it extremely sensitive to the effects of external influences, which act upon it in three different ways. First, if strong enough, they act upon it *forcibly*, precisely as upon any other substance of comparable sort, and quite without reference to whether it is living or not. Thus, heat burns it; pressure crushes it; and some chemicals dissolve it. Second, the forces when too weak to exert any forcible effects, can yet act *inductively* to promote, or to check, some of the processes in progress in the complicated chemical laboratory which the living protoplasm actually is, and thereby may produce a profound effect upon the behavior of the plant as a whole. Thus heat, in a degree far too low to injure the protoplasm, promotes the activity of those physical and chemical reactions which underlie the streaming, nutrition, growth and other activities of protoplasm; and this explains why protoplasm

streams faster, and plants grow better, in warmth than in cold. Light acts analogously on the cell-contents, and one of the results is the brilliant redness of autumn coloration. In some cases the external factors, especially some chemical substances, act repressively on the processes, which explains the action of anæsthetics. Third, the factors, when far too weak to exert even an inductive effect can act in a far more remarkable and consequential manner, for they can then serve as guides, or stimuli, in response to which the protoplasm can send its parts into positions found by past experience to be best for the performance of its functions or avoidance of dangers. Thus, light far too weak to be directly useful or injurious to the plant yet serves as a guide whereby stems can grow towards it, leaves across it, and roots away from it, those positions being the most advantageous for the performance of their particular functions. And innumerable other cases of this kind are known, of such interest and importance, however, that they must receive a chapter all to themselves under their proper physiological name of *Irritability*. It is enough for our purpose at present to make clear the existence of the three-kind relation between protoplasmic activity and the external world.

One does not go far with his studies upon protoplasm before he begins to take thought of its origin. In one way the problem is simple enough, for all of the protoplasm familiar to us originates obviously in only one way,—by growth and division from other protoplasm through reproduction. It is not so long since even scientific men held the contrary belief, still widely persistent among uneducated folk, that low forms of life could originate anew in slime or other fermentable masses; but later experimental studies, chiefly led by the great Frenchman Pasteur, have shown that in all such cases living germs are present, while if precautions are taken to kill all germs by heat or suitable poisons, then no life appears. Every known case of apparent spontaneous generation having thus been investigated and disproved, we infer that probably it does not now occur in our

world, and that all protoplasm nowadays originates from pre-existent protoplasm through reproduction. This much is easy. But when we try to trace back the continuously-reproducing chain to its very first origin in time, we come soon to the limits of our knowledge. Some philosophers have suggested that the germs of life were first brought to the earth in meteorites from other planets; but this merely sets back the difficulty one stage and does not remove it. Another explanation, which seems to be that most commonly assumed by scientific men, places its origin in spontaneous generation at some time in the earth's history when the favorable combination of material and energy happened to occur. Obviously, such a combination ought to be repeatable experimentally; and it is upon this assumption that many learned men, from astrologers of old to physiologists now with us, have sought, though in vain, to make protoplasm anew in the flasks of their laboratories. There is, however, a third explanation which I have already suggested in an earlier chapter,—namely, that the protoplasm known to us did not originate in its present form, but is evolved or descended from a simpler substance adapted chemically to the higher (or lower) temperatures which formerly prevailed on the earth, while that substance in turn was evolved from a still simpler, and so on backwards to a beginning cotemporaneous with that of inorganic matter itself. This view I hold to be the most reasonable and probable.

But, after all, the most impressive and important thing about protoplasm is its power to build those great and elaborate structures which we call plants and animals. For, structurally considered, a plant or an animal is nothing other than a mass of soft protoplasm which climbs aloft and reaches outward into the form of the plant or the animal, building itself meantime a skeleton for the support of its helplessly-weak substance. Now, in building these organisms, the protoplasm never exhibits the character of a continuous and homogeneous mass, but always separates partially into tiny structural units called cells, which are

mostly too small to be seen by the naked eye, but which appear prominently in every magnified view of any part of any animal or plant, as witness, for example, figures 2, 53, 73, 141, in this book. We must therefore consider with some care the construction of these cells,—a subject of the foremost importance in Biology.

The hairs earlier studied are fairly typical cells except that

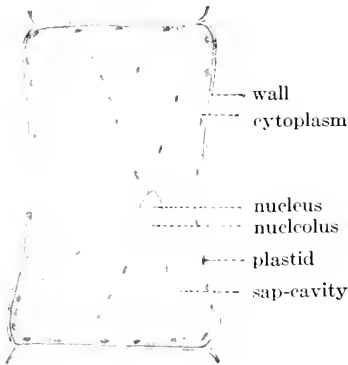


FIG. 47.—An optical section, highly magnified, through a cell of the Squash, showing all the parts of a typical cell.

they are partially isolated from their neighbors instead of deeply embedded among them, and are elongated rather than rounded. If one observes an example of these hairs, e. g., that of the Squash (figure 47), he is likely to notice first the clear-cut containing *wall*, inside of which comes a complete lining of soft gray-granular protoplasm, very likely in slow streaming motion, with threads of the same extending across the cell at various angles. This soft protoplasm is called *cytoplasm*. Some-

where within it, though not carried in its streaming, lies a denser, rounded granular structure, also living protoplasm, the *nucleus*, which often exhibits a round mass within itself,—the *nucleolus*. In the cytoplasm lie also certain scattered granules (not especially distinct, however, in these hairs), which are larger than food granules and otherwise unlike them; these too, are living protoplasm, and are called *plastids*. Finally, within the cytoplasm appear large open spaces, various in size and number but commonly merged to a single very large one in old cells; though apparently empty, they really are filled with a watery sap and therefore are known as *sap-cavities*. These parts, wall, cytoplasm, nucleus, plastids, sap-cavities, are the prominent parts of typical plant cells, and the great majority of cells possess them all. We can accordingly construct a conventionalized cell showing these

parts in their natural relations and fully-developed condition; and such a cell is represented herewith (figure 48).

We should now examine a bit further these parts of the cell and their meaning.

The wall is composed of a firm-elastic transparent substance called cellulose, whose chemistry is treated in the chapter on Metabolism. It is built by the cytoplasm, which, in suitable places, is supposed to lay down within itself tiny masses (bricks, as it were) called micellæ, of cellulose, and continues to add to

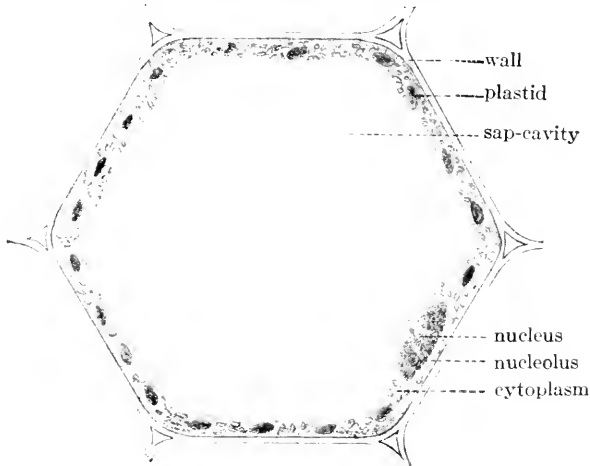


FIG. 48.—An optical section through a conventionalized complete plant cell.

their number until they accumulate to nearly a solid mass. I say "nearly," because apparently there always are left between these micellæ thin sheets of protoplasm, like the mortar between bricks, so long as the cells are alive, though they are withdrawn when the cell has reached full maturity. It is these thin sheets of cytoplasm, too thin to be visible even to the strongest microscope, which keep the wall alive, as it were, so that it can become enlarged, split, chemically changed, absorbed in places, and in other ways altered, a good while after its formation. But except for such subsequent alterations, the walls of contiguous cells re-

main parts of one continuous mass. As to the function of the wall, that is perfectly obvious,—it is the skeleton of the cell, the mechanical support for the gelatinous cytoplasm, which has not enough firmness of texture to raise itself unaided an inch from the ground. It is interesting to let the imagination picture what would happen to the loftiest and stateliest tree, if, by some subtle chemical magic the cell-walls could be suddenly re-converted back to the gases from which they were made; the protoplasm would simply collapse to the ground as a shower of slime.

The reader at this point will observe how different in principle is the construction of the skeleton in plants as compared with animals. In animals, in conformity with the much higher degree of division of labor in their parts, certain cells are set aside to build the skeleton for the entire individual, either a deeply-buried bony skeleton as in man, or a surface skeleton of lime or horn as in crabs and insects; while all of the remainder of their cells are without hard walls and devoted to other functions. In plants, however, every individual cell has a wall around itself, and the collective mass of these walls makes up the skeleton of the plant. Such a mass of cell-walls, however, by no means represents, though one might naturally think so, a lot of originally separate walls fused together. Observation of growing parts always shows (figure 101) that the new walls formed between dividing cells are thrown across the protoplasm as single solid structures, which may or may not in time become split and divided between the two cells. Thus the cell-wall system of a plant is one single mass from the beginning, just as is the wall mass of a building; and the protoplasm lives in cavities therein, precisely as people live in the rooms of a house they have built. The reason for the difference in the method of skeleton building by animals and plants is plain enough upon reflection. The method of animals permits jointing and muscular movement, as it must in order to allow the most fundamental of all animal activities,—locomotion in search of food; the method of plants

permits only a fixed position, which, however, is sufficient, since the materials for making their food are brought to them in the general circulation of nature. And these conclusions are all the more confirmed by the seeming exceptions, for some plants swim or creep freely about (e. g., swimming spores of Algæ and Slime Molds) in a very animal-like manner; but in these cases they lack the firm cellulose wall distinctive of plants. But although the skeletons of animals and plants differ, their protoplasm does not, for in all essentials the protoplasm of plants and animals is alike.

This brief account of the plant skeleton has touched incidentally on a matter which must now receive some further attention. As the student soon learns when he studies many cells with his microscope, they differ immensely in shape and in the thickness and composition of their walls, to such a degree indeed as to make them apparently too complex for analysis. Yet here, as elsewhere, further study gradually crystallizes out the essentials, when it appears that after all only a few ground forms exist, and then only in correlation with definite functions or influences; while all of the others are simply variations and combinations of these. As to the shapes of cells, the simplest of all, and the one to which all others tend to revert, is the sphere, that being the mathematical form in which the most contents can be comprised within the least wall. This shape, with the wall a spherical shell, is actually realized in those cells which float freely in water or air, as do the spores of many Algæ and Molds, and some pollen grains; and this shape may become elongated to ellipsoid and ovoid forms under particular conditions (figure 49, 94, 108). Where such cells occur inside the tissues of plants, however, and hence are hard pressed by their numerous neighbors, the spherical shape becomes necessarily modified to many-sided (polyhedral) or faceted; and this shape is approximately realized in many storage tissues of plants, where it comes measurably near to that twelve-faced shape which always results when equal-sized spheres are forced together by pressure (figure 49, 72). There is also some

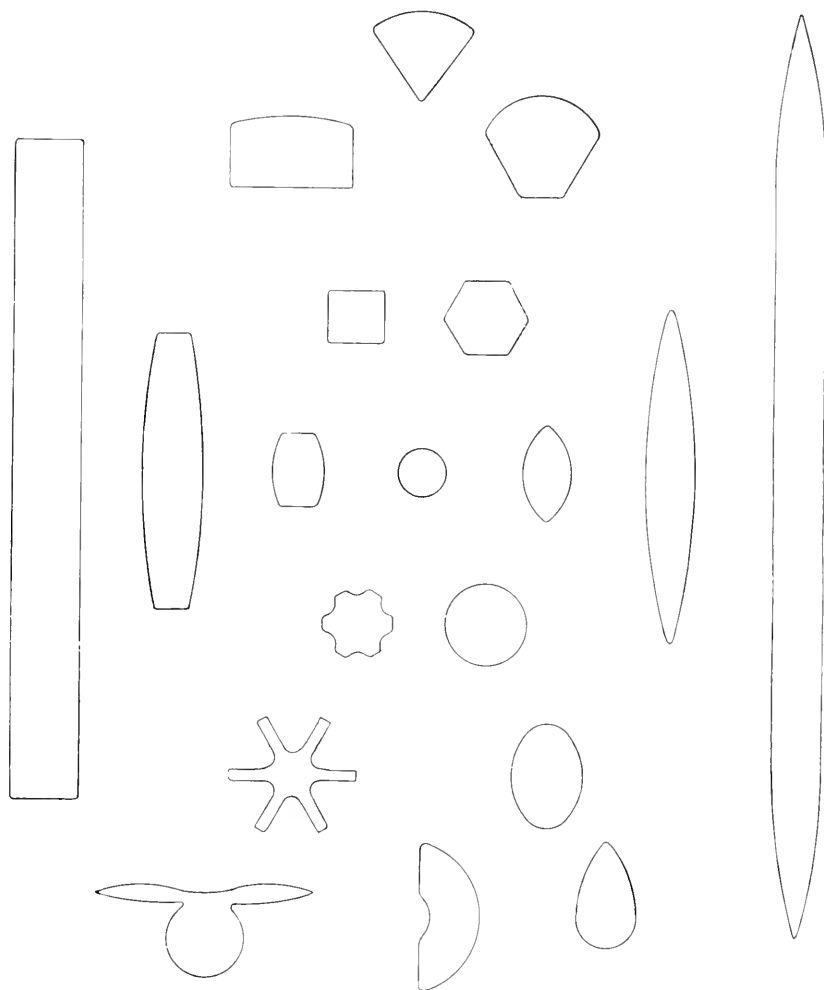


FIG. 49.—Generalized drawings of optical sections through the principal forms of plant cells, all of which are derivable by differential growth from the spherical form in the center.

approach to this shape in the green cells of leaves, (figure 2), although here a modification is introduced by the need for concentrating the chlorophyll grains towards the best-lighted surface, for which a cylindrical shape is the best (Plate I, *B*), or else

by the need for the presence of very large air spaces, for which a branching, or stellate form is most suitable. The polyhedral shape due to mutual pressures, in conjunction with the formation of new walls as plates thrown across cells from one wall to the other, results in the formation of cubical cells in growing points (figures 49, 53, 139 *C D*), or elongations thereof to four-sided prisms, as in the cambium cells, which form the growth zone between the bark and the wood in most trees (figure 139 *B*). In other cases the cells become flattened to tabular shapes, as in epidermis and cork (figures 2, 49); where the function of these cells as the protective skin of the plant obviously requires such a shape. Again, the spherical or polyhedral shape becomes elongated to a cylindrical or prismatic form where the function requires much length, as it does in the conduction of liquids through the plant; and it is a line of such cylindrical cells, thrown into a tube by absorption of the intermediate walls, which constitutes the water-carrying ducts, (figures 49, 53, 54 *C*, 72) while the food-carrying sieve-tubes are made in analogous manner (figure 72). Or, the elongation takes place at two opposite points, resulting in a spindle or fiber form, which is developed wherever tensile strength for resistance to strains is required (figures 49, 50 *d*). Finally, through the intermediation of a more active growth at several points, the spherical or polyhedral shape becomes modified to a branching, or even a star-shaped form; and this occurs in the spongy cells of green leaves as a means of providing generous inter-cellular air spaces, (figure 2, and *B* of Plate I): in some Rushes as a part of their very flexible pith (figure 49): and in certain excretion cells of Water-plants as a means of providing more wall for the deposition of waste crystals. Thus these few ground forms,—the fundamental sphere, with its lines of modification, shown by figure 49,—viz., ellipsoid-ovoid, polyhedral, tabular, cylindrical-tubular, spindle-fibroid, and branched-stellate, represent the mathematical possibilities upon which the cells can play, but by which they are also bound in their adaptations to

their various functions; and although innumerable forms occur not directly referable to any of these types, they are nevertheless only modifications and combinations thereof.

The cell-wall, however, is modifiable not only in shape, but also in thickness. Ordinarily very thin, it can become thickened to any degree required by function, even to the almost total obliteration of the cell cavity, as happens in some fibers (figure 50, *d*), where the need for additional strength is perfectly plain: in cells

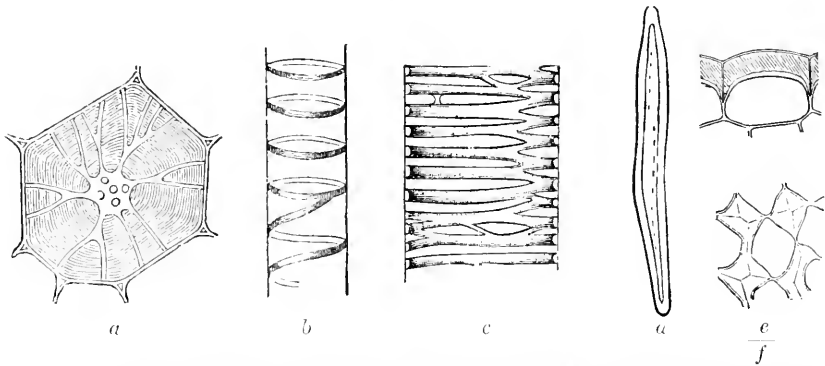


FIG. 50.—Various methods of adaptive thickening of cell-walls; further particulars in text. (All copied from von Mohl's classical work on the Plant Cell, 1851.)

devoted to the protection of something, notably in the shell of a nut (figure 50, *a*): and in cases where the formation of a thickened wall is a means of storing additional food, as in the Ivory Palm and Date (figure 36). A similar thickening is used also as a protection to the resting spores of Molds, Yeasts and disease germs, which thereby are so completely protected against all hostile outside influences that they can float uninjured for months in the air, and germinate finally in the most unexpected and least desired of places. In some cases the thickening is not at all uniform, but takes the form of rings and spirals, as in young ducts which they help to keep open while the walls are still very flexible (figure 50, *b*); or it makes an elaborate fretwork of strengthening ridges surrounding thin areas easily pervious to water, as in older ducts (figure 50, *c*); or it occurs upon one wall only, as

is frequently the case with protective epidermal cells (figure 50, *e*); or it affects only the angles, in some cells which combine water-storage with strengthening (figure 50, *f*); and it takes various other forms too many to mention.

Furthermore, the composition of the wall is alterable both physically and chemically. Cellulose is a very elastic substance, and where greater stiffness than it can afford must be had, the wall becomes penetrated by the far stiffer substance lignin; and lignified walls are wood. Both cellulose and lignin, however, allow ready passage of water, and where that would be a danger, as at surfaces of plants which grow in dry air, the wall is made waterproof by the formation all through its texture of a water-repelling substance, called cutin or suberin; and such is the case with the epidermis and cork which form the skin of plants. In other cases the wall softens to mucilage on the access of water, as in Flax seeds, though the reason thereof is not perfectly clear; and there are yet other such modifications of more special character and meaning.

It is thus plain that cell-walls are well-nigh indefinitely plastic in shape, thickening, and composition, while, moreover, any and all of these features can be combined in various ways and degrees in accordance with the particular needs or functions concerned. Furthermore, the cells are rarely isolated; but commonly coöperate in large masses of similar function called tissues. Masses of tissues coöperating in function, and mutually adjusted to perform their work to the common advantage, form organs, and organs make up the plant.

There remains one other matter of importance about the wall. Although, at first sight, it seems to shut off completely the protoplasm of each cell from that of its neighbors, minute observation exhibits the presence of definite thin places perforated by very fine pores which permit the passage of tiny threads of living protoplasm from one cell to another (figure 51). This continuity of protoplasm from cell to cell has been found in every part of the

plant, where it has been sought; and it seems clear that every living cell is thus in communication with its neighbors, and therefore with every other living cell of the plant. Thus the protoplasm though partially, is not wholly, separated into cellular masses, and is, after all, for any individual plant a single great continuous sheet.

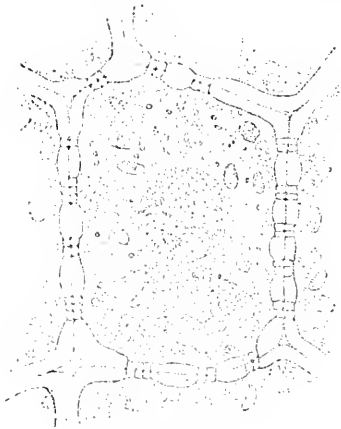


FIG. 51.—An ordinary cell specially treated to show the thin threads of protoplasm extending through the wall to connect its protoplasm with that of its neighbors. (Copied from Strasburger's *Lehrbuch*).

There is every reason to believe that impulses of different kinds can be transmitted from cell to cell through these threads, which, therefore, take the place in part of the nerve system of animals. This helps us to understand how it is that the plant can act as a physiological unit: how the different parts of a plant can be kept in harmonious coöperation: and how stimuli applied at one part of a plant, can produce their effects at a considerable distance.

Thus much for the wall of the cell, to which, it may seem to the reader, I have devoted a disproportionate space and attention. Yet while vastly less important than the protoplasm, the solidity, prominence, and relative permanence of the walls makes them far more accessible to study,—to such a degree indeed that our conceptions of cellular structure center much more largely around the walls than the protoplasm.* This, however, is less unfortu-

* The inconspicuousness of the living protoplasm of plants in comparison with the prominence of the walls it builds finds striking exemplification in the history of their discovery; for the mass of the walls was well described, and their cavities were named *cells*, by Robert Hooke as early as 1667, while they were elaborately described and beautifully pictured only a few years later, 1672-1682, in the fine books of Grew and Malpighi. But the protoplasm was not recognized at all as a constituent of cells until over a century and a half later, and was only first adequately described and named by von Mohl, in 1844.

Here is Hooke's sentence, of 1667, in which cells were first named. He is describ-

nate than it might seem, because the constitution of the walls is so closely interlocked with the functions of the cells that from the one we can infer much as to the other.

Passing now to the cytoplasm we can briefly dismiss it, for, being the typical protoplasm, it has already been fully described in the earlier part of this chapter. It is the working body of the cell, concerned with its nutrition, construction, etc., and the streaming movements are probably concerned with the transportation of substances through the cell, a view sustained by the fact that the streaming is most active in general in the cells which are largest. The cytoplasm does not differ particularly in appearance in different cells, excepting that it is more fluid in some and more solid in others. One point of present interest about it, however, is this, that just at this time of writing, certain newly found tiny bodies within it, called mitochondria, or *chondriosomes* are attracting much attention, and may prove to be very important.

We come next to the nucleus of the cell. It consists of living

ing the appearance presented by a thin section of cork placed under his microscope. "I could exceeding plainly perceive it to be all perforated and porous, much like a Honey-comb, but that the pores of it were not regular; yet it was not unlike a Honey-comb in these particulars."

First, in that it had a very little solid substance, in comparison of the empty cavity that was contain'd between, . . . for the *Interstitia*, or walls (as I may so call them) or partitions of those pores were near as thin in proportion to their pores, as those thin films of Wax in a Honey-comb (which enclose and constitute the *sextangular cells*) are to theirs.

Next, in that these pores, or cells, were not very deep, but consisted of a great many little Boxes, separated out of one continued long pore, by certain *Diaphragms*, . . .

I no sooner discern'd these (which were indeed the first *microscopical* pores I ever saw, and perhaps, that were ever seen, for I had not met with any Writer or Person, that had made any mention of them before this)." . . . (Robert Hooke, *Micrographia*, 1665, 113.)

Here is von Mohl's sentence, of 1844, in which protoplasm was first named:—"So mag es wohl gerechtfertigt sein, wenn ich zur Bezeichnung dieser Substanz eine auf diese physiologische Function sich beziehende Benennung in dem Worte *Protoplasma* vorschlage." (*Botanische Zeitung*, 1844, page 273); or, in translation, "Accordingly it may be justifiable if for designating this substance I propose an appellation having reference to this physiological function, namely, the word Protoplasm."

protoplasm, denser than the cytoplasm, and different, somewhat, chemically. It varies comparatively little in appearance in different cells, and ordinarily exhibits no particular structure; but when the cells are dividing or reproducing, then a definite number of rod-shaped structures become differentiated and perform remarkable manœuvres which we shall later consider in the suitable place along with reproduction (figure 101). These rods, called chromosomes, are the seat of the controlling power of heredity, and thus guide the constructive work of the cytoplasm in growth. The nucleus, therefore, bears to the cytoplasm a relation suggestive of that of the brain to the body. Indeed, the resemblance may extend pretty far, since there are those who maintain that heredity in the chromosomes is substantially the same thing as memory in the brain. But I hope the reader will not therefore call the nucleus the brain of the cell, for it isn't. As to the nucleolus, that is irregular in its appearance, and probably represents a reserve of chemical substance for use in the growth of the chromosomes.

The plastids, likewise, are living protoplasm, and are present in all cells of the typical plants, though sometimes they are inconspicuous. Thus, it is the plastids which hold the green color in leaf-cells, where they are already well known to the reader as chlorophyll grains, called also chloroplastids. In other cells, of some fruits, such as the familiar Jerusalem Cherry, they contain yellow or orange colors (chromoplastids), thus aiding to make the fruits conspicuous. And in other cells yet, especially in the storage parts of plants, they remain colorless and are called leucoplastids, but perform the remarkable and indispensable function of converting sugar to starch. It is, indeed, a fact of the greatest interest about these leucoplastids, that they and the homologous chloroplastids comprise the only places in nature, either within the plant or outside of it, where starch is known to be made. Starch is one of the substances which the chemist has not yet been able to make in his laboratory.

The sap-cavities are as simple in structure as they look. In very young cells they are absent, as a later picture illustrates (figure 129); but in those that are older little rifts appear in the cytoplasm and gradually grow larger until finally, in the fully mature cell, they become merged into a single cavity of very large size, as the figure of the conventionalized cell clearly shows (figure 48). This cavity is filled with water in which sugar and other useful substances are dissolved. It thus represents a storehouse of useful materials, but serves secondary functions, likewise, in pressing the cytoplasm against the wall, and in aiding growth, by methods which will later be described in the suitable chapters.

It is of interest to note that not only does new protoplasm in general originate only from preëxisting protoplasm, but new cells originate only from cells, nuclei from nuclei, and plastids from plastids; while the same thing has been claimed even for cell-wall and sap-cavities, or rather for the part of the cytoplasm which forms them, though here the evidence is not conclusive.

The question is now appropriate, why does protoplasm separate into cells at all, and what makes them of such minute size as they are? It is sometimes assumed that the plant-structure becomes cut up into cells in order to provide structural units of convenient size and form, after the manner of the bricks of the builder; but the analogy is wholly misleading, since the skeleton of plants is not built at all from originally separate units, as brick buildings are, but rather from a continuous mass of cell-wall substance comparable with the cement construction now coming into use. Another explanation maintains that each nucleus can control only a limited quantity of cytoplasm; and thus are established certain administrative units between which, naturally enough, the walls are built,—the resultant being cells. As to the reasons why their sizes are so small as to require a microscope to show them at all, we have again a few guesses, but no

exact knowledge. Possibly the chromosomes need a certain size in order to perform their functions; this would establish the size of the nucleus, and hence (on the explanation above noted) of the cell. Another explanation rests on a mathematical basis. We may assume that the typical cell is a sphere filled solidly with protoplasm. When a sphere enlarges in size, its bulk increases much faster than its surface, the bulk increasing as the cube of its diameter and the surface as the square thereof. Obviously it is through this surface that the spherical cell must absorb the oxygen for the respiration of the entire bulk of its protoplasm; it is therefore quite evident that there must be a certain size of the cell in which the surface is just sufficient to aërate the bulk of protoplasm within,—and that size would determine the average cell size. If the cell were to grow larger its surface would not suffice to aërate the bulk, while if smaller the surface would be needlessly great. In a general way this conclusion is sustained by the fact that where conditions for respiration are harder the cells are smaller, and vice versa. Moreover, the very largest cells occur in places well situated for aëration, and besides, possess accessory arrangements,—viz., the flattening of the protoplasm in a thin layer against the wall (figure 45), and protoplasmic streaming,—which aid to that end. These features prevail in the hair cells already observed by the reader, and in consequence those cells become large enough to be visible to the eye without the aid of a lens. In general, therefore, it does seem true that the relation of bulk to surface in a solid as affecting respiration is one of the principal factors, if not indeed the principal one, in making the size of cells what it is.

In comparing the functions of the cells of plants with those in animals, it soon becomes obvious that plant cells exhibit a far lower degree of division of labor; and this involves a remarkable consequence. It seems to be a fact that when protoplasm continues to perform a single function for long periods of time, as it does in the highly-specialized organs of the animal body, it grows

stronger and stronger and works better and better up to a certain culminating level, beyond which it tends to decline, and finally to cease work altogether. It is probable that the decline and cessation of work is dependent upon purely physical causes, somewhat as a bar of metal when too often bent, becomes weakened and broken at last; but in this peculiarity of protoplasm we find an explanation for the cycle of youth, maturity, old age and death. When, however, the protoplasm can periodically alter its location, habits, or functions,—can re-melt itself, so to speak,—it renews its youth thereby, and can continue its vigor without limit, thus becoming potentially immortal. In this fact is found the explanation of the benefit wrought by a change of scene or occupation, or a vacation, upon ourselves, though the effect is here limited; and if a way could be found to affect our protoplasm more profoundly,—to make it mix itself up periodically, even within the limits of the same cell,—then, it seems likely, man would have discovered the long-sought elixir of life and the secret of perpetual youth. This in fact is the case in full degree in simple plants like Bacteria. Each of these is made of one cell, and when it reaches full size divides into two, each of which grows up and divides again, and so on without limit, in perennial change, vigor, and youth. A similar rejuvenation takes place in sexual reproduction, when the protoplasm of two individuals mingles together in fertilization. Now, the higher plants possess no organs at all in which the protoplasm continues to work within the same cells throughout the life of the individual, but, as our chapter on growth will abundantly illustrate, the protoplasm is continually moving outward and onward into newly forming buds, leaves, roots, and stems; and this removal permits it to renew its youth perennially. Therefore plants should never grow old from internal causes, in the way that animals do,—and in fact they do not, the exception presented by annuals being only apparent and not real. Even the greatest trees continue to form new leaves and roots with unabated vigor until they are brought

to their death by external causes, chiefly connected with the large size they attain.

The manifestations of life, wherever we know them, are associated closely with constant changes of matter and energy, especially with respiration. But there is a case in which all of these processes seem suspended, for our most delicate methods of research fail to demonstrate them, and that is in resting structures such as seeds, Resurrection plants, and some low animals. Not only can dry seeds retain their vitality for a great many years, but in that condition they can withstand without injury a temperature above boiling point, or even two hundred degrees below freezing point. The question is important whether the usual changes are proceeding in these seeds, but too slowly to be measured, or whether all processes stop and the vitality is really suspended. The truth is not as yet known, but it is to be noted that there is no logical difficulty in supposing that all of the processes may slow down to a stop without any derangement of machinery, precisely as an engine is stopped for the night simply by withholding the steam, leaving it all ready to start once more in the morning.

When this chapter was finished down to this point, it was handed like all of the others to a critic for judgment. And this is in substance the comment with which it came back. "The chapter is clear enough in its statements, and appears to cover the subject, but somehow it leaves you with a very unsatisfied feeling." This opinion I take for a very high compliment, since it shows that my chapter reflects precisely the scientific situation of the subject.

CHAPTER VII

THE WAYS IN WHICH PLANTS DRAW INTO THEMSELVES THE VARIOUS MATERIALS THEY NEED

Absorption; Roots



IN the preceding chapters we have traced pretty fully the principal processes occurring within the bodies of plants. But as yet we have taken no thought of the ways in which plants absorb the various materials they need from outside; and this is the inquiry which now lies before us. I give the reader fair warning that the subject will lead us perforce into distant, unfamiliar, and recondite matters; but their study will have the advantage of illuminating a good many things besides absorption by plants.

Of all the substances absorbed by plants, the foremost is water, which not only makes up a great part of plant substance, but is also indispensable for various physical and chemical uses. This water is absorbed, as everybody knows, through the roots; but the fact is less familiar that the absorption takes place exclusively through the young white terminal parts. Upon these, accordingly, we now center our attention. They can be studied most easily, and without obscuration by adherent soil particles, in young roots obtained by the germination of seeds in flower-pot saucers kept shaded and wet. From such specimens it appears that young roots as a whole are remarkably alike, and possess several features in common,—viz., a slender white shaft with a yellowish tip, and a diaphanous garment of delicate radiating hairs,—features which are shown very well, except for the color, in the seedling of Mustard pictured herewith (figure 52). If

one centers observation more exactly on these hairs, he will see that nearest the tip they are plainly just forming, while farther back they are progressively longer, until a maximum is reached, behind which they are obviously withering and dying. Evidently the single hairs have each their little day and pass, while the zone as a whole moves forward in perpetual youth, *pari passu* with the advancing tip of the root. These hairs are of first importance to our immediate subject, for they are the active water-absorbing parts of the roots.



FIG. 52.—A seedling of mustard grown in dark saturated air; natural size.

Thus much can be seen with the eye and a lens, but hardly anything more. If, however, one cuts a thin section through the apex and along the central axis of a root, and magnifies this section with the microscope, he will have before him an arrangement like that of our picture (figure 53), with which it will be desirable to compare the generalized section of figure 139 C. At the tip is the *root-cap*, a cluster of cells which, continually renewed from behind, acts as a protection to the delicate tip in its passage through the rough and abrading soil; just behind lies a prominent focal center, the *growing point*, whose closely-packed cells are so densely filled with protoplasm that the characteristic yellowish color of that substance shows through to the outside; while radiating back from the growing point run long lines of cells which gradually merge into the differentiated tissues of the older root. These latter tissues, so far as they concern our immediate subject of absorption, are shown generalized in figure 54, D. Of the lines of cells, a few in the center constitute the pith, outside of which lie the long lines of water-tubes, or ducts, readily identified by their distinctive spiral markings. These ducts contain water, but, contrary to what one would expect, are otherwise empty tubes, possessing no living protoplasm after once they are formed; and they run in continuous strands from the tips of the roots all

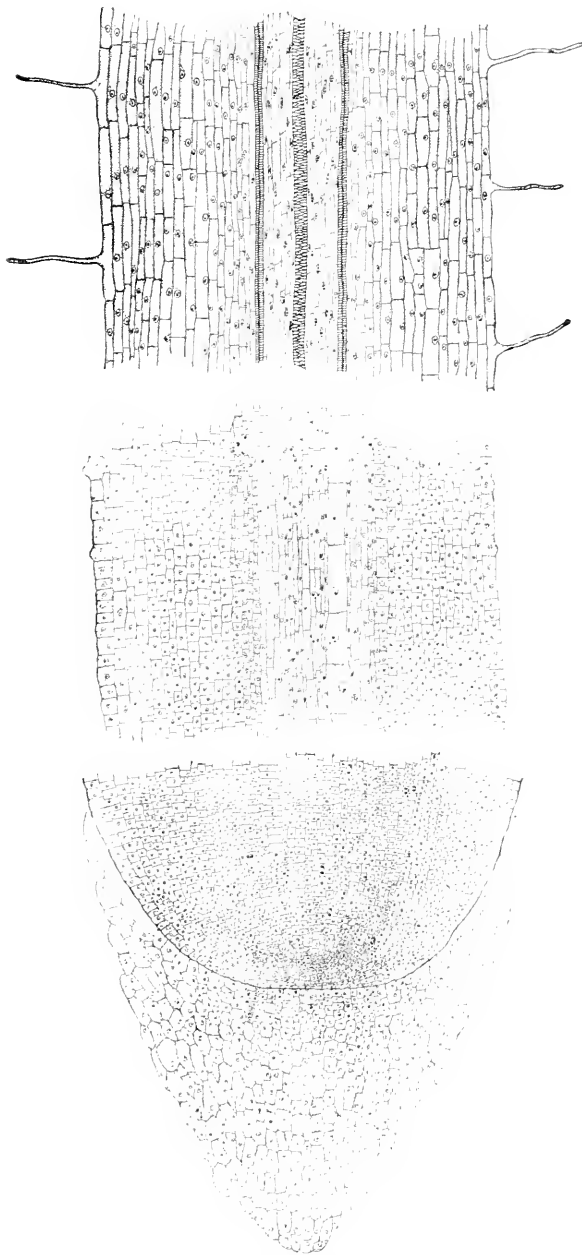
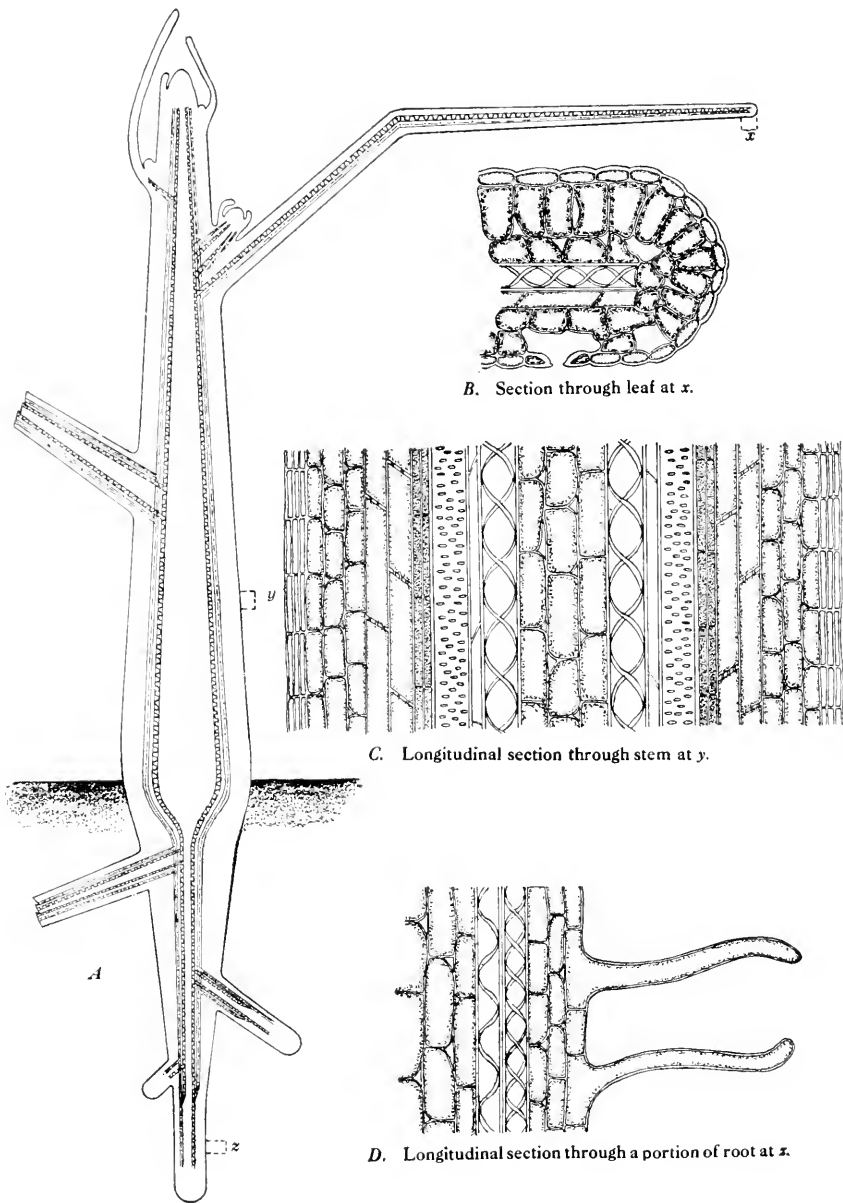


FIG. 53.—Typical parts of a section drawn lengthwise, cell for cell, through a young root of Corn. The entire section is not presented because its length would be much too great for the page. The tip portion is magnified more than the others.



B. Section through leaf at *x*.

C. Longitudinal section through stem at *y*.

D. Longitudinal section through a portion of root at *x*.

FIG. 54.—Generalized drawings illustrating the absorbing and conducting systems of the plant.

through the stems to the leaves, as shown very clearly in the conventionalized plant of figure 54, A. Outside of the ducts lie some rows of rounded-elongated cortical cells, each of which retains its lining of protoplasm and is shown by tests to contain a solution of sugar. Finally, outside of all lies the single thin line of epidermal cells, which display a very striking feature, viz., a great many are prolonged into slender cylindrical closed tubes, which are obviously identical with the root hairs already observed in the young living roots; and each hair is lined by living protoplasm and, as shown by suitable tests, contains a solution of sugar. Now the structures important from the view of water-absorption are the ducts, the cortical cells, and the root hairs; and these parts constitute the water-absorbing machine. And this machine, if reduced to a single cell of each kind, would be constructed somewhat as suggested by figure 55.

We turn now to the forces concerned in absorption. Most people, if questioned, would doubtless express the belief that roots suck up water in much the same manner that a wick sucks up oil, that is, by the power, called in physics *capillarity*,—the same which takes liquids up fine tubes. Indeed this was once the belief of botanists themselves, as witnessed by their former use of the term “spongiolæ,” that is “little

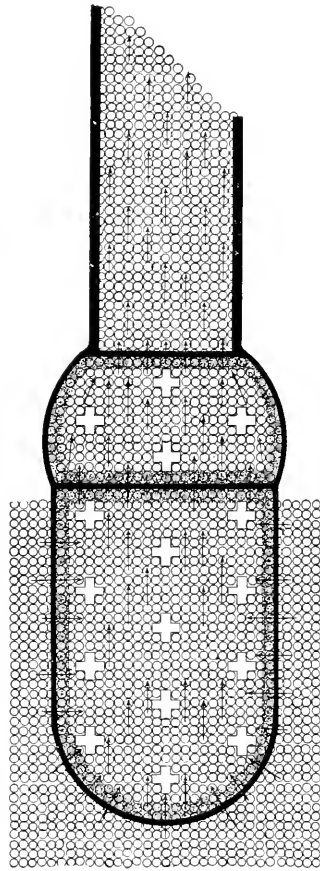


FIG. 55.—A diagram of the construction of the water-absorbing machine, as it would appear if reduced to a single root hair, cortical cell, and duct. Protoplasm is shaded; circles are water; crosses are sugar; the arrows show direction of movement. Magnification as in Fig. 6.

sponge," for the tip of the root, which was supposed to soak up water and pass it on to the ducts. Later it was found that the water enters chiefly through the hairs. But in these the conditions for capillarity are absent; for capillarity requires openings, and the hair walls contain none that even the most powerful microscopes can detect. The problem is, therefore, to explain an absorption of water through membranes that are imperforate, or solid, and through protoplasm-lined and sugar-holding cells into protoplasm-less and sugar-less ducts. But the very mention of absorption into sugar solutions through imperforate membranes immediately suggests a direction for our further inquiry, since it recalls a mode of absorption very well known in physics, and associated with those very conditions, viz., *Osmosis*.

So important is this subject of osmosis to an understanding not only of absorption of water by plants, but of many other notable phenomena as well, that the reader ought really to make its more intimate personal acquaintance. This he can do by aid of the following experiment, which is one familiar to all workers with plant physiology. Over the end of a large glass tube is tied firmly, by means of waxed thread, a piece of soaked parchment, (preferably a cylindrical parchment cup made for the purpose) which is a physical equivalent of the wall of the root hair; into the tube is poured a solution of sugar, for which molasses, a solution ready made and conveniently colored, is excellent; then the tube is supported with the parchment in pure water, the whole arrangement being much as displayed in the accompanying picture (figure 56). A surprising result always follows, for, without the operation of any visible machinery or forces, and in a manner which to me, despite long familiarity therewith, looks always anomalous and even somewhat uncanny, the liquid rises steadily though slowly in the tube, lifting its own considerable weight, until within two or three days it has reached a height of two or three feet or more. Indeed the process can be demonstrated even more strikingly than this, for, if the parchment cup be

made very large and the glass tube very small, as is readily arranged for purposes of demonstration, the liquid will mount steadily up before the very eyes to a height of several feet. Obviously there is only one possible explanation of the rise of the liquid against gravitation,—viz., water must pass through the parch-

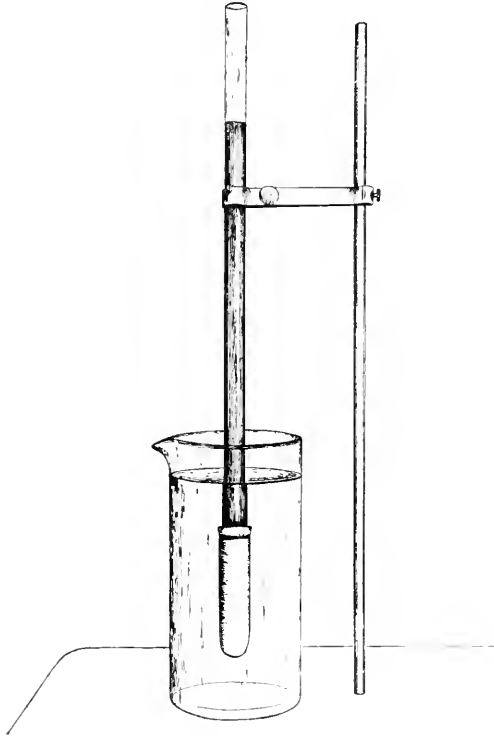


FIG. 56.—An osmoscope, using a parchment membrane; further particulars in text.

ment, and that not simply in a manner that is passive, but with a force sufficient to overcome a considerable resistance. The same result invariably follows, with a difference, however, in the rate of the ascent, no matter what solution is put inside of the tube, and follows, moreover, in case there is also a solution outside, if only the inner solution is the stronger. This is a typical example of osmosis under its simplest conditions, but it is representative of

all conditions, inside of plants and animals, as well as outside of them. It thus constitutes one of the great natural verities which may be stated as follows;—*when water and a solution, or two solutions of different strengths, are separated by a suitable membrane,*

there is always a forcible osmotic movement of liquid through the membrane from the weaker to the stronger solution. This is one of those elemental cosmical facts which the reader should fix in his mind as one of the pillars of his natural knowledge.

If, at this point, it seems to the reader that however interesting such experiments with parchment and tubes may be, they can have little to do with the processes inside of a living plant, let him take a leafy potted Begonia, Fuchsia, or Marguerite, cut everything away close down to the roots, and connect the stump with a plain glass tube like that which was used in the foregoing experiment. Then, I believe, he will change his opinion, for water always rises in the tube, though slowly, to a height of two or three feet (figure 57). There are of course plenty of

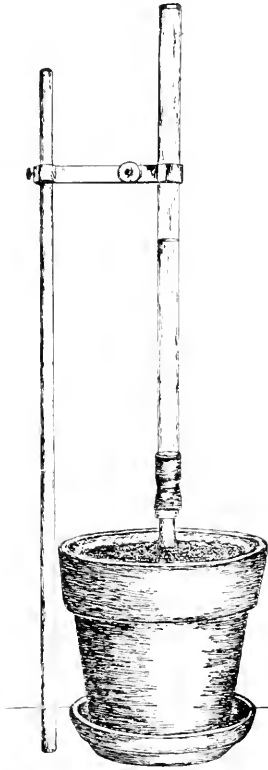


FIG. 57.—An arrangement in which the parchment cup of figure 56 is replaced by living roots.

differences in detail, but sugar-holding cup and live roots agree in the central and crucial feature that they absorb water into a sugar solution through imperforate membranes and force it up tubes against gravitation. There is no question that the primary forces are the same in both cases, and that the absorption of water by roots is osmotic.

We return for a moment to our osmoscope, for such is the name of our osmosis-exhibiting instrument. As the liquid ascends in the tube, a brown color appears in the water outside, showing that some of the molasses comes out, though of course in much smaller amount than the water which enters, else the liquid could not rise in the tube. This suggests at once the inquiry,—does the sugar in the sap of the root-hair cells also come out into the soil? It does not, as ample evidence attests. And if we seek in parchment cup and root hair for a structural difference to explain this difference in osmotic action, we can easily find it; for the hairs possess a complete lining film of living protoplasm to which there is no equivalent in the parchment cup. It is easily shown by experiment that this protoplasm really does stop the passage of sugar while permitting that of water; and this fact explains not only why no sugar passes out of the hairs into the soil, but also the equally striking phenomenon, that none passes out of the cortical cells into the ducts, for in general it is only pure water which ascends through the ducts to the leaves. Protoplasm, however, is not the only membrane of this type (which, because permeable to water but not to dissolved substance is called *semi-permeable*, in distinction from the ordinary kind which are *permeable* to both), for they can be constructed artificially from chemicals, and even laid down in a uniform film all over the interior face of the parchment cup. In this case our osmoscope becomes a very close physical duplicate of the living root hair, and likewise permits the steady absorption of water without the escape of any of the sugar whatsoever. My students have often constructed such arrangements, with results that were wholly satisfactory.

If, now, the reader will compare point by point, an osmoscope containing a semipermeable membrane, and the absorbing mechanism of the living root (which is diagrammatically represented in figure 55), he will agree that they match very closely in physical construction and operation except for one very notable difference,—namely, while the liquid which rises in the osmoscope is a mix-

ture of molasses and water, that which rises in the ducts is practically pure water. This difference, obviously, is correlated with a difference of structure, viz., in the plant the water has to pass through intermediate cells, which are wanting in the osmoscope. We have already learned why it is that the sugar does not pass with the water into the ducts (the protoplasm stops it), and our problem resolves itself into this,—how is it that the cortical cells send water into the ducts when all of the conditions seem rather to invite the absorption of water from them, exactly as the hairs absorb it from the soil? This question, I am sorry to say, I cannot yet answer, for it remains one of the unsolved problems of plant physiology, though one of the most inviting of them all. It is true, some physiological books attempt to explain it, but in all cases, so far as I have observed, either their physics is bad, or else their explanations are worded in a manner more lethal than logical. I suspect the explanation will ultimately be found in some ordinary physical or chemical processes working under control of some still unknown property of the protoplasm.

In the three or four paragraphs which follow I purpose to explain how it is that substances in solution can pass through imperforate membranes, and what are the forces which drive them. The subject involves a consideration of molecules, and things of that sort, and will require hard work from the constructive imagination. So the reader is given fair warning and may skip if he pleases, though I beg to remind him that this book makes appeal to his reason, and is an attempt to help him to share the spartan pleasures of understanding.

The most striking feature of osmotic absorption consists in the remarkable rise of a large body of liquid against gravitation without the operation of any visible forces whatsoever. Yet forces there must be, if not visible, then invisible; and accordingly we turn for the sources of the power deep within the constitution of the bodies themselves. As everybody knows, mem-

branes, water, and dissolved substances are all of them composed, according to the teaching of physics, of ultimate excessively small units, called molecules. In the solid or liquid state, the molecules are held together by a force of mutual attraction, called cohesion, analogous to the force which holds an armature to a magnet. But when heat in sufficient amount is supplied, there comes a point at which the cohesion of the molecules is suddenly overcome and replaced by an opposite tendency to spread or diffuse just as far apart as they can; and this is what constitutes a gas. The power that actuates the diffusion is heat, which, catching the tiny molecules in the swirl of the violently-vibratory ethereal waves of which it consists, imparts to them its own vigorous motion, whereby they are set swiftly darting and dancing hither and yon, bounding and rebounding energetically against one another, with a result that they work steadily outward, very much as a cargo of corks would be spread from a foundered vessel on the waves of a tempestuous sea. Familiar examples of this diffusion of gases are many,—for instance, the spread and ultimate disappearance of odors, and the penetration of cigar smoke through the house; but all gases diffuse in this manner. And here comes a curious and consequential fact about diffusion, namely, that it occurs not only in gases, but also in anything, whether solid, liquid or gaseous, when dissolved in a liquid. Examples thereof are abundant,—the gradual spread of a bit of solid dye when dropped into water: the spread of sugar through coffee or tea without stirring if only time be allowed: the spread of fertilizers evenly through soil though added in large lumps on the surface. By diffusion, also, the molasses reaches the water outside of the tube of our osmoscope. Such diffusion occurs, as it seems, because an adhesive attraction existing between the molecules of the substance and those of the dissolving liquid separates the molecules of the substance from one another, and thus brings them into a condition such that heat can exert upon them the same action as it does upon the separated mole-

cules of a gas (figure 58). And if the reader objects at this point that diffusion in a solution takes place at a temperature too low to permit this explanation, I remind him that days far too cold for our comfort are yet hot from the physical point of

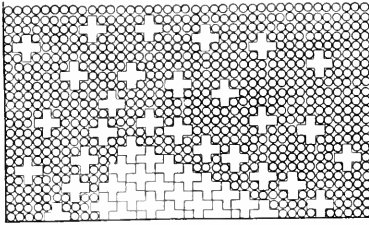


FIG. 58.—A diagram designed to illustrate the diffusion of a substance in solution. The circles are water, and the crosses are the dissolving and diffusing substance,—e. g., sugar. The molecules of water are supposed to have a stronger attraction for the molecules of sugar than these have for one another. Magnified as in Fig. 6.

view, for there is heat in the air at all temperatures above the absolute zero, which lies no less than four hundred and fifty-nine degrees below zero of our ordinary thermometer. And the phenomena of diffusion are precisely the same inside of plants and animals as outside of them. We are now prepared to summarize diffusion as another verity of nature, thus,—*when substances are anywhere brought into a state, whether by*

conversion to a gas or by solution in a liquid, such that their molecules are separated from one another, then those molecules, set into energetic action, and thereby given a mutually-repulsive motion, by heat derived from the surroundings, spread, or diffuse, forcibly outward from places of greater to those of lesser concentration.

Thus much for diffusion; we turn next to the other condition involved in osmosis,—the nature of the membrane. What can be the constitution of a body which, possessing no discoverable openings, will permit water and other substances to pass through with a freedom well-nigh as uncanny as if a fourth dimension were concerned? The membrane, of course, is composed of molecules, but there is also good reason to believe that, in walls at least, the membrane is composed of larger units, called *micellæ*, which are aggregates of molecules (or perhaps simply huge compound molecules) that may be represented diagrammatically as cubical (figure 59). Now these micellæ, although structurally separate, are held closely together by virtue of a certain cohesive affinity

for one another, somewhat as a magnet and its armature are held together by magnetism; and this explains why the membrane, although composed wholly of separate units, holds to-

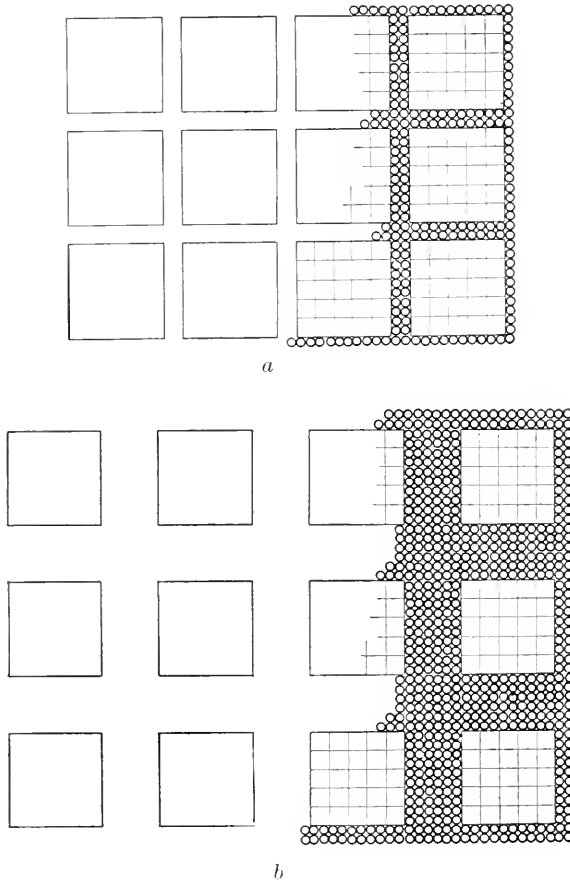


FIG. 59.—A diagram illustrating the construction of membranes. The circles are water: the smaller squares are molecules, and the larger are micellæ, of wall substance. *a*, represents a dry membrane (which always contains some water) and *b*, a saturated membrane, supposed to be seen in section, reduced to only a few micellæ.

gether as a solid. At the same time the micellæ possess a still stronger affinity for something quite different, namely water, which accordingly they can draw in as thin films among and

around themselves, thus forcing themselves apart against the resistance of their own cohesion. This explains how it is that membranes, and all bodies of similar constitution, like wood, can forcibly absorb water throughout all of their structure, and swell up in the process, the requisite energy being supplied by the adhesive attraction between water and wood. This intermicellar absorption of water is called *imbibition*, and is represented in the accompanying diagram (figure 59). But why, by the way, are the micellæ not driven entirely apart by the water, thus making the membrane completely soluble therein? The reason is believed to be this,—that while the adhesive attraction of micellæ for water, and the cohesive attraction of the micellæ for one another, are, like the attraction of a magnet for its armature, strongest when the parts are the closest and weaker with increasing distance apart, the adhesion is supposed to weaken with distance more rapidly than the cohesion; hence, although the adhesion between micellæ and water is at first stronger than the cohesion of the micellæ (thus drawing in some films of the water) there soon comes a point at which the rapidly-lessening adhesion between water and micellæ exactly balances the slowly-lessening cohesion between the micellæ, and this point of equilibrium is that where the membrane is saturated with water and swollen its greatest, as supposed to be represented in figure 59, *b*. In this condition the intermicellar spaces will possess a certain definite size, differing, of course, with the nature of the membrane; and in these different sizes we find the simplest explanation of the different behavior of the types of membranes, for the semi-permeable would be one with intermicellar spaces too small to allow the sugar or other large molecules to pass, while giving free transit to the much smaller water molecules, while the permeable has large enough spaces to permit both kinds to pass. The case in reality, however, is not quite so simple as this, for plenty of facts show that adhesion or solution relations between dissolved substance and the membrane play also a part. Moreover, the

condition of balance in a saturated membrane explains how it is that water can pass so readily through it; for the last films absorbed, those furthest from the micellæ, are held so very lightly that only a slight force is required to draw them from the membrane. What the nature of the force may be which withdraws the water from the inner face of the membrane in osmosis we shall consider in a moment.

Diffusion, imbibition, osmosis itself are typical examples of molecular forces, those operating between individual molecules, in contrast with the more familiar molar forces which act upon masses. There is also one other molecular force of some importance in the plant,—viz., *capillarity*, which we must now briefly notice. Capillarity is the well-known force by which water is raised in small tubes,—or any small passages no matter how irregular,—and the higher the finer the tubes, as our diagram illustrates (figure 60). It is the power by which a towel dries

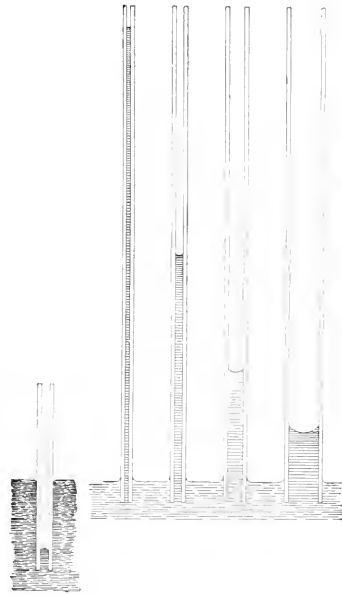


FIG. 60.—A diagram to illustrate the rise and depression of liquids in capillary tubes, drawn to approximately true scale. The liquid on the left is mercury, and on the right is water.

water from the skin, a blotter takes up ink, a wick raises oil, or any porous substance soaks up liquids. It is only with difficulty, and under suasion from my critic, that I forbear to explain this interesting process in detail to the reader; and I must regretfully confine my exposition to the following brief synopsis. The capillary rise of water is due to forces residing within the water itself. Because the attractions mutually exerted between the molecules inside of the liquid are not balanced at the surface by equivalent attractions towards the outside (fig-

ure 61, *b*), the surface layers of molecules are drawn strongly inward so that collectively they press on the liquid as if they were tightly stretched rubber,—a phenomenon known as surface tension. Now surfaces that are flat press inward with a definite force, but those which are concave, being partially buried, as it were (figure 61, *c*), within the body of the liquid, and therefore having the inward attractions of the molecules a little com-

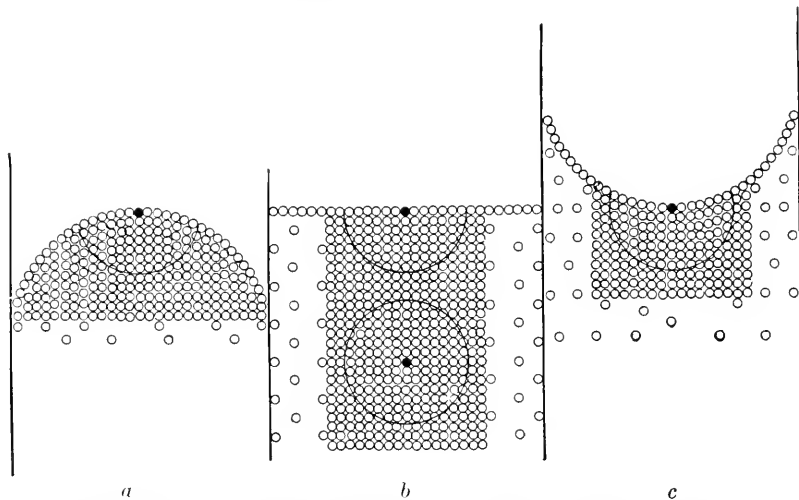


FIG. 61.—A diagram to illustrate the operation of forces concerned in capillarity, representing sections through convex, flat, and concave water surfaces. The small circles, open and solid, are water molecules, and the larger circles are the areas within which given molecules, represented black, are cohesively attracted by others. Where these areas lie wholly within the liquid, as shown in the lower part of *b*, the attractions balance one another, and no effect is produced; but where the areas fall partly outside of the liquid, the inward attractions are not resisted by equivalent outward ones, though the exact degree thereof depends on the form of the surface.

pensated by partial attractions outward, press inwards with less force, while those which are convex, projecting as it were outside of the liquid, have their molecules drawn in with an even stronger attraction than have those of a flat surface (figure 61, *a*). Therefore it follows that the very mobile water will always be pressed away from flat or convex surfaces towards those which are concave. Now it happens, furthermore, that water adheres both to glass and to wood, and hence in a tube of either of these substances

climbs up a bit on the wall, as our figure 61, *c* well illustrates, making the surface concave to a degree that is greater the smaller the tube. Hence the greater surface tension of the flat surface outside pushes the mobile water up against the lesser pressure of the concave surface inside, forcing it to rise against gravitation until equilibrium is established, which will occur at a higher point the smaller the tube. And the reverse process occurs with liquids which will not adhere to glass or wood, e. g., mercury, or with walls of such composition that water will not adhere thereto, as in some air passages of plants; for in this case the surface in the tube is convex, and presses the water down against the flat surfaces outside, so that the liquid stands below the outside level in the tube (figure 60, on the left), or, if the tube is not deeply immersed, will not enter at all.

Such is capillarity, deriving its energy from internal molecular tensions given release by peculiarities of external conditions, and, like all molecular forces, strictly limited in amount and without possibility of continuous action. Capillarity plays in the plant some minor part in the ascent of sap, in prevention of the entrance of water into some air passages, and in other processes later to be noted. Moreover, some physicists see in imbibition nothing but a refined capillarity, although as I think, the phenomena of imbibition of water vapor, presently to be noted under hygroscopicity, is hardly consonant with this explanation. Still another possible connection of a refined capillarity with osmotic absorption will be noticed in a moment.

We have now reached the place where the reader who may have used my permission to skip for a little must resume his grasp on this narrative if he is to understand the essentials of osmotic phenomena.

In watching the ascent of a liquid in an osmoscope, like that of figure 56, one sooner or later comes to wonder what would happen in case an insuperable barrier, e. g., a tight stopper, were interposed against the further rise of the liquid. The matter is

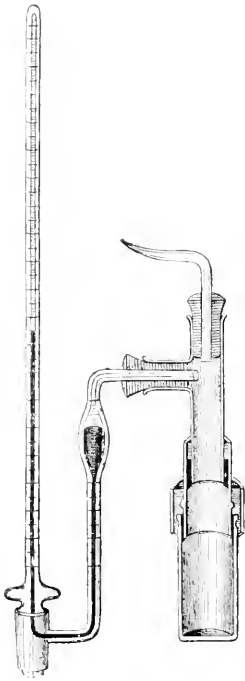


FIG. 62.—Pfeffer's cell, as pictured by himself in his own book (but reduced to $\frac{3}{4}$ his size).

A semipermeable membrane is formed all over the inner face of the porcelain cup, which is shown, in half, at the lower right of the figure. The cup, and all the remainder of the apparatus, is then filled with the sugar solution, which, absorbing water when the cup is immersed, presses the mercury up against the air in the gauge to a height which balances, and measures, the pressure. The remaining mechanical features are connected with filling and sealing the cup.

easy of experiment and the answer plain; the cup becomes stretched or even pushed from the tube, or sometimes (and always if provided with a semipermeable membrane) it bursts. This shows that osmotic absorption, if confined, develops osmotic pressure. Of course the pressures have been measured exactly, chiefly by aid of an instrument invented by the great botanist Pfeffer, and shown by the accompanying picture (figure 62). When its porous cup, lined with a semipermeable membrane, is filled with a solution of sugar like that in root hairs, and then is immersed in pure water, the gauge actually exhibits a pressure equal to that of three or four atmospheres, or fifty to sixty pounds to the square inch. Nor is this all, for when very strong solutions are used, which require, of course, an instrument of enormously greater strength, pressures of surprisingly high magnitude have been registered, even up to twenty-four atmospheres, or 360 pounds to the square inch,—a much higher pressure indeed than ever is used in the steam boilers of even the swiftest express locomotives; while recently even higher ones have been measured. Nor are such pressures of merely academic interest to the botanist, because others higher yet, above one hundred atmospheres, have been found to exist under special conditions in plant cells.

Here follows another paragraph which the reader may skip if such be his inclination,

since it merely concerns the explanation of osmotic pressure, and is not essential to the integrity of our subject. Now a very remarkable and important point about osmotic pressures is this, that in general they are the same in amount as would be given by the respective substances if converted into gases at the same volume, temperature and pressure. This carries the implication that osmotic pressures and gas pressures, being the same in amount, are the same in kind, the dissolved substance being practically a gas, and it, not the liquid, exerting the pressure. But while this explanation is satisfactory for most of the phenomena, it meets with the physical difficulty that the closely packed water molecules must prevent that freedom of back and forth movement upon which a gas pressure depends. Accordingly a second explanation has been given, really an old one revived, which finds the source of the pressure in an adhesive attraction between the molecules of the dissolved substance and those of the water, whereby the former draw all of the latter around them, and take more from the membrane (which easily recoups itself from the outside supply); and thus the solution swells and the pressure is obviously exerted by the substance and liquid in combination. Or, one can express the same thing by imagining that the molecules of the dissolved substance act like the micellæ of the membrane and absorb water (from the latter) by imbibition, with only this difference that the adhesion between substance and water is stronger for all distances than the cohesion of the substance for itself. And still a third explanation is possible, namely, that the spaces between the suspended molecules of the dissolved substance act like excessively fine passages along which the water passes forcibly by an extremely refined capillarity,—in which case the water, and not the substance, exerts the pressure. And if it seems that the correspondence between osmotic pressures and gas pressures must be conclusive for the first explanation against the others, it is to be said that this is not necessarily true, for the properties

of substances in solution and in the gaseous state are so closely and regularly interconnected, that the same mathematical relations apply to them all. And as to which of the explanations is correct, the future must decide.

The reader has now a sufficiency of data for understanding pretty fully the nature of osmotic absorption and pressure, which we may summarize here by aid of the accompanying diagram

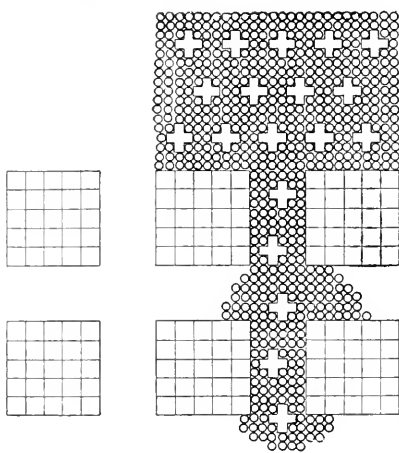


FIG. 63.—Diagram to illustrate osmosis through a permeable membrane; the symbols as in figures 58, 59. In case, however, the membrane is semipermeable the dissolved substance cannot escape through it.

(figure 63). The dissolved substance inside of a membrane is always tending to diffuse outward by the energy of its own diffusion pressure, which depends ultimately upon heat; and if the membrane be permeable, then the substance diffuses into and beyond it, as it did from our molasses-holding osmoscope; but if semipermeable then not. Meantime, whether because the interrupted diffusion-pressure acts like gas-pressure to swell the interior liquid, or because of adhesive attraction between substance

and liquid, or because of capillary action between substance and liquid, the substance draws on the water supplied by the membrane, which yields it very easily so long as it can recoup itself freely from the outside supply. Thus the solution swells and exerts pressure until the power of the substance to withdraw water from the membrane exactly balances the resistance interposed to its expansion. And this is all true inside of the plant or the animal as well as outside thereof, whence we may now deduce another of our natural verities, to this effect,—that *wherever the conditions for osmotic absorption exist, the membrane*

acts as a check, either partial or total, to the further diffusion of the dissolved substance while allowing the liquid itself to pass freely, as a result of which the dissolved substance, whether by gas-like expansion or direct attraction, draws liquid through the membrane, swells, and exerts an osmotic pressure proportional to its strength.

After this lengthy but needful discussion of physical principles, we turn to the actual osmotic phenomena displayed by plants, and here the reader who is skipping the hard parts must resume the narrative. The absorption of water by roots is the most important of these phenomena, but there are others of little less consequence. First among them is the maintenance of rigidity in very soft parts such as leaves, young stems and flowers. These parts consist mostly of water (fully 90 per cent), while the residuum of solid matter (about 10 per cent) is too small and unsubstantial to supply rigid support. Even the moderately firm veins, as everyone knows, are quite unable to keep a wilted leaf from collapsing. But every young cell, soft and weak though it is, can absorb water powerfully through its semi-permeable protoplasmic membrane into its sugar-holding sap, and thus swell to turgescence, stretching the walls until they are tense, and the structure is stiff. Again, osmotic pressure supplies the energy by which young cells can expand their walls in growth, overcoming the resistance of older cells around them; by which buds or flowers can swell and unfold; by which young roots can force a way through hard soil and even destroy masonry and lift curbstones; and by which soft-bodied fungi can burst pavements. Osmotic pressure is the mechanical power used by those parts in effecting their work.

Of minor osmotic phenomena in plants, some of them familiar in the household, there are many. Thus, if one places dry sugar on fresh strawberries, pretty soon it becomes a syrup, and the berries look shrunken; evidently the sugar, moistened by contact with the berry, makes a dense solution which draws water from the cells. The collapse of berries from this cause is very

evident when preserves are made with plenty of sugar, but fruits retain their shape in some of the processes where little or no sugar is used. Dry raisins and currants become plump when soaked, for their cells contain sugar though their protoplasm is dead; and the process is hastened by the heat of cooking. The crisping of celery or cucumbers when placed in water is a case of increased turgescence, the tense cells actually exploding, as it were, when crushed by the teeth. The reason, by the way, why the water must be cold for best crisping is this, that warmer water tends to drive out and replace the air of the intercellular passages, thus deadening the explosive action in which crisping consists. Moreover, the bursting of hard-skinned berries, like cranberries, when heated in water, though apparently an osmotic phenomenon, is primarily due to the swelling of the air confined by the skin, the same thing which occurs in apples when baking. A genuine osmotic bursting does, however, occur sometimes in fruits, like plums and grapes, while still on the plant, because of a great absorption of water from the ducts by the sugar-ripe cells under action of heat on bright summer days; and the calyx of carnations sometimes bursts from the same cause when the temperature rises in the greenhouse. There is in tomatoes an osmotic disease, called *Œdema*, due to an over-absorption of water by soft cells, and the consequent formation of blistery swellings. The swelling of soaking seeds with a power sufficiently great to result in the bursting of strong vessels, is chiefly due to osmosis though it is partly imbibition, and the same is true of the forcible swelling of dried apples. Sugar and salt are common preservatives, the one of fruits and the other of meats, though neither is really poisonous to the germs and molds which cause decay, while the former is actually nutritive; but in strong solutions they act germicidally, because they withdraw so much water from the decay organisms as to render these inactive. Moreover, either of these substances, when eaten in more than moderate amount, causes thirst, which results from

their osmotic action in withdrawing water from the walls of the stomach, whose dryness, from whatsoever cause, gives the thirst sensation. And there are doubtless other familiar osmotic phenomena which will occur to the ingenious reader, who can now have the pleasure of undertaking their explanation upon an osmotic basis.

To complete our discussion of water absorption by plants, we must consider the case of dry tissues like wood. Dry wood, as everyone knows, absorbs water eagerly and powerfully, swelling considerably in the action. The conditions for osmosis are absent, and all evidence goes to show that the absorption is due to imbibition into the solid cell-walls. This helps to explain a common phenomenon in connection with wood,—its warping. When water is placed on one side of a dry board, the board warps away from the wet side, often with power enough to tear it from firmly-fixed fastenings; but if the supply of water be continued, the board later flattens out, and a measurement will show that the saturated board is considerably larger than when dry, precisely as a membrane is. Evidently, the water forcibly absorbed by imbibition upon one side forces apart the micellæ and swells the wood on that side before it has time to reach the other, although, after the lapse of enough time, it penetrates to the other side, swells that, and thus straightens the board, as represented diagrammatically by a combination of the figures 59 and 64. It will here occur to the reader, incidentally, that boards often warp without access to water, and simply from the one-sided action of heat. The principle, nevertheless, is the same; even the driest boards contain some water, the drying of which from one side allows the water remaining in the other to warp the board in the usual manner. Furthermore, the reader may recall that a board will warp crosswise but never lengthwise, which fact is correlated, obviously, with another well-known fact about wood,—a fact of very great importance in building and carpentry,—viz., that wood does not lengthen or shrink lengthwise as it does so freely

crosswise. The basis of this fact is not known, but I venture to suggest as a possible explanation that the sides of the cubical micellæ facing towards the end of the wood (those towards and away from the reader in the sections of figures 59 and 64) have no attraction for water at all, and hence absorb none; and this view I propose that we hold as an hypothesis until it is disproven

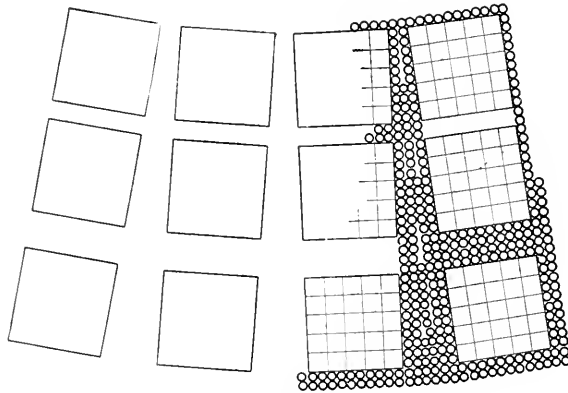


FIG. 64.—A diagram illustrating the molecular basis of the warping of wood. It belongs between *a* and *b* of figure 59.

or a better is offered. The supposition that micellar surfaces can exist without any attraction for water will help also to explain how cell-walls can be waterproof, as they actually are in cork and epidermis.

A special form of imbibition by dry tissues is the absorption of water vapor from moist air, with its return thereto as the air becomes dry,—a phenomenon called hygroscopicity. Familiar examples occur in the softening and sagging of paper in damp weather, in the uncurling and curling of hair, in the movements of the wood of old furniture, giving rise to snappings and creakings which are oft of uncanny effect when heard in the stillness of night. Now, in essence, hygroscopic movement is the same thing as warping, the water being absorbed as a vapor instead of as liquid. Furthermore, if the tissues are made very

thin, this warping may be rapid enough to be seen by the eye, and forcible enough to exert a considerable pressure; and advantage of these features is taken by plants, to produce, by aid of suitable mechanical arrangements, adaptive movements of various sorts. Of this nature are sundry hygroscopic movements described elsewhere in this book,—the self-planting of some seeds; the creeping of some fruits by the twisting movements of hygroscopic awns; the opening and closing, with changes of weather, of most spore-cases and anthers; and the forcible shooting of seeds by hygroscopically-bursting pods. Man has also taken advantage of this principle to construct instruments, called hygrosopes or hygrometers, for showing or measuring the amount of moisture contained in the air. By suitable mechanical arrangements the hygroscopically swelling or shrinking substance may be made to twist a pointer over a graduated scale, to cause suitably-clad little persons to make their exits and entrances to and from tiny houses, or to produce other visible results having appropriate significance.

So much for the absorption of water; we turn now to absorption of minerals, several kinds of which are needed for the various processes of metabolism inside of the plant. But the subject is comparatively simple. The plant can absorb only those minerals which exist in solution in the water of the soil, dissolved therein from the rocks or from various fertilizers added by man. And the minerals enter the plant with the water. In Water-plants, and the simpler sorts of the land, they enter mostly by diffusion from the outside supply, traveling everywhere through the water which saturates the plant. But in the higher plants they are swept in with the current through the hairs, cortex and ducts, from which they pass by diffusion to the places of use. It would seem at first sight that their passage through hairs and cortex would be forbidden by the semi-permeable protoplasmic membranes. But semi-permeability is wholly relative, and a given membrane which prevents the passage of the relatively large

sugar molecules, may permit the passage of the much smaller mineral molecules. But aside from this, the evidence shows that in protoplasmic membranes another influence comes into play, and that the dissolved substance, in order to pass through such a membrane, must be soluble in the material composing it.

There remains to be considered the absorption of gases, a matter of great importance because of the indispensable part played in the

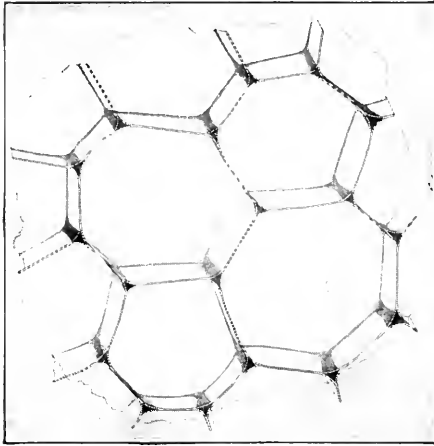


FIG. 65.—A cluster of cells in a piece of pith, showing the intercellular air passages (in black). (Copied from a wall diagram by Frank and Tschirch.)

plant's economy by both carbon dioxide and oxygen, the great reservoir of which is the air. The first requisite, of course, to gas absorption by the living cells, the most of which lie deeply buried within the body of the plant, is some system whereby those gases can be conveyed from the atmosphere into their presence; and such a system, as the reader already has learned in Chapter II, is provided in the inter-cellular air passages, which are shown

in a typical tissue, a bit of pith, in the accompanying picture (figure 65). These passages do not exist in young tissue where new cells are in process of formation, as figures 53 and 139 *C* illustrate; but as the young cubical cells grow larger, they tend to round off into spherical form, splitting in their mid-walls, first at the angles and then along the edges, until the final arrangement tends to approximate to that of the spaces and passages existing between balls in a pile. These passages once formed always persist, no matter what shapes the cells may assume; and therefore they form a continuous system ramifying everywhere throughout the plant, as is represented diagrammatically in the

accompanying figure 66, *A*. Here, for simplicity, the passages, represented in black, are imagined to fall into one plane; and here also, by the way, a partial interruption in the system due to the presence of the longitudinally-running woody bundles is shown by the blank spaces. In young green tissues, as shown by the detailed diagram (figure 66, *B*), in which, as in *C* and *D*, the air passages are partially reduced to one plane, the passages open through the epidermis by the stomata, while on older stems, where a corky bark has formed, they open through the lenticels (figure 66, *C*), those corky wart-like excrescences prominent on all young stems, and consisting simply of open gashes in the bark, partially sealed in the winter by corky cortical cells. In young roots, however (figure 66, *D*), neither stomata nor lenticels are present, but the continuous epidermis and hairs are commonly and normally covered with films of water, through which the gases diffuse in solution from the air spaces in the soil to those in the root, and vice versa.

Thus much for the aëration system, whereby every living cell of the plant is brought into communication with the external reservoir the air. But what is the power impelling the gases along these passages,—which are often of great length, small size, and extreme irregularity? Plants possess no mechanism for the forcible indrawing and expulsion of the air en masse, such as animals have developed in their muscular chest-and-lung breathing arrangements. In some degree a movement of air through the inter-cellular system is promoted by the swaying of parts in the wind, and by the expansions and contractions of the air under varying temperature and barometric pressure; but such effects are insignificant. The primary cause of the gas movement is found in diffusion, that process, already described, whereby the molecules, driven by the energy of heat absorbed from the surroundings, tend ever to move forward from places of greater to places of lesser concentration, and therefore from places where they are being formed or released to places where they are not,

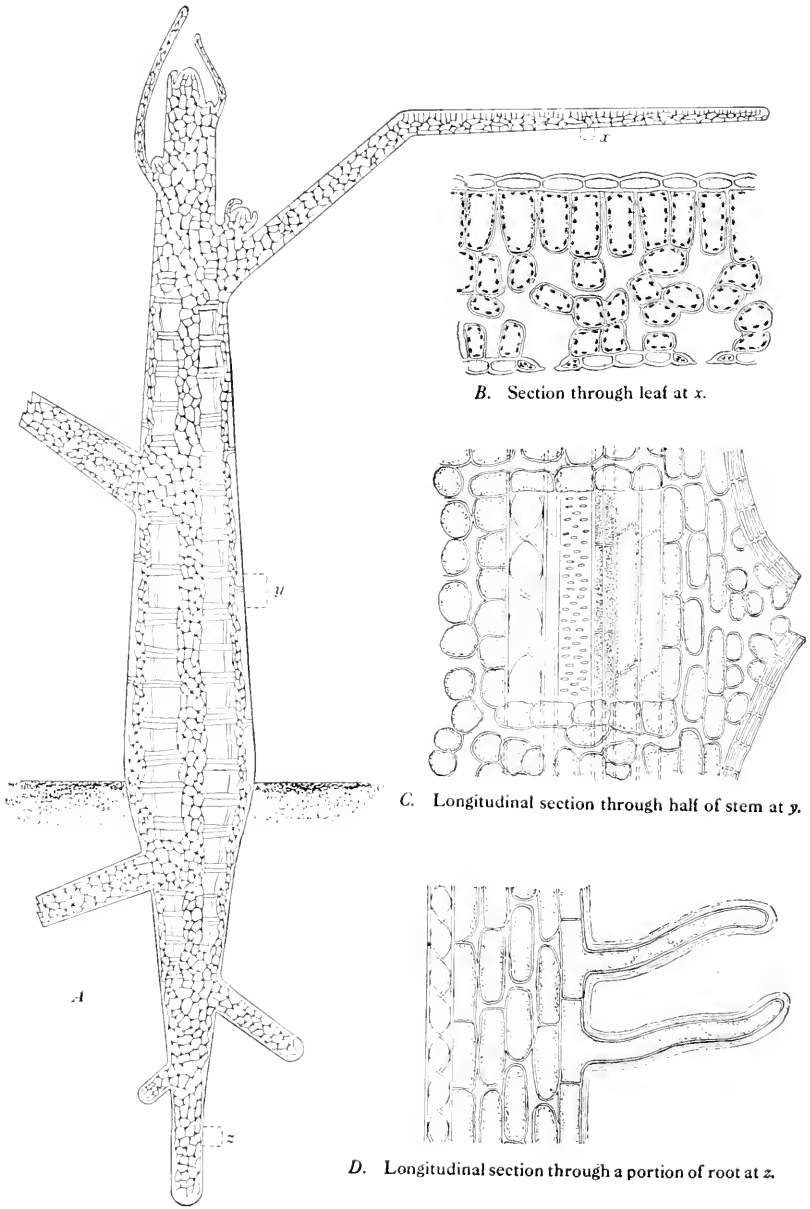


FIG. 66.—Generalized drawings illustrating the aëration system of the plant.

and from places where they occur to places where they are being absorbed. Moreover, each kind of gas diffuses by itself, no matter what others may be present, so that a gas in process of absorption by a plant can move inward in a steady stream through another which is not being absorbed, and even against the opposite stream of one in process of release. Thus, in photosynthesis, for example, a constant current of carbon dioxide diffuses into the leaf, through nitrogen which remains without movement, against a current of oxygen which is diffusing outward. It is a condition hard to imagine, it is true, but the facts declare it is so. The gases thus impelled along the passages by diffusion finally reach the living cells, and, being soluble in water, are dissolved by the moist surfaces, and then diffuse through walls and protoplasm to the places of use. And here I may add a suggestion, for the benefit of the reader versed in physics, that this movement of different gases in contrary directions along the same passages is explained much better by the old-fashioned idea that diffusion and gas pressure are caused by a mutual repulsion between the same kind of molecules than by the modern kinetic theory, which makes those phenomena the result of vibratory movements of the molecules; and moreover the very same conception explains perfectly how osmotic pressures and gas pressures can be identical in kind as well as in quantity.

A very special case of absorption occurs in those plants which absorb organic food substances already made. Such plants, of which parasites are a good example, have the power of excreting from their absorbing parts those special enzymes, or ferments, which render soluble the organic materials they touch. The dissolved substance then enters the plant by diffusion from the place of high concentration outside to the places of use and low concentration inside,—the intermicellar spaces, of course, being adjusted for the admission of these large molecules. The absorption by pollen-tubes of tissues through which they pass; of humus by the fungi which live thereupon; and of the materials

dissolved from the bodies of insects by the pitcher-plants or other insectivora, is also of this character. In all of these cases the materials are not drawn in, as by osmosis, but are driven in by the energy of their own diffusion.

In reviewing absorption by plants, the reader must be struck by the fact that the forces at work are chiefly molecular, and therefore slow and gradual, even though powerful in their action. Plants, as it were, arrange the conditions to permit the molecular forces to work for them. In this respect they stand in rather marked contrast to animals, which tend rather to make use of those larger or molar forces which permit greater rapidity and range of action. In this difference we have the explanation of the persistent placidity of plants in comparison with the abounding activity of animals.

This chapter is already so long that it is only with reluctance that I add anything more; but there remain a few matters which must receive some discussion in this immediate connection. First, we must examine a little farther the arrangements for aëration in plants, especially under unusual conditions. Wherever particular need exists, there the inter-cellular system may become much larger, as occurs conspicuously in leaves, which, requiring a carbon dioxide supply for photosynthesis ten times or more greater than the oxygen supply they need for respiration, exhibit a far larger aëration system than any part of the plant needing only a respiration supply; and that is why leaves have the markedly spongy texture they so commonly exhibit. Again, there are plants of such habit that their roots (as in Marsh Plants), or even huge rootstocks (as in Water Lilies), lie deep under water and must be aërated in some way from the surface. In such cases the inter-cellular system is immensely developed, even to the formation of elaborate passages, in the parts which lead from the surface to the parts under water; and this is the reason for the soft, open, spongy texture of the petioles of Water Plants, and the pith of Rushes and Sedges, and it explains why some plants

can grow in a soil that has no aëration. And it is interesting to note, by the way, that many interesting accessory adaptations are displayed by these plants, of which one in particular is here apposite, viz., the walls of the air passages in these Water Plants are so modified chemically that water will not wet them, and therefore will not enter them by capillarity, on the principle discussed earlier in this chapter. This is obviously an advantageous adaptation against the obstruction of these slender passages by water in case of sub-aqueous accident to the petioles or stems. In some other cases accessory aëration structures are developed which permit a shorter route from the air to the roots. Of this a conspicuous case has been claimed to exist in the great knees of the Bald Cypress of the Southern swamps, which rise above the water surface and contain an aëration system in connection with the roots; and other comparable cases are known. In some Water Plants, however, the aëration is of a simpler sort, consisting indeed of an absorption of air dissolved in the water, in precisely the manner used by the Fishes. In some kinds, for example some Eel-grasses, the leaves are so thin as to present a relatively great surface in proportion to the bulk of tissue to be aërated; while in others the leaves are cut to the finest divisions, presenting indeed a condition directly comparable physiologically with the gills of the fish. This is the reason for the tissue-thin and thread-fine structure of practically all plants which live wholly under water.

Finally we must give some further attention to the particular organs of absorption, the Roots. The structure of the young white tips has already been described except for one point, viz., the water-carrying ducts and the food-carrying sieve-tubes do not stand in-and-out from one another as in young stems, but alternately. In this arrangement lies an obvious adaptation, since it removes the sieve-tubes out of the path of the water from hair cells to ducts; and this conclusion receives some confirmation from the further fact that the arrangement is not main-

tained in the older part of the root, where the entire anatomy is closely like that of the stem. Roots, however, have no nodes, nor regular places of origin of new roots, which, unlike branches, originate deep in the tissues, budding out as it were, from the

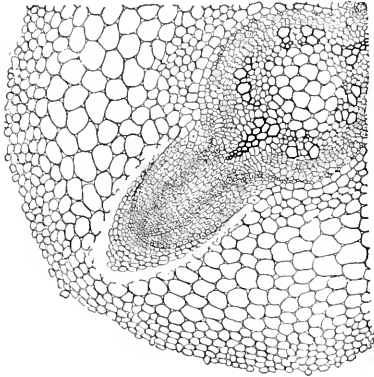


FIG. 67.—A cross section of a typical root, showing the way in which a side root originates. (Copied, reduced, from a drawing by H. O. Hanson, in Curtis' *Nature and Development of Plants*.)

fibro-vascular bundles (figure 67), and breaking their way (partially by the aid of enzymes) out through the cortex, at places determined by the stimulus of more abundant air, water, minerals, or space. This method of origin of side roots, by the way, stands in marked contrast with that of side stems, or branches, which always originate by a transformation of the cells of the cortex, as indicated in figure 137. Thus, the root system of any plant is always excessively irregular, although, on the other hand, differ-

ent kinds of roots present comparatively little variation in structure or appearance, as indeed is to be expected from the comparatively uniform conditions under which most of them live. Typically, roots are much more slender than stems, and have their strengthening tissues condensed nearer the center, in obvious correlation with the fact that they have no lateral strains to withstand, but only pulling strains exerted upon them by the stems for which they must provide a firm anchorage. Therefore, while stems approximate to hollow columns in construction, roots approximate rather to ropes or cables. Indeed, in many roots, one can trace a distinction between features connected with absorption and others connected with anchorage of the stems; and the difference in some cases goes so far that one distinguishes between absorbing roots and anchorage roots, which often occupy

different positions or directions in the soil, the former seeking usually the dampest places, while the latter tend rather to penetrate radiately from the stem into the earth.

While absorption and anchorage are the typical functions of roots, occasionally they perform others quite different, as we have noticed already in the chapter on leaves and stems. Thus, they become modified, with appropriate anatomical changes, to swollen storage organs, in the Sweet Potato; to slender and toughened climbing organs in English Ivy and many tropical climbers; to tough pointed spines in some Palms; to slender penetrating haustoria or sucking organs in some parasites; to flat green photosynthetic organs in some tropical orchids; and to yet other structures of minor account. Thus roots, like stems and leaves, formed for one function can be modified greatly for the performance of others, illustrating once more Nature's wonderful capacity for ringing changes on her favorite ideas.

CHAPTER VIII

THE WAYS IN WHICH SUBSTANCES ARE TRANSPORTED THROUGH PLANTS AND FINALLY REMOVED THEREFROM.

Transfer, Transpiration, Excretion



THE living plant, as the reader of the foregoing pages will surely agree, can be viewed as a kind of central station for the transformation of substance and energy, both of which forever are streaming into, passing through, and issuing forth from the plant, undergoing en route quite definite changes in correlation with adaptive results. These transformations we have already considered in our chapters upon Photosynthesis, Respiration, and Metabolism, while their Absorption was the theme of the chapter just finished; but we still have to consider their passage through the plant and their final removal therefrom. These matters can be treated conveniently together as they are in this chapter, although, for a practical reason which will later appear, we may best reverse the natural order, and treat first the subject that logically should be last.

The most abundant of the substances transferred and eliminated as well as absorbed, by plants, is water. Most people are aware in a general way that plants are forever giving off water as vapor to the air, although they have little idea of its amount. The fact can be demonstrated, by the way, very conclusively to the eye by placing a potted plant, of which pot and soil have first been enwrapped by a water-tight covering, in a glass case or bell-jar, after which, within a few minutes, there will collect on the glass a cloud of water-drops which can have come from

no other possible source than as vapor from the leaves. This is the source also of most of the moisture that collects upon windows near which house plants are grown, and likewise of the water-drops which gather, sometimes to annoying extent, on the glass faces of ferneries, though such water is commonly assumed to originate from evaporation out of the soil. This release of vapor from leaves or other green parts is a practically universal phenomenon in plants. It is called in physiology *Transpiration*; and I wish to warn the reader at this point, out of the depths of a considerable experience as a teacher, not to allow a mere resemblance in words to create any confusion in his mind between this and the utterly unrelated process of Respiration. Transpiration is one of the great primal physiological facts about green plants, and it has, like Photosynthesis, this further distinction, that it is one of the very few processes of plants for which there is no equivalent in animals, the animal process of perspiration being utterly different both as to method and meaning. The reader should therefore incorporate into the visualized picture of the living plant now under construction in his imagination, the idea of a tenuous cloud of vapor rising forever from all its green parts.

But no student of science, and therefore I hope not the reader, will rest content with the general fact that water is given off as vapor by plants, but will insist upon knowing the quantity. The most practicable and accurate of the several methods by which transpiration quantities may be determined lies in the use of the balance. If one takes an ordinary potted plant,—Fuchsia, Hydrangea, Rubber Plant, or other,—encloses soil and pot in a water-tight cover to prevent evaporation therefrom, then weighs the plant at intervals on an accurate balance, the comparative weights, aside from some minor, and largely self-compensating, errors arising from photosynthesis and respiration, must obviously exhibit the exact transpiration from the leaves and the stems. Such experiments are frequently tried in botanical

laboratories, and never without exciting an interested attention from all students, young or old. Some of the results are shown vividly in the accompanying photograph (figure 68), wherein the plant, with its pot and soil enclosed water-tight for this study,

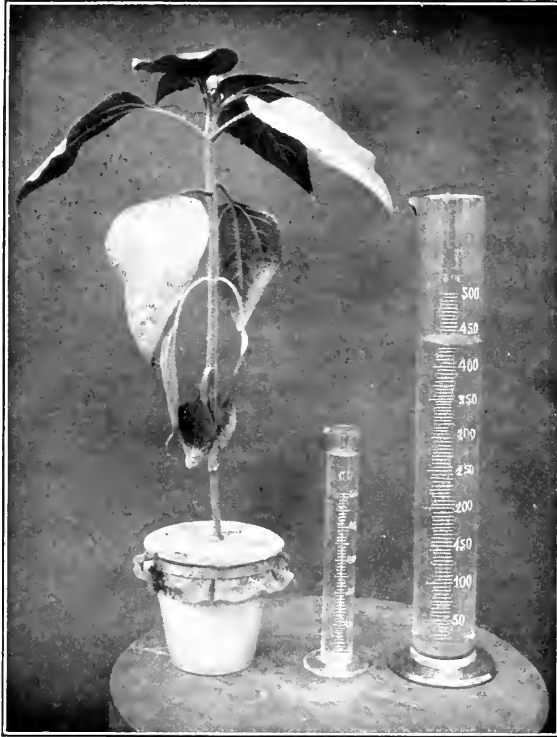


FIG. 68.—A potted Sunflower prepared for transpiration studies as described in the text. The measuring glasses show the number of cubic centimeters, and therefore of grams, of water transpired in twenty-four hours and in a week. In three and a half days the plant transpired a quantity of water equal to the capacity of the pot in which it is growing.

is shown standing beside measuring glasses which display the volume of its transpiration for a day and a week. The quantity of transpiration must necessarily depend on the size of the plant; and in order to compensate this variable, and at the same time to permit a comparison between different plants, it is customary

to express transpiration in standard units. For greenhouse plants, which have been the most carefully studied from this point of view, it has been found that while the transpiration in one hour from one square meter (roughly a square yard) of leaf ranges according to circumstances all the way from near nothing up almost to 300 grams (11 ounces), the generalized average, or conventional constant, is 50 grams per square meter (nearly 2 ounces per square yard) per hour, i. e., $50 \text{ gm}^2\text{h}$, by day and $\frac{1}{5}$ of this quantity, $10 \text{ gm}^2\text{h}$, by night, which equals 30 grams per square meter, $30 \text{ gm}^2\text{h}$ (an ounce per square yard) per hour, day and night together. Upon this basis, an average leaf during an ordinary summer season transpires an amount of water equal to its own area, and a centimeter ($\frac{2}{5}$ of an inch) deep. These quantities are well worth remembering.

The first sensation of the student as he really comprehends these data, especially whenever they are yielded by experiments of his own, is always one of surprise at the largeness of the quantity. It is, indeed, this copiousness of transpiration, rather than the existence of the process, which is the remarkable thing about it; and it helps to explain a number of more or less familiar phenomena. Thus, the rapidity with which leaves always wilt when cut from their stems, and the quickness and completeness with which plants can dry out the soil of their pots, are consequences of transpiration. In this way some plants can serve as good drainers of marshy soils. Thus Eucalyptus trees, especially active transpirers, have been used for this purpose in the Roman Campagna with such success that the marshes have become freed from the former scourge of malaria-carrying mosquitoes, and therefore habitable by man; while the malaria-repelling virtue often ascribed in this country to Sunflowers, which are sometimes planted around dwellings with this end in view, has the same genuine scientific basis. It is also transpiration conditions chiefly that determine which kinds of plants can be grown in dwellings as house plants. House plants are by no means the

most attractive kinds there are, but are the most attractive that can withstand the dryness that prevails in our houses in winter,—a dryness that is due not so much to the heat of the house as to the fact that the general atmosphere in the winter has a very low content of water vapor. A house plant in fact is one whose transpiration in that dry heat is no greater than can be completely compensated by the absorption and conduction of water from the soil. And this relation of transpiration to conduction explains another notable phenomenon in plant nature, namely the limitation in the height of trees, which in general are just so high as the water can be conducted in sufficient abundance to supply the transpiration from the foliage. When that height is reached the tree can still spread out laterally, which explains the flat tops of the largest Elms, Maples, Oaks and others, and of many forest trees when seen from mountain tops. A transpiration effect of a very different sort is displayed by a good many plants in the early spring. It is a fact that roots absorb water very slowly when chilled, and if they are kept for a time at a low temperature, while leaves and stems are exposed to conditions favorable for transpiration, as is effected quite easily by experiment, the plants will wilt very rapidly. These very conditions are often supplied naturally in the spring, for if the soil remains frozen or very cold after warm bright days have forced out the leaves, or if a cold spell that chills the soil is followed abruptly by very warm bright windy days, then the young leaves transpire so much faster than the water can be supplied by the roots, that they become dry-blasted as if by a frost, to which latter cause, indeed, this effect is commonly but mistakenly ascribed. This is the explanation also of the fatal browning of the leaves of many ornamental evergreens, whose leaves are awakened to active transpiration before the roots can supply the water they need; and it is, indeed, a chief cause of winter-killing generally. And finally, as to transpiration effects, there is one more way in which this process exerts a very remarkable influence upon

plants; for the necessity that it be regulated and minimized in places where water is habitually scanty, as occurs conspicuously in deserts, has resulted in the development of protective adaptations which, as the weird aspect of desert plants abundantly attests, affect the forms, sizes, and other structural features of plants more profoundly than does any other influence whatsoever

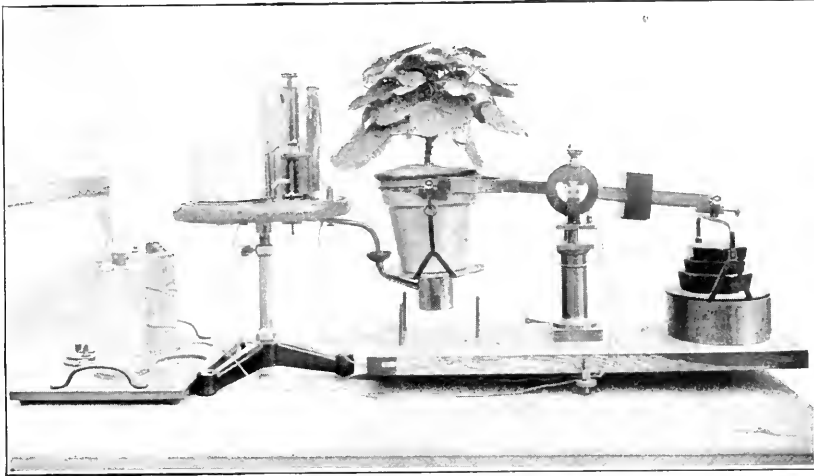


FIG. 69.—A transpirograph in action. The loss of a gram of water from the plant permits that end of the balance to rise and close an electric circuit; this acts, through an electromagnet, to force a pen against a revolving time-drum (seen on the left of the stand), and at the same time to drop a spherical gram weight from a cylindrical reservoir into the box under the scale pan, which is thus depressed, again breaking the circuit. Thus a record is made on the time-drum at each moment when the plant has lost a gram of water.

excepting only Photosynthesis. But this subject belongs really with a later chapter (on Protection), where it will be treated in detail.

The results of all experiments on transpiration show remarkable variations in its amount; but it soon becomes evident that such variations are correlated closely with changes in external conditions. This can be tested by weighing the plants while kept under somewhat extreme conditions of heat or cold, humidity or dryness, light or darkness; and the results are all the clearer if one makes use of some form of self-recording instrument, one of

which, called a Transpirograph (a little thing of my own, by the way) is shown in operation in the accompanying photograph (figure 69). By its use the plant is made to write, precisely and continuously for days together, a record of its own transpiration. Further, there also exist instruments, invented long ago for use in meteorological stations, which write continuous records of the very conditions that affect transpiration, viz., temperature and humidity, while light is recorded by a special method. When the contemporaneous graphs of transpiration and the external conditions are plotted together upon the same sheet, as in case of the accompanying graph (figure 70), the relation between process and influencing factors is displayed in a way which leaves little to be desired in the direction of exact and expressive exhibition of the relation between this physiological process and the external conditions. Indeed, I am accustomed to use this study with my own students as an example of a well-nigh ideal piece of physiological method, whereby Nature is compelled not only to display, but even to write down, for the edification of man, the tale of her own operations. I often recall with delight the remark once made by an eminent literateur who happened to visit my laboratory at a time when this experiment was in progress. As soon as he had grasped the full scope of the matter, he turned away with this comment,—“Well, I don’t see what there is left for Nature to do but lay down and holler.” In these words he expressed very well both the aim and the joy of scientific investigation, which after all is a kind of great game where one matches wits against Nature, and generally loses, but now and then wins and gathers the stakes, which consist in a share of her jealously-kept secrets.

But to return to our experiments on the effects of external conditions upon transpiration, they show these results. *Heat* increases, and *cold* lessens it. Heat, indeed, may hasten transpiration to such a degree that water is lost from the leaves much faster than the roots can absorb it or the stems conduct it, in

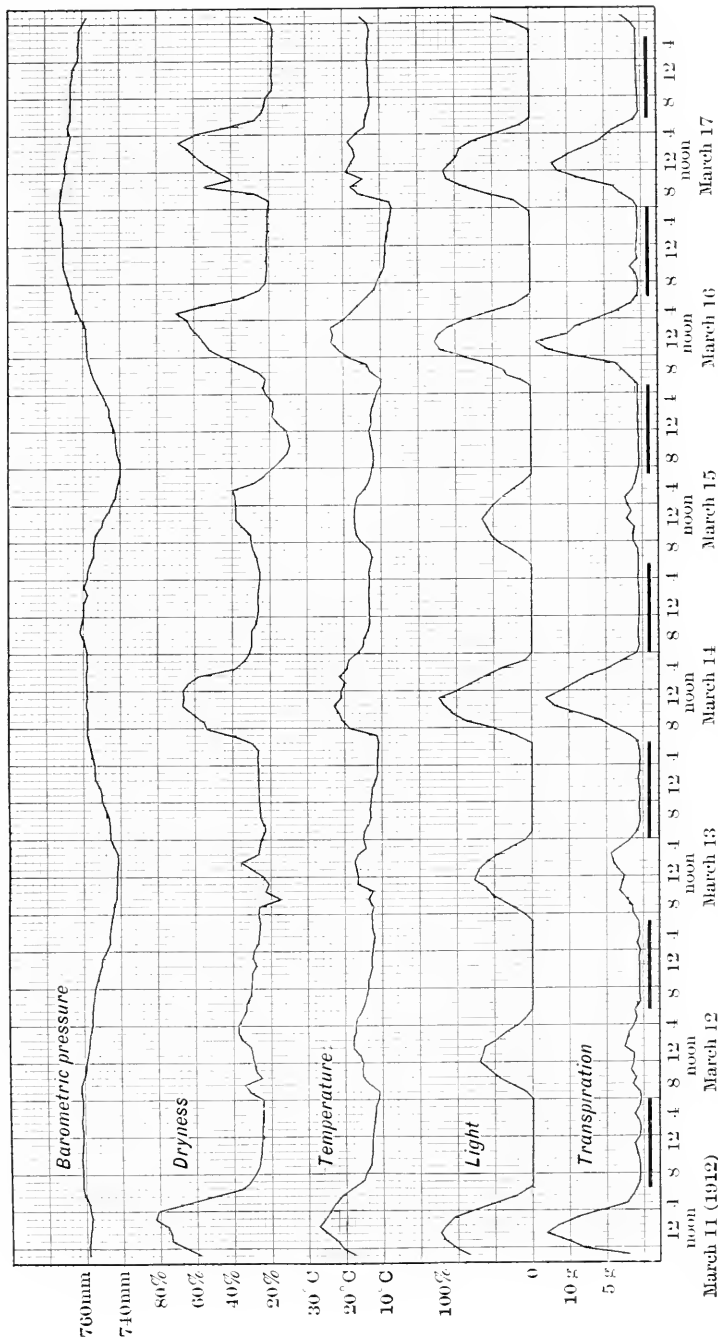


Fig. 70.—A complete Transpiration graph plotted from data supplied by self-recording instruments, except in the case of Light, which is recorded by a special method. The graph of Dryness is an inverted graph of Humidity.

which case a wilting results even though water is plenty in the soil; but plants thus wilted can quickly recover when the weather grows cooler, for then the absorption and conduction catch up, so to speak, and again fill the leaf. *Light* increases, and *darkness* lessens it. This harmonizes with our transpiration constants, which showed that in general the process is five times more active in daylight than at night; and it explains why plants that wilt in the day recover at night. *Dryness* increases, and *humidity* lessens it. This is the reason why most kinds of plants will not live in our houses, the air of which is so dry that the leaves lose their water much faster than roots and stems can supply it, no matter how plenty in the soil. It explains, too, why leaves never wilt in the weather called muggy, no matter how hot, and also why leaves that are wilted recover when sprayed, even though experiment proves that none of the spray is absorbed. As to other external climatic conditions, their influence is slight, except in the case of the wind, which always promotes it. Thus it is evident that in general transpiration is promoted by the very same factors which favor evaporation, though later studies have shown that the parallel does not hold true in detail.

We must now consider the structural basis of transpiration, with which, however, the reader already has incidentally made some acquaintance. If he will recall his knowledge of the cellular structure of the leaf, refreshing his memory, perhaps, by another inspection of figure 2, Plate I, *B*, and figure 54, *B*, it will be clear that every cell borders, for purposes of respiration and photosynthesis, upon the inter-cellular air-system, which ramifies throughout the leaf and opens to the outside world through the stomata, —the little slit-like openings through the otherwise continuous epidermis. Now these cells are all gorged with water, which saturates their walls; and where these border on the air spaces the water necessarily evaporates. The vapor thus formed saturates the air inside of the leaf, and is then moved by the force of its own diffusion along the passages and through the stomata to

the relatively dry atmosphere outside. Such is the structural and physical basis of transpiration, and it explains perfectly why heat, which is an evaporation accelerator, and dryness and winds, which are diffusion promoters, increase the process.

But though such is its basis, transpiration is really not so simple as this, for it is influenced much by another condition, and that is the number and size of the stomata. As to their number, that varies immensely with different kinds of plants, there being none at all on the upper surface of a good many leaves, while on lower surfaces they vary from a few up to near 500 to every square millimeter (one-twenty-fifth of an inch), with a conventional mean at 100; and this equals no less than 100 millions to the square meter (yard), which is another of our conventional constants. And it is worth while to add that when all of the stomata are open their widest, about one-hundredth of the whole area of the leaf is exposed. As to the size of the stomata, that not only varies with the kinds, but in each kind is highly variable, since they open and close, from near a circle through a narrowing oval to a slit and perhaps no passage at all, by the movements of two bordering cells called *guard cells*. These guard cells, as shown by the typical example pictured herewith (figure 71), are of aspect distinctive and unmistakable, with little resemblance to others of the epidermis. They are usually somewhat kidney-shaped, forming together two halves of an elongated oval, and they contain chlorophyll. Their construction is such, as figure 71, *lower*, illustrates, that the natural spring of their walls tends to bring them together and close up the stomatal slit; but the development of osmotic turgescence in their cavities rounds them out so that they separate, thus opening the slit. Now this turgescence of the guard cells is influenced much by the quantity of water contained in the leaf, rising and falling therewith, so that when water is plenty the stomata tend to be open, but when it is scarce they tend to be closed. Thus it seems as if the guard cells ought to act adaptively as regulators of transpira-

tion, keeping it down to safe limits when water is scanty, but allowing full play when water is plenty. The turgescence of the guard cells, however, is influenced also in another way; for

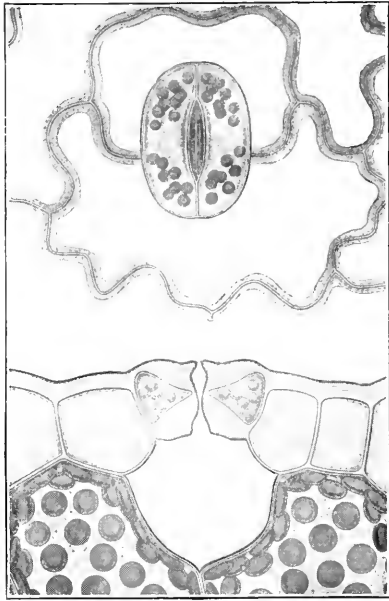


FIG. 71.—Typical guard cells, with a stoma between them, highly magnified, in surface view and cross section. The lower figure shows diagrammatically in cross section the method by which the turgescence rounding of their cavities opens the stoma,—the dotted walls showing the closed, and the unshaded walls the open, position. (The upper figures reduced from a wall-chart by L. Kny, and the lower from a much-copied diagram by Schwendener.)

they (and they only of epidermal cells), contain chlorophyll, which has to make sugar in light and thus increase their turgescence and cause them to open the stomata. This arrangement would explain to perfection why light increases transpiration so greatly quite apart from any accompanying heat, while a definite ecological advantage seems equally clear, viz., it should ensure opening of the stomata at those times when the demand for carbon dioxide is the greatest, and allow them to close with the lessening of this need. From the structure of the guard cells, therefore, we should expect them to serve as automatic valves, regulating transpiration adaptively to the external conditions; and thus they have usually been regarded by botanists. But this conception has not been sustained by later studies, which have shown so much irregularity, and even anomaly, in their action that we

have to remain in doubt until further researches shall give us the truth. Meantime we can only consider that any regulatory action they may have is clumsy at the best.

Such are the principal facts as to transpiration, and they bring us to the problem of its physiological meaning, upon which also there is uncertainty. The older explanation argued thus:—plants need in all parts, and especially their leaves, certain minerals from the soil: their only possible method, apparently, of raising these minerals to the places of use consists in absorbing and transferring them in water, and evaporating the latter to leave them behind: some of the minerals are so scarce that plants hardly ever can get as much as they need: the more copious the transpiration the more minerals are raised; presumably, therefore, transpiration is the mineral-raising process and is the more efficient the more copious it is. On this assumption, plants would be expected to develop adaptations for promoting transpiration, and a great many such have actually been claimed to exist, as will presently appear. A second explanation argues thus:—the stomata exist primarily for admission of carbon dioxide needed in photosynthesis (they occur, in general, only in green tissues): when open for this purpose, evaporation and diffusion of water will necessarily take place from the saturated cell-walls of the interior of the leaf as a purely physical operation which the plant has no power to prevent: presumably, therefore, transpiration is merely an incidental physical accompaniment of photosynthesis, a kind of necessary evil, as it were. Upon this explanation adaptations would be expected for its prevention, especially of a kind which would not interfere with photosynthesis; and of these a good many have been described, as we shall note in the following chapter. This explanation accounts best for most of the phenomena, and is the one that is generally accepted at present. A third explanation argues thus:—when full sunlight falls on a leaf, it beats thereon with an energy overwhelmingly greater than the leaf can employ in its work (for it actually uses no more than some three per cent): this energy, both light and heat, would work disaster to the living protoplasm unless dissipated in some manner: evaporation is a highly effective method of

energy-dissipation: presumably, therefore, transpiration is an adaption to protection against injury from the over-plentiful energy of sunlight. Each of these explanations has its merits and its difficulties, and no one alone is sufficient. Probably the truth will be found to involve some participation of all three; transpiration may be fundamentally a process which the plant cannot prevent, but that is no reason why the plant cannot employ it, and even develop it highly, as an easy method of raising its requisite minerals, and a convenient means for the dissipation of superfluous energy. But this question, too, is one of the many whose solution lies with the future.

Transpiration, however, is not the sole method by which water is removed from the plant. Everybody has noticed the clear shining drops which bejewel the margins of Grape leaves on mornings that follow hot days and cool nights; these drops are commonly thought to be dew but are not. They show very strikingly also on young plants of Nasturtium and seedlings of Grasses, where they can be made to appear whenever desired, simply by covering the actively-transpiring plants for a few minutes by a cooled, darkened, or dampened bell-jar. In a great many other plants, too, the drops appear and are mistaken for dew. The slender wet streaks often seen on the leaves of the Cannas just after sundown, come from similar marginal drops; and a tropical plant is said to exist from which water is projected in a very fine jet. In all of these cases the water is known to come from inside the plant, and the process, known physiologically as *guttation*, is a result of the following conditions. On very warm days the vigorous transpiration is accompanied by an equally energetic absorption and transfer, but the comparatively sudden check to transpiration caused by the cool of the evening does not at once affect the absorption; therefore water continues to be forced into the stems and leaves to an extent which might prove a serious detriment were it not for an avenue of escape provided by openings existing in the ends of the veins, for it is here

that the water-drops always appear. Guttation, therefore, is a kind of a safety-device for the plant even if transpiration is not. Furthermore, it happens at times that roots keep their vitality long after the stems have died, and continue to force up water which can find an outlet only through rifts that it makes in the withering stems. Besides, in cold weather all stems tend of course to contract, thus squeezing from such rifts any over-abundant water they may happen to contain. When water from either of these sources is forced out in cold weather, it freezes in lines, which soon become flat plates as more and more issues from the stem, pushing the already formed ice before it; and this is the origin of the ice crystals or shells, often of great beauty and commonly mistaken for "frost," which are seen on the stems of some plants in the early part of the winter.*

If I seem to have dwelt over-long on this matter of water-removal from the plant, I claim in explanation that the process, because of the profundity of its effect upon plant-structure and habit, is worth all the space I have taken; and the later chapter on Protection will help to support this conclusion. But now we are ready to proceed to the topics remaining, of which the removal or excretion of substances other than water comes naturally next. These excretions belong to four different classes. First, of course, are *the gases*, for oxygen is an excretion in photosynthesis, and carbon dioxide in respiration. But the subject is simple, for they pass off by diffusion, either through stomata and lenticels of leaves and stems, or in solution through the wet epidermis of

* A conspicuous case occurs in *Helianthemum canadense*, commonly called Frost-weed, which is described in Gray's *Manual of Botany* thus: "Late in autumn crystals of ice shoot from the cracked bark at the base of this and the next species, whence the popular name." Another, and even more striking, example is the Dittany (*Cunila Mariana*, or *origanoides*), in which the ice-forming habit has thus been described: "Our *Cunila* has attached to the stem a shell-work of ice, of a pearly whiteness, beautifully striated, sometimes, like a series of shells one in another—at others curved round on either side of them like an open, polished, bivalve; then, in others, again, curled over in every variety of form, like the petals of a tulip." (J. Stauffer, quoted in the *Botanical Gazette*, XIX, 1894, 326.)

the roots. Second, are various *minerals*, which in part are useless materials absorbed along with the useful kinds, and in part are by-products of chemical changes inside of the plant. For their removal plants have no regular excretory system as animals have, though a partial substitute exists in the fall of the leaves and the bark, which thus remove crystalline matters they contain. Other minerals are left behind as crystals in the old dead cells when the living protoplasm advances into the new ones it forever is building (compare figure 41). Third, are the *root-poisons*, little known to us yet and even by some experts not believed to exist. They appear to be highly complex organic substances, slow of diffusion and drainage, and poisonous to the roots which produce them though not necessarily to different kinds; and this fact gives a new explanation of the advantage of rotation of crops and of letting a soil lie fallow. Fourth, is *extra-floral nectar*, apparently identical in composition and mode of formation with the nectar of flowers, which performs the invaluable service of attracting cross-pollinating insects, as later we shall note in detail. The extra-floral nectaries are very tiny structures, sometimes marked by blotches of color, occurring commonly at, or near, the bases of leaves in young plants (e. g. in some Ferns, Horse Beans, Castor Beans and others), or with the spines (in Cactus), and elsewhere. They have been supposed to attract small ants which may perform some ecological service; but the evidence thereon is so unsatisfactory that it seems best to place this nectar for the present among the excretions, though surely it is a puzzling sort.

So, and by such means, are substances removed from plants. The reader knows also in what ways they are absorbed. Between absorption and removal they have to be transported, often for very long distances; and this is the matter which next needs attention.

The principal substance to be transported is water, of which transpiration demands so great a supply that it has to be moved

in a copious and continuous current through the plant. This involves of course a highly efficient water-carrying mechanism, which we should first consider. The principal feature thereof is the ducts, which are tubes, beginning near the tips of the roots (figure 53) and running in bundles throughout the length of the stem to the leaves, as our earlier generalization of the system so clearly illustrates (figure 54, A); and here they end in little areas of green tissue, as we have noted already in the description of the leaf. Structurally, the individual ducts are short, but the end of each one lies against the end of another with only a thin partition between; and therefore the practical effect is that of a continuous tube with occasional thin cross partitions. When roots and stems are young and flexible, the soft walls of the ducts are supported inside by ringed or spiral thickenings, which keep the cavities open when the young roots or stems become sharply bent back by accident, and also against the turgescence pressure of neighboring cells. The ducts formed later, however, when the tissues are thicker and harder, have not the spirals, but stiff bands or a fret work, or even a uniform thickening, pierced by thin areas for the escape of some water to the neighboring tissues. These distinctive features of ducts are very well shown in the picture given herewith (figure 72; also 54, C).

We turn now to the study of the transfer of water through the plant, or, as it may also be expressed, the forces impelling the ascent of sap. Transpiration makes very great demands for a water supply, especially in lofty and broad-leaved trees, and in weather that is bright, dry, and windy. By what forces is so weighty a volume of water raised so quickly to a height so great? Recently I had occasion to calculate the work done in a day in transferring the water from roots to leaves in one of the largest kind of trees, and I found it was just about equal to that which would be done by a man in carrying 500 large pailfuls of water up a ten-foot flight of stairs within ten hours. This is nearly a pailful a minute for ten hours without cessation, my figures being

expressed in this form in order to bring the matter home to my students. Now, strangely enough, the botanists are not yet agreed either as to the source of the energy or the precise physical method by which this considerable work is accomplished; and in default of precise information I can only present to the reader a synopsis of such data as we possess, along with some comments on their probable bearing. And here follow the principal explanations which have been offered for the physics of sap ascent.

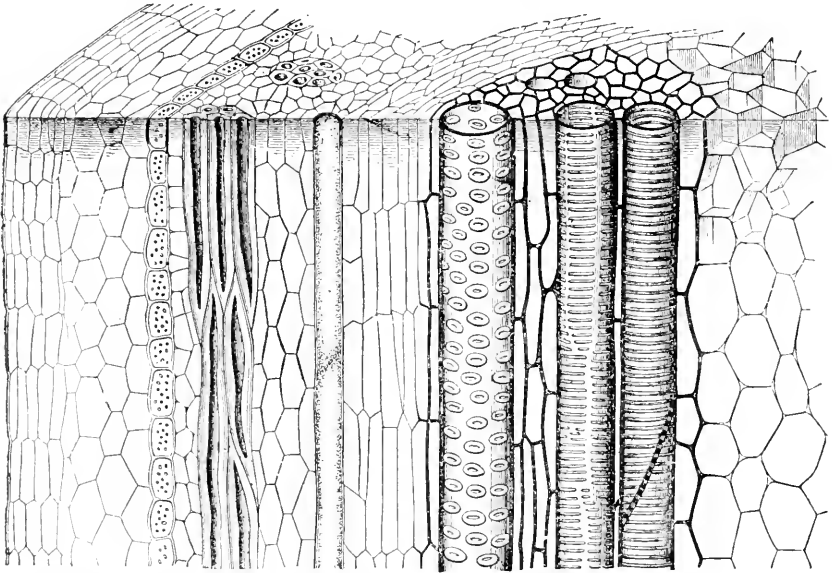


FIG. 72.—A generalized drawing of the tissues of a typical stem, showing the water-carrying *ducts* (the three larger tubes), and a food-carrying *sieve-tube* (the single dot-lined tube), with the associated tissues. (Copied from Kerner's *Pflanzenleben*.)

1. **Root pressure.**—In the preceding chapter it was shown that roots absorb water osmotically and forcibly start it up the ducts. But this pressure, which, in some greenhouse plants has been found sufficient to raise water 40 to 50 feet, and in trees up to 80 feet, is wholly insufficient to explain the ascent when trees reach 400 feet, as they do in some kinds of Australian Eucalyptus; and therefore this cannot be the explanation.

2. Atmospheric pressure.—This will suffice, when the suitable conditions are provided, as they are in a pump, to raise water some 32 feet, but no more; in the plant, however, the requisite conditions are wanting, while this height is obviously quite inadequate. Therefore this cannot be the explanation.

3. Capillarity.—This is the power, as the reader will recall, by which water, driven by its own internal molecular energy, rises in small tubes, the higher the smaller the tube. But even the slenderest ducts known to occur in plants are not small enough to raise the water more than a few feet even if all the other conditions were most favorable, which indeed they are not. Therefore this cannot be the explanation.

4. Imbibition.—This was the favorite theory of the great botanist Sachs, who defended it to the end of his life. He conceived of the wall-system of the plant as a kind of gigantic continuous membrane, extending all the way from the root hairs to the cells of the leaf; into this membrane, by forces and method already considered, water was absorbed by imbibition, and raised by the same energy, to be finally removed by evaporation at the leaf-cells. The theory is simple and plausible, but is shattered by one fatal fact,—viz. it requires that the transpiration stream shall move in the walls of the ducts, not their cavities (which Sachs took simply for reservoirs), whereas experiment proves beyond question that the water does move in the cavities. Therefore this cannot be the explanation.

5. Propulsion.—This theory maintains that the water is forced or propelled upwards by some action of the living cells distributed along the course of the ducts, each living cell being supposed to draw water from a lower duct and force it out into a higher. It really is an extension of root pressure to the whole stem, the living cells passing water from one duct to another precisely as the root hairs and cortex pass it from the soil into the ducts,—and by the very same physical power and method, which is still unknown in detail. It differs from the preceding explana-

tions in this, that it involves the activity of cells which are alive; and herein also it meets its greatest difficulty, because, according to some experimenters, when the living cells are killed by suitable methods, the water continues to ascend, at least for some time. Therefore, they say, this cannot be the explanation. But others are not convinced that the cells are really all killed in these experiments, and hold that this explanation is substantially correct.

6. Traction.—This, the most recent explanation, has been worked out by a botanist, Dixon, and a physicist, Joly, working in collaboration, and is often known by their name. It maintains, in brief, that water in very thin threads holds together, by the force of its own internal cohesion, with a tenacity sufficient to make it as strong as a solid fiber or wire; wherefore the thin threads of water in the ducts can actually sustain their own weight for a length as great as the height of the tallest trees. These threads being practically continuous from the tips of the roots to the cells of the leaves, hang, as it were, from the leaf-cells, into which they can be lifted by any power that can remove the water from those cells. This power is supplied by the energy of evaporation in transpiration, which latter process, therefore, lifts or drags the water threads up the ducts much as a man on a roof would pull up a rope from the ground. On this view the energy which raises the water in the tree is the same which lifts it to the clouds. This theory finds its chief difficulty in the lack of complete demonstration that the water can thus cling together in threads of such great length, and it has not been universally accepted.

It sometimes appears as if the extent of our knowledge of any subject were inversely proportional to its importance. At all events we found this to be true of the structure of protoplasm, and it also seems true of this subject of sap ascent. And at present there is a pause in the advance of our knowledge thereof. With this subject, as with others, we find out everything that existent methods of investigation can yield, then turn for a time

to other matters. Presently, however, somebody, working perhaps in a quite different field, chances upon some new method that happens to be applicable to this subject, to which students then turn once more, and make another long step in advance. The very fact that all knowledge thus grows by appreciable stages makes it all the more interesting to follow; and the watching for such new knowledge, and the grasping it when it appears, constitute the principal charm of the scientific life.

There remains but one other point in connection with the transfer of water. The current must supply not only the transpiration loss, but all the working needs,—chemical, osmotic and other,—of the various tissues besides. This matter, however, is simple, for all kinds of ducts possess plenty of thin places through which the water can pass outward, after which, by imbibition and osmosis, it gradually penetrates from cell to cell throughout all of the tissues that need it. And with the water in this way go the various minerals in solution, which explains their transportation, as well as their absorption, by the plant.

From the transport of water and minerals we turn to that of the various food-substances made in the plant,—a subject known in plant physiology as *translocation*. The subject is comparatively simple. In the first place such substances travel invariably in solution; and substances which are not soluble in water never move from their places of formation. The very physical nature of some substances, e. g. the sugars, makes them naturally soluble, but others, viz. starches, oils, cellulose, and most proteins, are for the same reason insoluble. In such cases solubility is obtained, for purposes of translocation, by their conversion (or *hydrolysis*) into closely-related substances which are soluble,—thus starch and cellulose into sugar, oils into fatty acids, insoluble proteins into peptones. These changes are effected by those remarkable substances called enzymes, whose method of action we have considered in the chapter on Metabolism. The enzymes are widely scattered through plants, and some of them are identical with the

digestive juices (diastase, pepsin) found in the alimentary system of animals; for the solution or hydrolysis of insoluble foods by enzymes constitutes digestion in plants just as truly as in animals. This digested material is then in suitable condition for transportation, which takes place in two ways. First, it may be carried with an onward-moving water current, as happens with the sap in the spring (witness the Sugar Maple), when the food stored for the winter in the roots or lower trunk of the tree diffuses from the storage cells into the sap current and rises therewith. Second, it may travel by diffusion alone, for a substance dissolved in water is in perfect physical condition for diffusion,—that is, has the power and the tendency to move outward and onward, by its own diffusive energy, from places of greater to places of lesser concentration until equilibrium is established. When, furthermore, the substance is being produced at one place, as occurs with sugar in the leaves during photosynthesis, and is being removed in another, as occurs in places of storage where it is converted into insoluble starch, then a steady diffusion current is established between the place of production and the place of use. And it is by such diffusion currents that most of the translocation of food-substances through the plant is effected, though it is to be remembered that diffusion alone, from its very nature, can never completely empty a part. This explains why some sugar and other food materials remain in autumn leaves when they fall.

This translocatory diffusion proceeds in part from cell to cell through the walls, the protoplasmic linings thereof being adjusted (by appropriate chemical modification or intercellular spacing, as noted earlier under Absorption) to permit the passage of the molecules of the substance; and, given time enough, there is no limit to the distance that substances may thus pass in solution. Obviously, however, such translocation through long distances must be greatly facilitated if long tubes replace the short cells; and such a system is actually found in the elongated sieve-tubes

which are very well illustrated in our figure 72. These sieve-tubes accompany the ducts all through the plant from root-tips to stem-tips and leaf-cells, as our generalized plant illustrates so clearly (figure 54), thus forming a part of the same fibro-vascular bundles. But sieve-tubes are more slender than ducts, and unlike them have thin soft walls, and a continuous lining of protoplasm; while the occasional cross partitions, thicker than the walls, are perforated by openings in a way which has given these structures their name (figure 54, *C*). The presence of this protoplasmic lining in the sieve-tubes when diffusion alone does not require its presence at all, suggests that it plays some part in helping to force substances along the tubes, perhaps in a manner analogous to the way in which the food is moved along the intestines of animals; but no such action has been proven. Doubtless the movement is aided materially by the swaying of branches in the wind, and, when it is downwards, by gravitation; but these influences are obviously both incidental and irregular, and diffusion is the only motive force in translocation that we surely know. The reader, therefore, must visualize this process as one of constant diffusion along the sieve-tubes. It is not an onward movement of the solution they contain, but a movement of the sugar and other dissolved substances through water that is standing still, a process in great contrast with the onward rush of sugar-carrying sap in the spring. The method of this diffusion, by the way, is illustrated diagrammatically in figure 6.

The sieve-tubes, in which translocation of food principally proceeds, lie in the inner bark of woody plants, down through which, accordingly, all summer long, there is a constant movement of food-substances towards the roots or other underground parts devoted to winter storage. That this is really the path is easily proven by experiment, such for instance as removing a narrow ring of the bark, or constricting it by a metal ring. This often happens by accident in Botanical Gardens where the encircling wires which support the labels are left too tight. In all

such cases the obstruction in the bark causes an accumulation of the food just above, with a resultant swelling of the tissues that often is very prominent. The same thing happens also naturally where a twining stem, such as that of a Bittersweet, tightly constricts a growing tree, in which cases the swelling stem always shows a very much greater enlargement above than below the vine.

Such is the method whereby food materials are transported from their places of formation to the places of storage and use. The same general method explains the transport and accumulation of all those special substances, usually of definite and adaptive functions, which we call secretions,—the volatile oils, nectar, some coloring matters, and others which have been considered in the chapter on Metabolism.

This is really the place to bring this particular chapter to a natural conclusion; and it is truly a pity that it cannot be done. For somewhere in the book we have to consider the prominent subject of the cellular anatomy of stems, and this is the most suitable place. However, the matter is not indispensable to a clear understanding of the chapters that follow, and therefore the reader may skip the remainder of this chapter if he wishes. And if the said reader should ask why I do not skip it myself, I would answer that the integrity of my subject requires its presence. For with regard to this book I feel with Nehemiah Grew, who wrote more than two centuries ago in the dedication to his great work on the Anatomy of Plants,—“Not I, but Nature speaketh these things.”

If, accordingly, in pursuit of a knowledge of the anatomy of stems, one cuts with a sharp knife a clean section across any young stem, he can always discover the ends of the fiber-like veins distributed in a uniform ground-work of tissue. And if, furthermore, he makes a thin section from a typical young stem, such as Castor Bean, and magnifies it moderately, he will have before him such an appearance as is pictured herewith (figure 73).

while a typical stem is shown generalized in our later figure 139 *B*. Among the many cellular elements in the symmetrical, almost geometrical structure thus displayed, it is easy to identify the bundles of *ducts* from their relatively large size and their obvious resemblance to the cut ends of round tubes. Associated with the ducts, and a little way removed towards the outside of the stem, lie clusters of smaller, thinner-walled, and more angular cells, which are also the cut ends of long tubes, the food-carrying *sieve-tubes*; while between sieve-tubes and ducts lie two or three layers of small squarish cells presenting an aspect which later the reader will learn to associate with growth, for they are the *cambium* cells which form new ducts

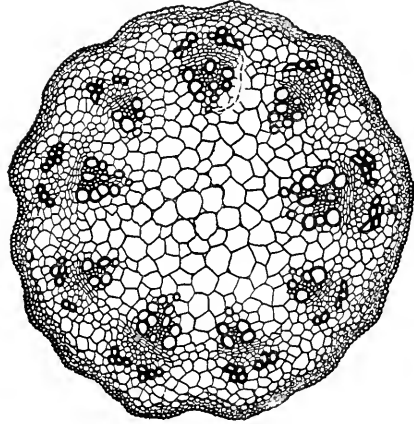


FIG. 73.—Cross section of a young stem of the Castor Bean, magnified about twenty times. (Copied, reduced, from a drawing by H. O. Hanson, in Curtis' *Nature and Development of Plants*.)

and sieve-tubes as long as the plant lives. Ducts, sieve-tubes and cambium, to which often are added strengthening fibers, grow all or a part of them together in bundles, forming *fibro-vascular bundles* which are identical with the veins,—both the kind that can be seen in young translucent stems, and also those familiar in leaves. The bundles begin, as our generalized picture of the conducting system illustrates (figure 54), near the ends of the roots, where they consist of a few ducts and sieve-tubes only; farther back they acquire cambium and fibers and enlarge greatly in size; in the stem they branch at the nodes and run out to the leaves, when they fringe away gradually to the veinlets, each of which ends as a single duct and sieve-tube in the midst of one of the ultimate areas of green tissue.

The fibro-vascular bundles have not only this definite com-

position, but a definite arrangement in the stem, where they lie in a ring, as our pictures illustrate (figures 73, 139 *B*). The tissue in which they are embedded consists mostly of thin-walled cells, of rounded or polyhedral shapes. The part thereof lying inside of the ring of bundles makes up the *pith*, which is commonly utilized for storage; that between the bundles constitutes the beginnings of structures later to be considered as the *medullary rays*; while the tissue outside of the bundles forms the *cortex*, which contains some chlorophyll, and aids in the photosynthetic work. This cortex, by the way, is continuous and morphologically identical with the green tissue of the leaf; and one can form a very useful and reasonably accurate conception of the anatomical relations of stem and leaf by imagining that one of the fibrovascular bundles of the stem is snipped out from among its neighbors, and, with its adherent cortex, bent outward at right angles to the stem and then flattened and fringed out to a network which the green tissue surrounds and fills in. But as to our stem, outside of the tissues aforementioned comes the single layer of *epidermis*, physiologically the plant's skin, with its distinctive flat chlorophyllless cells pierced here and there by the stomata. Finally, sometimes in connection with the sieve-tubes, sometimes as a ring or as scattered islands in the cortex, or just under the epidermis, occur masses of very thick-walled cells, showing long and pointed when seen lengthwise, which are the important *fibers* that give strength to the stem. Howsoever these fibers are distributed, there is always one constant feature about their positions, that they tend to keep close towards the outside of the stem. And the reason therefor is sufficiently plain,—it is a fundamental principle of mechanics that any given amount of strengthening material exerts its greatest supporting effect against lateral strains if disposed in the form of a hollow cylinder or tube, which is the reason why columns used in building construction are hollow, not solid, why a bicycle frame is constructed of tubes, not of rods, and why a great tree can stand as a mere shell of

wood long after its center has rotted away. It is true, this principle would require for greatest efficiency, that the fibers should lie on the very outside, as indeed they do in some cases; but such an arrangement would prevent all access of light and therefore the use of the surface for spreading of chlorophyll. It is easy to understand how the plant could find it advantageous to sacrifice a trifle of effectiveness in the strengthening system for the sake of the marked advantage of spreading more chlorophyll; and in this arrangement we see one of those innumerable compromises with which plants, like mankind, are accustomed to meet the conflicting problems of existence.

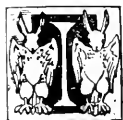
Such is the primary or ground structure of stems, as typically displayed in their earlier stages, and up to the time when they cease to be flexible, green and soft. Then they begin to undergo remarkable changes, connected adaptively with their continuous growth into trees; but these we can better postpone to our chapter on Growth, where the reader will find them fully described.

It will interest the reader to know that the principal theme of this chapter,—the transfer and transpiration of water,—will always be associated in the minds of plant physiologists with the foundation of their science; for to it, of all the phases of plant physiology, was first applied that exact scientific method of measurement which is the only sure means for advancing natural knowledge. Its founder was Stephen Hales, whose book *Vegetable Statics*, though published in 1727, might have been written yesterday so far as its spirit is concerned. He will always be considered the father of this science, and his book one of the greatest of botanical classics.

CHAPTER IX

THE PECULIAR POWER POSSESSED BY PLANTS TO ADJUST THEIR INDIVIDUAL PARTS TO THE IMMEDIATE SUR- ROUNDINGS

Irritability



IF the reader at this point will turn back to the Table displaying the plan of this book, he will see that we have now reached the end of our survey of the processes concerned with the nutrition of plants. These processes are primarily internal, but they are all more or less dependent, especially for their supply of material or power, upon some one or the other of the external conditions. Now these external conditions,—heat, light, water, minerals, and so forth,—are never distributed quite uniformly around any individual plant, but are more or less abundant in some spots or directions than others. Obviously it would be a very great advantage to plants if each separate one of their parts,—each leaf, stem, root, and so forth,—could be adjusted or swung individually into the direction or position that would enable it to work to the very best advantage under the conditions presented by its own immediate surroundings. Such a power, and in high degree of efficiency, plants in fact do possess, as we shall now proceed to consider. The reader will be surprised, I predict, by the importance and interest of the phenomena which belong under this head.

We may best begin our study of the subject by consideration of its most familiar example. When a potted plant, like a “Geranium,” is grown in a greenhouse lighted evenly all around, it assumes a symmetrical form, alike on all sides, as everybody

knows; but when the same plant is grown in the window of a room, where the light is wholly one-sided, it turns all its parts in that direction, even to the extent of seeming to reach out, as it were, after the light (figure 74). The same thing occurs commonly in nature, as may be noticed along the margin of shrubbery or close



FIG. 74.—Two "Geraniums" which for two or three days before their pictures were taken, were kept, respectively, in a uniformly lighted greenhouse and a chamber lighted only from the right hand side.

to high buildings or banks; and it can be demonstrated very prettily by experiment (figure 75).

A close observation of these cases shows always that stems and leaves behave very differently in relation to the direction of the light, for while stems point straight towards it, leaves set their faces across it. This suggests the inquiry,—what, then of roots?

And for answer we turn to experiment. If seeds of mustard or radish are started in water-culture vessels, by methods described in an earlier chapter (page 136), the young seedlings grow rigidly upright in darkness; but if, when well started, they are given a



FIG. 75.—Sets of Radishes grown side by side in a chamber lighted wholly from the right hand side; but those on the instrument were kept continually revolving.

one-sided light, they turn always as shown in our figure,—the stems to the light and the leaves across it as before, but the roots distinctly away (figure 76). And such conduct is typical of ordinary stems, leaves and roots.

This process of light-turning is called in physiology *Photo-*

tropism (pronounced with the accent on the second syllable), or *Heliotropism*. Parts that turn towards light are described as positively phototropic (with the accent, despite the seeming anomaly, on the third syllable), those that turn away as negatively phototropic, and those that turn across as transversely phototropic. Phototropism is so thoroughly typical an example of the power of individual plant parts to adjust themselves in relation to the immediate external conditions that we can use it as a basis for the analysis of the nature of this power, which is known physiologically, though not very happily, as *Irritability*. Now the elements entering into irritable responses are these:—

First, the reason why the parts do it.—As to this, the explanation must be amply obvious. The turning towards the window brings the leaves into positions where they secure the best exposure to light,—

the light which is indispensable to the photosynthetic function for which they exist. The best position for performance of this function must of course be that which sets them at right angles to the light; and this in turn requires that the stem, whose function is simply to carry the leaves, shall point or reach towards the light. As to the roots, not only does their function (the absorption of water and minerals), require no light, but their unprotected protoplasm is actually injured by exposure thereto; and this shows the advantage of their power to retreat from light. The reason for the characteristic phototropism of ordinary leaves, stems, and roots, respectively, is therefore to



FIG. 76.—A Mustard seedling germinated by water culture in darkness and then exposed to light falling from the direction of the arrow.

be found in an advantageous functional adjustment of those parts in relation to the direction of light. And this principle of advantageous individual adjustment of parts is characteristic of irritable adjustments in general.

Second, the mechanical method whereby the turning is effected.—

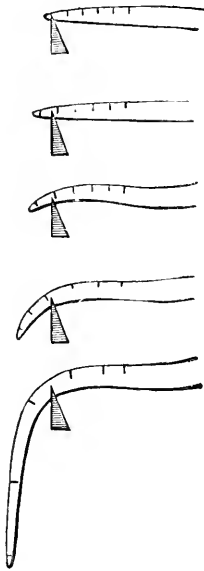


FIG. 77.—Successive stages in the downward turning of a root, showing, by the spread of the marks, that the apparent movement is effected by new differential growth and not by the bending of tissues already formed. The triangular piece is a paper index. (Copied from Sachs' *Lectures*.)

The turning of the leaves, stems, and roots into their respective new positions requires both a considerable power and a definite mechanism. Now it is quite evident that in phototropism neither of these is supplied by the light, for that has no power at all to lay bodily hold on the parts and forcibly pull, bend, or push them into their respective positions, while it is easy to prove on the contrary that the power is supplied by the plant, and derived from its own respiration. Thus, if oxygen be withdrawn from a chamber in which a symmetrical plant is subjected to one-sided light, not a trace of phototropic response ever follows. The connection will be clear to the reader:—The response requires energy, energy depends on respiration, respiration demands oxygen; therefore no oxygen, no response. And as to the mechanism of the turning, that also is easily determined by experiment, for if stems, petioles, or roots are marked across with evenly-spaced lines before the plant is exposed to one-sided light, then the marks

spread apart in a way to prove that the bending accompanies growth in those parts, and is due to a more rapid growth on one side than the other,—on just that side, indeed, where it is requisite in order to swing the parts concerned into the advantageous positions (figure 77). In phototropic adjustments,

therefore, the already-existent tissues are not forcibly bent, but the new tissues grow in such an unequal or differential manner as to swing the parts into their new positions. In these respects phototropic responses are typical of others, for in all cases the power is supplied by the responding plant; and the motor mechanism consists, as a rule, in such differential growth, though occasionally it is of different sort, as we shall presently note.

Third, the way the light operates in connection with the turning.— Since it is not the light but the plant which accomplishes the turning, we still have to seek the nature of the rôle that light takes in the process. In brief, observation suggests and experiment proves that in phototropic responses the plant parts, which in general can grow quite as readily in one direction as another, use the light simply and solely as a convenient guide or signal (called scientifically, but not very fortunately, a *stimulus*), indicative of the most advantageous direction to take. It plays, indeed, very much the same part for the plant that the compass does for the sailor, establishing a definite line of direction, towards, across, or from which, according to circumstances, definite movements may be made. This case is typical of the action of stimuli in general; they never take any part in the mechanical accomplishment of the irritable adjustments, but serve merely as signals for guiding, and sometimes for starting or stopping, the same.

Fourth, the way the light stimulus is perceived by the plant.— The plant has no eyes for the light, as the sailor has for his compass, yet it must possess some means of perception of the stimulus else obviously it could not react. The details of the matter are still much in doubt, but in general this much is certain, that the light falling on the sensitive protoplasm of the plant part sets up (probably by chemical means, since the blue rays are mainly concerned) a condition of irritation or strain, which puts the side towards the light in a condition different from the side away from it, and thus establishes the line of light direction. This case

is typical of all stimuli, which act by producing in the sensitive protoplasm on which they impinge a condition of differential irritation or strain which serves to impress a line of direction on the part concerned. Then the part is swung by the motor mechanism into a position where this condition of strain is the same all around, which position is kept in the subsequent growth. Obviously only those agencies can act as stimuli at all which can thus produce a differential state of the protoplasm, and conversely, any agency capable of producing such a condition can, theoretically, act as a stimulus. And as to how strong a stimulus must be to produce an effect, it is only essential that it have enough power to produce the impression of differential strain on the sensitive protoplasm; and above that degree its strength does not much matter.

Fifth, how it is that a single uniformly-acting stimulus can evoke different directions of turning.—The fact that in phototropism the light neither pushes nor pulls the parts to their positions, but acts simply as a guide to direction, involves the corollary which is confirmed by experience, that it is exactly as easy for parts of the plant to grow away from or across the light as towards it, precisely as the sailor, guided by his compass, which neither pushes nor pulls him over the sea, can steer as easily to the south, east, or west as to the north where it points; and the reader should learn to think of all stimuli in this way. But if the parts of the plant can turn as easily in one direction as another in relation to light, what feature of their growth-mechanism is it which sends stems so unerringly towards it, leaves across it, and roots from it? Here again there is very great doubt as to particulars, but hardly any as to principle, which can thus be illustrated. In a locomotive, as most people understand, there is a certain lever, which when set in one direction determines that the engine shall move forward, and when set in another, that it shall move backward, *after the steam is turned on*; and an engine is easily imaginable in which, with the lever in yet a third position, the move-

ment would be sideways. In all cases it is the same engine, the same machinery, the same motive power; the difference consists only in the way a small part of the machinery is set; and the reader will please to observe that this set of the machinery is not the cause of the movement of the engine, but merely determines the direction thereof when the power, which is steam, is applied. Now something of analogous kind, it is most probable, determines the direction of turning of the plant organs. The structure and motive power in all of these parts is substantially the same, but in each some portion of the machinery is differently set, so that the application of the power, which is growth, causes turning in the distinctive direction,—the stem towards light, leaf across it, and root from it. Of course the machinery is not metallic but protoplasmic, and in last analysis is probably of a chemical nature, while, moreover, the set of the machinery is usually not alterable at a touch, but is hereditarily fixed in each kind of organ. And the subject may stand out yet more clearly if we return for a moment to our sailor, who, in order to reach a certain eastern port, sets his steering gear to hold his good ship at one angle to his compass, and in order to reach a western port holds her at another. It is the same compass, ship, machinery, and power; only the set of the steering gear is different. This is the principle, I believe, which underlies the different kinds of responses to any single uniformly-acting stimulus.

Sixth, how the advantageous direction of response has become fixed in each part.—Or, in the simile of the preceding section, how did the machinery become set so differently in leaf, stem, and root; and especially, how did it become set in each of those organs in the manner most advantageous for the performance of its particular function? Now it is perfectly plain that the power of a part to respond advantageously to a stimulus, that is to say, the set of its responding machinery, is an hereditary and adaptive feature, and must therefore have arisen in precisely the same manner as any other adaptive features, including those of visible

structure,—precisely, for example, as chlorophyll has been developed in the leaf, a fibro-vascular cylinder in the stem, and hairs on the roots. Unless our whole philosophy of nature is wrong, there was a time when these things were not: now they are: at some time and in some way meantime they have arisen, and by gradual stages in the course of evolution. Our problem of the origin of the set of the machinery is therefore identical in kind with that of the origin of any adaptation, and thereby is transferred into that separate field of inquiry which forms the subject of our later chapter on Evolution and Adaptation.

The turning window-plant illustrates very clearly the nature of typical sensitive responses in plants; and all of the more complicated cases are identical in principle. Thus, not all stems turn towards light, for those of wall-climbing Ivies (e. g. the Boston or Japanese Ivy) turn away from it, as manifest by the way in which these plants grow into porches and windows. The advantage, however, is evident on reflection; if these stems turned towards light, like the ordinary sort, they would be carried away from the wall and the possibility of clinging thereto; but, turning away from the light, they are flattened up against the wall where their holding discs can secure an attachment. This example shows also that no necessary connection exists between stemness, so to speak, and a set of the growth machinery towards light, but that the set is developed in the organs in correlation with their habits quite regardless of their morphological nature. Again, not all leaves set themselves across the light, for a good many kinds belonging in places very brilliantly lighted, like sub-tropical plains, set their edges to the direction of maximum brightness. In some this position is permanent, and may thus bring the leaves to a vertical north-and-south position, as in the Compass Plant of our prairies, which owes its name to this circumstance; or, the leaves may change their positions, rising from horizontal to vertical at the time of maximum brightness, as in sundry plants of the Pea family (figure 78). The advantage

of these vertical light-positions is believed to consist in a protection given to the living substance of leaves against the full exposure to a brightness too intense for their good; for we know on the one hand, that too bright a light does chemical damage to protoplasm, even when partially screened by the chlorophyll, while on the other hand, leaves can make use of only a moderately strong light, the extra brightness being wasted upon them. It is this last-mentioned circumstance, by the way, which explains a problem that sooner or later will puzzle the reader, viz., why all the vegetation in the northern hemisphere does not have a turn towards the south where the sun is. This is no doubt because the diffused light falling on the plants from the north is quite as strong as they can use; and hence they have no object, so to speak, in turning to the side of the sun.

There remains one other phase of phototropism in leaves which must here be considered, and that is their lateral shiftings out from beneath one another's shade, a movement chiefly accomplished by twisting and lengthening of the petioles. The result is often to bring them, especially in spread-out plants like the vines, into a one-planed pattern where no leaf is overlapped by another,—an arrangement commonly known as a leaf-mosaic (figure 79); and there are even some botanists who believe that the angular shapes of such leaves (e. g. in the English Ivy) are partly determined by the advantage of interlocking to use all the space.

Such lateral shiftings imply that the whole upper surface of the leaf is equally receptive to the light stimulus; and a very



FIG. 78.—A plant of *Mimulus*, showing the position assumed in the bright sun by the leaflets which in weaker light are horizontal. (Copied from a paper by W. P. Wilson.)

ingenious and highly probable theory has been advanced in explanation, viz., that the epidermal cells, focussing the light in a special manner, are light-sensitive organs, and that the leaf keeps turning and shifting until all of these cells receive their full quota of light at the most desirable angle. In some other cases, however, the reception of the light stimulus is known to take place in a specialized spot, as for example in the seedlings of Grasses, which are light-sensitive only in the tip of the first sheathing leaf. The same thing is true, for several stimuli, of the growing-point of the root, and other cases are known. Evidently some such structures advance pretty far in the direction of the special sense organs of animals, such as eyes.*

Thus much for the phototropism of stems, leaves, and roots: what now of flowers and fruits? As to flowers, they turn their

* The localized reception of stimuli by the growing points of the roots is strikingly expressed by Darwin in the closing paragraph of his great book, *The Power of Movement in Plants*; and this passage illustrates so well a number of other phases of irritable responses that it is here reprinted in full.

"We believe that there is no structure in plants more wonderful, as far as its functions are concerned, than the tip of the radicle. If the tip be lightly pressed "or burnt or cut, it transmits an influence to the upper adjoining part, causing it "to bend away from the affected side; and, what is more surprising, the tip can "distinguish between a slightly harder and softer object, by which it is simultane- "ously pressed on opposite sides. If, however, the radicle is pressed by a similar "object a little above the tip, the pressed part does not transmit any influence to "the more distant parts, but bends abruptly towards the object. If the tip per- "ceives the air to be moister on one side than on the other, it likewise transmits an "influence to the upper adjoining part, which bends towards the source of moisture. "When the tip is excited by light (though in the case of radicles this was ascertained "in only a single instance) the adjoining part bends from the light; but when excited "by gravitation the same part bends towards the center of gravity. In almost every "case we can clearly perceive the final purpose or advantage of the several move- "ments. Two, or perhaps more, of the exciting causes often act simultaneously on the "tip, and one conquers the other, no doubt in accordance with its importance for the "life of the plant. The course pursued by the radicle in penetrating the ground "must be determined by the tip; hence it has acquired such diverse kinds of sensi- "tiveness. It is hardly an exaggeration to say that the tip of the radicle thus en- "dowed, and having the power of directing the movements of the adjoining parts, "acts like the brain of one of the lower animals; the brain being seated within the "anterior end of the body, receiving impressions from the sense-organs, and directing "the several movements."

faces, as a rule, directly to the light like the leaves, as anyone can observe in our house plants, or in those that happen to grow close to a building (e. g. a border of Nasturtiums), or against walls (e. g. Trumpet Creeper), or otherwise in one-sided light (figure 80). In a few flowers (e. g. Sunflowers), the phototropism even extends to the following of the sun through the day, though the adjustment is only moderately effective. Perhaps at first thought it will not be evident why flowers are phototropic at all,

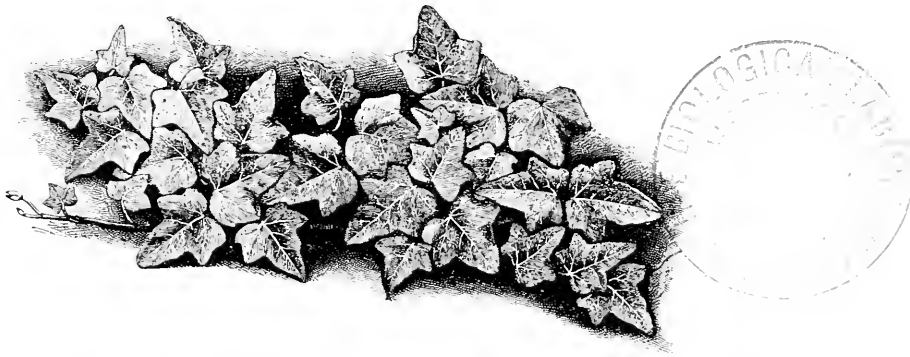


FIG. 79.—The adjustment of Ivy leaves (of English Ivy) into one plane, affording the best aggregate exposure to light. (Copied, reduced, from Kerner's *Pflanzenleben*.)

because, unlike the leaves, there is nothing in the function of the flower requiring the action of light. But on further contemplation of the use of the flower (a subject to be fully explained in the chapter upon Cross-pollination), and especially of the function of the showy corolla as an advertisement to show insects its position, the matter becomes evident; because obviously this function of conspicuousness requires that the corolla must stand out where the light can strike on it most fully. As to fruits, they are as a rule indifferent to light, though responsive to some other kinds of stimuli, as will later appear. One special case, however, deserves mention because illustrative of an additional fact about stimuli. There grows in Europe a little cliff-dwelling vine, *Linaria Cymbalaria* (figure 81), which turns its flowers as usual to the sun, but its ripening seed-capsules away therefrom.

In consequence these seed capsules are brought into contact with the cliff, and, moving about more or less, are reasonably sure to push into some crevice where the seeds can be dropped in position

for starting the new plant in its favorite habitat, instead of at the foot of the cliffs. There are two good reasons why I cite this example. In the first place it shows that the phototropism of a part may change—the lever may be thrown—during its own life, though this is not common. In the second place, the seed capsule has obviously no need to get away from the light as such, but simply to get back against the cliff. Since, however, there exists no cliff-ward stimulus, the light, which happens to act in the suitable direction, is used for the purpose. Light in this case acts as a foster-stimulus as it were, and may thus be described, in contrast with the direct stimuli of the examples earlier described.



FIG. 80.—A cut shoot of Bellflower, kept for two days in a chamber lighted wholly from the left. Observe the positive phototropism of the flowers.

There remains one other class of light responses,—the so-called sleep movements. It is very well known that some leaves

droop at night, as in Clovers, Wood-sorrels, Beans, and many other members of the Pea family (figure 82); and most people have seen, at some time or other, the remarkably tight-shut ap-

pearance presented by those plants at night. The same plants, moreover, can be put to sleep very easily, even at midday, by simply covering them up from the light. Now the exact meaning of the sleep movement is somewhat in doubt, as our chapter on Protection will show; but there is no question at all that light is the stimulus concerned. This response has, however, an interest in another direction, for the motor-mechanism is not growth, but a simple hydraulic contrivance contained in the clear little swellings at the bases of the sleeping leaflets. In the daytime,

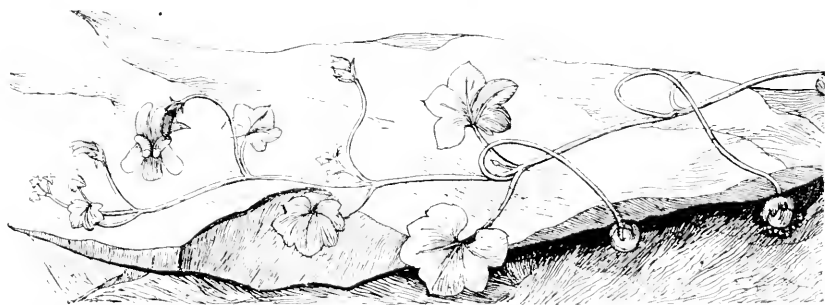


FIG. 81.—The cliff-dwelling plant, *Linaria Cymbalaria*, showing the positive phototropism of its flowers and the negative phototropism of its seed capsules, which thus are brought into advantageous positions for the deposition of the seeds. (Copied, simplified, from Kerner's *Pflanzenleben*.)

under stimulus of light, their cells become strongly turgescient and hold the leaves stiffly expanded; but at night the turgescence is lessened, and the spring of the tissues, aided more or less by gravitation, causes them to droop. It is perhaps simply a high degree of development of sleep movement which gives us the remarkably-balanced leaf mechanism of the Sensitive Plant, later to be considered.

In viewing these sensitive responses, and others of similar sort, one soon comes to wonder what the limits may be to the changes they can cause in the construction of the plant. This, like most of our problems, is amenable to experiment. If the most favorable possible conditions for one-sided stimulation are

supplied to a plant, it will turn to that side to a considerable degree; but the turning is never without limit, for, generally speaking, the farther it turns the more reluctant, so to speak, it is to turn any farther. If, on the other hand, the plant is so grown that it does not receive a one-sided stimulation, which is



FIG. 82.—A typical example of the sleep of plants. Both are *Acacias*, identical in kind and age, but the one on the right has been covered for an hour from light.

easiest accomplished by keeping the plant in continual rotation by aid of an instrument (called a clinostat) designed for the purpose (figure S3), then it always develops with remarkable symmetry, determined, very obviously, by internal and hereditary causes. The plant, accordingly, is born with an internal tendency to symmetrical form, but likewise with a considerable though not unlimited margin of possible deviation therefrom; and it is within this margin that the irritable responses take place. But

this margin has a greater interest than this, for it is characteristic of animals also, including ourselves, where it offers the basis for improvement of the body through exercise, and of the mind through education, while it is the field, as well, within which plays such freedom as is possessed by the will.

Phototropism has received this generous measure of attention because it is so thoroughly typical of irritable responses in general. Accordingly the remaining forms of irritability can be treated much more briefly.

Hydrotropism.—If one prepares a porous clay germinator of the cylindrical form represented in our picture (figure 84): fills it with water: hangs it horizontally: fastens small seeds along its sides: and places it in a chamber with a vapor-saturated atmosphere, then the stems

and the roots will grow stiffly up and down as shown by the first of the figures. But if the surrounding air



FIG. 83.—The clinostat, an instrument which allows the effect of one-sided stimuli to be neutralized through the continual slow rotation of the plant. Note the resultant symmetry of the *Nasturtium* which has been grown from seed on the instrument.

be partially dry, then the roots will cling close to the porous and water-soaked germinator, though the stems will act precisely as before. In the first case the moisture is the same all around;

in the second it is most abundant on the side towards the germinator. The experiment, therefore, shows that roots turn in the direction where moisture is most plenty;—that is, they possess a definite hydrotropism, another typical form of irritable response. The advantage of hydrotropism is perfectly evident when one recalls that the very first function of roots is the absorption of

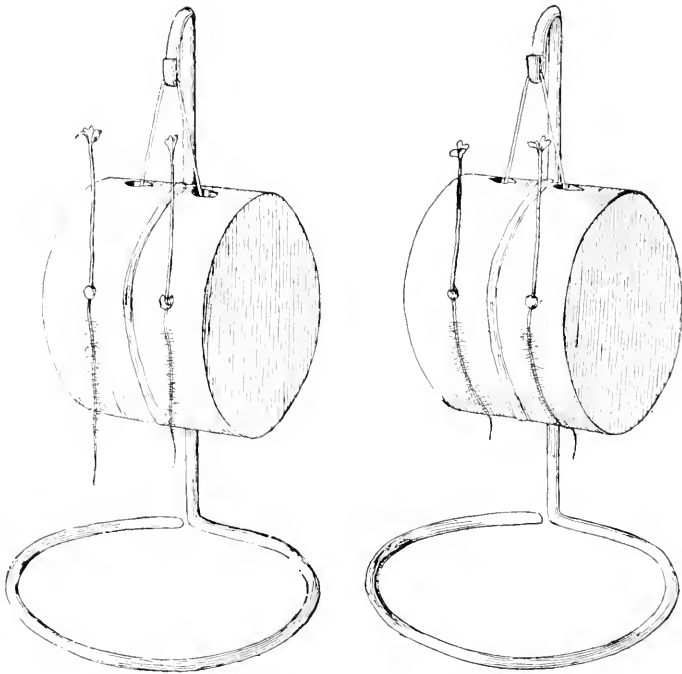


FIG. 84.—Porous water-filled cylinders, to which seeds of Mustard were attached. That on the left was then kept in a saturated, and that on the right in a drier, atmosphere.

water. The stimulus acts in this way; the water, absorbed more rapidly on the side of its greatest abundance, doubtless causes an osmotic swelling and tension stronger on that side than on the other; and this difference is ample to establish a line of direction towards which the roots turn in their growth. It is equally easy to see why stems and leaves display no hydrotropism at all, for, as they do not absorb any water under normal

conditions, its one-sided abundance is a matter of indifference to them. This fact illustrates anew the adaptive character of these responses; for it is a general rule that plant parts are indifferent to stimuli to which there is no profit in responding.

The hydrotropism of roots involves matters of some practical consequence. It is said that when trees develop in a uniform soil, the root tips tend to collect in a circle just under the outer drip of the foliage, which is obviously the place where the water is usually most plenty. But in case the soil is moister on one side than another, the roots grow more freely in that direction, and may even extend to a distance several times the diameter of the tree. In their progress thus towards the most copious wetness, they sometimes are led to a drain, and, insinuating themselves through some crevice left in the tiles, find therein a combination of water, air, and mineral substances so agreeable that they grow very profusely, even to so great a degree that they sometimes choke the drain quite completely.

Chemotropism.—But roots have also other irritable responses, notably to some chemical substances. Thus they turn, though rather feebly, towards a source of supply of some of the minerals they absorb, and this is typical chemotropism, with a very obvious advantage. But they turn much more strongly towards air (a special phase of chemotropism called *AËROTROPISM*),—of course for the oxygen it contains, which they need for their respiration. It is easy to see in these cases how the stimulus is received by the root, for the chemical substance, especially the oxygen, must react with some of the materials found in the complicated protoplasm with which it first comes into contact, thus originating a differential chemical disturbance which would establish the line of direction.

But other structures besides roots are markedly chemotropic. Thus pollen-tubes in their growth turn towards the substances secreted by stigmas and styles. In the fertilization of Ferns, an egg-cell at the bottom of a protective flask-like archegonium is

fertilized by a male antherozoid which swims through the water (figure 104). Now when this egg-cell is ready for fertilization, a weak solution of malic acid pours out of the archegonium into the water, and diffuses steadily outwards. As soon as some wandering antherozoid perceives the presence of the acid, it turns and swims directly towards the source of supply, and hence to the egg-cell, which otherwise it would have no means to discover. And there is reason to think that such a secretion of special chemicals at the time when the egg-cells are ripe is very wide spread through the plant and animal kingdoms, providing the method whereby the swimming or growing male cells are enabled to find the female cells. This function is obviously not simply advantageous but indispensable.

There are many important phases of chemotropism, but I have the space to mention only one more. Water-plants, which have floating leaves, alter the lengths of the petioles in accordance with the depth of the water, a matter which can be shown very beautifully by experiment. Now it is found that this regulation is chemotropic, or, more exactly, aerotropic, for, as experiment proves, petioles continue to grow until the leaves reach a supply of free oxygen, when they stop. This case illustrates an additional fact about stimuli, viz. that they can serve as signals to stop a process as well as to guide it; and other cases are known in which they act to start a process. Such stimuli are probably very important in controlling the various processes of growth, as our later chapter on that subject will demonstrate.

Thigmotropism.—This name is applied to those turnings and movements made in response to a touch as a stimulus. The most typical case is exhibited by tendrils, which, as the reader will recall, are those long slender structures sent reaching out for a support by a good many kinds of climbing plants. These tendrils sweep in long slow courses through the air until they touch some hard object, such as a stem, or a wire, around which they then curl in three or four turns (figure 85), thus obtaining

a grip which holds the vine firmly and permits a still farther ascent. Now it is easy to prove by experiment that it is really the contact with the support which constitutes the stimulus producing the bending, for anyone, by rubbing one side of a tendril with a pencil, can call out the turning, and watch all of the steps in its progress. Even a momentary contact is followed by a turning within a few minutes, though the tendril will straighten again in case the contact is not maintained; but if the contact be continuous the tendril will wind completely around the pencil. The advantage, the motor-mechanism (which is growth), and the mode of reception of the stimulus, in this form of thigmotropism, are all sufficiently obvious.

Most persons who have knowledge of plants would doubtless put forward a different case as a type of thigmotropism, viz., the well-known Sensitive Plant, which droops promptly and completely at a touch (figure S6). But I think this movement is only accidentally thigmotropic. Nobody has yet found, even after study of the plant in

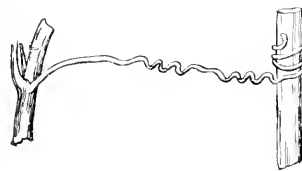


FIG. S5.—Four successive stages in the thigmotropic curling of a tendril around a support. (Copied, simplified, from a wall-chart by Laurent and Errera.)

its native home, any satisfactory reason why the plant should droop for a touch, while, on the other hand, it responds in the same manner to other kinds of stimuli,—a scorch of flame, a strongly-focussed light, a trifle of acid—to which there can be no question of adjustment. The leaves have, however,

yet one other marked response, and that most important, because, as is probable, it explains the original adaptation,—viz. a marked sleep movement just like those which we have noticed already under phototropism. The motor-mechanism underlying the droop of the leaves of the Sensitive Plant is a



FIG. 86.—Two Sensitive Plants, of which the one on the right was struck a sharp blow just before the photograph was taken.

particularly efficient example of the hydraulic type already mentioned; and probably it is so highly perfected and delicately-balanced that although developed originally in connection with sleep movements, it can now be set off, so to speak, by various other stimuli, such as touch,—precisely, for example, as a cannon can be fired by a lighted match, an electric current, some chemicals, or a sharp blow. The sensitiveness of the Sensitive Plant to touch is upon this explanation accidental; and there are probably yet other examples of such accidental stimulation in other phases

of irritability. Indeed, in the very highly complicated and unstable organization of the plant, it must often happen that the motor or growth mechanisms are set off, quite accidentally, by various wholly unrelated stimuli. Such is undoubtedly the nature of many of the "mechanical responses," which by some recent writers have been made the basis of all plant activities, development and evolution, quite regardless of the innumerable other elements and conditions entering into the constitution of organisms.

A good many additional cases of thigmotropic irritability are known. Thus, the leaves of some Insectivorous Plants close upon

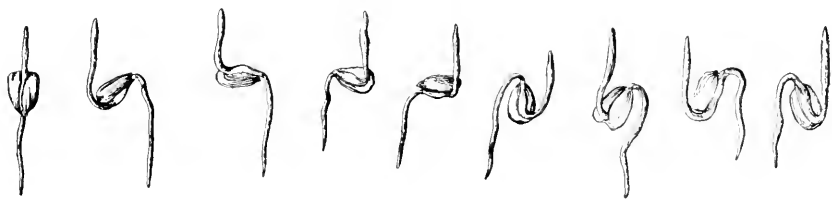


FIG. 87.—Corn seedlings, showing the uniformity of position assumed by the growing roots and stems, respectively, from very diversely placed seeds.

flies that alight upon them,—quickly in the Venus Fly-trap, and slowly in Sundew. Some stamens when touched by insects, move up in such a way as to dust those visitors thoroughly with pollen, thus aiding in the utilization of insects for cross-pollination of flowers, of which the importance will later become apparent to the reader. In these and some analogous cases, the advantage, mechanism, and method of stimulation are all more or less well understood.

Geotropism.—When seeds fall to earth, or are placed in the ground by a gardener, they come to rest in the most diverse positions, with their embryonic roots and stems pointing at any and all angles. Nevertheless, as they germinate, the young roots, with a singular unanimity, turn downwards and the stems upwards. The same thing can be shown very clearly by ex-

periment, for if a number of large seeds, such as Windsor Beans, or Corn, be fixed in the most diverse possible positions (figure S7), the new stems and roots will grow themselves round into the up-and-down directions respectively. Furthermore, the side

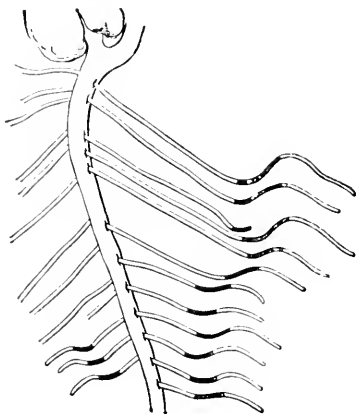


FIG. 88.—This Bean seedling was grown for a time in this position; then it was inverted, and the new growth is represented in solid black; finally it was returned to its first position and has made still further growth. The direction of growth is obviously geotropic, not relative to the main root. (Copied, reduced, from Sachs' *Lectures*.)

roots as they come out, and side branches as well, assume and hold for a time a definite angle to the same up-and-down line. That the positions of these parts are taken with reference to the up-and-down line, and not simply in relation to the main root and stem, is proven by a very conclusive experiment; for if the young plants, when their parts are well formed, are tipped over at an angle, or upside down as shown by our figure (figure 88), then all of the parts grow as quickly as they can into their former directions. A case of analogous sort is found also in Nature, where evergreen trees

that grow on irregular steep hillsides show no relation whatever to the slope of the ground, but grow as stiffly upright, and with branches as truly horizontal, as if the ground were quite level. These simple illustrations are typical of a well-nigh universal fact about plants,—that they send their first roots down and their first stems up, and their side roots and side stems out at definite angles to the up-and-down direction, regardless of the conditions under which they originate. This fact is fundamental in the economy of vegetation, for it helps to explain the way in which large plants can guide their growth into upright positions, and hold themselves therein, and how they can spread out their branches at such definite

angles as to give to these plants their characteristic outlines. Furthermore it also explains how stems can so readily recover their natural positions when the plants are over-turned, whether by accident, or by intention in experiment.

We must next turn attention to this crucial matter of the up-and-down line. Now there is in this world only a single determinant thereof, and that is the attraction of gravitation, which forever is drawing all objects towards the center of the earth. Gravitation, therefore, would seem to be the stimulus used by the plant in assuming the positions we are considering. In other words, the parts of the plant are geotropic;—and all evidence confirms this conclusion.

The wide use of gravitation as a stimulus raises at once the question as to the physiological value of gravitation to the plant. In itself, however, it has no value, so far as anyone has been able to discover. The plant has no object at all in sending roots downward and shoots upward merely to have them down and up; but it happens that down is the direction of moisture and minerals, which roots need, and up is the direction of light, which shoots need. No doubt those parts could be guided in the needful directions by their hydrotropism and phototropism respectively, but gravitation has this advantage over moisture and light as a stimulus, that, while happening to act in the suitable direction, it is present unvaryingly at all times, whereas light and moisture are most variable in quantity, and sometimes absent altogether. This is especially true of light, which is missing at night when growth is most active and the guiding stimulus most needed. Gravitation, therefore, is neither a direct, nor a foster stimulus, like those we have already considered, but a substitute stimulus, adopted by the plant in place of other stimuli because it acts better than they. The use of the compass has just the same advantage over observation of the sun and the stars, which would also take the sailor to his port; for the compass is constant in its action, while the sun and the stars not only

vary in direction all through the twenty-four hours, but oftentimes are obscured altogether. Moreover, this principle of substitution stimuli is often important in connection with the development of structures, for it helps to explain how an organ or other feature can form in advance of perception of the stimulus to which it is later to react,—e. g. the formation of the eye before birth in animals, and of chlorophyll in the embryos of plants.

The way in which the gravitation stimulus is perceived by the plant seems clear. Gravitation draws the heavier contents of the cells, especially the starch grains, down to the bottom of the cell, where their weight presses hard on the sensitive protoplasm and produces a condition of strain different from anything in the upper part of the cell; and this difference establishes the line of direction. Then the responding mechanism is so set that main roots are sent growing towards this pressure, main stems away from it, and side parts across it, precisely as in other typical responses. Geotropism, by the way, is a perfect illustration of the fact that a stimulus acts merely as a guide, and not as a physical aid, to responses; for while gravitation might be supposed to help pull roots downward, obviously it cannot be imagined to help push stems upward or to drive side parts out crossways.

Thus much for the geotropism of stems and roots; what of leaves, flowers and fruits? As to leaves, their geotropism is usually disguised by their stronger phototropism; but that they are geotropic is shown by the vertical or horizontal positions they assume when kept in dark rooms. We see another illustration thereof, as I take it, in Nature, in some of the broad-leaved shrubs which grow in the shade of the forest; here the diffused light is so evenly distributed that it exerts no one-sided stimulus, and the leaves are left free to assume their geotropic position, which is strikingly horizontal. As to flowers, they also, for the most part, are definitely geotropic. Thus, if one selects a long terminal cluster of unopened irregular flowers, such as Larkspur

or Snapdragon, bends it over and fastens it down at the tip, as shown by our figure (figure 89), then each of the blossoms, as it opens, turns over individually to the very same position it would



FIG. 89.—Flower shoots of Larkspur, the curved one of which was bent over and fastened a few days before this picture was taken. Note the uniform geotropic positions assumed by both buds and flowers.

have had in the vertical cluster. The position of each separate flower is here established geotropically, and for a very good reason,—viz., these irregular flowers, as our later chapter on the

subject will show, are specialized for cross-pollination in a way which makes the lowermost petals alighting places for insects; and therefore these petals must be kept horizontal. For the same reason the long tubes of Daffodils are geotropically horizontal, as one can prove by fastening the young flower-stems in horizontal positions; and there are other cases without number. As to fruits, they are mostly indifferent geotropically, but a few, e. g. Cyclamens and Pea-nuts, use gravitation as a guide as they bury their seeds in the earth.

So many and interesting are the manifestations of geotropism in special cases that I must take room for a few more examples. Trailing vines, whose main stems rest flat on the ground, like the Periwinkle, Twin-flower, and Ground Pine, and perennials with horizontal stems just beneath it, like Solomon's Seal, keep these positions by virtue of the fact that their main stems have not the usual main-stem geotropism, which is upright, but the transverse kind characteristic of side-branches; twining plants are kept encircling a vertical support under guidance of a lateral geotropism, and this is what prevents them from twining around horizontal branches or supports which would not take them up towards the light; the aerial roots of many tropical climbers, and most tendrils, have likewise this lateral geotropism, which keeps them swinging horizontally until they meet with a support; and there are many other cases of which some may be identified by the reader himself if he keeps observationally alert in his walks abroad in field, garden, or forest.

Of all of the stimuli made use of by plants for guiding their parts to positions of greatest advantage, gravitation is much the most important. Plants are born with an hereditary tendency to put forth their parts in a symmetrical manner, as can be demonstrated experimentally by aid of the clinostat; but they depend upon geotropism to guide those parts into the suitable positions, and thus to realize the ultimate shape of the plant. And this is the case no matter what the form of the plant may be,

whether a symmetrical cone of horizontally-spread branches radiating from a central main stem, as in the Firs or the Spruces, or a great urn of up-and-outcurved branches, as in the Maples and Elms, or in any of the intermediate shapes; and the reader should learn to visualize all of the main trunks and branches as thus developing in touch with gravitation and largely under its guidance. This applies, however, only to the main structures; the smaller branches and most of the minor parts are more or less controlled by other kinds of stimuli which determine the final details of form; and this is especially the case with roots. The fact that geotropism is thus ever tending to hold the plant to a certain upright symmetrical form explains why any one-sided turning in response to other stimuli, is of limited amount, and why the plant always tends to recover its former upright and symmetrical position in case it is disturbed.

Some minor tropisms.—These include,—**THERMOTROPISM**, a turning towards warmth, rather rare: **TRAUMATROPISM**, the turning of roots away from an external irritation or injury: **RHEOTROPISM**, a turning against a water current, which, however, has been shown to be only a special phase of thigmotropism: **ELECTROTROPISM**, a certain adjustment to mild electric currents; and some others of lesser importance. The case of rheotropism, by the way, illustrates a confusion of stimuli, the root apparently mistaking the pressure of the flowing water for that of some hard object in the soil. The case of electrotropism, involving response to an influence to which the plant is never subjected in nature and to which it cannot have become adaptively sensitive, illustrates the same thing, or else, perhaps, an accidental release of the motor-mechanism after the manner already described for the Sensitive Plant. And the occasional responses found in plants to other stimuli new to them (e. g. to X-rays, radium emanations), are likewise due without doubt to confusion of stimuli, or accidental release.

Thus far we have considered for the most part only cases in

which the stimuli act from a single direction, and therefore evoke only one-sided responses. But some of the very same stimuli may act in a diffused or all-around manner, becoming impressed on the sensitive protoplasm of the plant through a change in intensity; and in such cases the responses are all-sided or symmetrical. Thus the sleep movements of leaves, already considered, are of this nature, being a response to the change in intensity of the circumambient light; and the same thing occurs with some flowers, which close at night or in very dark weather. Other flowers, e. g Tulips, are affected in like manner by changes of temperature, opening as the weather grows warmer, and closing as it becomes cooler; and some evergreen leaves, notably of Rhododendrons, rise and fall in this way even in winter. Such responses are distinguished from the ordinary sort in scientific terminology by the termination, *nasty* (nastynasty, thermonasty, etc.); and we may note by the way, that the responses due to a free-swimming movement, as in the case of the antherozoids of Ferns already described, are distinguished by the termination *taxis* (chemotaxis, phototaxis, etc.).

There are, furthermore, several other types of responses to stimuli, some of them vastly important in connection with the growth and development of plants. Thus, it has been claimed that the strains set up by the swaying of stems back and forth, whether in nature by winds, or in the laboratory under experiment, serve as stimuli to the larger development of strengthening tissues in the places where the strains are most felt, thus producing a needed enlargement at those places. It is perfectly clear that the great knees which rise from the roots of the Bald Cypress of the Southern Swamps and which probably are aërating structures, are formed in response to the presence of water, for they do not form at all when these trees grow in soil that is well-drained. Other cases are known where the thickness of cell-walls, the arrangement of tissues, the sizes of parts, and other structural features are regulated by responses to well-known stimuli from

the environment. Again, the climbing roots of some Ivies, and the sucking roots of some parasites, grow out at those places where the stimulus of contact is felt, and therefore exactly at the places where they can best serve their uses; and the places of origin of even ordinary roots are largely controlled by the stimulus of especially abundant moisture or minerals, which explains why roots branch so profusely upon entering drains. Then there are stimuli which start particular stages of growth. Thus it is a stimulus given by some phase of fertilization which starts the formation of the fruit in the higher plants. The advantage is clear, since the fruit would be wasted, and its formation a useless drain on the plant, if no fertile seed were produced; for the dispersal of the seed is the function for which the fruit exists. Stimuli can also serve as signals to produce a cessation of growth, as in the case of the leaves of the water-plants already considered; and there are plenty of other cases where stimuli regulate growth and development in various ways, the further consideration of which we may postpone to the chapters which deal with those subjects, where also we may consider the correlation and linking of stimuli, with their very important consequences.

There is one other phase of responsiveness to stimuli which we must consider at this place. It is a familiar fact about organisms that they have a certain power of adjusting themselves, or becoming *toned*, as it were, so as to work their best under the prevailing conditions to which they are exposed; and when they are thus working in full harmony with those conditions they are said to be *in tone*. We have a familiar illustration thereof in our human affairs in the way we become accustomed to certain peculiarities of food, temperature, fresh air, occupations, etc., to such a degree that we become uneasy when exposed to any others, and hasten back with relief to the congenial conditions. Thus, most of us work our best at about 70° Fahrenheit and become very uncomfortable when the temperature rises to above 90°, though this is still much less than the natural heat of our bodies.

Moreover this condition of tone is more or less alterable under continuous action of new conditions, and such tonic adjustment to new conditions is commonly called *acclimatization*. We do not yet know much as to the nature of the process, but there seems little doubt that it is chemical in its nature, and represents a process of chemical adjustment to the external conditions acting as stimuli. An important phase of the same process is found in the formation in the animal body of those special chemical substances called collectively "antibodies," which neutralize chemically the injurious substances formed in disease. Probably the acquisition of tone and acclimatization are fundamentally similar in principle, consisting in chemical alterations in the protoplasm of such character that substances or features less efficient under the prevailing conditions are replaced by others more efficient. At least such seems to be the principle, though as to the details, they are still with the future.

As one views the various adjustive structures produced in response to external stimuli (such as the knees of the Bald Cypress just mentioned, the thicker epidermis of plants in dry places, and so forth), one cannot but ask how these may be distinguished from adaptive structures produced in the course of evolution; and whether, after all, the two may not be fundamentally the same thing. As to the first point, one cannot distinguish adjustive from adaptive structures by any evidence except the test of heredity, for adjustive structures are produced anew in each generation only in response to certain stimuli and are absent when the stimuli are lacking, while adaptive structures are produced regularly every generation quite regardless of the presence or absence of the given stimulus. The only thing that is hereditary in irritable adjustments is the capacity to make them. We have an analogy in the different methods whereby republics and monarchies are provided with rulers, for while the president of a republic is often indistinguishable in mode of life and other characteristics from a monarch, and may even surpass one in


power, he is chosen quite anew at regular intervals in adjustment to the popular demands of the moment, only the method of electing him being permanent, or, so to speak hereditary; while the monarch holds his office by heredity quite regardless of the fluctuations of politics. As to our second question, whether in the last analysis, the two may not be fundamentally the same, adaptive structures being only permanently-fixed irritable adjustments, the view is attractive but as yet unproven, as we shall further consider in the chapter on Evolution.

There remains one other important matter to mention in connection with stimuli. The response to a stimulus, while highly efficient, is blindly invariable, and not alterable for particular conditions. For example, if a wind-blown seed of an ordinary plant were to lodge in a cleft of an overhanging ledge, it would be an advantage for this plant to be able to reverse the usual positions of roots and stem; yet we know it would send its stem up, though only to die in the earth, and its root down, only to perish in the air. In this invariability of particular responses, and in many respects besides, these irritable responses of plants agree with the reflex actions familiar in animals; and it is now very clear that they are essentially the same. Furthermore, if two or more stimuli act upon the same part of the plant at the same time, the result is simply the product of the effort of the part to respond to them all. There is no sign of an attempt on the side of the plant to correlate these stimuli, so to speak, and to respond in a manner which would be best in the face of this particular combination. In this respect animals have gone far ahead of plants, for they have acquired that last-mentioned power. Herein we have the chief feature which distinguishes the higher animals from the higher plants, and also, I believe, the origin of consciousness. Thus, out of one and the same origin, plants have developed irritability, while animals have developed reflex action, consciousness, and ultimately reason.

CHAPTER X

THE VARIOUS WAYS IN WHICH PLANTS RESIST THE HOSTILE FORCES AROUND THEM

Protection

Y the methods considered in the preceding chapters, plants provide most effectively for their nutritive needs, and also for advantageous adjustment to the external conditions affecting the same. But they have not thereby solved the whole problem of daily existence, for they still have to reckon with the presence of a great many hostile external conditions. Thus the winds, which in moderation do no damage to plants and even may work them some benefit, occasionally swell to great tempests possessing a power well-nigh too great for resistance. Again, water, which is indispensable to plants in considerable quantity, becomes sometimes, through drought, quite dangerously scant, or through floods quite as dangerously plenty; while various parts and places of the earth,—deserts on the one hand and swamps on the other—though perfectly habitable by plants in all other respects, remain permanently in one or the other of these undesirable conditions. Further, light, which is likewise essential to plants, is in some times and places too weak for efficiency, and in others so intense that unprotected protoplasm can by no means endure it. And again, the food supply manufactured by plants, while ordinarily ample for both themselves and their hereditary dependents the animals, is in some parts indispensable to the continuance of the plants' activity, so that its destruction by animals would constitute a serious menace. Finally, while endowed with indefinitely

great powers of reproduction and growth, plants live in a world already quite filled, and are therefore exposed to a competitive struggle with one another, of which natural selection is the remorseless arbiter, and a survival of the fittest the inevitable outcome. In a word, plants live in a world that is generally friendly, but sometimes is hostile even to a mortal degree. Against the hostile features of the environment they have had to develop protective adaptations, some of which are extremely conspicuous and play a large part in the determination of the habits and aspects of plants. These protective adaptations, of course, must co-exist and compromise with those physiological adaptations in leaf, stem, and root, which we have already considered. The identification, separation, and definition of the structures and features of plants which are protective is the task that now lies before us.

To begin with, the protoplasm of plants is physically weak, but secures an efficient first line of defense by the most obvious of all methods, viz., through encasing each one of the soft-bodied cells in a separate coating of armor,—the cell-wall. As the reader will recall, from the description in the chapter on Protoplasm, the plant skeleton is constructed from the united wall-mass of the cells; and it thus combines both support and seclusion for the protoplasm in its cavities, very much as the walls of our many-storied houses do for us. Such a combination of skeleton and protecting wall is permitted only by the sedentary habits of plants, and stands in very great contrast with animals, whose locomotive habit requires a jointed skeleton, moved by masses of contractile, and therefore naked (muscular) cells.

Turning now in detail to the various hostile influences against which plants need protective adaptations, the most obvious is that of the winds, which, however, become a danger only as they rise into gales. Then, as all will agree who have seen a great tree tossed in the grasp of a tempest, protection is found in the slenderness and elasticity of the branches, which yield in great

curves that permit the smaller to stream with the wind in the lee of the larger, where they can tug at their anchorage in safety. Doubtless in a windless world the plant skeleton would be rigid and brittle, probably to such a degree that an ordinary one of our storms would shatter it to fragments, much as at times they do now with the ice of a silver thaw. As to older stems, we have learned already how it is with them; their hollow-column principle of construction holds them up against great lateral strains. Furthermore, a good many kinds of stems exhibit a special strengthening arrangement at the place of maximum weakness, which lies at the contact of stem and root, where the leverage exerted by wind on the top is most felt. Thus, some kinds of plants, like the Corn, develop prop roots that extend from the stem above ground diagonally down to the earth, while many tall trees possess buttress-like thickenings between the stem and the principal roots, as appears very well in some of our Elm trees, and especially in some of the tropical giants, where they attain a good many feet of height and breadth, though only a few inches of thickness. As to leaves, whose broad faces would present much exposure to wind, their slender-elastic petioles permit them to yield, and to swing like so many weather vanes, presenting only edges to the blast, while they can also sway accommodatingly to every irregular gust. In this adaptation, indeed, we find one of the principal functions of the petiole, as follows from a discovery made by one of my own students,—who found that the petioles from the exposed part of a tree average longer than those from more sheltered situations, although the leaves are smaller in the former locations than the latter.

But it is not alone on the individual tree that the sizes of leaves are inversely proportional to the degree of their exposure to winds, for it is true in general of plants as a whole. Do not the largest leaves that are known to the reader grow in the shelter of undergrowth? And if at first sight it appears that the gigantic fronds of Palms and Tree Ferns contradict this view, a second

thought is enough to confirm it; for, although morphologically single leaves, they are cleft to a great many small leaflets, each of which acts physiologically as a single leaf. This division, or "compounding" (as it is called scientifically), of leaves in such plants appears clearly to constitute a protective adaptation against the tearing action of winds; and I believe the same factor is the principal one in determining the compounding of leaves in general, though sometimes the compound condition, as in our undergrowth Ferns, means rather a persistence of an ancestral condition than anything of immediate importance. Nor is one's natural thought at this point, that the sizes of leaves are dependent on their thickness, correct. The thickness of leaves is determined by the depth to which sunlight can penetrate green tissues without losing all of its photosynthetic power; and hence it is approximately the same in all leaves exposed to the sun in the same climate, with a trend towards more thickness in extra-bright places, and thinness in shade. Undoubtedly the whole tendency of wind action is to produce an adaptive lessening in size, which is directly antagonistic to the tendency of photosynthesis to produce a larger spread of surface; and the resultant between the action of these two factors, modified it is true by certain other minor influences, makes leaves the sizes they are. This explains why our common deciduous trees of similar habit, our Oaks, Elms, Maples, and Chestnuts, possess leaves of much the same size, or at least of the same order of magnitude. That size represents the equilibrium between the contesting photosynthetic and wind factors acting on leaves of standard thickness growing in similar situations.

Another kind of strain to which plants are exposed is the weight of the winter's snow and ice. This danger is greater, of course, for evergreen than deciduous trees, but against it the conical shape characteristic of evergreens provides a manifest protection. This follows from the fact that only the ends of the branches are exposed to the falling load, while their slender forms

and horizontal positions permit them to yield greatly without damage, and thereby even to shed their burdens (figures 14, 15). No doubt the protective adaptation involved in the conical shape has operated along with the photosynthetic considerations earlier mentioned (page 56) to fix this form for evergreen trees, which in general are commonest in the snowiest regions; while, correlatively, the danger involved in the accumulation of snow upon the leaves borne by upwardly springing branches, like those of most of our deciduous trees, is doubtless one factor in making such trees drop their leaves in the winter.

This mention of the shapes of trees makes this a suitable place to consider their modes of resistance to certain other strains. The stems of trees have not only to carry great masses of foliage high up in the air, but also to support it out laterally for considerable distances, and all in opposition to a heavy downward strain from gravitation. In some trees, conspicuously those of the cone-shaped evergreen type (figures 14, 15), the branches spread horizontally from a central upright trunk; but this arrangement, however advantageous from other points of view, is mechanically the worst for resistance to gravitational strains, and is only possible with comparatively slender branches and special methods of strengthening the same. Thus, bracket-like swellings often occur in the angles between such branches and stems, while extra material is commonly placed all along the under side of the branch, making it excentric in cross section. In such cases the extra material acts much like a long stiff spring bent upward just enough to counterbalance the weight of the branch, whose horizontal position is maintained by the counteraction of the two forces, as is shown quite conclusively by the very great bending of such branches when spring and weight are allowed to act together by the inversion of the tree (figure 90). But a cone-shape of trees is uncommon in comparison with that in which great branches, often well-nigh as large as the trunk, rise up therefrom at sharp angles, swing gradually outward to near

the young parts, and then curve vertically upwards again to bear the new leaves,—the whole stem melting away, as it were, to a spray of such branches. This is the form prevailing in most of our deciduous trees, as the reader can see for himself by examining the tracery of Oaks, Maples, Elms, or Chestnuts when projected against the winter sky. Such a sigmoid form of the branches affords them the best possible anchorage in the trunk with the minimum of leverage on their heaviest parts, while

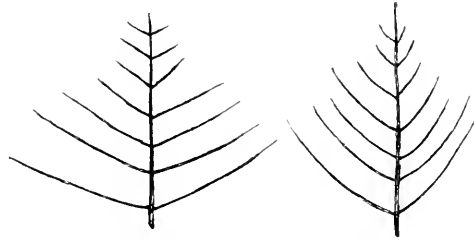


FIG. 90.—Tracings from photographs of the same Balsam Fir, in the natural position and inverted, illustrating a point explained in the text.

providing enough spread and a vertical tip for support of the foliage. If, now, we apply this sigmoid mechanical modification to the theoretical form of our photosynthetic tree represented in figure 7, we obtain the form illustrated herewith (figure 91). This theoretical form, modified by some minor and largely accidental circumstances, is very nearly realized in the noble Oak shown in figure 8, and by many of our common deciduous trees. The chief difference consists only in this, that whereas the theoretical tree is hemispherical, the actual kinds are often ovoid, cylindrical, or top-shaped,—in obvious adaptation, as I think, to a diminution of the excessive gravitational leverage that accompanies too extensive a spread.

We pass now to a second of the greater environmental influences hostile to plants, namely excessive light. The reader does not need to be told that light, and in large quantity, is indispensable to plants for their photosynthetic work; but it is an important physical fact that the amount they can thus use has a limit, above which any increase is not only useless but positively harmful. And that limit is often surpassed in the open sunlight of summer. However, not all of the mani-colored rays that make

up the white light are thus injurious, but only the blue-violet, and then only when received in great force; for these very same rays, like some of the red, are the ones that are useful in photosynthesis. They produce their bad effects, as it seems, through

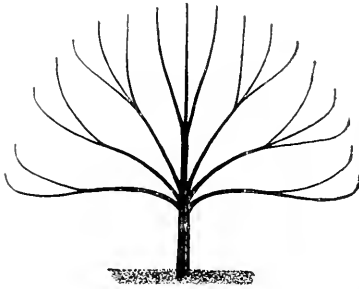


FIG. 91.—The theoretical form of a deciduous tree, consisting of the photosynthetic groundwork shown by figure 7 modified in adaptation to the mechanical support of the weight of the foliage.

their peculiar power of promoting chemical changes, whereby they induce in the complicated living protoplasm illegitimate reactions, as it were, which interrupt the orderly series of chemical processes in which the very life of the protoplasm consists. However, whether this be the correct explanation or not, it is nevertheless a fact that strong unshielded light, because of its blue rays, is always injurious to living protoplasm. This

is the reason why bright light is fatal to disease germs, or Bacteria, and explains the basis of the hygienic value of sunlight in the home; while blue light is used with success for the very same reason in the cure of some diseases of the skin. Now because the red rays of the sunlight are not only harmless but also useful, even in fullest intensity, while the blue rays are harmful only when intense, but otherwise useful, the problem of adaptive protection against too intense light resolves itself into one of tempering the blue rays without affecting the others. This can be perfectly accomplished through use of a screen which permits red rays to pass while checking the blue, and such a screen is of necessity red. It is upon precisely this principle that photographers use a ruby glass screen in developing their plates, for this color cuts off the blue rays, which are those that took the picture originally and therefore would spoil it in development, while admitting the red rays which are not only harmless to the plate but useful in showing the photographer what he is doing;—only the photog-

rapher needs a total exclusion of blue rays and therefore a screen of much deeper color than the plant requires for only a partial exclusion of those rays. Such is most likely the adaptive significance of that charming red blush which mantles the face of the fresh vegetation of spring, for, without some such protection, the young leaves and stems that push out of the buds before the formation of the chlorophyll, which constitutes later a sufficient though incidental protection, would expose their unshielded protoplasm to the full force of the bright light then prevailing. And there are some students who find a similar function in the redness of leaves in the autumn, believing that it shields the protoplasm after the chlorophyll has faded away; though here, as I believe and have argued in the second chapter, there is little warrant in the evidence. Certain it is that there are cases, e. g., the red under sides of leaves of some tropical undergrowth plants, where the explanation must be totally different. But the light-screen function explains very well the reddish or brownish colors of spores which must float long-time in the air exposed to the brightest of light, and perhaps it explains also the red color assumed by roots and underground stems when these become exposed to the light, though here the color may represent simply a chemical incident.

A second method of light protection may consist in those hairy or woolly coatings, or even in the waxy or resinous layers, which overspread a good many plants of open bright places, resulting in a distinctive aspect of grayness found especially often in plants of the deserts. Such covers must act to reflect and refract the light, without, of course, any distinction of rays, to an extent sufficient to weaken very greatly its power to penetrate the tissues.

The third of the methods of light protection, bound up, however, with protection against excessive transpiration soon to be noted, is more important. It consists in the assumption by the green tissues of a vertical position, whereby they present only a thin edge, or at least a low angle of incidence, to the mid-day

brightness of the sun, with the full exposure to its less intense action at morning and evening. Such a vertical position of the green surface is common in plants of open bright places,—in some, notably certain clover-like kinds, as a temporary and irritably-adjustable position of the leaflets (figure 78), but in others as a permanently vertical arrangement of the leaves. In the most perfect of the latter cases, all the leaf-blades present their faces to the east and the west, thus bringing their edges north and south; and such is the real meaning, and the reason for the name, of the Compass Plants, of which the most perfect and famous example occurs on our own western prairies. In some kinds, instead of the leaf-blade it is the petiole which is flattened and set vertically, the blade being suppressed, as in most of the Australian Acacias (figure 21). In others, advantage is taken of the naturally vertical position of the stem, the function of foliage being transferred thereto from the leaves which are simultaneously reduced or abandoned. This is the case with the Cactuses and innumerable other plants of the deserts, which sometimes acquire additional vertical green surface by the development of longitudinal ribs. The readiness with which the green tissue can be developed in one part of the plant as well as another helps, by the way, to explain some of the curious morphological overturnings represented by plants like the Butcher's Broom (figure 23), or, still better, the familiar Smilax of the florists, in which the apparent leaves are in reality branches, while the actual leaves are no more than tiny scales just beneath them. It is easy to understand that if plants of the desert have once transferred their chlorophyll to their stems, simultaneously suppressing or abandoning their leaves, and then a change of climate, or migration to a moister region, should require a larger spread of green surface, this would more easily and naturally be secured through a further flattening of the stems or branches than through a restoration of the lost leaves; and with time such branches would become more and more leaf-like even to the

extreme degree represented by the Smilax. This very overturning does actually occur in the Cactus family, in which, happily, all of the steps without exception are represented by still living forms. It is the relics, indeed, of such devious windings in the past history of plants which give us our principal morphological puzzles.

This consideration of light naturally suggests the question as to heat. This, likewise, is indispensable to plants, since it supplies a condition requisite for some chemical reactions and physical movements, notably diffusion. Heat also, like light, is more and more useful up to a certain intensity (about that of blood heat in ourselves), beyond which any increase is not only without benefit, but soon becomes an injury. Thus, plants in the fields in summer by no means thrive better the hotter it gets. It is doubtful, however, whether the natural heat of the sun ever attains an intensity dangerous to plants, and even if it does, the same structural adaptations, especially refractive coverings and a vertical position of green tissues, protective against light, would be equally effective against heat. And there is perhaps yet another method of protection against both, but especially heat, namely transpiration, which dissipates through evaporation the too intense energy of heat and light thrown into the leaf by the sunlight, as we have noted already (page 209). There is, however, one place on the earth's surface, and that is in hot springs, where low kinds of plants belonging to the Algæ can grow at a much higher temperature than the sun ever produces,—even a degree too hot for the hand to endure (up to 81° Centigrade or 192° Fahrenheit). In these Algæ no structural adaptations to protection occur (unless a certain slimy coating be such, though this is hard to believe), but the living protoplasm has apparently become acclimatized to the high temperature, probably by the elimination of all chemical constituents affected thereby and the substitution of others whose reactions are under full control at such temperatures.

Thus much for heat; at the other end of the thermometric scale more abundant and better marked adaptations are known, for the natural temperatures of the earth do fall plenty low enough to prove fatal to working plant protoplasm. The first of the methods of protection against cold consists in the elimination of water, for while moist and working protoplasm is killed near the freezing-point, the dry substance can endure temperatures of more than 200° Centigrade (over 400° Fahrenheit) below zero without injury,—and, by the way, in this condition, can also endure heat even above the boiling point of water. This power of resistance of dry protoplasm against cold and heat is doubtless due to the fact that the injury resulting therefrom is of a chemical nature, and the chemical changes in living protoplasm proceed only in solution, and solution requires water.

The protection against cold afforded by dryness explains how seeds, which become very dry, can withstand such low temperatures. Winter buds, however, and the other living tissues of plants become only partially dry in winter, and consequently are only partially protected by this method; the remainder of their safety is probably secured by the slight amount of heat released in respiration, which continues all winter, and which is effectively conserved by the non-conducting wrappings provided in the air-holding bark, and the woolly coatings of buds.

From these reasonably certain adaptations we turn to some others of rather a doubtful sort. The leaflets of many kinds of plants, and the flowers of some others, close together or “sleep” at night; and Darwin, who studied these movements most closely, thought they must form a protection against too great cooling at night. This has been doubted of late, and apparently with reason, but nobody has given as yet any more probable explanation. Again, the red color of the spring vegetation has been thought to provide a kind of mitigation of the effects of cold weather then frequent, in that by a certain power it possesses of converting light into heat, it warms up the parts in the bright

but cool days of early spring, when all the warmth procurable by the plant is desirable for hastening the development of the various parts. This explanation has been applied in particular to the red stigmas and styles of wind-pollinated flowers which ripen before the appearance of the leaves in the spring, the extra warmth thus acquired being supposed to promote the growth of the pollen-tube and hence to hasten the fertilization. But here we are nearing mere guesswork, and must not accept such suggestions as explanation, but simply as interesting hypotheses deserving of determination through the test of experiment.

We come now to the most deadly of all the dangers to which plants are exposed,—and that is dryness. As the reader will readily recall, water is not only the principal constituent of the bodily structure of plants and indispensable in their daily nutrition, but is also evaporating or transpiring,—constantly, copiously, and unavoidably,—from all of their younger aerial parts. Therefore plants need a constant and uniform water supply, but in fact rarely get it, for the most of the kinds, including all of those most familiar to us, live under conditions of extreme variability not only as to the quantity available for absorption by the roots, but also, and especially, as to the quantity forcibly transpired from their tissues,—these conditions, indeed, being linked with the most variable of all things, the weather. Against such fluctuations ordinary plants secure a tolerable protection, on the one hand through their power of absorbing even the hygroscopic water of the soil through their copious root hairs, and, on the other, by their complete waterproof epidermis, the few necessary openings in which are automatically regulated, albeit somewhat clumsily, in adjustment to the prevailing conditions. But in places where water is permanently scant, as it is extremely in deserts, these simple arrangements are insufficient and must be supplemented by special protective adaptations; and these take three different forms, under which heads we shall consider them,—(a), increased efficiency of the absorbing system,

(b), development of water-storing tissues and organs, (c), arrangements that minimize loss by transpiration.

The absorbing system of typical plants, as the reader now knows very well, consists principally in the innumerable root hairs, which draw water osmotically from a wide area all around them. Plants that live in dry places usually exhibit, either as an individual adjustment or a structural adaptation, a marked intensification of one or more of the features involved in this absorption;—that is, the number of young roots is larger, the hairs are more profuse, the osmotic solutions are stronger, or the total range of the root system through the soil is greater. The increased profusion of hairs in drier situations is manifest when young roots are grown in damp air, where they make a far greater display than ever they do in the soil; while the much wider range and greater freedom of branching attained by root systems in plants that grow in dry places, helps to explain why it is that the plants of the deserts are spaced so widely apart, with large open areas between them. The presence of stronger osmotic solutions inside the absorbing root hairs is distinctive not only of some desert plants, but also of others which grow in a different situation where water is hard of absorption even though present in plenty,—namely, in salt marshes, where the water itself is a markedly osmotic solution of appreciable strength. As was shown in the chapter on Absorption, osmotic absorption by roots is dependent on a superiority in strength of the inner over the outer solution, and is the slower and harder the more nearly the two approach the same concentration. It is this difficulty of osmotic absorption from salt water which explains why large vegetation, while crowding as close as it can to fresh-water streams and lakes, keeps away from the corresponding situations along the margin of the sea.

The storage of water is the second of the methods protective in plants against dryness. All living cells of all plants, indeed, possess plentiful stores of water in their sap-cavities, which

explains no doubt the reason for the prevalence of the large cell-cavity in the construction of plant cells. But many of the plants of dry places develop great numbers of specially-large cells obviously adapted to water storage in particular, and the presence of such cells makes the parts that contain them swollen, rounded, soft-textured and translucent. This is the origin of the type of plant-structure commonly described as *succulent*, and distinctive of many Cactuses, Euphorbias, Mesembryanthemums, House-leeks, and others, all of which grow either in deserts, or in other places, such as the clefts of rocky hills, where water is scanty for long times together. This storage of water is naturally combined in a great many cases with the storage of food, in which case the parts display a firmer texture and whiter aspect in section, as illustrated for example by the Century Plants. And the examples above given show that the storage organs can be leaves, as well as stems, while roots are frequently used for the same purpose.

The minimization of transpiration is the third and most important of the protective adaptations against dryness. We have noted already the method by which ordinary plants are protected against drought, viz., the possession of a waterproof epiderm is whose only openings, the stomata, are protectively guarded. Now there is apparently no limit to the thickness and perfection of waterproofing that can be given by plants to their epidermis; and if it were possible for them to exist without the stomata, then plants in dry places could wrap themselves up in a way to conserve their indispensable water without limit. But as the reader well knows, green plants in order to live must have food, which is made by photosynthesis, which requires a supply of carbon dioxide, which must be drawn from the atmosphere outside. Thus is necessitated the existence of the stomata, which must be open for a time and extent directly proportional to the food to be made; and this means that water will escape, or transpire, incidentally but inevitably, through those openings to an

amount proportional to the food manufactured. This inevitable linking of transpiration with photosynthesis is one of the most fundamental of all facts in the economy of green plants. Some plants of dry places, especially the deserts, have solved the adaptive problem thus presented by condensing all of their photosynthetic work into the brief moist season (for all deserts where plants can grow at all do possess such a season), spending the remainder of the year in a resting and dried state, comparable with that assumed by our plants over winter. But others, illustrated by the Cactuses conspicuously, continue their activity all through the season, in reliance upon a copious store of water and sundry devices for rigid economy of the same.

This matter of economy in transpiration is so important and interesting that we must give it a little further consideration. The first and most obvious method thereof consists in the reduction of total green surface, which of course is carried to a degree sufficient to keep the unavoidable loss within the limit of safety. This is the reason why the plants of dry places, and especially of the deserts, are comparatively small, why they are so commonly compacted in form, and why they so often are leafless,—the very object of the existence of the leaf, as the reader will recall, being that of spreading more surface. A second method consists in the provision of an especially efficient epidermis, preventive of transpiration except through the regulable stomata; and so thick and strong does it become in some plants that it is hard to cut and impossible to compress with the hands, and actually resembles a coating of horn spread all over the plant, as some of the Cactuses illustrate. But a third and most interesting method of transpiration economy consists in certain arrangements which hinder somewhat the transpiration without interfering with the gas diffusion. This to some degree is accomplished by a vertical position of the green tissues, for while the diffusion of carbon dioxide through the stomata takes place with equal facility in any position of the tissues, the tran-

spiration is much less from vertical surfaces, since the force of the sun which supplies the transpiration energy is obviously much less powerful upon vertical than horizontal surfaces. Doubtless, by the way, this factor is much more potent than those of protection against light and heat in determining the prevailing vertical position of green tissues, whether of stems or of leaves, in plants of dry and desert places. And this conclusion is strongly confirmed by the fact that salt marsh plants, which need protection against much transpiration though hardly at all against light and heat, especially in northern regions, show a notable tendency to a vertical position of leaves and other green tissues. But the very same end is also attained in a different way by the provision, outside of the stomata, of chambers in which the escaping vapor is held for a time, thus checking transpiration a little, somewhat as a damp atmosphere would do, while the inward diffusion of carbon dioxide is not appreciably affected. In some plants these chambers consist of deep pits in the thick epidermis with guard cells lying at the bottom; in others the same effect is produced by coatings of hairs or scales; while in still others the leaves are inrolled to tubes into which the stomata all open. The same result follows, as well, from the dense crowding together of leaves, such as desert plants show not infrequently (figure 12, *center*). And many other arrangements, notably hardness of tissues, and the presence of gelatinous substances, both contributing to water conservation, have been described.

Thus much for dangers from dryness; the other extreme,—too much water,—likewise constitutes at times a danger to plants, rarely, however, in any direct manner, but indirectly through prevention of the access of air supply. But this matter has already been considered along with respiration and aeration, where the various protective adaptations (air passages, aerating structures, utilization of the dissolved air of the water),—have been sufficiently described. A very different kind of protective

adaptation against damage by water has been claimed by those who believe that transpiration is not simply an unavoidable evil, but a process of value in itself. The presence of water on leaves, derived from dew or the rain, must check transpiration, partly by blocking the stomata, and partly by the creation of a moist atmosphere around the leaves during its evaporation; and any arrangements tending to prevent the wetting, or facilitate the drying, of leaves would thus be protective. Such arrangements do, apparently, exist in those waxy or other unwettable coatings which enable leaves to shed water in small drops as one can see readily in the Garden Nasturtium, the Pond Lilies, and a great many others, some of which show a silvery film of air all over the leaf when plunged into a vessel of water. The same result is claimed to follow in a different way in those very many leaves of tropical rainy regions which taper off to a long slender tip ending in a very small point; these tips collect, as it were, the water-drops as they slip down the hanging leaf, and guide them to the point whence their own weight makes them drip to the ground, leaving the surface well drained, and ready the sooner to begin transpiration.

There is, however, one way in which water can damage plant-structures directly, and it actually happens with grains of pollen when these are touched by the rain. The functions and mode of growth of these grains, which will be fully described in the following chapter, is such that their walls are necessarily thin and their contents osmotically attractive to water, whence it happens that if they become touched thereby, they absorb it, swell up, and burst, as can be seen very clearly when the water is added to grains under the microscope. The pollen, therefore, needs protection from rain, whereto a good many adaptations have been found, as can be considered, however, more appropriately along with the Flower in the chapter devoted to that subject. It has also been claimed that the surface-cells of the simple and soft-bodied plants of fresh water are subject to a similar osmotic

absorption, especially in very warm weather; and this might, if too sudden, produce damaging distension and perhaps rupture of the walls. But these plants are commonly covered by a thin coating of jelly, which is known to greatly impede the rapidity of water-passage, thus allowing enough time for an equalization of pressures through the stem. This is very likely the adaptational significance of the jelly, or slime, of water plants generally.

But the forces of the air, the earth and the waters are not the only ones hostile to plants, for among their worst enemies are other plants, and animals. As to plant enemies, the most deadly are the parasites, the Bacteria, Molds, Mildews, Blights, Rots, Rusts, Smuts, and other Fungi which often destroy their host plants entirely. Yet few, if any, positive adaptations have been found in plants protective against these parasites, although some of the oils and resins occasionally found in leaves do appear to afford a moderate protection against Fungi as well as against animals. Practically all of these plants reproduce by spores which are blown about by the wind; and when these fall upon suitable plants they germinate into slender threads. These, for the most part, have no power to penetrate the epidermis, which is thus somewhat protective against them; but they enter the open stomata and thus reach the soft food-filled cells of the leaf, which they proceed to devour. Thus the necessity for the existence of stomata involves another danger besides that of excessive transpiration, and in this case one against which plants seem well-nigh helpless. However, plants differ immensely,—not only different species but even different individuals of the same species,—in their susceptibility to injury by parasitic Fungi, and there is very good reason to believe that the differences have a chemical basis, some kinds possessing a chemical constitution hostile to the growth of the parasite while others do not. These differences offer a basis for the attempts now being made in many experiment stations, to combat plant diseases by breeding immune varieties,—the less susceptible

individuals being preserved for breeding in each generation. And perhaps it will yet be found that plants can be rendered immune by acclimatization, so to speak, to their diseases, as animals can be to theirs. But of these matters we know little as yet.

We come finally to the last of the environmental factors hostile to plants, and that is the depredations of animals. These, indeed, cannot be otherwise than constant and great, since in the long run every jot of the food that is eaten by animals has to be ravaged from plants. The general defense of plants, however, is passive and indirect, consisting chiefly in a reliance upon their own superabundant powers of growth, regeneration, and reproduction, in which features they surpass animals many fold. So great are these powers, indeed, that plants are enabled to produce organic material in vast excess of their own needs, upon which fact depends the very possibility of the existence of animal life. And it may be true that the use of this surplus by animals is not only of no damage to plants, but may even be useful in removing superfluous material and making room for a more active evolution of that which remains. In any case it is a generous payment for the various services which animals render to plants.

Although plants thus appear to possess few adaptations against animal attacks, especially in their vegetative parts, there appear to be notable exceptions. Thus, a good many herbs develop various substances in their stems or their leaves,—bitter oils, turpentine resins, acrid glucosides, astringent tannins, alkaloids, or even needle-pointed irritating crystals,—which render those plants distasteful to herbivorous animals, including all kinds from the greatest of beasts down to slugs and innumerable insects. Everybody has noticed the clumps of such plants left standing quite isolated in pastures by cattle which browse the grass well-nigh to the roots all around them. In these cases, however, the protection is perhaps incidental rather than adaptational, and may be defensive against Fungi rather than animals;

but there are other instances where the actual adaptation seems reasonably clear. Thus, in the desert the conditions of life are so hard that plants can scarcely produce any surplus above their own needs, while the very precious store of water laid up in their stems, and essential to their own safety throughout the dry season, is particularly tempting to large animals. In such plants, accordingly, we find the best development of features that appear to be most protective against animals,—either distasteful secretions, which are especially common and virulent in plants of the deserts, or else a horrid armature of thick-set and dangerous prickles and spines through which animals can penetrate but painfully if at all. Furthermore, a few desert plants are known which resemble so closely the background against which they grow,—either the rough gray surface of the soil (as in the case of the half-buried flat-topped “Living Rock” Cactus of the American Southwest), or else the drab pebbles in the beds of dry water-courses (as in a number of plants described from the peculiar flora of South Africa),—that it seems as if such plants must surely escape notice by animals, and secure a protection, by this form of mimicry, though here again it may be true that the result is incidental rather than adaptational. But while a protective mimicry seems reasonable in plants of this kind and habit, the same can hardly be said of those cases in the flora of ordinary climates where some kinds have been claimed to secure protection through their resemblance to Nettles, or Poison Ivy, or other plants actually noxious. Indeed, so far as concerns a protective function for the poison of plants like Poison Ivy, there is a difficulty in the fact that the repelling effect is not felt until long after the plant has been injured. I think we do not yet know the meaning of the poisonous quality of plants.

An injury done to the vegetative parts of plants does not extend to other parts, and is easily replaced; but damage to the machinery of growth and reproduction is serious, in correlation with which fact we find in those parts a good many apparently

protective adaptations. Thus, the preservation of the store of food laid up for starting the new vegetation in the Spring is obviously of vital importance. We find in fact that the sugar and starch stored up by perennial or biennial plants is placed underground in bulbs, tubers, or rootstocks, where it is well out of the sight and reach of large animals, especially when the ground is frozen in winter; while in woody perennials, where the food must remain largely above ground, it is scattered thinly throughout a large area of tough woody tissue. As to seeds, they are often protected by hard coats or extra shells, impervious, for the most part, not only to gnawing teeth but also to the digestive juices of animals, though in the case of large nuts the teeth of the squirrels have won a trifle of the same advantage over the hardness of the shells that the gunmakers have won over the armor makers among our own civilized selves, and doubtless after much the same kind of long evolutionary struggle between the two. Adaptations to protection of the food supply in these nuts while still growing and before the hard seed coats are formed have been found in such spines as the Chestnut and Horse Chestnut display: in the bitter taste of some pods: and in their green color which has been taken for protective coloration, though it is also readily interpretable as simply the usual utilization of all available surfaces for the spread of more chlorophyll. The greenness of edible fruits prior to their ripeness has also been interpreted as protective until the time when they turn red or other color and aid in dissemination of the seeds, as we shall consider at length in the fifteenth chapter. Flowers, likewise, exhibit some remarkable adaptations to protection against animals, though in a different way, and combined with some more remarkable adaptations for attracting them, though this is a subject which can be considered more conveniently in our chapter on the Flower. As to protective adaptations of the growth machinery, which is principally the buds, there appear to be several. Not only are the buds important as the originators of new growth, but con-

sisting as they do of a rich store of succulent food, they cannot but prove attractive to smaller animals. Thus, a good many kinds, as in the Grasses, place their buds underground, whence they send up their stems and leaves to the light. In buds that must grow in the air, every soft protoplasmic growing point is deeply buried by the leaves it is forming, for these at first lie tightly against it, and only later open out to the light. Their green color, moreover, must afford an appreciable measure of protective coloration, which is doubtless the chief explanation of the prevalent greenness of the calyx of flowers. In some desert plants, where true leaves are wanting, the buds are sunken deep in a hollow formed by the older tissue, and often are further protected, as in the Cactuses, by a perfect *cheveux de fris* of tough and interlocking spines. The growing points of roots are well protected by their position underground, while the cambium cylinder, likewise richly stored with the most nutritious of food, is deeply enwrapped by the tough fibrous bark, which often contains in addition a great deal of tannin,—a substance strongly distasteful to most gnawing animals.

In viewing this list of adaptations, one is constantly reminded of the fact that they never are perfect in operation, since animals do successfully attack plants against every one of these protections. Like so many others of the adaptations of plants, they are real and are useful, though clumsy. However, they do obviously afford a considerable measure of protection, enough, as it seems, to permit plants to hold their own in the struggle; and in a world that is full this is all that they need.

CHAPTER XI

THE WAYS IN WHICH PLANTS PERPETUATE THEIR KINDS, AND MULTIPLY THEMSELVES IN NUMBER

Reproduction



IF all the facts about life, no one is more fundamental or familiar than this,—that individuals inevitably die. Obviously they must be replaced if the race is to continue, and this replacement is the office of reproduction, which we must now proceed to consider. Our study of the subject will have all the more interest for the reason that, like several others of the physiological processes, reproduction is substantially identical in meaning and method in animals and plants, differing only in some external features connected with their differences in habit. Therefore any knowledge acquired in one kingdom can be transferred to the other; and one may learn from plants the essential nature of reproductive processes in animals, including mankind.

The central fact of reproduction is the formation of new individuals capable of growing into kinds closely like those which produced them. Associated therewith, however, is the further fact that usually the formation of a new individual requires the coöperation, through the act of fertilization, of two parent individuals of different sexes; and so prominent is this feature, especially among the higher animals, that most people consider it an indispensable feature of reproduction. This idea, however, is not correct, and the two things,—formation of new individuals and sexual union,—though so often associated, are quite independent in their nature, as is shown by the fact that purely non-sexual, or asexual, reproduction exists abundantly, not only

among plants, but among the simpler animals as well. We may best consider this asexual type before proceeding to the more familiar sexual kind.

Asexual reproduction is effected through the separation of a portion of plant structure capable of growing into a new plant without any preliminary fertilization or other influence of sex.

In the higher and more familiar plants it is rather rare. Almost anybody can recall the dark, ovoid bodies which are borne by Lilies in the axils of their leaves (figure 92), and which easily separate and produce new plants. These, though seemingly seeds, are really a kind of bulblet specialized for this sort of *vegetative multiplication*; and equivalent bodies are found also on a few other kinds of plants. Again, the runners,

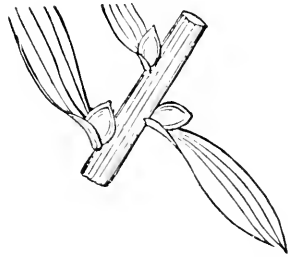


FIG. 92.—A portion of stem, with leaves, of a Lily, showing the axillary bulblets mentioned in the text. (Copied from Gray's *Structural Botany*.)

suckers, stolons, and other similar structures sent over or under the ground by Strawberries, Blackberries, Grasses, and many wide-ranging weeds, produce vegetative shoots at their tips, and thus propagate vegetatively while securing a kind of dissemination, as we shall note more fully in our chapter on the last-mentioned subject. It is, however, a fact of great interest, and likewise of much practical consequence, that although most of the higher plants have lost their power of propagating themselves vegetatively, they can yet be made artificially to reproduce in that way. Thus, the propagation of plants by slips or cuttings of any sort is artificial vegetative reproduction. Great numbers of plants will strike root of themselves and grow when slips thereof are placed in the earth; others which will make no roots in this way can be made to do so by various devices of gardeners; while still others which cannot be made to strike roots at all can yet be fitted with a set, so to speak, by the operation of grafting, as the reader will learn more fully in our later chapter on Growth.

Asexual reproduction in the lower and simpler plants takes place in two principal ways. In the tiniest plants, which comprise the Bacteria, or Germs, and some of the simplest Seaweeds,



FIG. 93.—Stages in the division of a one-celled plant, *Pleurococcus* highly magnified. The cells later fall apart. (Copied from the Chicago Textbook).

the entire plant body consists of no more than a single cell, which in reproduction splits directly across the middle; the two parts then grow promptly to full size, only to split again, and so on without limit (figure 93),—a method called *fission*, or *division*. Nothing could be simpler, which explains the extreme rapidity of multiplication in the forms that possess it. And it is interesting to observe that this is exactly the method whereby single cells reproduce in even the highest of plants. A second method

of asexual reproduction in the simpler plants consists in the formation of *asexual spores*, which, under great diversity of habit and form, exhibit these features in common,—that they are single cells separated off from the parent plant, and capable of growth directly each to a new plant. In some Seaweeds they are provided with swimming appliances whereby they can move through the water in a manner so suggestive of animals that they are known scientifically as *zoöspores* (figure 94), though in other Seaweeds they are drifted passively about by the water-currents. Non-motile spores occur in many land plants:—are formed in profusion in the gills of Mushrooms, the capsules of Mosses, the brown spots (or sori), on the under sides of the fronds of

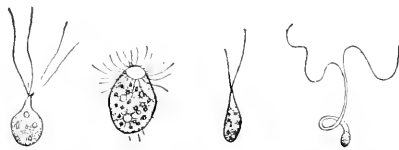


FIG. 94.—Forms of free-swimming reproductive cells, of which the two on the left are asexual zoöspores, while the two on the right are sexual cells, later to be described.

Ferns, and in the black stalked heads that develop on various Molds (figure 95), whence they are wafted on the wings of the wind to the uttermost parts of the earth. Oft-times these asexual

spores are provided with coats of such thickness and hardness as to make them immune against every natural condition of dryness and heat for weeks, months or years together; which fact, in conjunction with their power of floating with the dust in the air, explains their ubiquitous penetration into all kinds of strange places. It is thus that Bacteria and Yeasts, for example, are enabled to spread so widely as they do.

Such is asexual reproduction, which never involves fertilization, and has no relation whatsoever to sex. In sharp contrast stands sexual reproduction, involving the coöperation, through fertilization, of two parents which are usually, though not always, of different sexes.

We may best begin our study of fertilization with the more familiar plants, where it occurs in the flower, which is a structure specially adapted thereto. In a typical flower, as everyone knows, the outer green protective calyx and the inner colored showy corolla together enclose the stamens and the pistils (figure 96). The stamen consists of a slender stalk crowned by a chamber, the *anther*, containing a fine yellow dust, the grains of *pollen*, inside of which develop the male cells of the plant. The pistil consists of a rounded chamber, the *ovary*, extending upwards into a lengthened stalk, the *style*, ending in a roughened swelling, the *stigma*, and containing one or more *ovules* in which develop the female cells of the plant. If, further, a critical examination is made of a typical ovule, by aid of longitudinal sections and microscope (figure 97), it is found to enclose inside of some coats a definite cavity, the *embryo sac*, within which in turn is considerable protoplasm and several cells, including a larger one close to the end where an opening (the *micropyle*) is left through the coats. This larger cell is the female generative cell, the exact equivalent

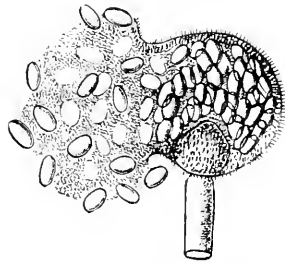


FIG. 95.—The spore case of a Mold, discharging its asexual spores; highly magnified. (From a much-copied picture by Brefeld.)

of the egg in animals, and hence called the *egg-cell*. Thus much for the female reproductive apparatus; turning now to the male, we find it in the pollen grain, which, examined microscopically, is found to consist of at least two cells (figure 98), of which one

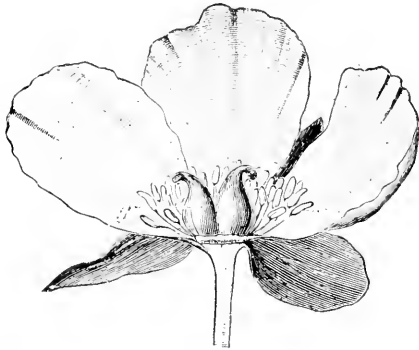


FIG. 96.—Interior view of a typical flower (of Peony), showing the four distinctive parts,—the outer calyx, made up of sepals, the more showy corolla, made up of petals, the many stamens, and the two pistils, which in this case show typical ovaries, but very short styles and small stigmas. (Copied from Strasburger's *Textbook*).

gives rise to the male, or sperm, cells, presently to be further described. Such is the floral structure, and such the appearance and locations of the sexual cells, when fully ripe and ready for fertilization.

The process of fertilization itself can be followed in detail by aid of the microscope, and is shown in essentials by our generalized drawing (figure 99). The first step is pollination, or the transfer of the pollen grain from the anther

to the stigma, and since the pollen is usually brought from a separate plant, the process is far more elaborate than one would imagine, and one, withal, which involves so many striking and interesting features that we must treat the subject in a chapter by itself; and that chapter follows. When the pollen grain reaches the stigma, to which it is held by a certain roughness aided by a sugary stickiness, it immediately begins to send out a slender tube. This tube, which carries in its tip two nuclei that represent the essential parts of two male cells, grows down into the tissues, through which it dissolves its way by aid of enzymes secreted by the tip, the dissolved substance being absorbed for food; and thus the tube literally digests its way down through the tissues of stigma and style to the cavity of the ovary. Here it passes out from the solid tissue, and, guided as it

seems by some chemical vapor exuded from the micropylar opening of the ovule, grows straight thereto and enters, pursuing its way until its tip comes to lie flat against the egg-cell. Then one of the male nuclei moves out of the tube into the egg-cell (figure 100), and across it to the nucleus thereof; then the two nuclei touch, flatten a bit against one another, and finally fuse and intermingle completely. Thus the egg-cell comes to possess a nucleus made up from the two parents, male and female; and this is the central and most essential feature of fertilization. The fertilized egg-cell is now ready to grow into an embryo, which, with certain accessory parts, forms the seed, and later grows to an adult new plant.

I have described somewhat fully this process of fertilization as it occurs in an ordinary plant because it is typical in principle of all fertilization through the plant and animal kingdoms. The machinery varies immensely of course in detail. In some kinds of plants the sperm cell is not carried by a growing tube, but, guided by certain attractive chemicals exuded by the female parts, swims of itself in water to the egg-cell, as is the way in Ferns, Mosses and many Seaweeds. In most animals, however, the male cells (called spermatozoids) are brought by suitable organs to the near vicinity of the egg-cells, to which they finally

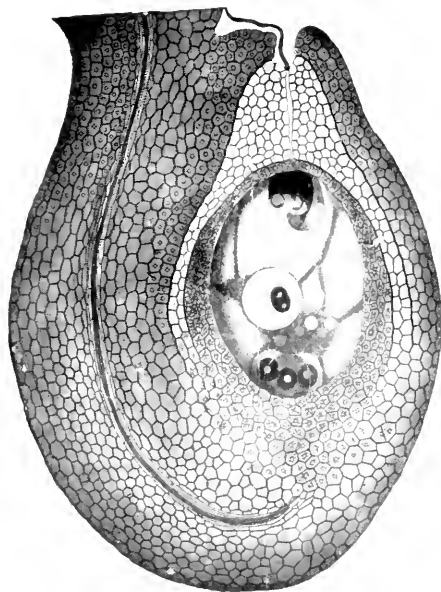


FIG. 97.—A typical ovule (of *Narcissus*), seen in optical longitudinal section, highly magnified. The parts may be identified from the text, the most important being the egg-cell, which is the larger of the three cells lying in the upper end of the embryo sac. (Copied from a wall-chart by Dodel-Port).

swim of themselves. But in all cases the principle is the same; by suitable structures and accessory adjustments and adaptations,

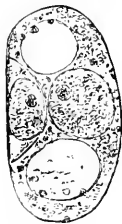


FIG. 98.—A typical pollen grain (of *Tradescantia*), seen in optical section and highly magnified, showing, on the left, the cell which produces the male, or sperm, cells. (Copied from Strasburger's *Textbook*).

the male cell is brought into contact with an egg-cell, to which it passes over its nucleus, with more or less cytoplasm; the two nuclei then fuse, and thus is formed a fertilized egg-cell from which the new individual develops.

In following this process it becomes evident that the object of all the elaborate machinery of fertilization is to secure the union of the male and female nuclei, for that is the one feature which is completely constant throughout. This of course raises the question as to what the nucleus actually is. As our chapter on Protoplasm showed, every nucleus contains a certain peculiar matter called chromatin, which, ordinarily scattered throughout the nucleus, collects itself at times into a definite number of rod-like structures called *chromosomes* (figure 101). The evidence seems to show beyond question, though the method thereof is in doubt, that these chromosomes embody within themselves the characteristics of the parent plants, (or, constitute the working plans or patterns thereof, so to speak), and in such manner as to exert control over the development of offspring, and ensure that new individuals shall grow up in resemblance to those that produced them. Now in fertilization each nucleus contributes its chromosomes, so that the nucleus of the fertilized egg-cell contains a double number derived equally from both parents (figure 100). The significance of this fact, however, becomes apparent only as we follow the behavior of the chromosomes during the development of the fertilized egg-cell into an adult plant; for in such development, the egg-cell first divides across into two, and then its parts into two, and so on until the whole plant is completely grown. Now in the first division each one of the chromosomes, both those

derived from the male and those derived from the female parent, split lengthwise into two, and one of the halves goes into one new cell and the other into the other; and they absorb nourishment and grow with the cell. This process is then repeated with every subsequent division, so that finally every cell of the adult plant contains chromosome material derived from each one of the parents of that plant. This fact helps to explain how it is that a plant or an animal can resemble either one of its parents in any detail of its structure.

At this point I will pause for a moment to consider two matters of minor importance which may have occurred to the reader. If the fertilized egg-cell contains the sum of the chromosomes of the two uniting nuclei, why is not this number doubled again in the next generation, and that again doubled in the next, and so on to their enormous multiplication? The explanation is simple; at some period in the development of the new sexual cells, by a method which we need not here trace in detail, the number of chromosomes is reduced to one-half. In the second place, if every cell contains within itself chromosome matter derived from both parents, and therefore has the possibility of resembling either one of its parents in any detail of its structure, what is it that determines which one it shall resemble? This we do not yet know, but the probability would seem to be that in each case the stronger of the two elements overpowers the other and reproduces its like.

The equal contribution of chromosome matter by male and female nuclei, together with the subsequent regular splitting of

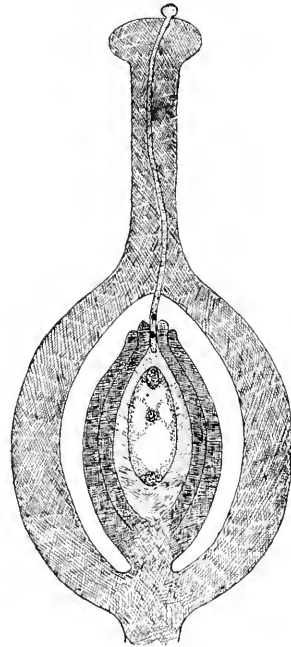


FIG. 99.—A generalized drawing of a simple ovary and ovule seen in longitudinal section, showing the parts concerned in fertilization.

each chromosome in cell division, carries an implication of great importance to an understanding of the nature of sexual reproduction, namely, it implies that both parents contribute exactly alike to the characteristics of the offspring, the selection between the double set of paternal and maternal characters being made in the course of development of the offspring itself. This view is dia-

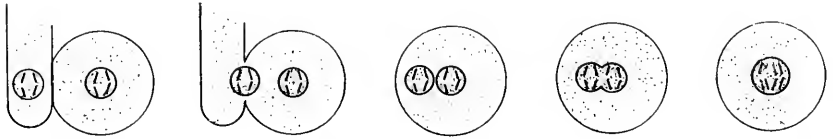


FIG. 100.—A diagrammatic representation of fertilization, showing the passage of the male nucleus from the pollen tube into the egg-cell, and its fusion with the nucleus thereof. The black rods in the nuclei are chromosomes, described on page 284.

metrically opposed to the older idea, once advocated by some biologists, that each parent contributes something the other does not; and it is obviously quite different from the various popular notions, which, naturally, are largely erroneous.

But now there arises this fundamental question. If the two sexes contribute substantially alike to the offspring, why are they not substantially alike in structure? What is the meaning of the differences between the sexes? Or, to go a stage deeper, why does sex exist at all? Happily these questions can be answered with reasonable certainty through evidence supplied by a study of existing transitions from the simplest plants, where sex has not yet developed, to the highest plants and animals, where it is fully differentiated. Thus, there exist some simply-organized seaweeds which throw out into the water a great many reproductive cells, all exactly alike and provided with suitable structures for swimming (figure 102). These move towards one another and come together in couples, which then fuse completely, uniting their nuclei; and thus is formed a "fertilized" cell which gives origin to a new plant precisely as does a fertilized egg-cell. Obviously fertilization in this case occurs between sexual cells precisely alike;

or, if one pleases, it is fertilization without sex. In the next place there are other and more highly organized seaweeds in which the reproductive cells given off into the water are of two different kinds, although produced by the same parent plant. One kind is very much larger, round, and without arrangements for locomo-

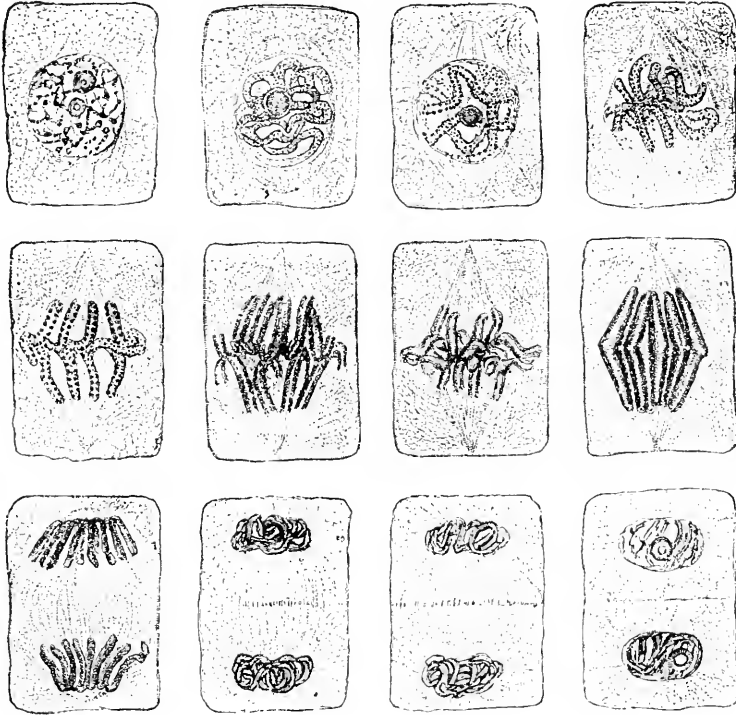


FIG. 101.—The appearance and behavior of the chromosomes during the division of a typical plant cell, as seen, somewhat generalized, in a series of optical sections highly magnified. A fuller description of the division of the chromosomes is given on page 284 of this book. (Copied from Strasburger's *Textbook*.)

tion, while the other is much smaller, of elongated shape and provided with good swimming organs (figure 103). All of the movement necessary to bring the two cells together in fertilization is made by the active smaller cell, which, guided no doubt by some chemical secretion, swims to the passive larger one and fuses therewith; the two nuclei then unite and from this fertilized cell

a new plant is developed. Now the difference between the two cells is known to consist in this, that the larger possesses a store of food substance, which is used in giving a start to the new individual,—the presence of this food substance in the cell being re-



FIG. 102.—Typical free-swimming sexual cells (of the Water net), highly magnified. At the left is a single one and at the right a pair in process of fusion. (Copied from the Chicago *Textbook*.)

sponsible both for its larger size and its loss of locomotive power. The smaller cell, on the other hand, contributes no food for starting the offspring, but elaborates the features concerned in locomotion, thus ensuring that the two cells shall be brought together. This difference does not imply in the least that the two cells contribute differently to the offspring, for the food substance supplied by the larger cell has no more to do with determining the essential characters of the new individual than has the food we eat in

determining our essential characters; the characters are determined by the chromatin in the nuclei, which the two cells contribute equally. But in this comparatively minor feature of division of labor between the two kinds of cells we have the origin of sex, for the larger cell we recognize as female and call it the egg-cell, and the smaller we recognize as male and call it the spermatozoid (or antherozoid). This difference between a large immobile egg-cell and a tiny active male cell, once established, persists and prevails in principle, though with numerous variations of detail, throughout all of the more highly organized plants, and throughout all of the higher animals, inclusive of man; and it is the foundation of all the phenomena of sex.

The essential characters of the sexual cells being thus established in these comparatively low plants in a degree of development as high as they ever attain, the sexual developments in the higher plants are concerned not with the sexual cells, but with the various accessory structures contributing to ensure fertilization under the conditions to which those plants are exposed. A first

step in the development of such secondary sexual structures is found even in the higher Seaweeds (the Red Algae), in which the egg-cell is not cast loose, as in the lower forms, but remains attached to the parent plant that forms it and supplies its store of nourishment; while simple arrangements exist to facilitate the access of the male cell. But far more important is the step taken

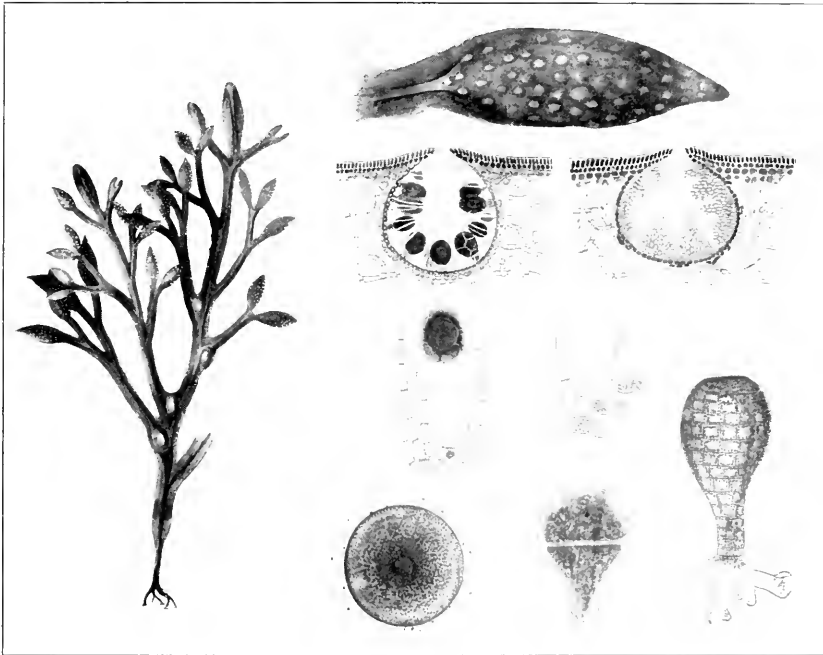


FIG. 103.—A series of figures illustrating the reproduction of the common Rockweed. In the middle lower part is the spherical female (egg) cell, highly magnified, surrounded by a number of the very much smaller free-swimming male (sperm) cells.

in the simplest land plants, like the lowly Liverworts and Mosses, and the fertilization stage of the Ferns, i. e., a stage in which the plant is a tiny thin leaf pressed close to the ground. In all of these plants the very delicate egg-cell and the subsequent embryo need protection from the dryness to which they must occasionally be exposed,—and a protection, of course, which does not interfere

with a ready fertilization. The structure which has been developed in adaptation to these conditions is in form of a flask-shaped covering to the buried egg-cell (figure 104); the end of the tube opens when the egg-cell is ripe and water is present, and exudes a special liquid chemototically attractive to the spermatozoids,

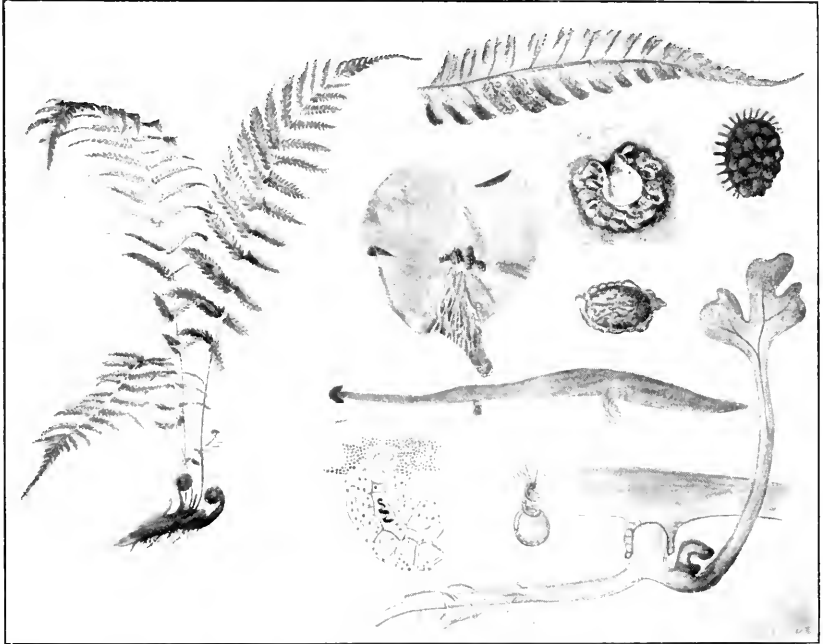


FIG. 104.—A series of figures illustrating the reproduction of a common Fern. The sexual cells are borne on the under side of a small thin leaf-like part close to the ground. In the lower middle part of the picture is a squarish egg-cell with prominent nucleus, buried in chlorophyllous tissue, and covered with an elongated-tubular structure, down the cavity of which a spiral-shaped male cell is proceeding to unite with the egg-cell.

which then swim towards and down the neck to the egg-cell. But such plants are as obviously dependent upon water for fertilization as are the Seaweeds; and hence they are confined to places habitually wet, or must grow so close to the ground that fertilization can be effected during flooding by rains. Still another step, but this time the final one for plants, in the evolution of secondary

sexual structures, is taken in the flowering plants, which carry their sexual parts high up in the air. In consequence of the greater dryness of that situation, they have had to bury their sexual parts far more deeply (viz., deep inside the ovules and anthers), and have had to abandon the free-swimming sperm cell of all the lower kinds and replace it by the growing pollen-tube, which carries the male cell to the female cell in the way we have already described. In a word, the structures developed adaptively in response to the conditions of protection and fertilization in these highest plants are the stamens and pistils, the essential parts of the flower which we have already described. But all such structures, like all of the sexual parts and adaptations developed by animals, are in reality secondary, being merely arrangements to enable the male cell to effect fertilization and the female cell to receive it. The central and essential feature of fertilization and sexual union, viz., the union of nuclei carrying the hereditary qualities of two parents; and the central and essential feature of difference between the sexes, viz., a division of labor between the two parents;—these remain the same throughout the plant and animal kingdoms from the lowliest of the seaweeds up to man himself.

Sex, therefore, does not arise in any essential difference of relation of the two parents to offspring, but in a minor and mechanical matter of division of labor between the sexual cells, involving secondary differences in various accessory structures. Sex, so to speak, is not a matter of method but of mechanism, and exists not for the sake of the formation of offspring but for giving it a more certain and better start in its life. That cell, structure, or individual, which is devoted to nourishing and protecting the young individual formed as a result of fertilization we call female: that cell, structure, or individual, which is devoted to bringing the two cells together for fertilization we call male. This difference is the central feature of all the phenomena of sex, although worked out with infinite variety of detail and more or less interlocked with other considerations; and it explains not only sexual structures in

plants, but in animals also, including man. With man, indeed, the principle that the female is the receptive and protective element, and the male the aggressive element, is not limited to physical structure alone, but shows its influence in some of the profoundest facts of his actions, thoughts, laws, and social customs.

At this point the reader may demur to this explanation of sex on the ground that it seems too superficial for the profundity of the phenomena. But one should take care not to extend to all Nature conceptions derived alone from mankind, where all sexual matters are vastly exaggerated in apparent importance by sociological considerations. In Nature at large sexual differences are prominent rather than profound. Even in plants that are highest in the evolutionary scale, sexual differences never affect the plant-structure very far away from the pistils and stamens; and all of the remainder of the bulk of the plant has nothing whatever to do with sex, but is strictly nonsexual or asexual. Even the occasional cases, described by the term *diacious*, where one plant bears only pistils and another only stamens, is no real exception, though we often describe these plants, very naturally, as male and female respectively. The individual, therefore, in plants is sexual only in limited spots, it is never sexual as a whole. The same is true of the simpler animals, but in the more highly organized species it is somewhat different, for in them each individual bears only one kind of sex cells, and has only one kind of sex organs; while the high specialization of these parts affects somewhat the whole individual so that we distinguish male and female individuals. But even in mankind the structural differences between the sexes are insignificant as compared with the structural resemblances between them.

Whatever else my discussion of sexual reproduction may have meant to the reader, it will at least have demonstrated this, that sexual reproduction is a far more complicated process than asexual, involving the construction and manipulation of adapta-

tions wholly needless in the asexual methods. Yet plants can reproduce perfectly well by the direct and simple asexual methods. In what, then, consists the superiority of sexual reproduction that plants and animals should not only take so great trouble to secure it, but should even abandon in the higher forms the asexual method entirely? Many answers have been proposed for this question, and we do not yet know the truth with certainty; but the most probable explanation is derived from the fact that sexually produced individuals are usually more variable, adaptable, and vigorous than those asexually produced, and hence in the long run overcome the latter in the struggle for existence, and survive while the others die out. An asexually generated individual is naturally no more than a chip of the old block, and can differ but little therefrom, while one sexually produced has the possibility of combining the good qualities from two parents. Now if conditions surrounding plants were unchanging, and all plants were adapted the best possible thereto, then the asexual method might be really the better; but the conditions of the world are continually changing, and therefore those animals and plants which possess the most variability and adaptability have the best chance of maintaining themselves therein. This is the reason, I think, why sexual reproduction, despite its complications, has displaced the far simpler asexual kind.

The greater constancy of characteristics usually distinctive of asexual reproduction, in comparison with the greater variability associated with the sexual type, has some very practical consequences. Thus, as everybody knows, we can reproduce Bartlett pear trees by the asexual method of grafting, and keep the fine qualities of the fruit; but if we propagate them by seeds, which of course are formed only as a result of fertilization, we do not get Bartlett pears at all, but just a plain mongrel variety; and the same thing is true of many other kinds of highly perfected garden plants. This principle is so well understood by gardeners that whenever they seek to secure new forms of plants, they make use

of seed propagation; and whenever they have obtained a specially good kind, they try to preserve it by propagating it asexually. But we are verging over to the subject of plant breeding, which is a matter so important that it must later receive a chapter to itself.

We must here turn back to fertilization in order to consider another important phenomenon in connection therewith. Although in the higher plants both pistils and stamens are usually associated closely together within one flower, it is only exceptionally the case that egg-cells are fertilized by pollen from that same flower. On the contrary there exist the most elaborate arrangements adapted to prevent such a close fertilization, and ensure that the sex cells which unite shall come from different flowers, and usually indeed from different plants. It is in adaptation to such cross pollination that plants have developed the more conspicuous features of the flower, the nectar, odor and showy corolla in particular, as will appear in the following chapter which is wholly devoted to this interesting subject. Indeed, in some plants the arrangement is such, notably where the stamens and pistils are borne on quite different plants, that close fertilization is not even possible; and this arrangement is universal among the higher animals. Now it is quite plain that the fertilization of an ovule by pollen from the very same flower would be vastly easier of accomplishment than is the elaborate cross fertilization,—requiring no more, indeed, than a simple turning of the stamen over against the stigma, when the growth of the pollen-tube would accomplish the rest; and the fact that plants not only choose the most difficult method, but also even abandon in the higher forms the very possibility of the simpler, shows quite conclusively that cross fertilization has some great merit above close fertilization. And the reason for the superiority is not difficult to find. It was first indicated by the experiments of Darwin, who showed that the progeny resulting from cross fertilization can be more vigorous and numerous than those from close fertilization; and the same

thing is confirmed in general by the experience of animal breeders who know that the parents must be not too nearly related if the offspring are to be of the best. Indeed, it is evident that if pollen and ovule belong to the same flower or even the same plant, we have a near approach to vegetative reproduction; while the full value of fertilization can be realized only when the uniting sex cells come from different individuals. In a word, cross fertilization has much the same advantage over close fertilization that fertilization has over asexual reproduction; and this advantage has sufficed to enable the kinds which have developed it to triumph over those which have not. If it seems to the reader that in cases like these Nature goes to a trouble out of all proportion to the advantage attained, I would remind him that life is a kind of race in which only a few can be winners; and that no effort can be too great to put forth when to live is the prize and to lose is death.

There is, furthermore, still another matter of the highest importance which must receive our attention in connection with fertilization. Everybody has heard something about Mendel's Law, though it is not, as yet, widely understood. Mendel was an Austrian monk, who, in his monastery garden, a half century ago, began experimenting systematically upon heredity, and thereby discovered the most important facts we yet know about that fundamental subject. In order that the characters transmitted by each parent might be distinguishable in their offspring, he selected as parents not plants of the same variety, but of distinct varieties differing markedly in some given features; and furthermore, in order to avoid the complications caused by cross fertilization, he chose kinds which fertilize themselves, as do a number of cultivated species. Accordingly, taking Peas, which fulfil these conditions, he bred together a kind with green cotyledons and another with yellow cotyledons. The resulting offspring were of course hybrids, but their cotyledons were not, as one would expect, greenish-yellow, or yellowish-green, but were all yellow

like those of one of the parents and quite free from the green of the other. These hybrids, when grown, were also self-fertilized, and produced a large number of offspring; and as a result a remarkable fact came to light,—namely, that although approximately three-fourths (75%) of these plants possessed yellow cotyledons, one-fourth (25%) had green cotyledons just like those of one of the grandparents. Furthermore, when these green-cotyledoned forms were propagated by self-fertilization, *all* of their numerous offspring had green cotyledons, and never yellow, which color was thus permanently bred out of these plants and their descendants. But when the 75% of yellow-cotyledoned forms were self-fertilized, their offspring gave this striking result, that one-third of them (and therefore one-fourth, or 25%, of the entire original number in this generation) produced only yellow-cotyledoned kinds, as did their offspring, and theirs again indefinitely, the green being thus bred permanently out of these forms and their descendants. But the remaining two-thirds of the yellow kind (forming half, or 50%, of the total number), acted, when self-fertilized, precisely as their parents had done, producing 25% green, and 75% yellow kinds of which latter 25% bred permanently yellow; and the same thing was repeated in the next generation, and so on without limit. The method of this distribution of characters in the offspring is shown graphically in the accompanying diagram (figure 105), in which, however, the exigencies of printing forbid the use of color, for which reason the yellow cotyledons are represented by the solid black circles, and green by the white ones. Moreover, the first generation, (and half of the later individuals) though themselves possessing yellow cotyledons as a visible or so-called *dominant* character, have obviously the power of transmitting the green as an invisible or *recessive* character; and this fact is represented in the diagram by giving to those individuals a white center. It is not yet wholly clear, by the way, why Peas which have the power of transmitting both yellow and green cotyledons should always have yellow ones;

but such is the fact, and such dominance of one character over another is always a feature of Mendelian inheritance.

Now this remarkable distribution of contrasting characters is true not of the cotyledon color of Peas alone, but of their flower colors, their height, and other characteristics; and not of Peas alone but of innumerable other plants, and likewise of the most diverse animals, in the most diverse characters. Moreover, while discovered and most conspicuous in hybrids, it is also true in principle of all kinds which breed together; and while its mathematical basis can be traced clearly only in self-fertilizing forms, it holds true, though of course with proportional complications, in

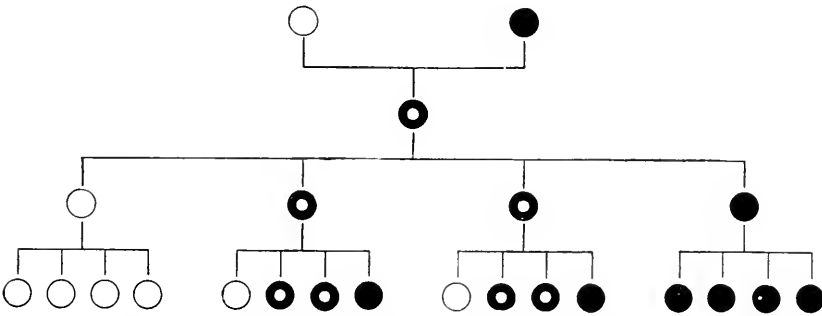


FIG. 105.—A diagram illustrating Mendelian inheritance. It is fully explained in the text.

cross-fertilized forms. There is, indeed, no longer any doubt that it represents a very wide spread principle of heredity. Indeed, were it not for the numerous complications introduced by the complexity of life-phenomena, it would probably be found to hold true universally.

Mendel's discoveries have thus shown not only that heredity is correlated with a certain mathematical principle, but also that any undesirable feature can be rapidly and surely bred out of a race, and need not require the slow process of dilution out, so to speak, as was formerly supposed.

There is one fact about this Mendelian distribution of characters which will illuminate the whole subject greatly if the reader will

but grasp it clearly at the start,—namely, that it applies only to single individual characters, never to large collections of them, and much less to the whole aggregate of characters displayed by each parent. Each of the many characters transmitted by parents to offspring conforms to this general principle, but they are transmitted to no two of the offspring in the same combinations. The offspring are thus like the different patterns displayed by the same pieces of colored glass in the turning of a kaleidoscope; and this is very well exemplified in the familiar cases among mankind, where the characteristics of two parents reappear in the most different combinations in their children. Nevertheless, in self-fertilized races of plants it is possible to fix permanently certain combinations of characters by breeding out their opposites, and then these combinations repeat themselves with the greatest fidelity. Such combinations we shall meet again in our chapter on evolution under the name of genotypes.

Finally, we consider for a moment the explanation of the remarkable mathematical arrangement revealed by Mendel's Law. In the first place it is plain that each definite character of the adult individual is represented by some kind of determiner in the germ cells (i. e. egg-cells and sperm cells), and that any individual is a mosaic of characters of which the germ cells (or, rather, their chromosomes), are collections of the corresponding determiners. Also, the facts show that, in harmony with the behavior of the chromosomes in cell-division and fertilization, while every body cell of each individual contains two determiners for each character (one derived from each parent), every germ cell, because of the reduction division earlier mentioned (page 285), contains only one or the other of these determiners and never both, a fact expressed in the phrase "purity of the germ cells." Thus in our Peas, earlier instanced, each of the male cells, and also each of the female cells, contain a determiner for either a yellow or a green cotyledon, but never both. Now if large numbers of such male and female germ cells are allowed to come together at hap-hazard, as in

fact they do in fertilization, then a certain proportion of those containing yellow determiners will unite with others containing yellows, and green will be excluded from the resulting individuals; a certain proportion of greens will unite with greens, thus excluding yellow; a certain proportion of greens will unite with yellows, and a certain proportion of yellows will unite with greens. These proportions (allowing for the fact that the yellow-green and the green-yellow are indistinguishable) will be precisely those actually found by the law to exist, as above described, and precisely those shown in our diagram.

There remain a few miscellaneous matters, connected with reproduction, which must be considered before this chapter can be brought to a close.

It is almost invariably the case that an egg-cell must be fertilized by a male cell before it will grow to a new plant, but a few exceptions are known. In some few plants of the Composite family, and in the Plant Lice among Insects, the egg-cells grow directly into new individuals without any fertilization or other connection with the males,—a phenomenon appropriately called parthenogenesis. It is a kind of asexual growth of the egg-cell, comparable with the growth of a tiny bud; and possibly the essential meaning of the process lies in its asexual character. It is conceivable that these particular kinds of plants and animals have reached the highest practicable stage of adaptation to the conditions around them, in which case it would be natural for them to preserve their characteristics unchanged by resorting to asexual propagation, using the method which entails least disturbance to existent structures and habits.

In my account of fertilization I showed that the pollen grain when it enters the embryo sac contains two separate nuclei, only one of which is needed to fertilize the egg-cell. The fate of the other is most peculiar, for in some plants at least, and probably as a rule, it fuses with a nucleus belonging to the embryo sac itself. The resultant cell grows into the mass of food substance

(the *endosperm*), devoted to nourishing the embryo in its growth. At first sight it would appear as if the embryo and the endosperm were brothers, so to speak, one of which later feeds cannibalistically upon the other; but probably this is not its meaning. It is more likely that the fusion is simply a method of providing a stimulus for the formation of the endosperm;—a signal, so to speak, to the waiting embryo sac nucleus that fertilization has really been accomplished and therefore the endosperm will be needed,—for the endosperm does not form unless fertilization is accomplished. The matter, however, would have a purely scientific interest were it not for a rather well-known phenomenon it explains. Most people are aware that some varieties of corn produce red ears while others have white ones, and that sometimes, where the two kinds grow together, red grains appear on the white ears. This has long been known to be due in some way to the influence of the pollen of the red kind upon the white ears, but the remarkable matter about it was this, that the color was not in the embryo, where its presence would be natural, but in a part of the grain which was apparently made by the white parent. Here was a case in which the male parent not only fertilized the egg-cell, but even seemed to affect the structure of the female parent, a phenomenon called *xenia* in plants, and often reported, though never confirmed, among animals. But the discovery of this double fertilization removed all mystery from the matter, for the color in the red grains resides wholly in the endosperm, which is a kind of a hybrid between the male and female parents, sharing in the characters of both.

As our chapter on Protoplasm showed, individuals tend to wear out and die when their protoplasm repeats longtime the same function; but they can live potentially forever if the protoplasm can change periodically its internal arrangement,—can go, so to speak, into the melting pot, and be cast anew. Now there is no more effective remelting than that accompanying sexual reproduction, for a greater change in the constitution of the protoplasm

could hardly be imagined than that which occurs through the commingling of two different cells. At all events fertilization is always followed, especially in animals, by that display of vigor and activity which we call youth or juvenescence, whereby the racial vigor is periodically renewed in each generation. Indeed, so prominent and advantageous is this rejuvenescence that some biologists have thought to find therein the chief utility of sexual reproduction. Perhaps it does indeed play some part, for sexual reproduction, like many other physiological processes, is probably not the expression of a single factor, but the resultant of the co-operation of several.

Replacement of the individuals which must die is no doubt the first meaning of reproduction, but therewith is often associated the idea of multiplication in number. Multiplication, however, is more seeming than real, as shown by this fact, that in general any kind of animal or plant, no matter how numerous its offspring, does not alter its numbers appreciably from one year to another. Thus, in general, there are no more Mushrooms, Dandelions, or Robins in a given county this year than last, and the numbers of each kind remain for decades substantially stationary. Even the occasional exceptions caused by the introduction of new weeds or animal pests, or by the expansion of man himself, is no real exception, for after a time these also attain a condition of numerical stability. Hence, the offspring formed by animals and plants do not in general increase their numbers, but simply make up for losses. In reproduction, therefore, multiplication is subordinate to continuance of the kind.

Reproduction, as we have seen, is essentially Nature's method of continuing the kinds of plants or of animals as the individuals perish. This being true it follows that if the individuals were immortal, there would be no need for reproduction, after once the world was fully populated. This view receives confirmation from the balance which exists between the vegetative prosperity of the individual and its reproduction,—anything favoring the one

tending to check the other. Thus, many simple forms will not form reproductive parts so long as the solutions in which they live contain plenty of food, and the other conditions are favorable; and it is only when they begin to feel the effects of insufficient food or temperature that they will begin to form reproductive bodies at all. Even in the higher plants the same principle holds, and all farmers know that when soils are too heavily fertilized many plants tend to "run to leaf," and flower very badly, while there are plants of our greenhouses (e. g. *Bougainvillaea*) which must actually be partially starved before they will form any flowers. The same principle holds good with animals; they must not be too highly pampered and fed, else their reproductive powers suffer. I believe that we have the operation of the same principle upon a very large scale among mankind in the fall of the birth-rate amongst the most highly civilized races, and the highest classes of each race. In general the birth-rate is lowest where the hygienic and other conditions are most favorable for the preservation and comfort of the individual, and the birth-rate grows higher among peoples and classes in which the conditions of life are markedly harder. Harder conditions of life presage an earlier end to the life of the individual, and Nature seems to have adopted their presence as the stimulus or signal for setting the reproductive apparatus more actively at work.

CHAPTER XII

THE MANY REMARKABLE ARRANGEMENTS BY WHICH PLANTS SECURE UNION OF THE SEXES

Cross pollination; Flowers



THE preceding chapter should have made it quite clear that plants possess sex; that this is the same, both female and male, as it is among animals; that a union of the two is generally needful for the production of offspring; and that the offspring is usually better in quality if the uniting sex cells are derived from separate parent plants. But the union of sex cells from separate parents presents a difficult problem to those plants which, including all of the higher and more familiar kinds, are sedentary, and therefore unable to come together by their own powers of locomotion, as animals, and indeed some of the water plants, so readily do. Specifically, their problem is this, to secure the transfer of the small and light pollen grains, which contain the male cells, from the anthers of one plant across some space to the stigmas, which give access to the female cells contained in the ovules, of another, after which, of course, fertilization proceeds by the methods already described very fully in the chapter on Reproduction. The problem of cross fertilization, therefore, resolves itself in such plants into one of cross pollination, which is effected by methods that we must now consider in detail.

Let us first dispose of the simpler methods displayed by the Water plants, which in some cases possess an animal-like power of independent locomotion by swimming, particularly in their

male cells. In most of the Seaweeds (or Algae), of both salt and fresh water, both kinds of sexual cells are cast out into the water, where those from different plants become completely commingled, especially under action of currents, waves, and the

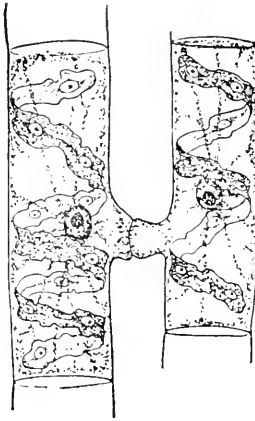


FIG. 106.—Cells, from distinct plants, of the Alga *Spirogyra*, highly magnified, showing the formation of a fertilization tube. (From the Chicago *Text-book*.)

power of the male cells to swim freely about; and apparently mere chance under these conditions is enough to ensure a sufficiency of crossing between different parents, although, for all we know, elaborate physiological arrangements, comparable with some of those which will presently be described for the higher plants, may exist to prevent union of sex cells produced by the same plant. Such arrangements, indeed, are known to occur in the higher kinds of plants fertilized in the

water, notably the Ferns, where the male and female sex cells produced on the same plant ripen at different times. Again, in some other kinds of low Water plants, whose habits are such that the many long threads of which their bodies consist live tangled or felted together, slender tubular projections (a kind of premonition of the pollen-tube), grow out and connect one thread with another (figure 106); and through the passage thus formed the contents of one cell can unite with another in cross fertilization, though plenty of cases are known in which the same method is used in the fertilization of one cell by another within the same thread.

While the Seaweeds, or Algae, are the distinctive plants of the waters, a good many kinds of Flowering plants, originally inhabitants of the land, have been forced into life in the water, developing, of course, appropriate adaptations thereto. Of these, the conspicuous kinds, like the Water Lilies, secure their cross pollination by the very same methods as the showy-flowered

plants of the land, which we shall consider a few pages later; but a great many others of simpler sort, including especially the lowlier Waterweeds, cast their suitably-protected pollen out into the water, to be drifted about by the currents until it reaches the stigmas. In some kinds, as in most of the Eel-grasses, where the pollen is thread-like in shape, the pollination occurs under water; but in others, for example the Freshwater Eel-grass, *Vallisneria spiralis* (figure 107), it takes place on the surface, to which the staminate flowers rise from their place of formation, and on which floats the ripe ovary with widely-spread stigmas. Then the movements of the surface currents, with aid of the wind, bring the pollen sooner or later to the stigma.

But far more striking and important are the adaptations to cross pollination found in plants that live out on the land, including the kinds with which we are most familiar. These, having no power at all of locomotion, have had to secure the

transport of their pollen in some different way and that way consists in the utilization, by aid of suitable adaptive mechanisms and methods, of such motive agencies as happen to exist in the world around. Now of all such agencies, the most ubiquitous and the easiest to utilize is the wind. Accordingly wind pollination prevails

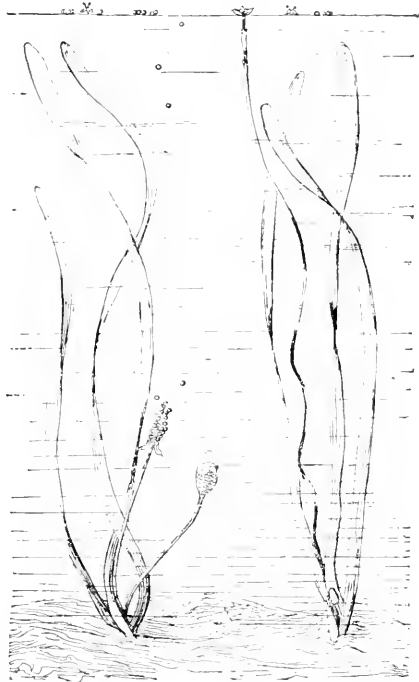


FIG. 107.—Cross pollination in the Waterweed, *Vallisneria spiralis*, which is shown about one-third the natural size. The staminate flowers may be seen rising to the surface, where they open and are drifted about until their stamens come into contact with the long-stalked floating pistillate flowers. (Copied, somewhat simplified, from Kerner's *Pflanzenleben*.)

in a good many plants, especially trees, and, in lesser degree, shrubs, for these are most exposed to the sweep of the winds; while it is rare in herbs and confined mostly to those that grow in fully exposed places. In such plants the smooth light pollen grains often possess bladders, or wings providing more surface for action of the wind (figure 108), while, moreover they are produced in vast

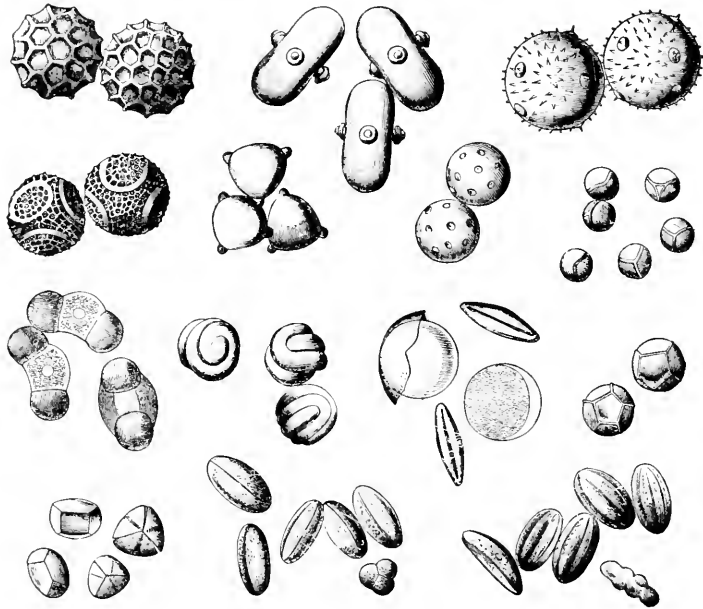


FIG. 108.—Typical pollen grains, highly magnified. On the left next above the bottom row, are three from the Pine, showing the attached bladders. The very rough kinds, especially those of the upper row, are carried by insects, to whose hairy bodies they are thus adapted to cling. (Reduced from Kerner's *Pflanzenleben*).

quantities to compensate for the inevitable waste inseparable from this method. For this reason the staminate blossoms of such plants far outnumber the pistillate, as witnessed by the fact that long hanging staminate catkins, from which one can dislodge a cloud of fine yellow dust by a touch, are familiar to everybody in Birches, Alders, Poplars, Butternuts, and other trees in the spring; while the pistillate blossoms, which commonly occur on

separate plants, or at least in separate flowers, are comparatively so inconspicuous that they scarcely are known at all, and need a considerable search to reveal them. The relative conspicuousness and abundance of the two kinds of blossoms are typically shown by the Hazel (figure 109). When found, however, these pistils are distinguished by large, and usually branched or hairy, stigmas,—an obvious net spread for the stoppage of the wind-drifted pollen. Thus the “silk” of the Corn, wherein each strand is a style along which grows a pollen-tube to each grain, stands out from the young ears when their grains are ready for fertilization, as a feathery cluster of styles and stigmas, which catch the pollen carried by wind from the staminate tassels, though later when its usefulness is past, the silk withers limply down. In cases where no stigmas are present, as for example in many cone-bearing plants, like the Spruces and Pines, there is usually some arrangement of smooth scales which guide the incident pollen down to the vicinity of the ovules. Furthermore, it is obvious that the efficiency of wind pollination depends on the greatest possible freedom of wind action through the branches, and therefore on absence of interference by the leaves. This is the reason why so many wind-pollinated flowers open

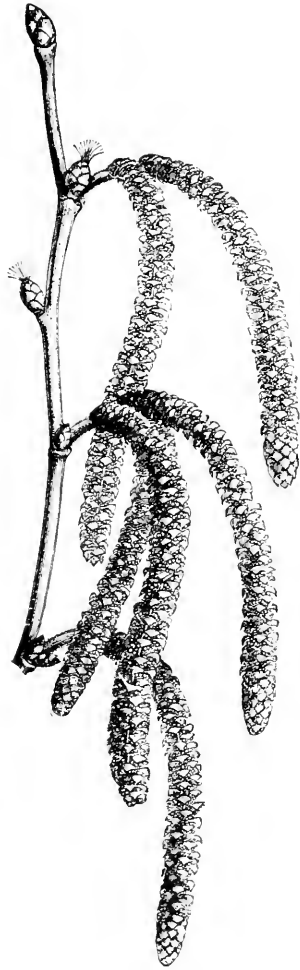


FIG. 109.—Flower clusters of the European Hazel, a typical wind pollinated plant, showing the great disproportion in bulk between the male and the female flowers, the former being the long drooping catkins, and the latter the small ovoid-tufted structures. (Copied from Kerner's *Pflanzenleben*.)

in the very early spring before the leaves have appeared, as catkins for example all do, and the flowers of some Maples; while that first feathery bloom shown by Elms against the spring sky is caused by the wind-pollinated flowers, and not by the leaves as most folks think. The same end is attained in a different way in those cases where the blossoms are borne out at the extreme tips of the branches, as in most kinds of evergreens, while a still more notable example is found in the Grasses, which raise their spikes or panicles of inconspicuous greenish blossoms high over the leaves, as any meadow well illustrates. And a good many other adaptations to wind pollination are found in particular cases. But in general these features,—occurrence on trees in particular; light and superabundant pollen, and therefore relatively prominent male blossoms; much-branched stigmas on prominently placed though rather inconspicuous female flowers; an early blossoming period or an exposed blossoming position—distinguish the wind-pollinated plants. And to these characters may be added another, of a negative though no less distinctive sort, that such flowers possess hardly any of the features that we commonly associate with the name,—no bright colors, aside from an occasional case of the early spring red, no odors, no nectar, no striking forms, no great size. The reason for their absence is obvious enough,—such features are not needed in wind pollination.

But wind pollination, widely used though it is, becomes almost insignificant when compared with a different method which surpasses it many fold in economy, efficiency and extensiveness of use. A great disadvantage of wind pollination consists in its wastefulness; for of all the great quantities of pollen cast out on the winds from the anthers of plants, not more than an insignificant proportion can happen to fall on receptive stigmas. One can gather, indeed, a vivid idea of the wastefulness of this method from the fact, which some of my readers may have seen for themselves as I have, that in northern countries, where wind-pollinated

trees, especially the cone-bearing kinds, are particularly abundant, the little lakes of the woods are covered in the spring time with pollen enough to make a continuous film all over the surfaces, while of course an equal amount must fall on the land. So plenty at times is the pollen in the air of those countries that it receives the expressive appellation of "sulphur-shower." Now pollen, composed as it is almost wholly of the richest protoplasmic material, is one of the most difficult and expensive of substances for plants to manufacture; and therefore the wastefulness of wind pollination must entail a great drain on these plants. Obviously, any method which would ensure the transfer of pollen direct from the anthers of one plant to the stigmas of another would be greatly superior in both economy and certainty to wind pollination. Such a method, indeed, plants have developed; and it consists in the utilization of the locomotive powers of animals, especially insects.

We turn, accordingly, to the study of the cross pollination of flowers by insects. Obviously a first requisite of the method is an arrangement that will lead insects to go directly from flower to flower,—a thing which they will not do unless induced by some attraction or compulsion. The inducement takes the form of a store of nectar,—a sugary liquid both nutritious and palatable to insects, and easily made by plants in little superficial glands. These nectar glands, which often pour their product into special receptacles called nectaries, and which exhibit a great variety of forms in different flowers, are of course placed in close juxtaposition to the stamens and pistils (figure 110). They constitute the most fundamental feature of insect-pollinated flowers; and those plants which possess them along with stamens or pistils but no other parts, for example the Willows and some Maples, represent a first stage in the evolution of the insect-pollinated flower. But a second requisite of the method is some arrangement by which the position of the inconspicuous nectar (and therefore of the stamens and pistils), can be made evident to the insects; and this

is accomplished by the provision of a blotch of color, which is formed and spread in a special set of leaves developed for the purpose,—the corolla. This is the reason for the existence of color in flowers;—it is a notice or signal, advertising to insects the position

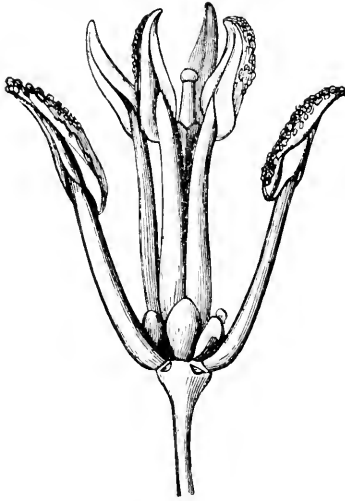


FIG. 110.—A flower, enlarged, of the Rape, with petals and sepals removed to show the contiguity of the nectar glands (the ovoid structures near the base) to the stamens and pistils. (Copied from Goebel's *Outlines of Classification*.)

of the nectar, which is the real attraction. Finally, a third requisite of the method is such a construction of the flowers as will make it inevitable that the insect, as it enters a pollen-ripe flower in the quest for its nectar, shall receive on its body a supply of the pollen which it will as inevitably leave on the stigma in entering an ovule-ripe flower. And this is the explanation of the principal peculiarities of shapes and sizes in flowers, which, because insects are most diverse in form and habits, are themselves equally diverse in details of construction. Furthermore, it is plain that the reason for the separation of the stamens and pistils into separate flowers in the wind-

pollinated kinds does not hold in those that are pollinated by insects; for in these, on the contrary, there are advantages, as to economy of number of blossoms and also of insect visits, in having both stamens and pistils associated in the same flowers. This, accordingly, is the prevailing condition in showy blossoms.

Thus it is evident that the most striking features of the flowers of the higher plants, including the ones with which our very conception of the flower is most closely associated,—the colored corolla, nectar, odor, and striking peculiarities of shapes, exist in adaptation to cross pollination by insects. Or, the matter can be stated in this way,—*the flower is an organ evolved in adaptation to*

the advantage of the coöperation of two parent plants in the production of offspring.

In my discussion of this subject I am assuming that the reader already has some general knowledge of the relationship existing between flowers and insects. Surely there is no one whose attitude towards nature is such as to lead him to read thus far in this book, who has not observed with interested attention the actions of insects among the flowers in a garden; and a little more watching will always reveal the same things in the flowers of field, roadside or forest. But it may be well if I insert at this point, in further illustration of our subject, a description of some conspicuous examples of adaptations to cross pollination.

There grows commonly in Europe, and sparingly in this country where it has been introduced, a small upright herbaceous plant called *Aristolochia Clematitis*, whose yellow tubular blossoms, an inch or so long, stand upright and invitingly open when ready for fertilization. It is cross pollinated by small flies, which, bringing pollen on their bodies from other flowers, slip easily down the tube through the downward-pointing hairs (figure 111). Then, working around after the nectar in the middle part of the chamber, to which they are confined by other hairs in the base, they leave their pollen on the stigmas (the hooked structures of the figure), which soon curl back out of the way of further pollination. Immediately the hairs in the base wither up, and the insects go there

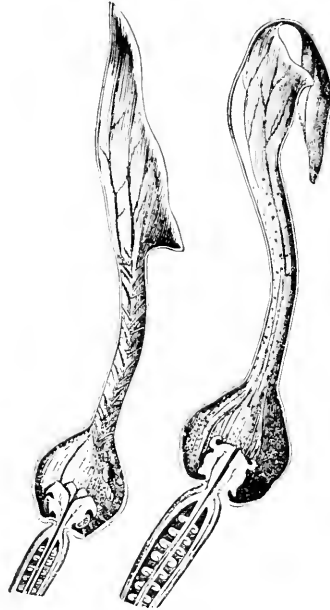


FIG. 111.—Flowers of *Aristolochia Clematitis*, just before and just after pollination, the method whereof is explained in the text. (Simplified somewhat from Sachs' Lectures.)

for the nectar, when the anthers open and shed new pollen on their bodies. Then the nectar-secretion ceases, and simultaneously the hairs in the throat, hitherto impassable in an upward direction, wither up, and the insect hies him away with his

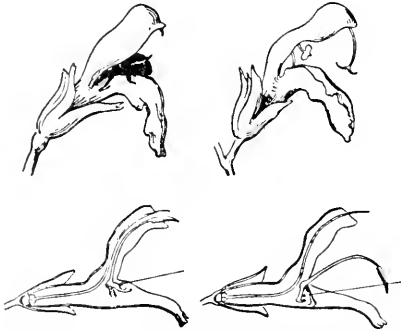


FIG. 112.—A *Salvia* flower (substantially like *S. pratensis*), in general view and in section, showing the mode of cross pollination described in the text. The line on the sections indicates the direction of thrust of the insect's proboscis. (Copied, with slight simplification, from the Chicago *Textbook*.)

load to another one of the flowers. Finally the flower becomes partially closed at the mouth, as the second figure shows, and droops on its stalk; then it is sought no more by insects, whose visits would obviously be useless.

Another common European field plant, sometimes seen in our gardens, is that Mint called *Salvia pratensis*, whose inch-long, bright-blue, horizontally-set, irregular flowers possess stamens remarkably hinged on their stalks (figure 112). These stamens are constructed on the principle of the lever, with the long arm carrying the anthers up inside the upper lip, and the short arm resting down like a valve over the entrance to the nectar tube. The cross pollinators are bees, and when one of these insects, coming to a pollen-ripe flower, alights on the lower lip, which is suitable in size, form and position for its reception, it pushes its head into the tube for the nectar and thus forces back the short arm of the lever, which, swinging on the intermediate hinges, brings down its longer pollen-laden end on the back of the bee in just the position where that insect is struck by the overhanging stigmas as it enters another flower that is ready for fertilization.

One of the most wide spread of American Orchids is the little wood-dwelling *Habenaria orbiculata*, which sends up a long loose cluster of greenish-white flowers from two glossy round leaves

spread flat on the ground. The flower, which is shown greatly enlarged in the accompanying picture (figure 113), has a structure so remarkable that without elaborate observational studies no one could ever imagine either the identity or the use of the parts. But the strap-shaped piece in front is a petal; the opening at its top leads into the greatly-elongated nectar tube shown next behind it; the two structures converging above this opening are the halves of one anther, each of which contains a great many pollen grains tied together into one mass by threads; these threads collect together into two sticky discs shown as two white oval structures each side of the opening; and the darker space between anthers and opening is the stigma. The reader will readily recognize how different is this construction from that of an ordinary flower; and the implication that the parts must possess unusual functions is correct. The cross-pollinating insect is a moth, with a proboscis (ordinarily carried in a pendant close coil) having a length sufficient to reach to the bottom of the nectar tube (figure 114). It alights upon the strap-shaped petal, whose narrowness compels its approach in a very definite position, and, as it pushes far down for the nectar,

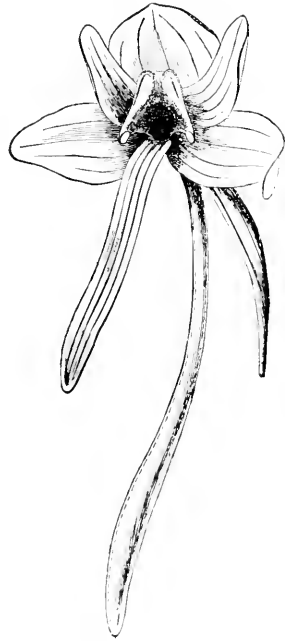


FIG. 113.—Flower, much enlarged, of an Orchid, *Habenaria orbiculata*, cross pollinated by the remarkable method described in the text. The hindermost part, not there mentioned, is the ovary and stalk. (Reduced from Gray's *Structural Botany*).

it brings the two sides of its head,—its huge eyes, to be exact,—into contact with the two sticky discs, which come away with their attached pollen as the insect withdraws. Moths have often been caught with these pollen masses attached to their eyes, which were formerly supposed to be afflicted by some kind

of strange parasite. Almost immediately,—during the flight of the insect from flower to flower in fact,—these pollen masses droop on their stalks, and hang down in such position that when the insect probes into a new flower they do not strike the anther but are pressed down directly on the sticky stigma, which holds them tenaciously. And thus is cross pollination effectively performed.

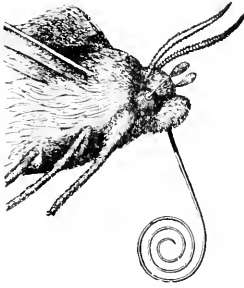


FIG. 114.—Front part of the moth which cross pollinates the *Habenaria* of figure 113; the pollen masses are attached to its eyes. (Reduced from Gray's *Structural Botany*.)

These three cases have been chosen not because they are especially remarkable, but because they illustrate several different features of cross-pollination methods. Indeed, the number of equally-striking cases is legion, requiring whole volumes for their adequate description; and many of the arrangements might well stagger belief were they not fully confirmed by the critical studies of large numbers of competent investigators. But while we cannot take space to describe any more individual cases, for which the reader, if interested, may turn to the works described in the footnote,* we must follow somewhat farther a few of the matters brought up in the foregoing discussion.

*The principal works upon cross pollination likely to prove of interest or use to the reader are the following: The foundation of all is Sprengel's book entitled (in translation, for the work is in German) *Nature's Secret displayed in the Construction and Pollination of Flowers* (1797), a classical work a half century ahead of its time, and a treasury of accurate information on its subject, though it missed, of necessity, the central illuminating idea of the value of cross as compared with close pollination. Next in importance came three of Darwin's greatest books, *The Various Contrivances by which Orchids are Fertilized by Insects*, *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*, and *Different Forms of Flowers on Plants of the same Species*, which three works contain a greater amount of new observation and illuminating explanation than any others we possess. The first general summary of the entire subject was Müller's *Fertilization of Flowers*, a translation of a German work, which is admirable in all respects, and superseded only by the cyclopedic work by Knuth, *Handbook of Floral Pollination*, just completed, likewise a translation from the

In the first place what is it which prevents close pollination in flowers where both sexes are present? Against this obvious difficulty, however, floral evolution has made ample provision. The simplest method is a physiological one, viz., a flower is sterile to its own pollen, that is, a given stigma will not permit the growth of its own pollen thereon, doubtless for some chemical reason; while another phase of the same thing is the fact true of some plants, that if close and cross pollen happen to fall simultaneously on a stigma, the cross pollen is the one that grows fastest and produces the fertilization. But far commoner is the simple and perfectly effective device of making the stamens and pistils of each flower ripen at different times, an arrangement called *dichogamy* (figure 115), and found in a good many common plants. Again, close pollination is prevented by mechanical arrangements, usually the interposition between anther and stigma of some specialized outgrowth, as shows very well, for example, in the common Blue Flag, or Iris (figure 116). Still another arrangement is displayed by the Primroses, Bluets, and Mayflowers, which possess two kinds of flowers bearing stamens and pistils in different positions, with corresponding differences in



FIG. 115.—Dichogamous flower of *Clerodendron*, on two successive days, showing the different time of ripening of stamens and pistils. (Reduced from Gray's *Structural Botany*.)

German. The best general account of the subject, admirably written and beautifully illustrated, is contained in Kerner's *Natural History of Plants* (another translation from the German), while his smaller volume, *Flowers and their Unbidden Guests*, is a charming presentation of that subject. Brief and popular summaries have been given by various writers, notably by Asa Gray in his all too brief *How Plants Bchare*, by Lubbock, in his *Flowers, Fruits, and Leaves*, and by W. H. Gibson in his *Blossom Hosts and Insect Guests*, which is the most readable of all the works on the subject. All of these books should be found in the public libraries.

pollen and stigmas (figure 117);—a plan of structure called *dimorphism*. When the suitable insect visits in succession several flowers of the different kinds, it receives pollen on its body from the upper stamens in a position to leave it on the tall stigmas, and

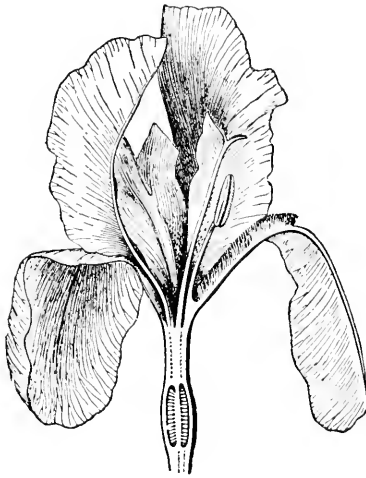


FIG. 116.—An Iris flower in partial section. Above the stamen is a petaloid style ending in a projecting shelf of which only the upper surface, shielded from the stamen, is stigmatic. (Copied from Gray's *Structural Botany*.)

the same for the shorter kinds; while any accidental pollination of a stigma from the same or a similar flower produces no effect, because of the differences in pollen and stigmas aforementioned.

But although such elaborate arrangements exist in adaptation to the prevention of close pollination, in other kinds of flowers there are features which as obviously secure it. Thus, in a great many of the simpler and regular kinds of flowers, the pollen falls normally on the stigmas of the same flower, and produces close fertilization in case no cross pollen is received, though if cross pollination does

occur, then cross fertilization is effected instead. But a much more extreme case is found in those flowers which never open at all, and in which the pollen-tubes grow out from the anthers to the immediately contiguous stigmas, and thence effect fertilization in the usual way (figure 118). Such flowers, called *cleistogamous*, lie close to the ground, and are well known in Violets and some kinds of Oxalis; but this fact is conspicuous about them, that the same plants in all cases possess also the ordinary showy kinds of blossoms cross pollinated by insects. Obviously, therefore, cleistogamous blossoms, like the cases of close pollination earlier mentioned, represent a method of ensuring close fertilization in case a cross should happen to fail,

on the principle that although cross fertilization is better than close, a close fertilization is better than none. And for this principle there is much other evidence. In all of these cases, however, at least an occasional cross fertilization must be effected; and there is good reason to believe that while many kinds of plants can endure close fertilization for a considerable time, they must have an occasional cross in order to retain their full vigor.

But we must turn for a moment to view cross pollination from the side of the insect. Our discussion thus far may have seemed to imply that insects exist in certain sizes, forms, and habits, fixed by other considerations, and that the adaptations between them and

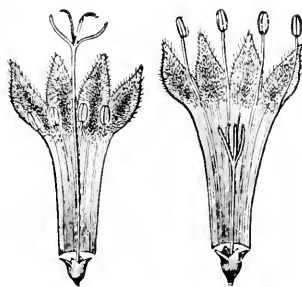


FIG. 117.—Dimorphous flowers, enlarged, of Partridge Berry, further explained in the text. (Reduced from Gray's *Structural Botany*).

flowers have been wholly effected by modifications of the flowers. This, however, is not correct, for there is every evidence that in the course of evolution, insects have become adapted to flowers as well as flowers to insects, as indeed we might expect from the fact that while it is an advantage for flowers to have their pollen carried by insects, it is an advantage to insects to be able to obtain their food from the flowers. There are, of course, many kinds of insects which never visit flowers at all; and it is only the kinds which are nectarivorous, so to speak, that plants have been able to provide an attraction for, and only these kinds show adaptations to flowers.

For the success of cross pollination of flowers by insects, it is obviously essential that the insects shall habitually visit plant after plant of the same kind, rather than first one kind of plant then another, which happen to blossom together. For no result follows a cross pollination between different kinds. Observation always shows that in fact insects do as a rule visit the same kinds

of plants successively, as anyone can see for himself in a garden; while experiment indicates that they are primarily guided by color, which, probably, in their equivalents for minds, becomes associated with flowers in which the nectar is ready. This process



FIG. 118.—A plant of the common Blue Violet, displaying the contrast between the familiar showy flowers and the cleistogamous kind, which are the bud-like structures on the recurved lower stems. At the right is a cleistogamous flower in section, showing the contiguity of anthers and stigma. (Copied from Atkinson's *Textbooks*.)

is greatly aided in nature by a correlative peculiarity in the plants themselves,—namely, that different kinds of flowers which blossom together at the same time are usually strongly contrasted in color, as any meadow, or brookside, or autumn roadside illustrates. It is true that the insects do not visit only one flower

on a plant and then visit only one on another, as would be theoretically the best of arrangements; for on the one hand that were too difficult a thing for the plant to be able to induce the insect to do, and on the other it is needless. What happens in reality is this, that an insect in visiting a plant usually goes successively to all the flowers that are open, and thus becomes thoroughly dusted all over by a mixture of pollen, which is ample in quantity to allow some for each stigma of all of the flowers on the next plant that it visits. Of course there is mixture of pollen, and a great deal of pollination between different flowers on the same plant; but the method makes probable the presence of some cross pollen on each stigma, when the selective power of the stigma for cross pollen, already mentioned, ensures cross fertilization. And the matter is aided a good deal by a peculiarity of blossoming which practically all plants show, that no large number of flowers are open at one time in the same cluster,—no more, one may say, than as many as an insect can pollinate by the quantity of pollen it can carry on its body from a previously-visited plant. Of course none of these arrangements are exact in their working, but are general, or average, or clumsy, with many individual failures. But on the whole they suffice.

That insects find flowers chiefly through the colors seems undoubted, but there is more in the subject than appears at first sight. The chief essential of floral color, from this point of view, is conspicuousness, which of course involves contrast with the background; and as this is commonly green, therefore white and yellow and red are the commonest of floral colors, especially in flowers that nestle among foliage. The less contrasted blue is rather more common in flowers that stand out by themselves, whether singly or in long terminal clusters. Furthermore, it is true that some kinds or groups of insects show preference for certain floral colors; and, correlatively, the flowers having such colors are prevailingly of a size and construction better fitted to the visits of those insects than of others. Thus, most small and

regular open flowers are yellow or white, and visited by a great variety of small insects, especially flies. Blue flowers, however, are visited mostly by bees, and, as the Larkspur and Monkshood well illustrate, possess in general a position of nectar, a compulsory mode of access thereto, and an arrangement of stamens and stigmas such that bees can best of all insects get the nectar and most surely carry the pollen. Red flowers, such as the Pinks, are oftenest visited by Butterflies, whose probosces are long enough to reach to the bottom of their slender tubes for the nectar which is there inaccessible to the very much shorter probosces of Bees. Again, white flowers, in highly specialized kinds like the Orchids, are preferred by Moths, which are indeed the only insects possessing probosces of a length sufficient to reach to the bottoms of the unusually long nectariferous tubes. The reason of course why the insects prefer the respective colors is because these have come to be associated with a construction of flower from which they can easily draw nectar, while that nectar is pretty sure to be present because other kinds of insects are largely excluded. These relations, as before, are not precise in detail, but operate as a general principle; and, as a general principle, also, it is true that insects, floral colors, and floral structure have evolved together in harmonious correlation.

While considering this subject of floral colors, I may here add a number of miscellaneous matters of particular interest. Thus, as to white color, it is found to distinguish most flowers that bloom in the dusk of the evening, that being of course the one color which is most conspicuous in darkness; and such flowers commonly exhibit the very long nectar-tubes and other constructional features adapting them to the visits of moths, which are chiefly night-flying in habit. This is the explanation of the peculiarities of the Night-blooming *Cereus*, *Nicotiana*, and some *Jessamines*. Quite a different aspect of floral conspicuousness is involved in the brilliant coloration of flowers that grow in rather inhospitable places, such as Arctic shores, Alpine heights, and desert wastes.

Alpine plants in particular are famous for their beautiful coloration. An explanation thereof has been found in adaptation to the comparative scarcity of insects in these places, the extra brilliancy representing the extra difficulty of ensuring their visits. Again, a good many flowers exhibit a considerable variegation of color, consisting chiefly of definite spots or lines quite different in hue from the ground color of the flower as a whole, as Forget-me-nots and Nasturtiums well illustrate. But these markings are found always to have one feature in common,—that they indicate the position of the nectar. The floral color as a whole brings the insect to the flower from a distance, and these markings then show it the place to probe for the nectar,—which of course brings it into the position where it can best leave its pollen and receive an additional supply. Again, the effectiveness of color is obviously increased by massing, which explains the value of clusters of flowers, especially for kinds that are small. Finally, as to this matter of color, we need note but one more peculiarity. Some kinds of flowers, though none that are very familiar, change color immediately after fertilization; and it is claimed that such flowers are no more entered by insects, whose visits would obviously be useless to both the flowers and themselves. The same end is here attained, though by a different method, as in the case of the drooping flowers of the *Aristolochia* already described. The advantage to the species as a whole of preventing useless visits of insects, and thereby conserving their services for flowers which still need them, is sufficiently obvious.

As an advertisement to insects of the position of the flower, color often is aided, and sometimes replaced, by odor. It has even been claimed in late years that insects are guided to flowers much more by odors than colors, many of such odors being hardly, or not at all, perceptible by us; but the evidence on this point has not yet won acceptance. However, there is no question at all as to the assistance rendered by odor to color in those cases where color alone cannot be made sufficiently conspicuous. This is true

especially of night-blooming flowers, in which the association of sweet odor and white color is very common. This same aid of odor to color is found in those flowers which bloom in very inconspicuous positions, such as close to the ground, or among leaves in the shade, as the Mayflower illustrates; and in general odoriferous flowers that are not night-blooming are the shy little kinds of the woods. Odor also aids color, or acts as a substitute in some flowers which have not attained to a corolla, or have lost it, as in some Willows and Maples. On the other hand, flowers that grow in exposed places, and display an abundance of color, very rarely possess any odor, as the tall kinds of the meadows, the river-banks, the autumn roadsides and the prairies all illustrate,—the absence of sweet flowers from the prairies in particular being matter of common knowledge and frequent comment. And finally, as to odor, we need note but one more point, that while most floral odors happen to be pleasing to us, there are some that are not, as in case of the Skunk Cabbage and a good many others of that family. But such odors have their lovers among insects to which they are doubtless more sweet than all of the spices of Araby. Indeed, it is only a fortunate accident that any of the odors of plants give us pleasure at all; for in their evolution our tastes in the matter were not in the least consulted.

Color and odor suggest nectar, which is the real attraction to insects in the great majority of flowers. It can usually be seen very easily at the bottoms of floral tubes where it lies as a clear watery liquid; and sometimes in special receptacles of more open flowers it stands out in great glistening drops, as conspicuously illustrated by the Crown Imperial. However, a good many flowers are without it entirely, in which case the attraction is pollen, then produced in unusual abundance; for some insects prefer pollen to nectar, making use of it not only for food, but also for building their honeycomb cells. And if the reader should ask me why some flowers use nectar while others use pollen as their means of attraction, I agree that I will tell him when he has

told me why one man is a carpenter and another a farmer; or why the Latin races are artistic while the Teutonic are practical; or why the Germans are the best scientific investigators in all the world.

The symmetry of my subject would seem to demand that I add to these paragraphs on color, odor, and nectar, another devoted to the mechanical arrangements in flowers in relation to cross pollination. But I despair of giving any adequate idea of this subject in the space that remains at my command, and it must suffice to say that such arrangements are both remarkable and innumerable, involving not only the most extreme modifications in all of the parts, but such special features as sensitively-bending stamens (in the Barberries), closing stigmas (perhaps, in *Mimulus*), springing stamens (as in Mountain Laurel), explosive stamens (as in Mallows), forcibly-projected pollen-masses (as in some Orchids), and others as striking, which the reader may follow as far as he pleases through the many good books devoted to the subject.

It is doubtless sufficiently obvious why insects are the animals most used for cross pollination by plants, for their small size, active flight, and especially their nectarivorous habits, make them especially available for this purpose. But it must at the same time be remembered that those very features have doubtless in large part been evolutionarily acquired in conjunction with the corresponding features of the flowers. Insects, however, are not the only animals thus utilized, for certain nectarivorous birds, of which the Humming-bird is the most familiar example, cross pollinate flowers in quite the same manner as the insects. Everybody has seen in our own gardens the Trumpet-creepers and Nasturtiums and Scarlet Salvias visited by Humming-birds. There are plenty of tropical flowers, displaying for the most part large tubular corollas, abundant nectar, and scarlet colors, which have a form, size, and shape well suited to the flying-habits of those birds. Among other animals that effect cross pollination

are the Snails, which are said to visit some low-growing flower-spikes of tropical plants for the soft tissue that grows abundantly among the blossoms; and thus they transfer pollen from one plant to another. But the other groups of animals are unavailable, for obvious reasons of habit, size, structure and the like.

As an earlier chapter (on Protection) has indicated already, plants are obliged not only to develop structures in adaptation to the performance of their functions, but also to protect them when made from hostile external forces which would work their destruction. This is all very true of the highly complicated and greatly exposed flowers. A certain protection against hostile weather conditions is attained by a control over the time of blossoming, which occurs in most plants only at times and seasons when the conditions are favorable for cross pollination, the blossoms opening in fine weather when insects are about, but not during rain-storms, when they remain under shelter. One of the greatest dangers to which the cross-pollinating mechanisms are liable is the influence of rain on the pollen, for water is absorbed osmotically by many kinds to a degree which causes the bursting and destruction of the grains. Accordingly, in flowers many arrangements exist in adaptation to protection of pollen from rain, aside from the great one already mentioned,—the failure of blossoms to open in stormy weather. Thus, in a great many blossoms the anthers are safely sheltered under an overhanging upper lip, as in most irregular flowers, like the Mints, Monkshood, and others of horizontal position, while in some kinds they are guarded by bands of unwettable hairs. Again, some kinds of flowers close in threatening weather, while others, arranged in flat-topped clusters, turn upside down in a rain-storm, presenting an aspect which leads most people to imagine that they have been beaten over by force of the rainfall.

But an especial protective need of flowers is against insects that are not adapted to cross pollinate them, and which would remove the nectar without rendering any service in return,—against

“unbidden guests,” as Kerner so happily called them. In one instance, at least, plants seem quite helpless against such an attack, for Bees often puncture the nectariferous spurs of Columbines and Larkspurs in our gardens without entering the flower at all; but this is exceptional, and presumably a recently-acquired habit of those insects. A partial protection against unbidden guests is secured by the adaptation of floral to insect shapes already described, in correlation with which most insects visit only the flowers to which they are fitted, leaving the others alone. But there is one kind of insect, whose small size and other characteristics make it useless as a cross pollinator, but which is at the same time a particularly pertinacious nectar lover, and that is the Ant, against which, accordingly, especial protection is needed. A number of adaptations preventive of its access to nectar appear to exist. Possibly the extra-floral nectaries earlier described (page 212), may provide a bait to keep these insects from the flowers. Furthermore this is probably the explanation of the closure of the throats of flowers, best exemplified in the Snapdragon, in a way to open by the pressure of a large insect's weight or strength but not to the small body of an ant; while the rings of scales or hairs in the throat or somewhere in the tube of the flower (figure 119), or sticky glands all over the outside of the calyx or neighboring parts (figure 120), have probably the same explanation, as have a number of other arrangements of minor account described by Kerner in his charming book devoted to the subject.

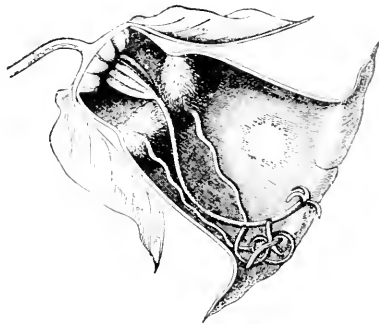


FIG. 119.—Interior of a flower of *Cobaea scandens*, showing the masses of hairs commonly believed to protect the nectar from insects unadapted to effect cross pollination. (Copied from Kerner's *Pflanzenleben*.)

It is thus plain that flowers, like other parts of the plant, are

never the expression of adaptation to some single function alone, but represent a resultant or compromise between adaptation to some leading function and adaptation to a number of minor ones,—the whole being further modified by the influence of a quantity of other factors,—mechanical, incidental and hereditary.



FIG. 120.—A flower of the *Linnaea*, or Twin-flower, showing the adhesive glands on the base of the flower, supposed to protect it from access of creeping insects.

In this discussion of cross pollination and the flower, which involves some of the most complicated and efficient of all known adaptations, the reader must have noticed how closely the mode of presentation of ideas, and even the language that is used, correspond with those which are commonly employed in describing some great product of human activity,—the organization of society, government, or a great business. And this peculiarity of exposition is not confined to the present writer alone, but seems unavoidable by any author who seeks to make the subject understood. It arises of course in some part from our common custom of personifying nature for purposes of convenient, economical, and vivid expression, but in much larger part, I am convinced, from a more or less unconscious recognition of the fact that there is an actual correspondence, or even an identity, between man's way of effecting results, and nature's. It is not that nature thinks things out as a man does, but that mind in a man works things out as nature does. This must be true, indeed, on theoretical grounds, else we must maintain that the mind of man is not an evolution with its roots in the rest of nature, but a special creation of its own separate kind; and against such a conception is arrayed all of the natural knowledge we possess. In all exposition, therefore, it is, as I think, scientifically correct as well as practically convenient, to personify nature.



CHAPTER XIII

THE WAYS IN WHICH PLANTS INCREASE IN SIZE AND FORM THEIR VARIOUS PARTS

Growth; physiological



IF all the physiological processes of plants, the one that possesses the greatest interest for most people is Growth. It is really a remarkable phenomenon, no matter how one views it,—whether in the unfolding and perfecting of some favorite flower, foliage, or fruit: in the development of a single microscopical egg-cell through embryo seedling and sapling to a mammoth tree: or in the seasonal procession of vegetation from the dormance of winter through the unfolding of spring, the maturity of summer, and the fruition of autumn. I take it the reader does not share in the mischievous fallacy that to know the causes of things is to lessen one's enjoyment of them, and I shall try to describe the way in which these various results come about.

At first sight the phenomena of growth seem too heterogeneous for analysis, but, like many another complication, they separate out in their true proportions under persistent investigation. And the first far-reaching fact which stands out is this, that growth consists of three operations, which, often in progress together, are really distinct in their nature and can proceed quite apart from one another. These are,—formation of new parts, or *development*, increase in size, or *enlargement*, and ripening for the final function, or *maturation*. The distinction comes out very well in the case of the spring vegetation. Everybody knows that the flowers

and leaves which burst forth at the first coming of spring were formed, or developed, the season before, and existed over winter tucked away very snugly in well-covered buds. In a Horse Chestnut bud, for example, one can recognize by dissection, at any time in winter, the flowers and leaves which are to come out the next spring; and the same thing can be seen even more clearly in sections made through flowering bulbs (Hyacinth, Tulip, Crocus). Seeds with their embryos act the same way. In all of these cases the formation or development of the parts takes place in early fall; the principal part of their increase in size, or actual growth, occurs the next spring; while the full ripening of parts, such as leaves, for the complete performance of their functions, follows in summer. This shows how distinct the three phases of growth can be. Accordingly we can best consider them separately, and for practical reasons may begin with the most familiar,—increase in size, or enlargement.

Plants, unlike animals, grow by repetition of similar parts,—new leaves, stems, roots, flowers, and fruits being formed in an endless succession. We shall therefore first direct our attention to the growth of these individual parts, of which the stems grow the fastest and are easiest to study. Anyone can determine the rate of growth of stems in a general way by making frequent measurement with rulers placed alongside the plant. For scientific purposes, of course, very exact ways have been devised, not only for measuring growth, but even for compelling a growing stem to register its own growth upon paper. One of the best of such instruments is shown in our accompanying figure (figure 121), and the reader may confide in my judgment of its merits, because I am myself the inventor. To the extreme tip of the stem is attached a thread, which is then run over a small wheel, as shown in the figure, and there fastened. Around the rim of the larger wheel, which is one piece with the smaller, runs another thread which passes over a small pulley-wheel and carries a pen against a paper-covered cylinder. The weight of this pen just suffices to

turn the wheels and keep the threads taut; and therefore, as the plant grows, the pen descends, making its mark upon the paper. The descent of the pen, however, is obviously faster than the growth of the plant in just the proportion that the greater wheel is larger than the smaller, this arrangement of the wheels being

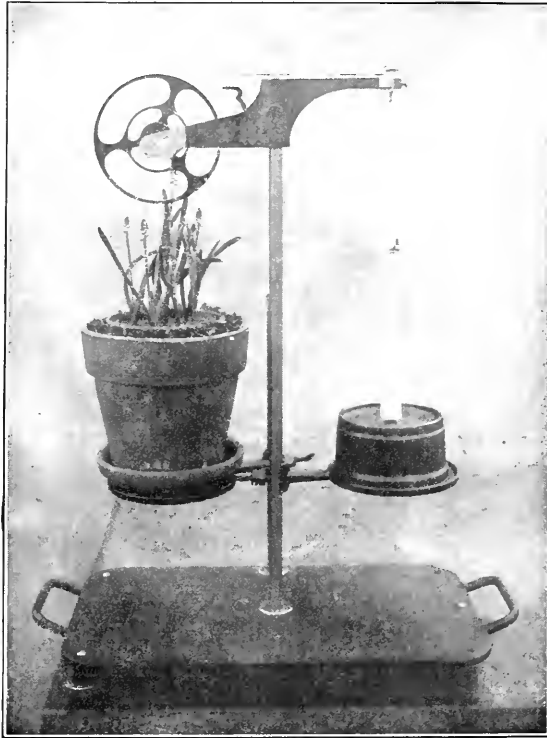
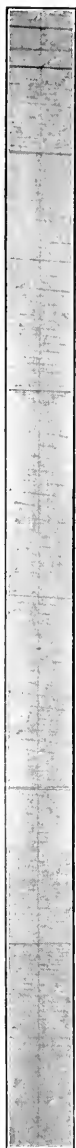


FIG. 121.—An auxograph, or recording growth measurer, in action. Its construction is explained in the text. Unfortunately the record, in the form of a spiral line on the cylinder, does not show in the picture.

adopted in order to space out the growth record enough for clear visibility. The cylinder, however, is revolved continuously by clockwork, making a complete turn once every hour; and therefore the descending pen traces not a straight, but a spiral, line, which every hour crosses a vertical line ruled on the paper, mark-



ing off thereon the precise growth, magnified of course proportionally throughout. The papers can then be removed from the cylinders and joined end to end in a continuous roll, or else a flat band. Thus is a plant made to write its own record of growth in a way convenient for scientific use. Such a record, obtained by one of my own students, and showing the growth of the flower-stalk of a Grape Hyacinth from its first appearance above ground to the completion of flowering, is shown, greatly reduced of course, in the accompanying illustration (figure 122). And by suitable modifications of the same auxograph (for so it is called because it is a growth writer), the growth of roots, leaves and other parts can likewise be registered.

A growth record like that of our figure is very expressive, but the facts can be brought out still better in the form of a graph like that which already has been used and described under Transpiration; and such a graph is presented in our figure 123. The base line is laid off in divisions of time, each space representing one hour, while the vertical lines are marked off with the number of millimeters of growth (magnified) per one-hour period, these marks being joined by straight lines in the usual way. In the resulting polygon, as the reader can see, the rise and fall of the lines corresponds to the rise and fall in the rate of growth. The reader must remember that such a graph represents the *rate* of the growth, not its amount, which fact explains the feature, puzzling to some people, that a growth graph can fall as well

FIG. 122.—Photograph, reduced to one-tenth the true size, of the record papers taken from the cylinder of the auxograph (of figure 121) during the growth of a flower-stalk of Grape Hyacinth. The heavier cross lines indicate noon of each day.

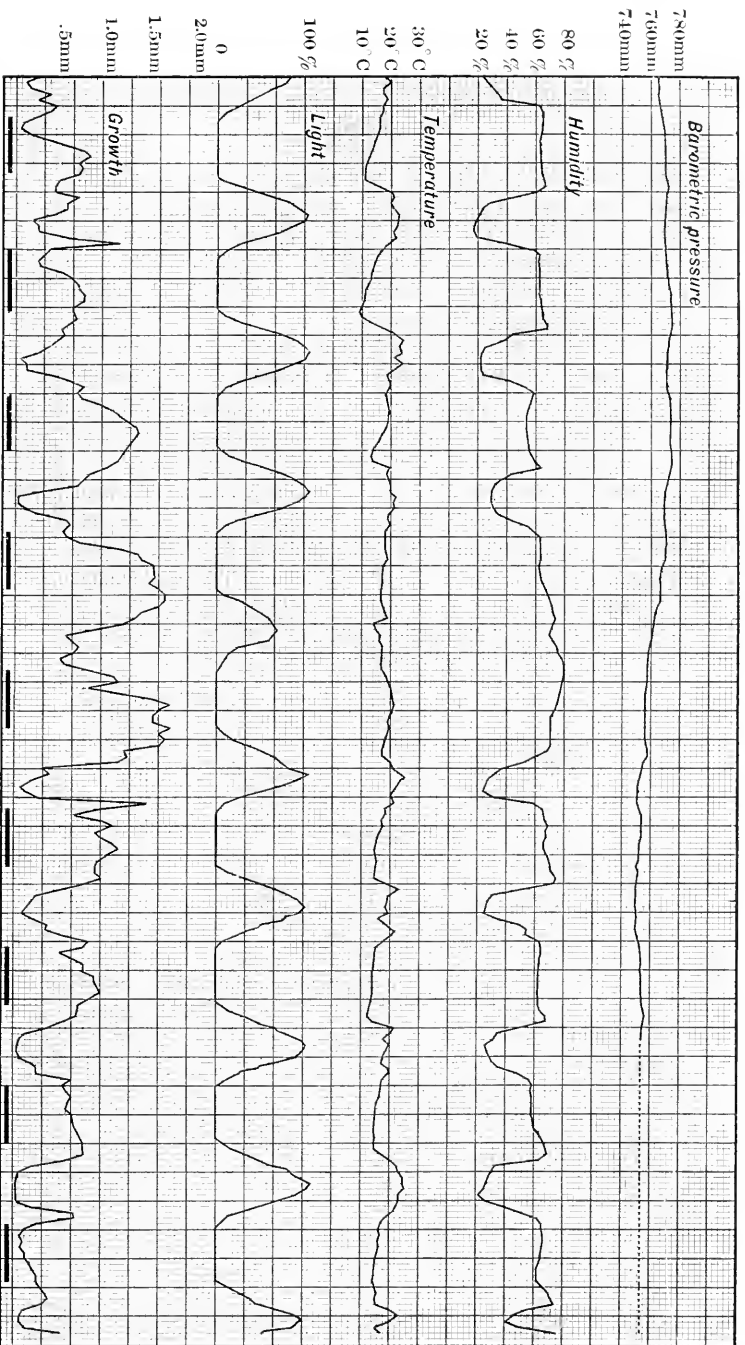


Fig. 123.—A graph illustrating the growth of a flower-stalk of Grape Hyacinth in relation to the principal external conditions. It is explained more fully in the text.

When, now, we inspect this graph somewhat closely we find its most remarkable feature to consist in its great irregularities; and the same thing appears in any others, from whatsoever source they are taken. In other words, the growth of plant-structures is extremely irregular in rate. It will not take the reader very long to ascribe the irregularities to the real cause of the most of them, namely,—variations in the external conditions of temperature, light, moisture and so forth. In order to determine the precise effect of each of these conditions, it is only necessary to plot the simultaneous graphs of temperature, moisture, and light, obtained as already described under Transpiration, upon the same sheet with the growth graph; and this has been done in the example presented above (figure 123). This subject of the effect of external conditions upon growth is, however, so important, that it must be considered somewhat farther.

First, as to the effects of temperature upon growth. Everybody knows, in a general way, that plants grow faster in warm weather and slower in cold; and in the early spring we see ample illustration thereof in the way the grass comes up fastest in the warmest corners, or in places where warm pipes, such as sewers from houses, cross lawns,—marking their courses by the early greenness above them. In our graphs the reader can see how closely the rise and fall in growth rate is connected with the rise and fall of the temperature. The same thing is shown, and very much clearer, by an instrument, devised for the purpose, and shown in our figure (figure 124). It must suffice to say that by its aid one can determine in a continuous band of soil the lowest temperature at which a plant can be made to grow (the *minimum*), the temperature at which it grows its very best (the *optimum*), and that above which it will not grow at all (the *maximum*). Between the minimum and maximum, the tips of the growing plants plot, as it were, their own curve of the relation of growth to temperature, culminating at the optimum, as our picture well shows.

These three cardinal points vary much with different plants, ranging lower in those of cold regions and higher in those of the tropics; and plants can thrive only in climates where the range of usual temperature corresponds somewhat closely with their cardinal points. This will explain why the Orange will not grow if planted in Canada, or Barley and Rye if taken to Florida. In plants of our own climates these points approximate on the average to 5° – 30° – 40° Centigrade respectively (or 40° – 85° – 100° Fahrenheit), which means that most of our plants do not grow appreciably below 40° ; they grow best at about 85° ; and

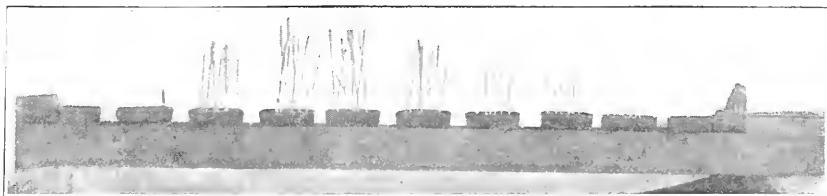


FIG. 124.—A graphic illustration of the relation of growth to temperature. The copper trough is heated from one end (the left), and chilled from the other, with the result that the temperatures grade evenly between.

hardly grow at all above 100° . This will explain why it is that when the temperature of our fields rises higher than 100° in the sun, the extra heat is no aid to plant growth, being rather a hindrance thereto. The same thing would happen also in greenhouses in summer were it not for the shading, which is added to reflect both the heat and the light.

The reason why heat has this effect upon growth is fairly well known. Growth depends upon a number of chemical and physical processes which are kept in orderly coöperation by the protoplasm. All of these processes, in general, are promoted by higher temperature, which fact explains the more rapid growth up to the optimum point; but, as the temperature rises higher, to degrees beyond those to which the plant is accustomed, the processes get beyond control of the protoplasm, or run away, so to speak, thus injuring and finally destroying the coördination and stopping the

growth. Other things, also, contribute to the result without doubt, such as the commencement of injurious chemical reactions under the higher temperature, and the accumulation of the waste products which are formed faster than they can be removed. But in general the relations existing between temperature and growth are determined by the power of the plant to control the chemical and physical processes concerned.

Second, as to the effects of light upon growth. At first thought one would suppose that plants must grow best in bright light, since light is essential to the making of their food, which supplies both the material and the energy for their growth; but in truth it is usually more rapid in darkness. This fact is brought out in our graph (figure 123), though here, as is usually the case, the matter is much complicated because the temperature commonly falls so greatly at night as to neutralize any tendency the plant may possess to grow faster at that time. But when the temperature remains even, as happens at times on warm nights out of doors, and in greenhouses artificially heated, then most plants show a tendency to grow faster in darkness. These are the conditions under which the farmer comments on the great growth that his cucumbers, for example, made in the preceding night. Plants make ample food in the day to supply the growth through the night. When, however, plants are kept continually in the darkness for days together, their growth becomes spindling and weak, and their chlorophyll disappears, as our picture will illustrate (figure 125). The results of such growth are comparable, in general, with the weakening activity of a fever.

The reasons why plants grow best in the dark are several. A part of this growth consists in that adaptive lengthening (the "drawing" of gardeners) already considered in our third chapter, whereby plants reach up after light. It is well illustrated by the great length of the stems in our picture (figure 125). A part may result from the fact that during the day all other processes are subordinated to photosynthesis, while at night growth has the

field to itself. A part depends on direct injury done by bright light through the injurious chemical reactions set up in the complicated protoplasm,—a matter we have considered pretty fully under Protection. On green plants, of course, the action of light is far less injurious than on colorless kinds, because the chlorophyll incidentally forms an excellent protective screen. In chief part, however, the lesser growth of plants in light is due to the



FIG. 125.—Pots of Scilla, started alike; but that on the right was kept in a dark room.

great promotion of transpiration by the light and its associated heat, whereby so much water is removed from the plant as to lessen the supply available for swelling the growing cells,—for such swelling is essential to their growth, as will be noted more fully a few pages later.

Thus, it is plain that light, like heat, can become too strong for the best growth of plants. We have seen already that even in photosynthesis plants cannot make use of all the light supplied by direct bright sunlight. These facts together explain why so many

plants thrive better in some shade than in full sun; and it is interesting to note that man finds it best to temper the light for some of his crops. This is the reason why shading is placed upon greenhouses in summer, and why better tobacco is grown under light cotton tents than in full sun, though here the protection given by the tents against hail storms and wind is also important. In Florida, pineapples grow better under a lattice work shade than in full open sun.

Third, as to the effects of humidity upon growth. A full supply of water in the soil is essential to the process, for this is the source of the water used in swelling the small new cells to their full adult size. But in addition the amount of moisture in the air has an important influence. Most people know that plants grow best on the kind of day we call "muggy," i. e., one in which the air is humid, even to the point of discomfort for us; and it is a familiar experience that upon such a day the grass of a lawn fairly grows before the eyes. The influence of humidity in promoting growth can also be traced in our graph (figure 123), which shows that in general growth increases with atmospheric humidity. The chief reason for this relation is easily found. Increased humidity checks transpiration, and therefore leaves in the plant a larger water supply for use in swelling the growing cells.

Fourth, as to other influences which affect growth. These are few and comparatively unimportant. Electricity, applied experimentally in limited amount, stimulates growth to a certain extent but in larger amount checks it; but its influence is not wholly separable from that of heat, and the matter is not so very important, since plants are hardly at all exposed to it in Nature. Poisonous substances in soil or atmosphere often stimulate growth a little at first, though ultimately they check it, through the injury they do to the living protoplasm. The presence of a little ether in the air seems, however, to promote growth without subsequent detriment, though the reason for this effect is not understood. The varying pressure of the atmosphere, recorded by the

barometer, should theoretically have some slight effect, but hardly any is appreciable in practice.

If now, we return to the graph of growth (figure 123) and proceed to eliminate those fluctuations which are traceable to temperature, light, and moisture, there still remains one peculiarity of much consequence, viz., a gradual rise in the graph as a whole, followed by a more abrupt descent. This means that the flower-stalk of the Grape Hyacinth, even when all disturbing external factors are eliminated, does not by any means grow at a uniform rate from start to finish, as one might naturally suppose, but, after beginning, grows faster and faster up to a point of highest rate, beyond which its growth is slower and slower until it stops. This peculiarity of growth, however, is not confined to the flower-stalk of this plant, but is very wide spread; and it has even a name of its own, viz., the "grand period." Thus, it is characteristic of winter buds; and this explains a phenomenon in connection with their opening which most people must have noticed, viz., that buds swell very slowly at first in the spring, seeming to take an interminable time before they show their green leaves, after which they open out very quickly, almost over night as it seems, to nearly the full size of their parts; and then they complete their final growth rather slowly. This opening takes place on the crest of the grand period as a rule, although it is complicated of course more or less by the effects of temperature. Leaves, single flowers, germinating embryos, fruits, and a good many other parts display the grand period. It is not, however, universal; for some structures, like stems which continue their growth all summer, pursue an even course affected only by varying temperature, moisture, or light.

By suitable modifications in details, records may also be secured by the auxograph for the growth of leaves and of roots. The graphs in general are very similar to those obtained from stems. But there is one feature of the growth of leaves, stems and roots, about which the auxograph gives no information,—namely,

the place of most active growth in each part, whether at tip, base, or all through the structure. This, however, is easily determined in another way, viz., by marking the parts when young by evenly-spaced lines, the spread of which, as the parts grow up, must

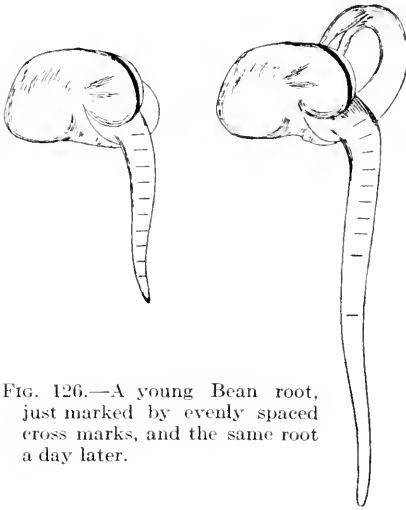


FIG. 126.—A young Bean root, just marked by evenly spaced cross marks, and the same root a day later.

reveal the place where these grow the most. If a young root be thus marked by cross lines, the result is like that of our figure (figure 126). Evidently young roots grow almost wholly at their tips. If stems be marked in the same way, the result is somewhat different (figure 127). Evidently young stems grow mostly at their tips, but over a much larger area than the roots, as indeed one might infer from the way in which the nodes of young stems

spread apart. It is no trouble at all to find an adaptive reason for the difference in the mode of growth of roots and stems, when one recalls that roots must pick their way through the irregular interstices of a closely-pressing soil, while stems have all outdoors to expand in. As to leaves, their shape makes it necessary to mark them by cross lines, forming squares, and when thus treated the spread of the lines shows that leaves, unlike roots and stems, grow all through their structure (figure 128). Slender leaves, however, especially the kind that grow up from bulbs, grow almost wholly at the base.

Although growth is typically accompanied by increase in length, it sometimes is correlated with shortening. One case thereof is found where a straight structure becomes a spiral, as in tendrils, which thus pull their plants closer to a support, or in the peduncles of some water plants, which thus draw their

ripening fruits to a safer position under water. But an actual shortening occurs in the roots of some herbaceous perennials, like the Dandelion, which thus are enabled to keep their stems safely underground despite a certain annual increase in length.

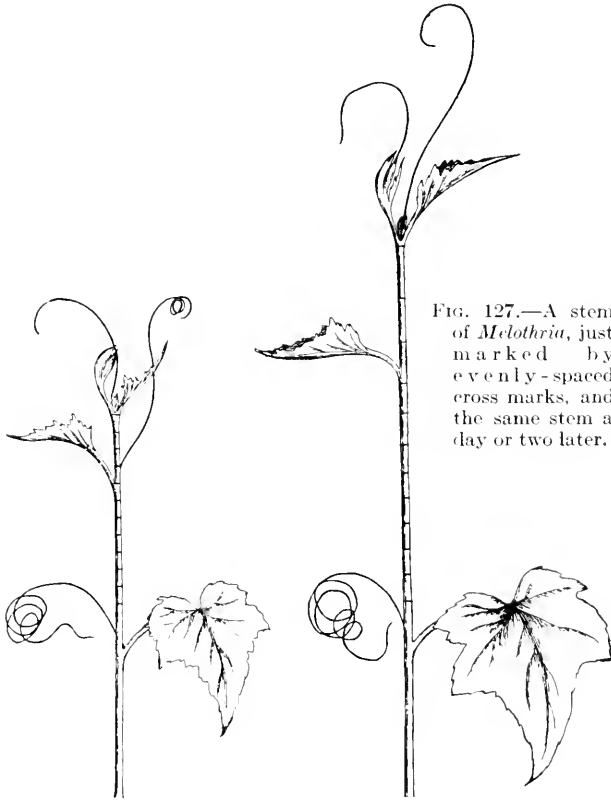


FIG. 127.—A stem of *Melothria*, just marked by evenly-spaced cross marks, and the same stem a day or two later.

The same thing is said to occur in the lateral rootlets of some bulb-bearing plants, like the Tulips, with this marked advantage, that the newly formed bulblets are drawn clear of the old parent bulb. Mechanically, this shortening is variously effected, but chiefly by a forcible lateral expansion of the tissues, somewhat on the principle by which a muscle is shortened; and as a result such roots commonly show a number of transverse wrinkles.

Such are the principal phenomena of that phase of growth which is concerned with enlargement. Another phase is concerned with the formation of new parts, or development. But the relations of the two will be much plainer if, before proceeding with the latter, I describe the cellular basis of both. As to this, we may anticipate a little by saying that in general, enlargement

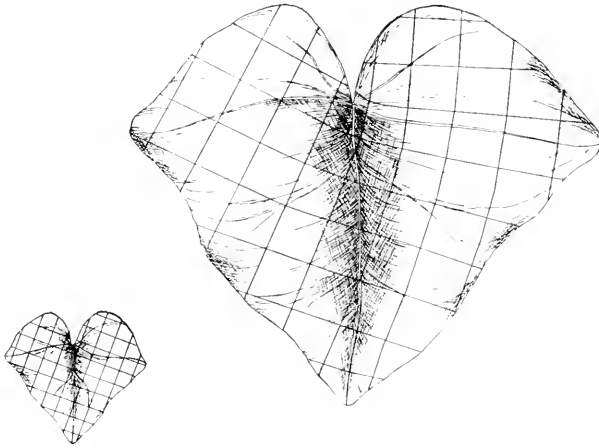


FIG. 128.—A young leaf of English Ivy marked in regular squares, and the same leaf a week or two later.

depends upon swelling of cells already formed, while development, or the construction of new parts, rests upon the formation of new cells.

The mode of formation of new cells is singularly uniform throughout all plants. It takes place, as a rule, only in small compact thin-walled cells densely filled with protoplasm, the kind technically known as *meristem* and best shown at the growing points of stems and roots (figures 53, 137, 139, *C. D*). The details cannot be seen in living cells, but can be inferred from the appearances presented by cells killed, stained, and sectioned for the purpose. The first sign of new cell formation occurs in the nucleus (figure 101), where the granules become more conspicuous and collect into stout threads which then sort themselves out in the form

of a definite number of the bodies called *chromosomes*; and these become arranged in a plate across the cell. Meanwhile the boundary of the nucleus has vanished, and a spindle-shaped framework of very fine fibers has formed at right angles to the chromosome mass. Then each chromosome splits lengthwise into two, and the spindle draws these halves apart towards its two ends, where they become surrounded anew by a nuclear boundary. Thus is the chromosome matter divided evenly between the two new nuclei. The chromosomes then lose their distinctness and gradually merge away to the threads, and finally to a granulation similar to that of the original nucleus. Meantime the spindle fades away and a new wall forms across the cell between the new nuclei. Each of the new cells then grows to the original size and is ready for another division.

The object of this elaborate process is without doubt the equal division of the chromosomes. These, it will be remembered, are derived equally from the two parents of the plant, half of them from one parent and half from the other; and although they absorb nourishment and grow and divide, they never lose their identity. The equal division of the chromosomes in every division of the cells, therefore, carries some of the substance derived from each parent to every cell of the adult plant, thus explaining how it is that any part of a plant can resemble either one of its parents.

Cell division underlies all development of new parts, for every structure—leaf, stem, root, or other—begins with the formation of just so many cells at just such places as will produce, when they swell to full size, the characteristic size and shape of the fully-adult organ. But at first these cells are all small, and densely packed with protoplasm and food substance. Such is the condition in a bud or an embryo, as our figures illustrate (figures 137, 139, C). One must not, however, lay too much stress upon the cell divisions in particular, for they are without doubt a result, rather than a cause, of the outgrowth of new parts. It is in reality the living protoplasm which pushes out into new structures; the cell divi-

sions take place as a secondary architectural arrangement. It is easy to follow the method whereby the individual cells grow from the tiny food-packed condition to the large protoplasm-lined and water-filled state that distinguishes them when adult; and the matter is well illustrated in the accompanying figure 129. First of all, inside the dense protoplasm there appear little rifts which contain a sugar-rich sap. Into these little sap-cavities water is absorbed osmotically, making them swell and exert pressure which pushes the protoplasm against the walls and stretches them tensely. But this pressure is relieved by the deposition of new substance all through the innermost texture of the stretched wall; and this allows a still further stretching, and so on until the cell is

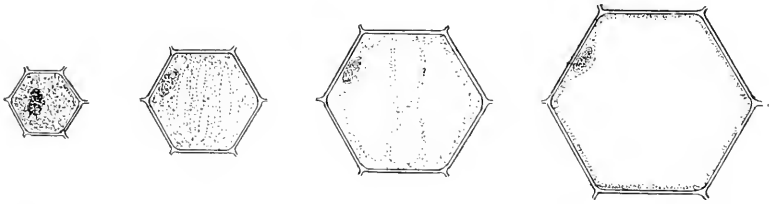


FIG. 129.—Generalized drawings, in optical section, of a cell during enlargement from the newly developed to the fully-adult condition.

full grown. The sap-cavities, meanwhile, are not only enlarging but are merging together; and the food substance originally stored in the cell is being transformed into new cell-wall, protoplasm, and materials dissolved in the sap. The final product is a fully-grown cell, many times larger than its embryonic original and provided with a tightly-stretched wall against which lies a thin lining of protoplasm, enclosing a single sap-cavity well-nigh as big as the cell itself. The exact direction of expansion of the cell, and therefore its final shape, are of course by no means accidental, but are under control of the living protoplasm, which thus simply makes use of osmotic pressure as the mechanical power for forcing cell enlargement. And the degree to which that enlargement may proceed, from the newly-developed to the

fully-adult cell, is sometimes surprisingly great, as the accompanying example well illustrates (figure 130).

From these considerations it will be plain that the fully-adult cell consists largely of water, with comparatively little solid matter, in great contrast to the embryonic cell which is largely solid. This is shown very clearly by the great collapse of fresh plant-structures when dried (for often they shrink away to a mere wisp of their former selves), and also by weighings, which prove that most fresh plant-structures consist of more than 90 per cent water. A plant as large as that shown in our figure, for example, (figure 131), can be contained when dried in the tiny vial beside it. The same thing is true also of seedlings and the spring vegetation from buds; when the water is expelled, it is found that the fully grown structure is not only no heavier than the embryo or bud, but even lighter in weight,—the loss of course being due to the removal of material by respiration. Thus in general it is true that developing structures gain weight, while growing structures lose it.

That growth consists chiefly in swelling of cells already laid down in development is shown very beautifully by comparison of some embryos with the seedlings that grow from them. If cross-sections of embryos and seedlings be made in about the same place, it is found on the average that although the cells differ very greatly in size, their number is approximately the same, though in one case they are tiny, squarish, densely packed and full of substance, while in the other they are large, rounded, loosely-arranged, and contain little but water. This separation of development and growth is more common than one would suppose, for



FIG. 130.—The comparative sizes of a pith cell in the newly developed and the fully-adult condition, as seen in optical section. Traced from accurate drawings on a wall-chart by Frank and Tschirch.

even in structures which grow on continuously, and in which it would seem that the two phases must be mixed up together, they are separated in space, although not in time. Thus, in roots, the development of new cells occurs in the growing point (figure 53, 139, *D*), while the enlargement of cells to full size takes place in the

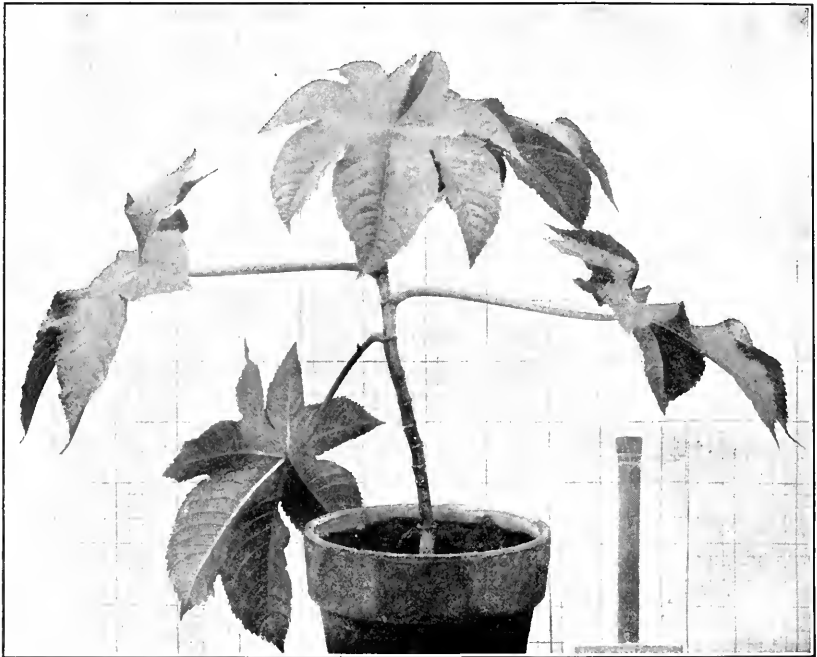


FIG. 131.—A Castor Bean plant, with its dry substance in a vial alongside. (The vial, of course, was photographed later, and worked into the plate.)

zone just behind, a fact which explains the enlargement of that zone as shown in our earlier figures. The same is true likewise of the stem, though less strikingly. Moreover, it is also a very interesting fact that if a plant is suddenly called upon to increase beyond the normal, as for example in the longer leaf-stalks demanded of water plants forced to grow in deeper water, or in the leaves of plants whose buds have all been destroyed, the enlargement is

attained by increasing the size of cells beyond the normal, not by increasing their number.

But while enlargement and development are separate in their nature, and commonly occur apart from one another, nevertheless they are often intermingled more or less. The very act of development, indeed, entails some increase of size, and enlargement is attended by some cell divisions in connection with adjustment of parts; and no doubt, furthermore, there are structures which develop and enlarge simultaneously.

As growth comes near to completion, and sometimes much earlier, the cells undergo such further changes as fit them more perfectly for particular functions. Such changes are designated maturation. Walls thicken in places and are absorbed in others; they develop spirals, rings, or other thickenings, and hollow pits or other depressions; while various changes take place as well in the contents, which often are transformed to secretions of very specialized function. Moreover, as cells increase in perfection of adaptation to their functions, they lose at the same time their power of division, so that when fully mature they are incapable of further development or reproduction. But these changes in the main have already been considered in the chapters on Protoplasm and Metabolism.

Before leaving this aspect of growth, we should summarize for completeness the other physical and chemical phenomena thereof, most of which have been considered in various connections earlier in this book. Thus, there is always a large conversion of stored food into new walls, protoplasm, and sap substances, resulting in the collapse of the storage parts of sprouting structures, like potatoes, bulbs and seeds. Again, respiration, the releaser of energy, is indispensable to growth, which demands much of it; and so close is the connection of the two, that whatsoever stops the one stops also the other. Therefore, oxygen being essential to respiration, if the oxygen supply be cut off from the growing plant, as happens often in nature through flooding with water,

and as can easily be effected by experiment, then growth ceases; and indeed death ensues unless the supply be admitted again. Furthermore, in the chemical reactions of growth, some waste by-products are formed, of which a part are dropped with the

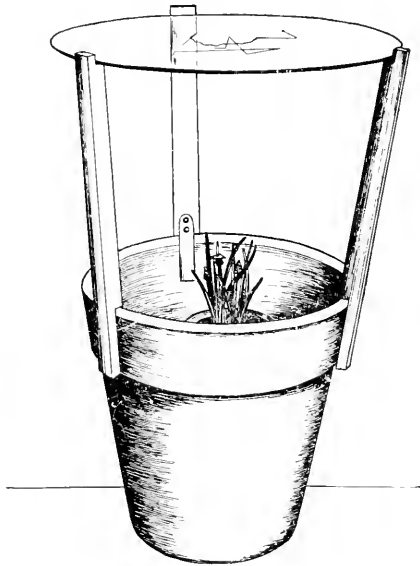


FIG. 132.—An arrangement (about one-sixth the true size), for the study of circumnutation, using a method described in the text. The glass filament and paper triangle, somewhat exaggerated for visibility in the drawing, may be seen near the center of the picture.

bark and the leaves, a part are stored in out of the way cells, and a part are apparently excreted into the soil, where they act poisonously, and produce economic and ecological consequences already described.

A notable feature of growth is its accompaniment by a number of different movements. Many of these are clearly adjustive of the parts to the particular conditions of light, moisture, and so forth prevailing in the immediate environment, and as such have been considered already in our chapter on Irritability, while they will also receive further mention in suitable places in the chapter that follows. There is, however, one movement of which the description belongs here, since it is an incidental accompaniment of all growth. It is that which was named by Darwin, its discoverer, circumnutation. So slow is it, ordinarily, however, that special methods are needed to render it apparent. If one takes some young seedling, such as Radish or Corn, attaches alongside its tip by harmless cement a slender projecting glass filament, places black reference marks on the end of the filament and on a bit of white paper at its base, and then supports a pane of

glass horizontally a foot above it (figure 132), he can, by sighting his reference marks, record on the pane the spot to which the filament is then pointing. But if, a half hour later, he sights again, he finds that the filament, and therefore the tip of the plant, points in another direction, and later in another, and so on. By drawing straight lines through the points thus established, one obtains a kind of polygon representative crudely of the magnified course of the moving tip of the seedling; and a few of these records, traced by one of my own students, are given herewith (figure 133), while Darwin's book, *The Power of Movement in Plants*, contains a great number. These are not by any means isolated cases, for comparative studies have shown that such movements are distinctive of most if not all growing parts,—stems, buds, leaves, roots, tendrils, flowers and their parts, and many others,—all of which move during growth in slow, irregular, and jerky paths, that are longer and more rapid the more active the growth of the part. While the movement is thus well-nigh universal, it is not popularly known because of its slowness. If its rate could be magnified a few dozens of times, what a different aspect would vegetation present! Then all the visible parts of all the growing plants of a garden, a meadow, or a forest, would exhibit a constant irregular movement, which collectively would seem of a tremulous character,—much, I imagine, as would be shown if the plants were shaken by continuous little earthquakes.

As to the cause of the circumnutation, that is known, in principle at least. It results from the fact that all growing structures, utilizing as they do osmotic turgescence for the expansion of their tissues, are under strong internal pressures which hold them in a highly tense but unstable stiffness. Now the readjustment of these pressures in growth cannot proceed with perfect evenness all around the stems or other parts, whose great length and slenderness cause a large magnification of even the slightest disturbances of the equilibrating tensions,—and circumnutation results. These movements, therefore, are simply an incidental by-product

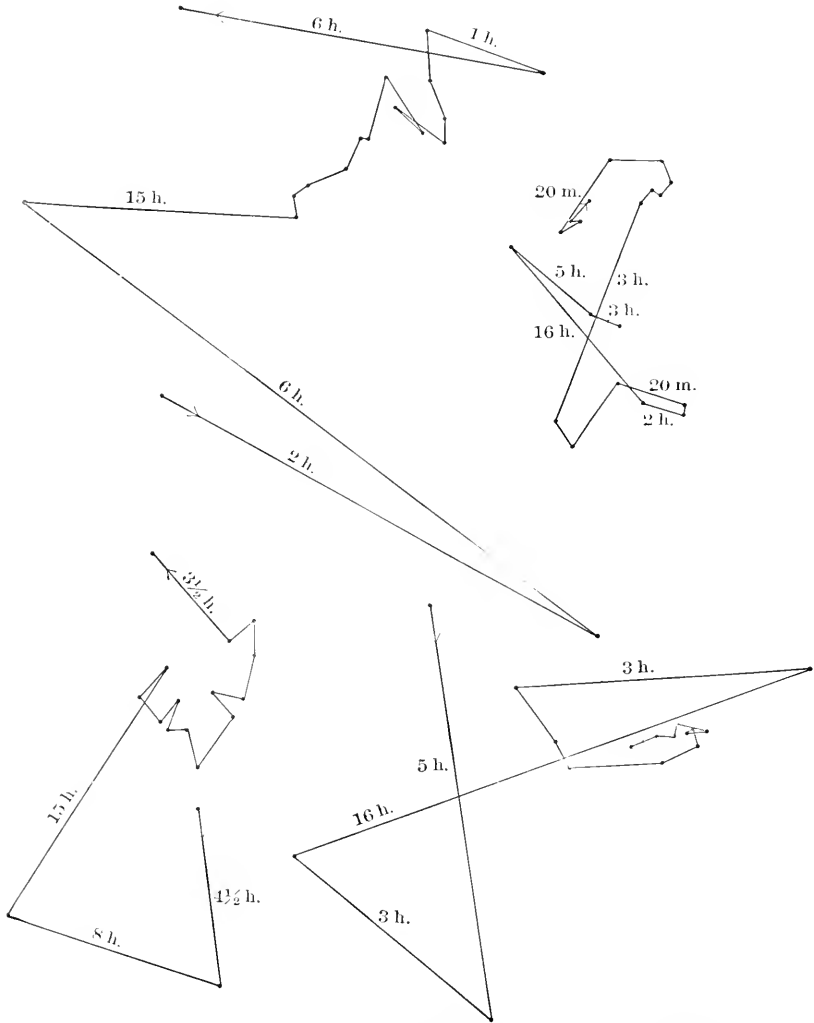


FIG. 133.—Records of the circummutation of some common plants, obtained by the method illustrated in figure 132. The letters *h* and *m* signify hours and minutes between observations.

of growth, and one of those incidental phenomena which possess no adaptational significance; and it is partly because it is so good an example of such incidental phenomena (of which autumn coloration, forms of starch grains, and phyllotaxy, are instances

earlier described in this book), that I give to it here so much attention. There is, however, another reason for its consideration, namely, that Darwin considered it the starting point for most of the useful plant movements,—the twining, sleep, geotropic, hydro-tropic and other adjustive movements which we considered under Irritability. His conclusion on this point, has not, however, been accepted by later investigators, though the present status of the matter may be expressed by saying that his view is unproven rather than disproven.

Finally, as to the physiological phases of growth, there remains one matter which is both scientifically interesting and economically important,—and it concerns grafting. Everybody knows that small twigs of apples, cherries, pears and many other plants can be cut from those trees and inserted into the stems of others in such way as to grow and form structurally an integral part of the new tree. Furthermore (and this is what gives to grafting its great economic importance), the inserted twig and everything which subsequently grows from it, continues to produce its own kind of leaves, flowers, and fruits substantially unaffected by the plant into which it was grafted; while, correlatively, the stock plant into which the graft was inserted continues to produce its own kind of vegetation unaffected by the graft, even though this may in time become the greater part of the tree. Thus it is possible to graft a number of very different varieties of apples, or of cherries, into a single trunk and produce a tree which bears all those varieties as long as it lives, without any visible sign to show that it was ever anything other than one tree from the start. It is in this way that highly specialized forms of fruits, leaves, or flowers, which appear mainly as sports (to be further considered in our chapter on Plant Breeding), and which cannot be grown from seed, are propagated and multiplied indefinitely.

Turning now to the purely physiological side of grafting, the first fact of prominence is this, that the twig, which is called the *scion*, (or *cion*), and the plant into which it is inserted, called the

stock, must be closely related, else no union of tissues takes place. We find the same necessity in hybridization, or crossing of different varieties of species by pollination; and indeed the possibilities of grafting and of hybridization have much the same limits, being comparatively easy between varieties of one species, much less so between species of the same genus, extremely rare between different genera, and unknown outside of the same family. Probably the reason is a chemical one—the more distantly related the forms the more likely is their protoplasm to contain chemicals which react on one another in a way to produce disturbing if not injurious or fatal compounds, thus preventing a normal or orderly continuance of growth. But when the protoplasm of scion and stock is actually congenial, so to speak, then the two grow together precisely as a wound on one plant would heal up, and the tissues unite and thereafter grow as one single mass. It is necessary that a considerable area of living tissue be brought into contact, which is comparatively easy in these plants possessing a cambium cylinder (i. e. a continuous growth system soon to be described), but it is practically impossible in others. This fact explains why no grafting is possible among plants belonging to the groups of the Corn, Lilies, Palms, wherein no cambium exists.

Although, in general, the scion and stock retain each its own characters unaffected by the other, a partial exception occurs in some minor features, such as earliness of blossoming, resistance to frost, and even some slight alterations in flavor of fruit or its color. In all these cases, I believe, such characters can be traced to the influence of the sap, which of course moves from stock to scion, or of the food substance, which moves from scion to stock. The living protoplasm, however, does not thus move from one to another, but remains within the original cells, or those which grow from them; wherefore the characters which depend on the protoplasm, including substantially all of those which give the distinctive characteristics to plants, are never transferred from stock to scion, or vice versa.

From the facts just stated, it would seem impossible for graft hybrids, that is, intimate mixtures of the protoplasm of stock and scion, to exist. Yet graft hybrids have actually been claimed to occur, though very rarely. And here opens up one of the most interesting chapters in recent experimental studies, for it has been found possible to produce experimentally such apparent graft hybrids. But the very same experiments have shown that they are really not hybrids at all, but merely mixtures of the tissues of the scion and stock, and not a blending of their protoplasm. These experiments were made by grafting a part of a bud of the scion to a part of a bud of the stock, when the resultant branch displayed a most remarkable mixture of the colors, shapes, tissue characters, and other features of scion and stock—not a blending but a mixture. Sometimes the upper side of the branch would be all scion with the characters thereto appropriate, and the under side all stock; sometimes a sheath of stock enwrapped a core of scion; and other mixtures of other sort occurred. Such graft products are not hybrids, and have been named *chimæras*. But are graft hybrids then impossible? Theoretically they are not, for if one cut cell of the stock and one cut cell of the scion should happen to match together, and if then their two nuclei should fuse together (as they well might, for we know cases of fusion of nuclei other than in fertilization); and if from this hybrid cell there should then develop a branch by the ordinary process of cell division, then the cells of that branch would all possess protoplasm and chromosomes from both stock and scion, and a true graft hybrid would exist. This alluring possibility has naturally attracted the eager attention of the experimenters, and already they have announced success, though as yet of a somewhat unsatisfying character. And if by good fortune I have ever the privilege of preparing a new edition of this book, I shall probably be able to describe much that is important and interesting in this connection; for this line of experimentation has opened up much more than merely this question of graft hybrids.

CHAPTER XIV

THE ORDERLY CYCLES PURSUED IN GROWTH, AND THE REMARKABLE RESULTS OF DISTURBANCE THEREOF

Growth: structural



THE reader may possibly wonder, as he contemplates the chapter before him, what reason there is for its separation from the one that precedes it, when both are concerned with the very same subject and closely interconnected. So I may as well make the confession that it has not a much better basis than the reason assigned by an early French naturalist for excluding the Crocodiles from Insects,—the animal seemed to belong there, but would make quite too terrible an insect! I like to conceive of this book as read one chapter at a sitting by a reader who has interest enough in the subject to make its careful perusal the chief feature of an evening's business; and so much must be said about growth that it cannot be followed unweariedly without some kind of division or intermission. However, the matter is really not quite so desperate as this, for the physiological and structural phenomena of growth are in fact sufficiently different to make a division between them not wholly unnatural.

Of the structural phenomena of growth, the most striking and important are concerned with the cycle of development of the individual plant from its very first origin up to its adult condition; and this is comprised in four stages.

1. **The Growth Cycle; from Egg-cell to Embryo.**—This stage is rather well represented, albeit somewhat diagrammatically, by

the accompanying picture (figure 134). The reader will recall that the egg-cell is the female reproductive cell formed inside the embryo-sac within the ovule, and that it needs to be fertilized by a male cell brought by a pollen-tube, before it can develop to an embryo. Immediately after fertilization, the egg-cell divides into two; these grow in size, and again divide, and so on in a way to

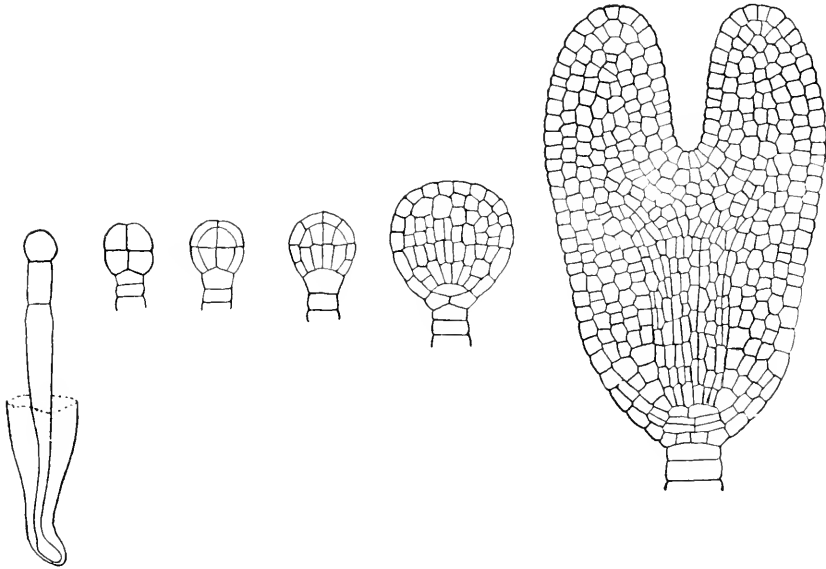


FIG. 134.—Typical stages in the development of an egg-cell into an embryo (of Rape). The original egg-cell lay at the bottom of the embryo sac of which a part is shown in the figure on the left, while the other figures show the development of the initial cell, at the top of the suspensor, into the embryo. (Adapted from pictures on a wall-chart by L. Kny.)

produce a line of cells forming a structure called a *suspensor*, which carries a terminal, or *initial*, cell out into the middle of the embryo-sac, where there is ample space for the development of the forthcoming embryo. Then the initial cell begins to divide, first at right angles to the earlier divisions, then again and again in other planes with great regularity, as represented in our pictures, until finally a many-celled ball is produced. Then the regularity ceases, and cell division becomes more active at two

definite places, resulting in outgrowths which wax greater and greater until they become the thick leaves that later are called the *cotyledons*. Meanwhile the original ball is growing more actively at the opposite end, there producing a cylindrical structure

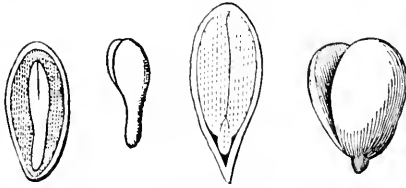


FIG. 135.—Typical seeds, with embryos, of the two leading types;—“aluminous” (a Barberry) and “exalbuminous” (an Apple), as further explained in the text. (Copied from Gray’s *Structural Botany*).

structure which forms the stem, or *hypocotyl*, of the embryo, while a group of growth cells at its tip forms the foundation for the forth-coming root, and another between the cotyledons forms the foundation for the first terminal bud. Thus are the first leaves and stem,

and the foundations for the first root and bud, of the new plant laid down wholly inside the embryo-sac of the ovule, forming the structure which we call the *embryo*. Simultaneously the coats of the ovule are growing thicker and harder, the suspensor is being absorbed, and a supply of food substance, the *endosperm*, developed in a manner already described (page 299), is filling all the space in the embryo-sac not preoccupied by the embryo. The resultant structure, a combination of embryo, food substance, and protective coats, is the *Seed* (figure 135, on the left).

Such is the typical method of development of embryos and seeds, though of course a great many differences occur in detail. In some seeds the development stops at the point here described, leaving the young embryo surrounded by copious endosperm or “albumen”; but in others, for example, Peas and Beans, the embryo continues its development until it has absorbed all the endosperm and everything else inside of the seed coats, in which case it usually develops also the first bud, called the *plumule*, between the cotyledons (figure 135, right). In any case, the seed is now ripe. It gives up most of its water, hardens its coats, separates from the parent plant, and goes into that resting state, in which

some kinds may remain, with vitality intact, for years and decades, and even a century, though not for the ages implied in the current but groundless belief that genuine seeds from the wrappings of mummies will germinate. In this condition, small and light, and independent of external food or water supply, the seed is capable of wide transport; and thus forms a natural stage for dissemination, in adaptation to which its coats or neighboring structures often develop wings, plumes, hooks, pulp and colors, as we shall consider more fully in the following chapter. It is not of course because the seed has these characters that it is utilized by the plant as its dissemination stage, but it is rather because it has been developed as the dissemination stage that it has these characters.

In following the sequence of cell divisions involved in these results one cannot but wonder what the nature of the controlling power must be. Structurally considered, cell division can take place just as well in one direction as another, yet in fact it takes place in substantially the same directions as in preceding generations of embryos,—directions which bring an adaptive result. What is it which compels the developing egg-cell to form a line of cells instead of a ball, and the initial cell to form a ball instead of a line; which leads the ball to push out the two cotyledons in definite places, and to make the hypocotyl and root in another? In some way, it is certain, the control issues from the chromosomes, which alone hold the knowledge of how the former generations developed; but through what mechanism do they exert their authority? This question, for the most part, we cannot yet answer, but in some part we can; for it seems reasonably certain that most of the changes consist in responses to stimuli, the nature of which was explained in our chapter on Irritability. Perhaps the pressure of the egg-cell against the end of the embryo-sac is the stimulus which sends the suspensor developing as a single cell-line in the opposite direction; perhaps the freer osmotic absorption permitted by the arrival of the initial cell into the more fluid

central part of the embryo-sac is the stimulus which sends this cell developing into a regular mul-ticellular ball; perhaps the beginning of pressure on this ball as its expansion brings it against the protoplasmic lining of the embryo-sac, is the stimulus which sets the cotyledons developing at their definite places, which places themselves may be fixed by the positions of least pressure; perhaps the contact of these growing cotyledons with one another is the stimulus which starts the development of the plumule between them, and starts also the extension to form hypocotyl and root in the other direction. Maybe, or probably, I am wrong as to the details of these stimuli, but if it is not these it is some others of similar sort; and in any case my speculations illustrate the principle of the matter. The idea is confirmed by the fact that there is one case of growth stimulation of whose nature we are reasonably certain. The reader will recall that the stimulus given by the fusion of the second nucleus of the pollen-tube with the nucleus of the embryo-sac starts the development of the endosperm (page 299); and this, or some other phase of fertilization, is the stimulus which starts not only the hardening of the seed coats and the development of other typical seed features, but also the many large processes involved in the formation of the fruit. It is a fact that ordinarily neither endosperm, seed coats, nor fruit, develop unless fertilization is effected,—an arrangement that is obviously adaptive, since without fertilization they would all of them be useless, and a wasteful drain on the plant. This kind of “linking up” of the processes together through the connection of stimuli is believed to be representative of the method whereby the development of plants, and animals too, is kept in harmonious and continuous progress. It is essentially the same method as that by which the parts of a complicated machine are kept working effectively together, each special part of the mechanism being geared or connected to some of the others in such manner that the movement of the mass as a whole compels each part to perform its destined office at just the right moment and place.

The analogy, indeed, goes a long way farther, for, just as the accidental loosening or breaking of some connection causes the machine to work irregularly, or even causes its different parts to work independently of one another,—so the failure of the stimulus-connection in the organism may release some parts from the regulatory control of the remainder and cause them to work more or less independently. Such is without doubt the explanation of the abnormal or monstrous growths presently to be considered. The same thing is well known in the animal kingdom, where tumors, for example, are known to be growths released in some way from the regulatory control usually exercised by their connection with the rest of the organism; and we have the same thing in mental phenomena, for dreams, in all probability, are simply mental processes whose correlation is temporarily lost in sleep, while insanity is the same thing with the correlation more or less completely or permanently lost.

While the embryo is thus developing from the egg-cell and the seed from the ovule, the fruit is developing from the ovary and other parts of the flower; and this fruit aids in dissemination, by the methods we shall later consider. During dissemination, and often for long after, the seed remains in a resting state, with its vitality suspended. In most seeds this resting period is compulsory for a time, at least for several weeks, within which period the seed will not germinate no matter how favorable the conditions that may be offered. The same thing is true, by the way, of winter buds, bulbs, and some other plants, though it is interesting to note that many cultivated plants, notably the grains, have lost the resting period, and will germinate as soon as ripe, even sometimes in the seed pod. The advantage of the resting period to the plant is sufficiently plain: it gives time for dissemination and it prevents premature germination, such as might happen during a warm time in winter, resulting in the destruction of the embryo by the subsequent frosts. It is effected and controlled, of course, by the protoplasm, which uses various arrangements for the purpose,—

sometimes seed coats so constituted as to take days or weeks for water to penetrate them, sometimes a delay in the development of the enzymes needed to soften the endosperm, sometimes no doubt in yet other ways that are still undetermined.

Thus is the new plant developed in the seed prior to its birth.

2. The Growth Cycle; Germination.—This is a very distinct though brief stage. When the resting period is completed, the seed germinates on the first access of water in conjunction with warmth. The water is absorbed and passed on to the embryo,

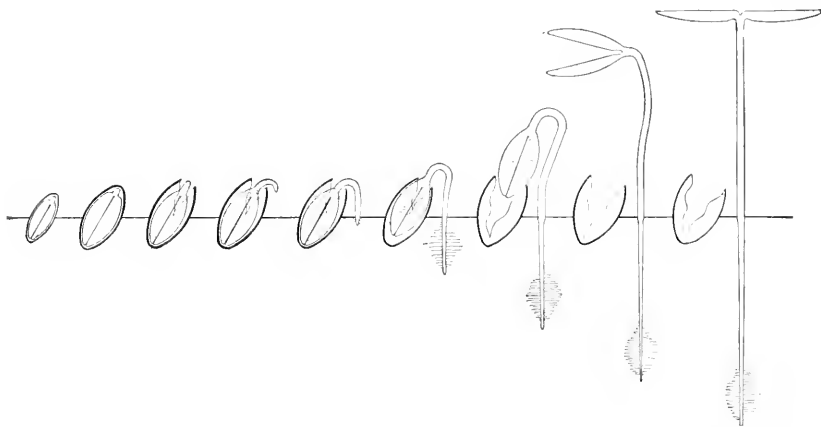


FIG. 136.—A generalized drawing of a typical case of germination, from the dry seed to the fully grown embryo. The controlling factors are discussed in the text.

which swells powerfully, and thus bursts open the seed coats. Immediately the root grows rapidly out, and, no matter in what position the seed or embryo may happen to lie, invariably turns downward under the stimulus of gravitation, and, developing a zone of anchoring and absorbing hairs, proceeds to grow straight into the earth (figure 136). This is an obvious adaptation to the new plant's first needs, a firm anchorage in the soil and a supply of water therefrom. When the root is thus firmly anchored, the embryonic stem, under the stimulus of gravitation, begins to turn upward, and, guided by other stimuli, works the cotyledons out of the seed, and carries them upward, where,

responding to the stimulus of light, they open out, turn green, and serve as the first foliage. At least such is the procedure in the most typical cases, though there are many variations in detail, including especially a great many cases in which the cotyledons remain in the seed, sending up only the plumule. Meanwhile this embryo has continued to absorb water, with which its cells have swelled greatly; and its stored food has been largely converted to new wall and living substance. Finally it stands up stiffly, many times larger than at first, but with no new parts and even less of solid substance. It is now all ready to begin its independent life.

Thus is the new plant born.

3. The Growth Cycle: the Seedling.—The stages of development, while distinct in the main, overlap in some places. Thus the root develops considerably in germination, and early in this stage begins to branch. Its new cells are all formed at a definite growing point, whence they radiate in regular lines backward, increasing in size, as shown very clearly in our earlier figure 53, and diagrammatically in a later figure, 139 *D*. The branches of roots start always from the fibrovascular bundles and have therefore to break or dissolve their way out through the cortex (figure 67), a method which seems clumsy, but is doubtless the best that the plant can do. Their places of origin are fixed largely by external stimuli,—the contact of greater warmth, moisture, aëration, mineral supply and the like. The guiding stimulus of their subsequent growth is gravitation, which sends them radiately outward in directions of least interference with one another, though they, and especially the later branches, are swung from the geotropic angles, and given their final details of position, by advantageous responses to various minor stimuli. Thereafter, so long as the plant lives, these roots grow, branch, and are guided continuously in this manner. Meantime the embryonic cells between the cotyledons become active and push up a cone of cells which constitutes the first bud. As this bud becomes larger the

cell divisions become more active at definite points near its base, and push out flat projections which develop and grow into the leaves, as shown by our accompanying figure 137, and diagrammatically by figure 139, *C*. Unlike new roots, the leaves have their places of origin determined not by stimuli from without, but by internal influences, for they come out from the bud in accordance

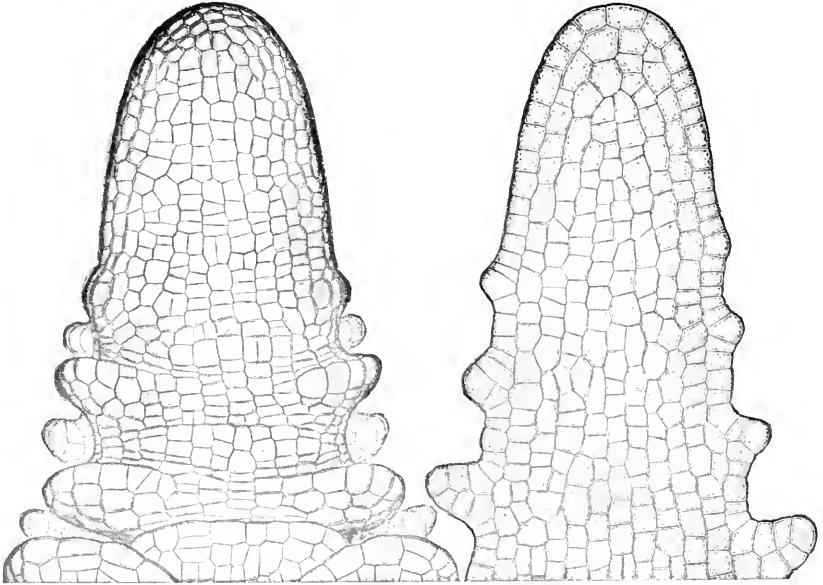


FIG. 137.—A bud (of *Elodea*, a water plant), in surface view and section, showing unusually clearly the mode of development of new leaves. (Copied from a wall diagram by L. Kuy).

with definite mathematical systems, as we have considered already under phyllotaxy (page 62). In their early stages, and while their tissues are still young, the leaves are flattened closely over one another into the conical structure we commonly call a bud; but as they become old enough to be useful they bend outward and ultimately present their inner faces to the sun. As they grow, their blades tend to take horizontal positions under guidance of gravitation, but they are easily swung therefrom, and given

final direction, by the stimulus of light, to which they set their blades at right angles. As the leaves develop, embryonic tissue in their axils becomes active, and develops into new buds precisely like the first bud produced by the embryo,—the stimulus thereto being probably the pressure exerted upon them by the developing leaf. It is easy to see an advantage in this axillary position of buds, for their first need is abundance of food, and the leaves are the source of supply. From these buds grow branches, the primary directions of which are assumed under guidance of gravitation, whereby they are sent radiately out into positions of least interference with one another, although the details of their ultimate positions are fixed by a variety of minor influences, precisely as in the case of the root-branches above mentioned.

Such is the complete structure of a seedling, of which a typical example is here represented (figure 138).

4. The Growth Cycle: the Adult.—The seedling continues development and growth for a considerable time in the manner just described, branching continuously into new roots and stems, and making new leaves. Its transition to the adult condition may be considered as marked by the beginning of reproduction, even though the plant may by no means have reached its full size. Suddenly, at some time in the plant's growth, without any apparent reason, some buds begin to produce flowers instead of more leaves. The central features of flowers are in reality the pollen grains and the embryo-sacs, and there can be

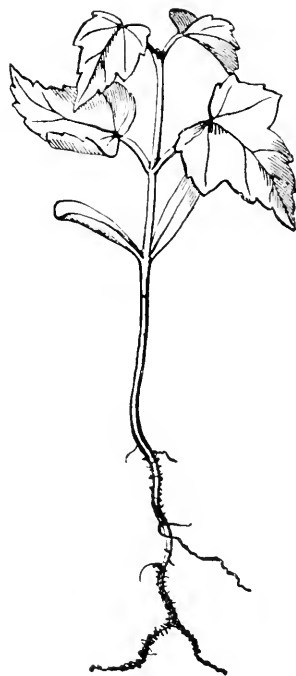


FIG. 138.—A typical seedling (of a Maple), showing the distinctive parts, excepting that the axillary buds are not sufficiently visible. (Copied from Gray's *Structural Botany*.)

little doubt that it is the beginning of the formation of these which gives the stimulus to the formation of sepals, petals, stamens, and pistils, instead of ordinary leaves. But it is not yet clear what it is which starts this formation of pollen grains and embryo-sacs, though it must result in part from some outside stimulus, since plants can be made to flower much sooner by making the external conditions somewhat harder. The flower, once formed, secures pollination or cross pollination preparatory to fertilization, as described in our earlier chapters, and is followed by the fruit which aids in dissemination, as we shall consider in the chapter that follows. But with the flower, indeed, we are back to the fertilized egg-cell with which we began, and thus is the cycle completed.

A matter of very much interest in connection with the growth of plants from the seedling to the adult concerns the changes in their tissues. The tissue of the young embryo is all capable of cell division (is *meristematic*, in anatomical language), but as the embryo germinates, only the tip of the root and the first bud, together with a thin hollow cylinder of *cambium* connecting them, remain so, while all the remainder of the cells grow large, assume special functions, and lose their power of division. The new growing points as they originate, whether on stems or on roots, establish connections with this cambium cylinder so that together they form one continuous system, in which all of the growing points are connected with one another by hollow cylinders of cambium, and conversely, the cambium cylinder branches into numerous tapering tubes terminating in the growing points, as our diagrammatic figure illustrates (figure 139). Meantime the cambium grows steadily outward, as the growing points grow steadily onward, each forming permanent tissues behind them. This separation of growth and permanent tissues makes it possible for a plant to go on growing without limit, and were it not for the restrictions imposed by external physical conditions, there is no reason why trees should not be immortal. In this possession of

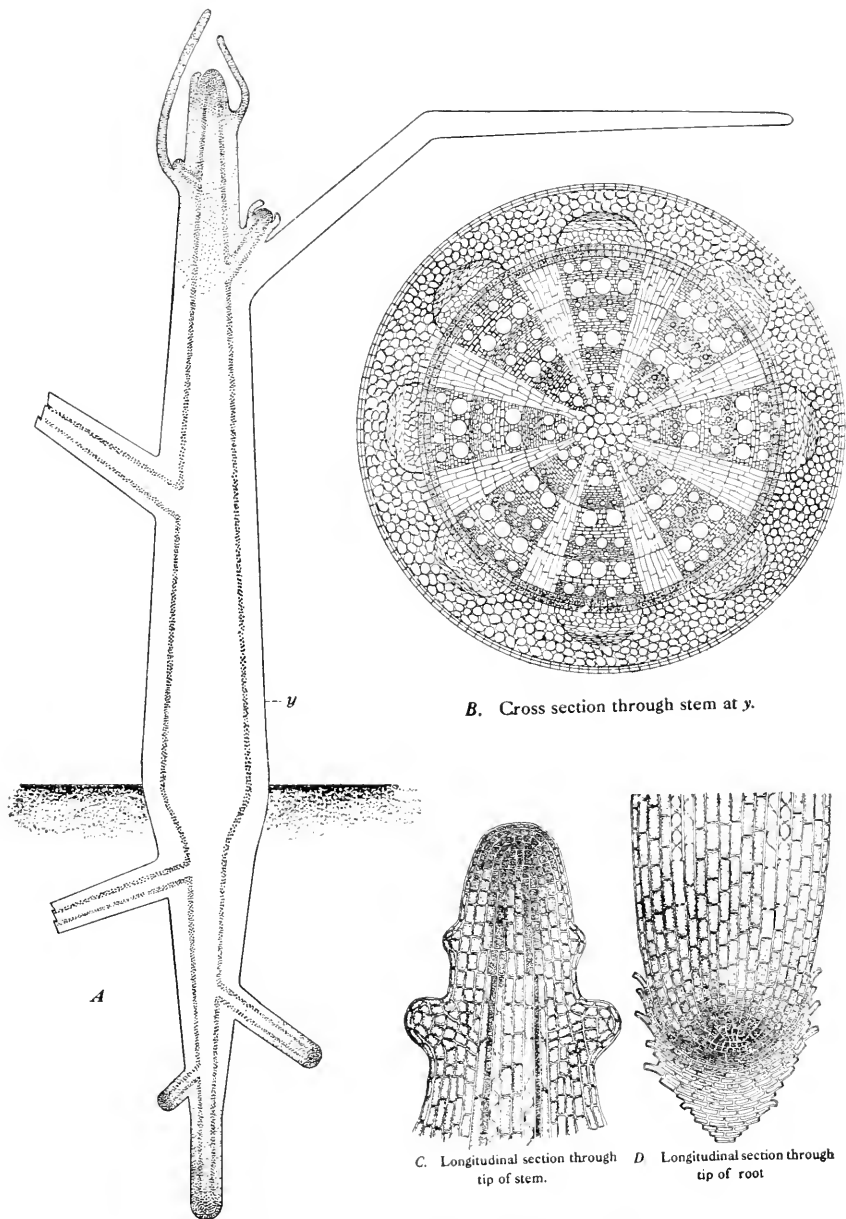


FIG. 139.—Generalized drawings illustrating the growth system of the plant.

continuously working embryonic tissues, plants are sharply distinct from animals, all of whose tissues sooner or later become of the permanent kind, thus limiting their further growth.

Although the most typical stems possess this remarkable cambium system, there are others which lack it. In these the further growth takes place by the addition of new fibrovascular bundles, or veins, among and outside of the old ones, so that the



FIG. 140.—Cross sections of stems of the two typical kinds,—*endogenous* with scattered bundles (the Palm on the left), and *exogenous* with the bundles in rings (the Scotch Fir on the right). The matter is further explained in the text.

fully-grown stem is composed of separated bundles scattered irregularly through the ground tissue, as well seen in the Corn, or a Palm stem (figure 140, left), or any plants of the great classificatory division of the Monocotyledons. Observation alone, of these stems, conveys the impression, though a false one, that the new bundles originate inside of the old ones, whence they have been described improperly as *endogenous*, in contrast with the *exogenous* growth from cambium (figure 140, right). The growth of exogenous stems involves matters of much interest, as figure 141

will help to illustrate. Although these stems possess separate fibrovascular bundles with intervening plates of soft tissue at the start (compare figure 73), the continuous growth of the cambium, which forms new duct tissue on its inner and new sieve tissue on its outer side, gradually fuses the bundles into one woody mass, although preserving, more or less perfectly, the intervening plates of tissue called *medullary rays*. The growth of the cambium, however, is periodically checked by the winter, and the contrast between the small compact autumn-formed cells and the large loose tissue of the spring (figure 139, *B*) gives rise to the familiar phenomenon of the *annual rings*, which appear also, though faintly and in reverse order, and ultimately crushed to unrecognizability, in the bark. Most of these features show well in such a wood as that of the Oak, where the annual rings, and even the separate ducts, are easily visible to the eye, while the medullary rays become the broad shining plates which give distinction and value to quartered oak. Meanwhile corky waterproof layers are forming in the outer part of the bark, which

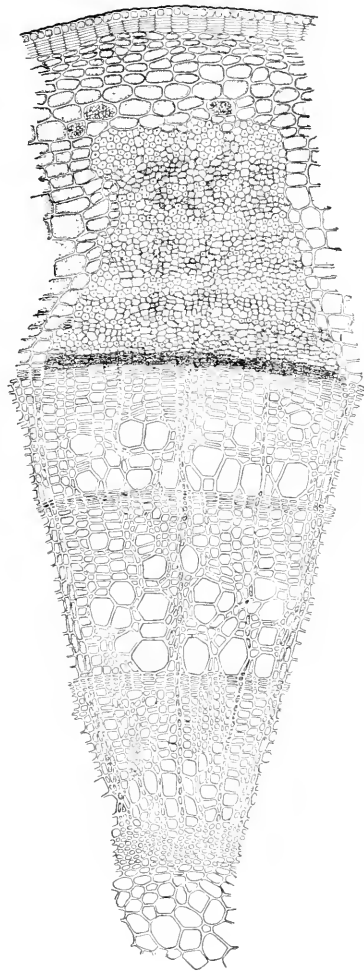


FIG. 141.—A segment, including a three year old fibrovascular bundle, of a typical stem, the Linden, showing the annual rings of the wood, the cambium cylinder, and the annual rings (less prominent) in the bark. Compare with a single bundle in figure 139, *B*. (Copied from a wall-chart by L. Kny.)

includes everything outside of the cambium. Though the bark, like the wood, thus increases in thickness as long as the tree lives, at least theoretically, in practice it weathers away about as fast on the surface as it forms inside. It will now be clear why this exogenous mode of growth permits the indefinite expansion of woody stems.

In close relation to the age at which flower buds first appear is the length of life of the plant. When plants come to flower the season they germinate, all of the food they can make is thrown into their seeds, and the soft stems then die, root and branch: such plants are *annuals*. Other kinds, however, make only leaf buds the first season, and store up food in some underground part to which they die down; then this food is made use of in forming new stems, flowers and seeds the next season, after which the plants perish completely: such plants are *biennials*. Yet other kinds, in the second season, instead of throwing all of their food into seeds, store a part underground, die down thereto and then send up a new flowering stem the next season, and so on year after year: such plants are *herbaceous perennials*, which include so many of the favorites of our gardens. Finally, there are many others which do not die down to the ground at all, but harden their stems to wood, and thus can stand upright over winter. Thereafter, each season's growth, whether in length or in thickness, is built upon that of the preceding, and the structure thus grows both in length and in thickness as long as it lives: such plants are *woody perennials*, which are principally shrubs and trees. Since this method admits of indefinite increase in size, and since, moreover, it involves a constant rejuvenescence of the protoplasm (the significance of which is discussed earlier, on page 162), it is obvious that trees have no limit set to their growth by internal factors, but their maximum size is imposed by the action of extrinsic causes,—such for example as the increasing difficulty of conducting sufficient water supply through the greatly lengthening stems. Thus, with increasing size it becomes

more difficult for them to transfer a sufficiency of water and minerals to their more distant parts, whose vitality is thus checked. At the same time the increasing exposure of parts to the winds, and the greater leverage thus given, leads to breakage, and hence the admission of rot-producing fungi, which sooner or later bring the loftiest tree to the ground. Thus trees, though they grow very large, never really stop growing in size; and, moreover, they never grow old in the sense that animals do, but come to their end while their individual parts are still in full vigor.

Such is the cycle of growth in the most highly organized plants, and very different it is, as the reader will have noticed, from the cycle displayed in the highest of animals. For animals construct but a single set of organs, which last without renewal through life; and when these have each grown to full size the growth of the individual is stopped, though it may live for a very long period thereafter. Inside of these organs the protoplasm goes on working without chance for rejuvenescence, and therefore gradually wears out and dies, thus fixing an internal limit to the length of the animal's life.

Through such a complex though orderly cycle do the most highly organized plants all swing in the course of their development and growth. In tropical climates the cycle is accomplished without pause, except for a brief time during dissemination, but in temperate regions the continuity is rudely disturbed every year by the advent of winter, to which all vegetation must in some way make adjustment. One could hardly believe, a priori, that plants could accommodate themselves to ranges of temperature from forty degrees below zero to a hundred and twenty above it;—yet such is the fact. This adjustment of vegetation to winter introduces a secondary seasonal cycle, which has the four following stages:

The Winter is the season of dormance, in which vitality is suspended. The protoplasm, giving up the most of its water, ceases to move, becomes hard, reduces all activities to a minimum, and

goes into a resting state. Its condition in the buds, the cambium, and the other living parts then approximates to that of the seed. This is the season of gray and brown colors, which are distinctive of dried tissues and of the non-conspicuous protective bark and bud scales.

The Spring is the season of unfolding, when the plant absorbs water, the sap rises, and the protoplasm awakens to a new and exuberant life. Then all of the structures developed in the buds the preceding season enlarge rapidly through their grand period, and unfold to soft-textured foliage and flowers, transforming the whole face of Nature. This too is the principal season of fertilization, and of germination, and of new life in various forms. It is the season of delicate colors, for not only is it the time of most flowers, and of the softest foliage green, but much of the young vegetation is overspread by a blush of rosy red, which perhaps is the protective and warming screen to the much exposed protoplasm before the chlorophyll is fully made.

The Summer is the season of accumulation. The green leaves, in the full vigor and strength of maturity, are engaged in the making of food, which passes steadily away to the places of storage or use, providing for current needs and preparing a new store for the future. It is the time of development of embryos, and formation of fruits. It is the season of greenness, the typical time of vegetation, the state that is permanent in the tropics.

The Autumn is the season of fruition,—the time of ripening which is always a preparation for the future. The tissues are strengthened and hardened; the parts to come out the next spring are completed in the buds and enwrapped with protective covers; the fruits are brought to perfection and made ready for their function of dissemination; the leaves are emptied of their valuable matters and made ready for their annual fall; the protoplasm throughout the plant gradually yields up its water and assumes its resting condition. It is the season of brilliant colors, red, purple and yellow, a part (those of fruits) serving definite uses, but the

most of them (the autumn foliage), a chemical accident, though one with the happiest consequences to the pleasure of man. Then the winter comes again and the seasonal cycle is closed.

There remains yet one other aspect of growth, and that of no little importance,—namely, the remarkable results that ensue from its disturbance. All growth when left undisturbed tends of itself to produce symmetrical structures. In evidence thereof one has only to recall the superb symmetry of an Elm or a Maple when growing alone in a meadow, or the perfection of conical form in a Fir tree which springs up in some field that is abandoned, or the regularity in arrangement of leaves which develop within the protection of a bud. And the same thing can be shown very beautifully by experiment. Accordingly when a plant deviates from symmetry it is always because of disturbing influences, of which there are some four classes.

Disturbance of Growth by Accidents.—These are many and so obvious as hardly to need comment, including overcrowding by other plants, breaking of branches by wind or ice, destruction of parts by animals or Fungi, scalding of newly exposed bark by the sun, drying back of parts through failure in water supply, poisoning by bad gases, and many others of various sorts. And it is important to observe that the destruction of parts of a plant by any of these agencies is followed as a rule by an effort at replacement and the restoration of the symmetry, as can be seen in trees which have lost some of their branches.

Disturbance of Growth by Adaptive Adjustment to the Surroundings.—This subject received full treatment in an earlier chapter, where it was shown that individual plants can alter greatly the details of their form, size, or structure, in adjusting themselves to take advantage of the best conditions of their immediate environments. It is most conspicuous in connection with adjustment to light, towards which a plant will often bend its entire structure; or in connection with adjustment to moisture, towards which an entire root system will often extend in a very unsym-

metrical fashion. Such disturbances of symmetry are wholly natural and healthful, unlike the cases which follow.

Disturbance of Growth by Parasitic Stimulation.—The parasites of plants are of two general classes, Insects and other plants, mostly of the simple kinds called Fungi. Everybody knows the structures called Galls, especially common and typical upon Oak leaves, where they appear as rounded, almost nut-like, often hairy, sometimes red swellings which, when opened reveal always the presence of a living insect larva. There are hundreds of kinds of these galls, very different from each other but each kind so distinctive that an expert can distinguish them easily, and even identify the insect which made them. Other galls are almost hair-like, others are globular swellings of very slender stems, while yet others include the terminal buds, and involve the leaves in a way to produce those compact rose-shaped structures often called willow-roses. They are all made in substantially the same manner; an insect lays its egg in the growing soft tissue, and the developing insect causes the plant tissue around it to form such a structure, and to lay up such contents, as will provide both a safe home and a sufficient food supply for the larva until its maturity, when it makes its way out and away. But just how the result is effected by the insect is not at all certain, whether by mechanical movements or chemical secretion. Nor is it yet certain just what the plant's attitude is towards the gall. It can hardly be true that the plant derives benefit from the excretions of the insect, since the original substance to make those excretions is mostly supplied by the plant itself. It seems much more probable that the plant is passively affected by the insect, which has discovered, so to speak, just the chemical substance or the developmental stimulus which happens so to fit some peculiarity of the metabolism of the complicated protoplasm as to stimulate it to the formation of structures and substances adaptive to the uses of the insect. Theoretically, man ought to be able to affect plants in analogous ways, and it is not unlikely that the horticulture of the

future may embrace wonderful new vegetables or fruits produced by the injection of chemical substances into the young growing tissues of ordinary plants.

Of somewhat analogous nature are the abnormal growths produced by the presence of parasitic plants. A typical case is found in those remarkable dense growths of many slender upright twigs, found often on Spruce trees and commonly mistaken for nests of big birds. They are generally known as Witches Brooms, and are caused by the presence of a Fungus which sends its nutritive threads into the young growing branch, and seems to produce a paralysis of the delicately-balanced controlling power of growth. As a result all the buds in that region proceed to develop, though ordinarily they would mostly be suppressed, and each grows for itself without any geotropic correlation with its neighbors. Of precisely similar nature



FIG. 142.—A "wooden flower" from Guatemala, one-third the natural size. It is explained in the text.

are those spiral-radiate-saucer growths on the roots of tropical trees, often sold to tourists as curiosities under the name of "wooden flowers" (figure 142). Unlike the case of the galls, there is no obvious advantage to the parasite in these methods of growth of its host, and the result seems purely incidental to the paralysis of the regulatory power,—the direction that anarchy takes, as it were, when the hand of the law is removed. We see something of the very same sort in the animal world and especially in mankind, in tumors and other abnormal growths, which are likewise a continuation of growth without

control. From such elaborate structures as the Witches Brooms there are all grades downward to those so inconspicuous as hardly to attract notice, including some very simple kinds of excrescences.

Results very similar to these may be caused by external mechanical injuries. Thus, when tree trunks are injured in the cambium, this also loses its regularity of growth, and becomes thrown into various contortions, producing gnarly fibrous growths which often appear as large burls on the trunks. Moreover, the injured cambium at times attempts to put out adventitious buds, which, forming in large numbers but without proper control, just about keep pace with the expansion of the trunk. The resultant masses of wood show the characteristic rings of buried branches, often in patterns displaying great beauty, of which the Birdseye Maple affords a conspicuous example.

Disturbance of growth by Internal Causes.—In addition to the external and visible causes which throw growth into confusion, there are others which appear to be internal. One of the simplest cases is that in which the correlation between the different parts of a plant becomes weakened or lost. This correlation is beautifully shown in the familiar fact that if the young tip of the main stem of a Spruce or a Fir tree be cut away, one of the nearest branches will grow up and take its place, although, had the tip remained, that branch would have grown like its neighbors horizontally outwards. It is indeed this correlation of the geotropism of the branches which makes possible the symmetrically radiate shape of a tree, each branch as it grows assuming the correct geotropic angle to form either the cone or the ball of foliage as the case may be. Now in old trees this correlation is sometimes lost, perhaps through the interruption of the protoplasmic connections along the stem, and then each new branch grows upward precisely as if it were the only main stem, as our accompanying figure illustrates (figure 143). Obviously such cases are related in method with the Witches Brooms and the like, earlier mentioned. Somewhat the same thing occurs in

the case of branches, or sprouts, that spring anew from old trunks.

More profound disturbances, also of internal origin, result in the formation of monstrosities, or in common language, "freaks." They are really rather common, and attract much notice because of their oddity. In general they may be distinguished from the effects of fungus or insect action by the fact that although they look odd they also look healthy. Very typical are those called *fasciations*, which arise in this wise, that, from causes unknown, some terminal bud, instead of developing as a single cylindrical structure, becomes partially split into a number of points, which usually spread out like a fan, and produce a flattened or corrugated stem with many little terminal points. A remarkably fine example of a fasciated Pineapple is shown by the accompanying picture (figure 144), and most people have seen fasciations in Asparagus, Hyacinths, or other strong-growing plants. Fasciations are also the basis of the crested forms of Cactus and other plants, and give the "cockscorn" to the plant of that name, in which, as in some other cases, the condition is hereditary. Fasciations can also be produced, by the way, by external injury, such as the bites of some insects, though when produced in such manner they are not hereditary. They are of all degrees of complexity, down to a simple forking of the growing point, which may sometimes result in the formation of double fruits, though these are more often the result of the fusion of two buds in a sort of natural grafting. It is obvious that such fasciations come very close to the condition which originates the Birdseye Maple, or rather that the latter

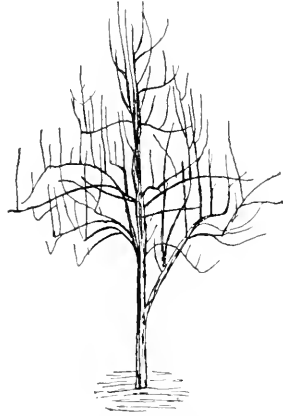


FIG. 143.—An old Apple tree, in which the geotropic correlation of the branches has been lost, leaving each bud free to develop as if it were the only one. (Traced from a photograph.)

in reality is a kind of fasciation. It is perfectly impossible to draw any sharp line between these different forms of clustered abnormal growths, or between external and internal causes of their formation.

Somewhat similar is the origin of twisted stems or *torsions*. These occur in small herbs, but are often seen to perfection in dead standing trees, or even in the logs of fence rails; but here the



FIG. 144.—A fasciated Pineapple, resulting from causes explained in the text.

process is hardly abnormal, since, as seems likely, the twisting of the cambium cylinder, to which it is due, is a result of normal growth processes in the plant.

A second common form of monstrosity is that known as *proliferation*. Sometimes the stem of a pear, or a strawberry (figure 145) grows on beyond the fruit, producing there a cluster of leaves. In one way these cases are easy to understand, for they

are simply instances wherein the stem, which ordinarily ceases to grow in a flower bud, keeps on growing just as it does in the leaf buds, though why it should do so is not as yet known. We have a partial case of the same thing in the navel orange, in which the receptacle or stem grows part way up through the fruit and makes there a second series of carpels, which constitute the secondary orange within the navel; and the same thing carried farther in apples sometimes gives us a two-storied fruit.

As to other monstrosities they are legion,—enough, indeed, so that their mere synoptical description suffices to fill large volumes devoted to the subject. Flowers double profusely; leaves instead of their characteristic flatness exhibit often the form of a pitcher or cup; pistils become open leaves, exposing the ovules, which themselves become altered at times to tiny leaflets; apples and cucumbers produce leaves on the sides of their fruits; flowers become green, and bracts of the stem assume the colors of flowers; and so many other alterations of form, color, size and regularity occur that it sometimes seems as if every deviation from normality structurally possible in any and every part of the plant became sometime or other actually realized in fact. Some of these monstrosities are hereditary, though mostly they are not, and many of them could be propagated by grafting if it were thought worth while. It is evident that they merge without break over into those extreme variations which are called, horticulturally, sports.

Monstrosities are sometimes reversions to an ancestral condition, and formerly they were thought always to be so. Hence they were supposed to throw light upon evolution and classification, an idea embodied in Goethe's saying that "by her mistakes



FIG. 145.—A Strawberry, in which the stem that forms the fruit has grown out beyond it into a leafy branch. (Copied from Masters' *Vegetable Teratology*.)

Nature betrays her secrets." But so many monstrosities are known which cannot be interpreted as reversions that we must consider them rather as results of disturbance of the growth processes, though we have no idea as to the ultimate causes. They can mostly be interpreted in terms of failure of action on the part of the suitable stimuli. Thus, in green roses, the stimuli

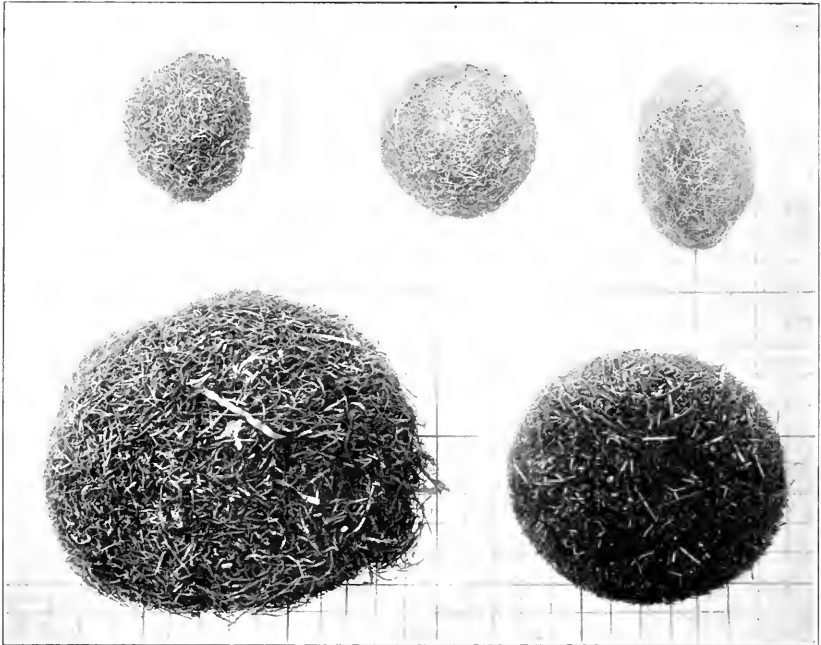


FIG. 146.—Typical examples of water-rolled weed balls, photographed about two-fifths the natural size (the squares of the screen are each one centimeter). The largest is composed of various Algae; the next in size, of Spruce needles; the next, of Pipe-wort; the oval one, of hair; while the composition of the fifth is uncertain.

which started the formation of a flower bud instead of a leaf bud worked properly, but those which controlled its farther development did not. But as to the causes of such failure of stimuli we have no information.

In connection with plant-structures of odd mode of growth, we must take note of one having a very different character. On

some sandy shores of the sea, or of freshwater lakes, the visitor sometimes finds balls of vegetable matter a few inches through, of a roundness and symmetry wholly surprising. Naturalists once thought them a species of seaweed, while peasants and doctors ascribed to them medicinal virtues. In reality they are nothing other than masses of the fibrous parts of half-decayed plants, matted, compacted and rounded by the gently-rolling action of the underwater parts of waves acting over smooth sandy bottoms. They are made up of the most diverse materials,— plant-fibers, fine seaweeds, needles of pines, spruces and hemlocks, and even such adventitious materials as shavings and hair. A number of different kinds are well shown on the accompanying plate (figure 146). These are not the only kinds of vegetable balls that are known; others, sometimes called *bezoars*, are formed by the rolling and matting of indigestible fibers in the stomachs of cattle. Somewhat analogous is the curious algal paper, sometimes formed by the drying of continuous masses or sheets of matted Algae left by the falling water of lakes. And doubtless there are other structures also, which appear to be products of some special mode of growth while in reality they are merely a result of the play of natural forces.

CHAPTER XV

THE MANY REMARKABLE ARRANGEMENTS BY WHICH PLANTS SECURE CHANGE OF LOCATION

Dissemination; Fruits



ONE of the most obvious and consequential of the facts about the typical plants is their sedentary habit;—they are rooted immovably in one spot. Yet all of the kinds are able at some stage in their lives to change their locations, though the methods whereby this is done are most diverse, as the following pages will abundantly demonstrate.

We make sure, first of all, why a change of location is needed. To take the most obvious reason, it is evident that if all of the seeds that any plant ripens were to fall direct to the ground and germinate there, a jungle would result so dense that few, or perhaps none, of the plants could survive. A power to spread from their parents is therefore essential in order that individuals may find space in which to develop. But there are reasons, as well, of a secondary sort. Thus, any kind of plant, whether because it exhausts from the soil some material it needs in its growth, or because it imparts to the earth some excretion injurious to itself, cannot grow a very long time in a single location without deterioration of vigor. Again, in an ever-changing world, it is an advantage to any species if it can leave a situation becoming less favorable for its life and migrate to some other that is becoming more favorable. Furthermore, it seems true of plants as of men that an occasional change to different surroundings acts stimulatingly upon health and adaptability, and therefore is distinctly

advantageous in the struggle for existence. And other reasons exist, of lesser weight, which combine with those given to explain both the need and the value of a change of location.

The methods whereby plants secure this change of location are many and various, but fall somewhat naturally under these divisions:—

1. Independent Locomotion
2. Extension through Growth
3. Projection by Elastic Machinery
4. Waftage by Winds
5. Flotage upon Water
6. Carriage by Animals

The roll of these methods will recall to the reader our discussion of the use of the very same ones in connection with cross pollination. They are, in fact, substantially the same, as would be inferred from the similarity of the problems presented to the plant in the two cases. The chief differences are connected with the greater difficulties of cross pollination (for here a definite goal as well as a definite starting place is imposed), and with the extreme fineness and lightness of pollen, which makes its propulsion from plant to plant impracticable. But the identity of method in the two processes should not be permitted to create any confusion between them in the mind of the reader, who should keep very clearly in mind the totally different object in the two cases.

1. Independent Locomotion.—Although none of the higher, or familiar, plants possess this power, it is well developed in the simpler kinds which lack the firm cellulose skeleton; and the method thereof is precisely the same as is used by the simpler animals. Thus, some kinds creep, as in the case of the Slime-molds (or Myxomycetes), with which the reader has already made acquaintance in the chapter on Protoplasm; these opaque-white gelatinous masses are sometimes seen in damp places,—on decaying wood, wet earth, or neglected flower pots,—where they creep about,

though slowly, by the simple device of directing their protoplasmic streaming in one constant direction, precisely as is the habit of the much smaller *Amœba* among animals (figure 147). Other plants, again, or their reproductive spores, can swim freely in water, in a

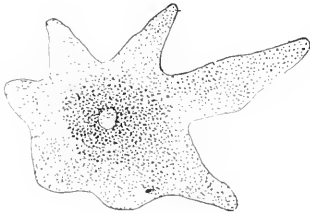


FIG. 147.—An *Amœba*, greatly magnified; a creeping organism mentioned in the text.

manner so like that of animals that they are known as “animal spores,” or zoöspores; and these are very abundant and characteristic in the Algae or Sea-weeds (figure 94). The motion is effected either by the action of innumerable cilia, tiny hairs which all in unison beat the water more strongly in one direction than the other, or else by

flagellae, which are structures suggestive of tails, except that instead of pushing the spore, they pull it behind them by an action the reverse of the one used in the tail of a fish. These movements of flagellae and cilia, by the way, depend upon the power of contractility in protoplasm, a form of the motility which has already been described as one of the physiological properties of that substance; and this same contractility, also, is the basis of the muscular mechanism of the higher animals. Other kinds of water plants, notably the Blue-green Algae, make use of vibration of their rod-like bodies, securing their movement, I suppose, in essentially the same way that a piece of flexible steel is shot through the air after having been bent between thumb and forefinger and then quickly released. Other kinds push out protoplasmic threads, which work against the bottom, as is the way with the Diatoms,—those tiny plants whose wonderfully-sculptured shells are the favorites of every happy possessor of a first microscope. In all of these modes of locomotion, the resemblance to animals is not accidental, but a persistence from an ancient condition in which the two kingdoms were one.

2. Extension through Growth.—The stems of the higher plants, as the reader will recall, are usually so made that elongated inter-

nodes separate the bud-bearing nodes, which, moreover, in most soft-textured plants, can readily strike root. It is plain that if stems are sent out horizontally in such manner as to touch the ground, the nodes at their tips may strike root and send up new shoots, thus originating new plants at some distance from the parent, from which they will later be cut loose by the death of the intermediate stem. Plants have not been slow to take advantage of the possibilities of this method. Everybody knows the typical case of the Strawberry, with its long slender *runners* which bear tiny plants at their tips; and the same thing is found in the House-leeks, and others too many to mention. Some plants send the stems underground, after the manner of roots, and form new plants, called *suckers*, at places not possible to predict; and this makes them hard to exterminate, as in the case of the Yarrow, and some other weeds of pertinacious character. Suckers, by the way, spring also from roots, some kinds of which can make buds, especially when injured; and this is the way with some fruit trees, like Apples. In a similar manner, the horizontally-radiating underground equivalents of roots, the mycelial threads, of some Mushrooms, send up the new Mushrooms at so regular a distance from the parent as to form a conspicuous ring, whose name "Fairy Ring," implies an ancient belief as to its origin, (figure 148). Again, among the more familiar plants, there are shrubs, of which our Briars and Blackberries are examples, with stems so slender as to curve over and bring their tips to the ground, where they take root and produce new plants, known as *stolons*; and these connecting stems for a time form a trap for the feet of the unwary, giving name to the various shrubs called Hobble-bush. The Walking Fern gives another example of this method.

There are plants, however, in which the main stem itself creeps on or just under the ground, striking root and sending up shoots as it goes, thus spreading its own growths to new ground. This is the way in the Grasses, whose creeping stems run and branch so freely, and interlock so closely, that they form the dense mats we

call turf. Our native ferns, as well, have stems that creep, and send up the beautiful fronds from new soil. There are other plants, like Solomon's Seal, which grow onward under ground year after year, the old parts dying behind as the new are developed in front; and such plants may wander a considerable distance through the woods, carrying their new branches ever into new ground. In the tropical forests there are epiphytes which wander in this manner over tree trunks, and certain undergrowth kinds which grow forward a little on stilt-like aerial roots.



FIG. 118.—Fairy Rings, of Mushrooms, originating as explained in the text. Three complete rings and a partial one appear in the picture. (Reduced from Kerner's *Pflanzenleben*.)

Roots possess a certain power of shortening their length during later growth, and advantage thereof is taken by some bulbous plants, like the Tulips. New bulblets are formed in the axils of the scales of the old ones, and then are pulled an appreciable distance from the parent by the shortening of their own radiating roots after these have become fixed in the soil. And there are other minor ways in which growth helps to spread plants, though I think the aforementioned include all of real consequence.

It is obvious that the ways described in this section, while efficient so far as they go, secure no wide spread for plants; they are, indeed, supplementary, or extra, methods which happen to be rendered available by some peculiarity of growth or habit in the plants concerned, all of which possess also the far more efficient methods we are now to consider. As to these latter, they depend in reality upon a single principle. Forbidden by their mode of life to move when adult, plants have taken advantage of that stage in their lives when they are small and therefore easily transportable, —the stage of the embryo. This embryo, with its vitality suspended for a time, together with its store of food substance and protective coats, constitutes the Seed, which is severed from the plant and can then be transported in various ways as we shall now proceed to consider.

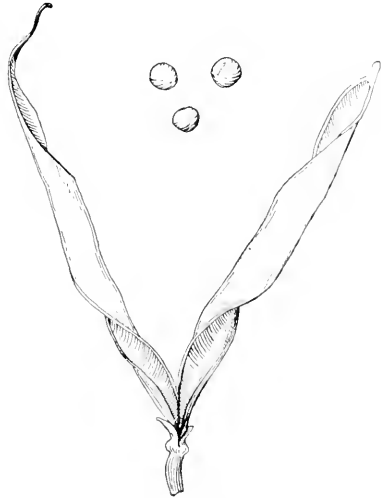


FIG. 149.—Pod of a Vetch, explosively propelling its seeds.

3. Projection by Elastic Machinery.—The appreciable size and weight of seeds makes possible their projection to some distance by a sudden application of sufficient power; and this fact has been readily turned to use by plants for their dissemination. The propelling machinery is variously made. In some kinds of seed-pods, definite bands of cells ripen in a state of stretched tension, which presently becomes so great that the pod bursts suddenly, hurling out the loose-lying seeds to a distance of several feet. In the Vetches, the two halves of the pea-like pods twist suddenly apart in opposite directions (figure 149); in the Wild Geranium, the ripening styles suddenly curl up from the lengthened receptacle (figure 150); the valves of the capsules burst

apart explosively, shooting out the seeds, in the Castor Bean, the Witch Hazel, the Acanthus (figure 151), or the West Indian "Sand Box," whose report is said to rival that of a pistol. In all of these cases, the propulsion of the seeds may be seen,

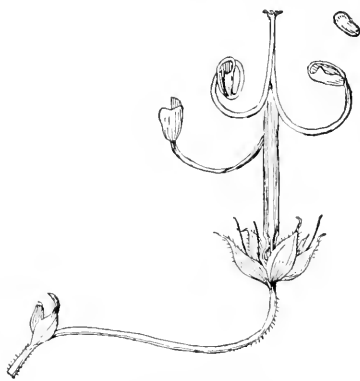


FIG. 150.—The seed-propelling fruit of Wild Geranium, explained in the text.

heard, and even smartly felt by the reader, if, when the pods are near ripeness, he will bring them to the room where he spends most of his time. In the Violets the sides of the ripening pods come to press harder and harder upon the smooth seeds which are held in the angle between them, until finally the seeds are shot out of the pods in precisely the same way that a smooth bean or a nut can be shot from between the tightly-pressed fingers (figure

152). In all of these cases, the seeds show approach to the qualities best in all shot,—they are round, smooth and relatively heavy.

Instead of the springing force of elastic dry tissues, some plants make use of turgescence,—that is, of the pressure developed by tensely-gorged cells against lines of a weaker sort, ending in explosive rupture and flight of the seeds. This is very well known in the fruits of the Jewel-weed, called also Touch-me-not, a common wild plant which takes its name from the habit. In the descriptively-named "Squirting Cucumber" of the East, the entire pulpy contents inside of the firm-skinned fruit ripen so turgidly that pulp and seeds together squirt out to a distance when an outlet is made by the breaking of the fruit away from its stem (figure 153).

Related to these ways in its principle, though differing much in detail, is the method used in those cases where small round and relatively heavy seeds come to lie loosely in open-topped

capsules on long stiff-elastic stalks. When the stalks are shaken by gusts of wind, or the impact of animals passing, the seeds are thrown out by the movement, especially the jerky recoil. The exit of the seeds from some of these pods lies along smooth grooves so placed as to guide the seeds at an angle best for their flight to a distance. These features appear well in the Poppies (figure 154), upon which observation and experiment are easy; but it really is one of the commonest of the modes of dissemination, prevailing through several large families of plants, notably the Figworts, Bellworts, Primroses and Pinks. And other methods of projection occur, as the reader may see for himself in the field, or find described in the works on the subject.



FIG. 151.—The pods of *Acanthus* explosively projecting its seeds.

A special form of projection through movements of ripening tissues is shown by those seeds which are pushed along the ground by movements of hygroscopic hairs. The causes of hygroscopic movements were considered in the chapter on Absorption; and it will here suffice to say that some tissues, by absorbing moisture from the air, or giving it up thereto, can swell and twist very forcibly, though not suddenly. In some Clovers hygroscopic hairs are so placed in conjunction with backwardly-directed parts, which act as “chocks,” that every movement of the hairs pushes the seed along the ground (figure 155). The arrangement is yet better in the curious “living Oat” (*Avena sterilis*), which can

creep appreciable distances within a few hours, and which, when placed with clothes in a drawer, burrows among these in a fashion quite uncanny. Hygroscopic movements also aid dissemination indirectly; for hygroscopic hairs, or equivalent structures, in some

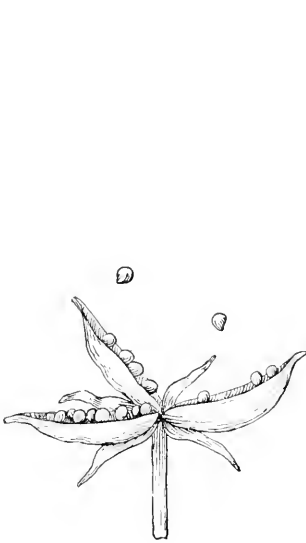


FIG. 152.—The pod of a Violet projecting its seeds by a method explained in the text.

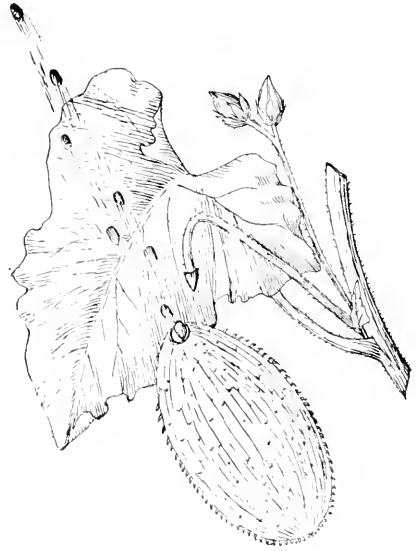


FIG. 153.—The Squirting Cucumber, projecting its seeds as explained in the text.

Orchids, Mosses and other plants, push seeds or spores from the interior of the capsules to the surface, where they can be reached and transported by action of the wind. Hygroscopic movements have also a part in the final bursting of seed pods in some of the cases described a page or two earlier.

But the method of projection, though effective in principle, has marked limitations, since the maximum distance to which seeds can be thrown, no matter how great the power may be, does not exceed a dozen or two feet. This is enough for very small plants and limited spread, but does not suffice for much larger kinds or a wider dispersal. It is fortunate, therefore, that a

method more effective is available. This method, in brief, is this,—the provision of appliances which ensure that the seeds shall be carried away by moving agencies that exist in the world around. These agencies are principally three,—winds, water-currents and animals. There is also a fourth,—gravitation,—but it acts in a profitless direction, although indirectly it contributes some aid to dissemination by making round seeds roll down slopes, and causing elastically-walled heavy seeds, such as

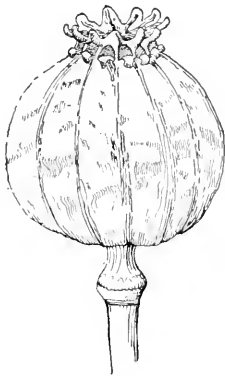


FIG. 154.—A pod of a poppy, showing openings for exit of the seeds.



FIG. 155.—A fruit of Clover, showing the hygroscopic hairs.

many trees have, to rebound from hard surfaces with a force which must oftentimes remove them considerably away from the plant that produced them. The other three agencies, however, are vastly important in dissemination, as the following descriptions will amply attest.

4. Waftage by Winds.—Of the motive forces of nature, winds are one of the most ubiquitous, and the easiest of all for plants to make use of. They occur in all grades from the wildest of gales, creating disturbance through hundreds of miles, down to the faintest of zephyrs confined to a limited region; and they include as well those upward currents of air which rise over heated places in summer to a height where wide-ranging breezes prevail. To utilize these winds for their spread, plants have only to attach

to their seeds such devices as shall make them expose a great surface in proportion to weight, and this they have done in manifold ways.

The simplest way of causing a seed to expose much surface to wind lies in the addition of a broad flat sail, or a wing. Everybody knows the seed of the Maple, with the lengthened wing growing out from the wall of the fruit (figure 156), and the Elm, with a similar wing except that it encircles the fruit. The conspicuous



FIG. 156.—Winged fruit of a Maple.

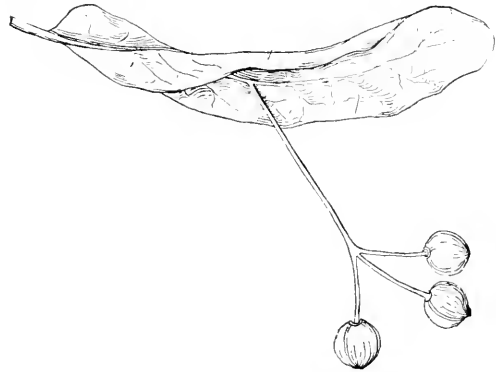


FIG. 157.—Winged fruits of the Linden.

way in which these seeds in their season are blown about our streets proves the efficiency of the arrangement. The seeds of the Linden, or Basswood, are likewise transported by a very fine wing, made from a bract grown fast to the stalk (figure 157), while in Pine and Catalpa the wings grow out from the coats of the seed. These are representative examples; and there are others as well, but less common, in which the wing is supplied by calyx or corolla.

Acting like the wings, and in some ways still more simple and effective, are large bladders, in which the seeds lie. Some approach thereto is made by those kinds of the Pea Family which have pods greatly swollen but very small seeds; but it reaches more typical development in cases like the Bladder Nut, where

the ovary forms a very loose envelope, or in some Orchids, where it is made from a greatly inflated seed coat (figure 158). In all of these cases the principle is the same,—that of a great spread of surface accompanied by very light weight.

Another fine method for giving much surface, consists in the provision of long soft hairs, or plumes; and seeds displaying this arrangement are plenty. The Cotton seed, for example (figure 159), develops hairs of such number and length that they serve not only to spread it afar under action of wind, but prove

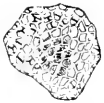


FIG. 158.—The seed of an Orchid, showing through its loose bladder-like coat.



FIG. 159.—A cotton seed, with its long soft hairs.



FIG. 160.—A plumose fruit of *Clematis*.



FIG. 161.—The parachute fruit of the Dandelion

incidentally a great utility to man, since they yield him the fiber for the commonest of all of his fabrics. The familiar silky plume of the *Clematis* (or *Virgin's Bower*) is made by the outgrowth of hairs from the style (figure 160); the parachute plume of the *Dandelion* from the calyx; the soft tuft of the *Milkweed* from the seed coat; the nebulous mass of the *Smoke bush* from stalks of unfruitful flowers. The phrase "parachute plume" used above was carefully chosen because of its suitability. For in the *Dandelion* (figure 161), and some other plants, the plumes are spread out horizontally, and keep that position in flight because of the

weight of the seed which hangs some distance below. Thus the seeds can be lifted over the tops of the trees by those currents of air which rise upward from places that are heated in summer, whence the wind may transport them to far distant parts. It is largely, no doubt, because the Dandelion, and its relatives in the family Compositae, have developed so efficient a mode of wind transport, that they constitute the largest and most widely diffused of all the existent plant families. And it is also of interest to note that these wind-carried seeds exhibit a very effective secondary adaptation to wind-transport, namely, great lightness of build, which even extends to the employment of oil, a lighter material than starch, as food in reserve for the embryo. And other modifications of this principle of plume-transport exist, as the reader may learn from his own observation, or the several good books on the subject.

If one compares the habits of plants whose seeds are winged or are plumed, respectively, he will find that in general the winged seeds belong to trees and the plumed seeds to herbs. It is easy to imagine a reason for this. Plumes are a better lifting device than are wings. The extra height and better exposure to wind of the tree gives its winged seeds a start which is ample for transport to sufficient, if not to the greatest distances. Moreover, some tree seeds possess such a relation of weight to wing form that they do not fall directly to earth, but only after whirling through long spirals, thus giving the wind a longer action upon them. But with herbs in their low sheltered positions, the wing would be far less efficient; and the lifting action of plumes is a notable advantage. The plume is actually a better device than the wing, and there is reason to think it a later evolutionary development; for our modern herbs, I believe, appeared later in time than our trees.

There is still another method, quite different in principle, of increasing the surface in proportion to weight. It consists in excessive reduction in size. It is a mathematical fact that as a

sphere or other rounded body diminishes in size, its bulk, and therefore its weight, diminishes far faster than its surface; or, in other words, the smaller such a body becomes the more surface does it spread in relation to weight. A body has only to reach a certain point of smallness, therefore, when the very slightest air movements are enough to blow it away, and to keep it suspended indefinitely in the air. This is the reason that dust floats as it does; and amongst this dust, and a part of it, float the spores of Bacteria, Molds, Yeasts, Ferns and other spore-bearing plants, which depend on this method for their dissemination. There can be little wonder that such plants are found so widely distributed when we remember how far this dust can be carried by any summer breeze. Among seed-bearing plants, however, the habit of forming a many-celled embryo before separation of the seed from the parent plant, makes the seed too large for this method to be used, though in some Orchids the embryo formation is postponed, leaving the seed small enough, especially when a loose open sac is added, to be transported in this manner.

The reader who is versed in morphology will observe that I often ignore the distinction between the seed and its accompanying fruit. From the point of view of the principle and efficiency of dissemination, it makes no particular difference whether the disseminating mechanism is formed from a part of the seed itself, or from the associated receptacle, ovary, style, calyx, or corolla. And if one asks why a particular plant forms its wing or its plume in this way, and another in that, we can only reply that herein lies another illustration of the first law of adaptation,—that a new structure when needed is formed from the part which happens to be most available for the purpose, and sometimes that part is one thing and sometimes it is another. Next after the seed itself, however, the disseminating mechanism is most often constructed from the part next contiguous, the ovary; and the frequency of its use for this purpose has caused its retention with the seeds long after the other parts have fallen. It is this per-

sistent ovary, modified to aid dissemination, and often accompanied by contiguous parts of the flower, which constitutes the *fruit* of the plant.

For the sake of completeness I should add yet another to the methods by which the wind aids dissemination, although it is

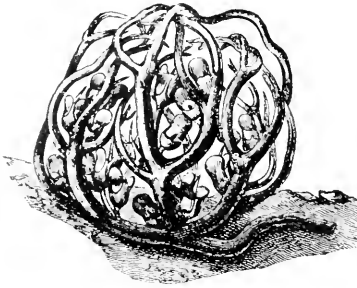


FIG. 162.—The Rose of Jericho, explained in the text. (Reduced from Kerner's *Pflanzenleben*).

only of minor importance. Not only seeds, but some other parts of plants which are capable of growth, are also transported by winds, especially when these rise into gales. It is thus with some leaves, in Begonias and Life-plants (*Bryophyllum*); joints of stem in some Cactuses; buds or bulblets in some Sedums and Lilies; the brittle twigs of Willows. The fact that in

such cases the transport is incidental rather than adaptively developed makes it none the less real; while moreover, the very accidentality of the method illustrates to perfection the way in which many, and perhaps most, adaptations begin. Again, some kinds of plants that live in open dry places roll their branches inwards at times to form a kind of ball, and in this state may be blown from their anchorage and sent rolling across plains or the frozen snow, to take root again in new places, often scattering their seeds or spores as they go. Such plants, called "tumble-weeds" and especially characteristic of prairies or plains, are well exemplified in the Russian Thistle, a troublesome new weed of the west, the Rose of Jericho, mentioned at times in the Scriptures (figure 162), and the Resurrection Plant of the southwest. Sometimes it is not the whole plant but only its fruit-cluster, as in members of the Parsley Family, which is thus broken loose and sent rolling away. A simpler method is displayed in those flat pods, such as some Locusts possess, which, curling into loose spirals that catch every wind, are rolled over smooth ground or the snow.

5. **Flotage upon Water.**—When water moves onward in currents, whether merely those minor and temporary kinds made by winds in their sweep over lakes, and by rains in the rivulets they cause, or in the mighty and permanent streams of river and ocean, it forms a good agency of transport even though less widely useful than winds.

With water-currents, as with others of the methods, some transport is incidental, as when floods tear out whole plants from the banks and leave them to grow anew in another location when the waters subside, or as happens when rivers sweep broken twigs of Willow to new places where they readily strike root. Again, rain drops splash out from open capsules, spores or small seeds which are carried away in rivulets to places where they are left in dampness good for their germination. Thus also are carried little buds (gemmae) of the Liverworts, and probably the axillary bulblets produced by several kinds of plants. Besides, most wind-scattered seeds are so light that they float well upon water, and thus effect a still wider transportation. But these incidental methods are insignificant in comparison with those which are secured by adaptation in the plants.

In the first place, some kinds secure transport by water-currents through their very habit of life, which indeed may be partly determined to this end. Such are the free-living submerged Algæ, which include vast numbers of the simpler kinds of Seaweeds, and the free-floating plants like our Duckweeds (figure 163) and the Water Hyacinth, with similar kinds of the tropics. And a modification of this habit is found in some sorts of our own, like some Watercresses, which are only lightly attached and are readily moved to new places; while many kinds of our water-weeds form naturally-detachable buds which are easily floated afar.



FIG. 163.—The Duckweed, a floating plant. (Copied from the *Chicago Textbook*.)

But the most perfect transportation by water is found in those cases where seeds are adapted expressly to this method, which requires some kind of a float, and a power to resist decay for a considerable time. Thus in the African Lotus, or *Nelumbium* (figure 164), the great top-shaped and air-filled receptacle, well known from its conventionalized use in the art of the East, forms a very effective float for the seeds which are dropped here and

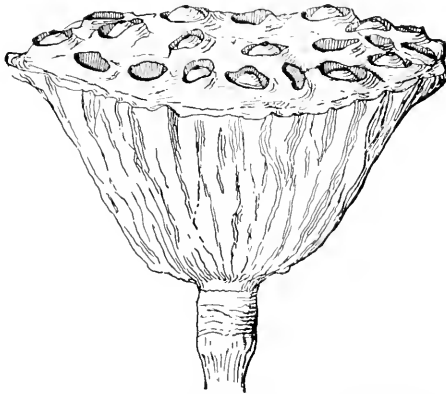


FIG. 164.—The floating receptacle of *Nelumbium*, showing a part of the seeds.



FIG. 165.—The seed of a water-lily, with its flotation bladder. (Copied from Gray).

there as it goes. In some Water-lilies, the float is an air-filled bladder formed by a loose seed coat around each single seed (figure 165); and in other commoner kinds the float is a swollen wall of the ovary. In the Coconut the great air-filled husk is a development of the ovary, and so perfect a flotation device that this plant forms the chief one of the palms that rise in the tropic isles throughout the seven seas. So perfect, by the way, is the power of this husk to resist decay in the water, that a cordage, called coir, is made therefrom for special use where resistance to decay in salt water is particularly needed. And by analogous methods other seeds as well have been carried over vast reaches of ocean.

6. Carriage by Animals.—Most ubiquitous of all of the moving

agencies of nature, so far as utilization by plants is concerned, are animals, which forever are roaming among plants in their search for food or for shelter. And in general where plants are most plenty, there animals too most abound. There is, by the way, a kind of poetical justice in plants making animals do service for them as some return for the priceless benefits they confer upon animals.

The ways in which animals are made to cooperate in the dissemination of plants are various. In the first place, as in case of other methods, some transport is incidental, that is, it occurs without the existence of any particular adaptations

thereto. Thus the seeds of some water plants are carried vast distances embedded in the mud which adheres to the feet of the larger and wide-ranging water birds, some of which have been shot with such seeds attached to their feet or their feathers. Again, some heavier seeds, such as nuts, are carried away by squirrels or birds to be eaten elsewhere or stored up for winter; but some are dropped on the way and others never are used, so that they come to grow in new places. Probably also the scattering of spores of Mildew, or other leaf Fungi, by temporary adhesion to the slimy bodies of snails is of similar nature.

Turning now to the definite adaptations which fit seeds for transport by animals, we find first of all a simple and obvious method in the provision of hooks or other arrangements suitable for attachment of seeds to fur or to feathers. Everybody will recall the case of the close-clinging Burdock (figure 166), while the Cocklebur and the Agrimony are equally efficient. Some striking examples occur in the plants of great plains, where large animals are especially abundant, as for instance the Unicorn Plant of the west (figure 167) which catches in the tails of horses, and the Grappling plant of South Africa (figure 168), which entangles



FIG. 166.—The hooked fruits of Burdock.

itself in the fur of lions. But innumerable small plants use this method, as one's clothing bears visible testimony after rambles through fields in the autumn. The hooks are most diverse in form as well as morphological origin, some coming from seed coat, some from ovary, some from calyx, some from bracts,—no doubt in each case along the lines of development that were easiest at the moment. However tightly these hooks may cling,

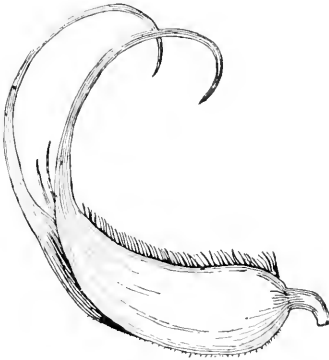


FIG. 167.—The Unicorn plant, explained in the text.

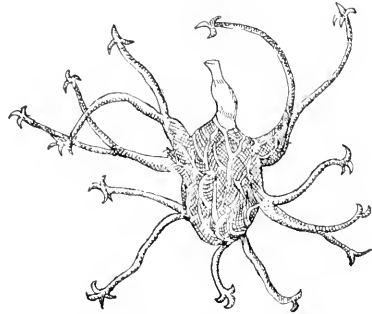


FIG. 168.—The Grappling plant, explained in the text. (Copied from Miss Stoneman's *Plants of South Africa*.)

the seeds sooner or later fall to the ground, either brushed away by contact with some hard object, or else dropped when the hair of the animal is shed. Nor is the employment of hooks confined only to seeds, for they exist also on some separable joints of small Cactus, or the slender stems of the Bedstraw or "Tear-thumb," both of which secure some transport through the contact of wandering animals.

Hooks are efficient with fur but less so with feathers, to which some adhesive material is better adapted. Thus, seeds which are carried by birds commonly possess a covering of mucilage, as in very many water plants; and so effective is this method, in conjunction with that where the adhesive is simply the mud of a pond, that water plants are among the most widely-distributed

of all living things, some kinds actually occurring in all of the continents. Especially effective is the very sticky "bird-lime," formed by Mistletoe berries and many other parasites; such seeds adhere to the feet or feathers of birds and thus obtain attachment upon trees, the only positions in which they can grow. Some low-growing herbs like the Twin-flower (figure 169), attain the same end by the possession of adhesive glands on the fruit.

There remains but one other method of utilizing animals in the transport of seeds, and that is the most striking and important of all. It consists in providing the seed with some form of indigestible covering, surrounding the same with a nourishing and appetizing pulp, and giving the whole a bright color which conspicuously displays its position. Such fruits are then eaten by animals, and the seeds pass through their bodies uninjured, after an interval that usually ensures their discharge at a place considerably distant from where they were eaten.

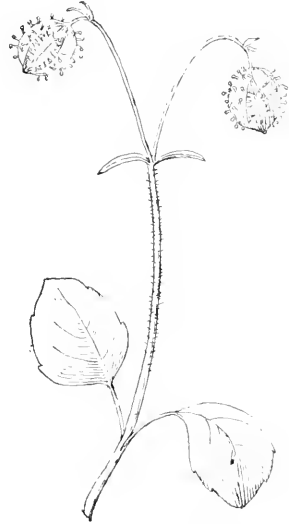


FIG. 169.—The glandular-adhesive fruits of the Twin-flower.

This without doubt is the explanation of the existence and characteristics of colored and edible fruits in nature; and so abundant and familiar are they that we need hardly cite any examples. So common, indeed, are edible fruits, and so effective their use, that this method of dissemination must rank very high among the modes of plant transport, and is second, if to any, only to wind waftage. To this method of seed transport, birds are better adapted than other animals, since their smaller size makes it possible to attract them with not too lavish provision of pulp, and their very active habits ensures their movement over considerable spaces. Accordingly, colored fruits are especially abundant on trees, shrubs,

and tall-growing vines, where birds most frequent; though they are by no means absent from low-growing herbs where they are eaten by ground birds or some of the smaller mammals. The indigestible coatings are formed either by seed coats, as in Grape, by ovary walls, as in Strawberry, or by a part of the ovary, as in the stone of the Cherry. Sometimes instead of the hard coat, an inedible core is developed, which is carried away but not eaten, as in Apples, while in yet others the slippery seeds are hardly swallowed at all, but are scattered around as the pulp is devoured, as in Oranges. The pulp is formed from the most diverse parts,—one can almost say every possible part,—from ovary as in Grape, receptacle as in Strawberry, bract as in Juniper, seed coat as in Yew, calyx as in Wintergreen, placentæ as in Watermelon, or hairs as in Oranges. The colors in general are such as are most conspicuous under the special conditions prevailing where the fruit ripens. Thus red is the most common of the colors of fruits, and it is that which is most conspicuous against the green of foliage; but purple or blue is more common in fruits of the autumn which ripen when the foliage has turned yellow or red, while white occurs in some berries which grow in the dusk of shady places near the ground. Before they are ripe these fruits are commonly sour, or astringent and unpalatable, and, moreover, are green in color, precisely like the foliage. This color may serve to prevent their notice by animals before the seeds are ripe, although such a function for the green color is probably wholly incidental and secondary to its use as accessory food-making tissue.

A special phase of dissemination by animals, the importance of which has only lately been realized, is the transport of seeds of low-growing herbs by ants. Such seeds are mostly small and light, but are provided with an attached reservoir of food-material (called the *caruncle*), attractive to ants, which carry the seeds to various distances from the capsules, leaving them where the food has been used. It has also been supposed that some seeds which

happen to resemble the larvæ of ants are transported some distance towards their nests by the same more industrious than sensible insects. It is possible, furthermore, that a somewhat similar explanation applies to certain seeds or fruits which look remarkably like beetles, as do some Castor Beans, or like caterpillars, as do some members of the Pea Family (figure 170); for such seeds, which are protected by hard coats against digestion, are supposed by some naturalists to be swallowed by birds in the belief that they are really live insects. Again, brightly-colored hard seeds, protectively coated, appear to be swallowed by birds, as are other bright objects, simply because of their attractive or conspicuous appearance. But these latter matters are doubtful, and perhaps are fancies rather than facts, though we must remember that strangeness or seeming improbability are not valid scientific objections to any explanation of a natural phenomenon. Not only birds and small mammals, but also bats, snails, insects, fish, and perhaps other animals, have been detected in carrying seeds by some one or the other of the various ways we have mentioned. The subject is by no means exhausted, and most interesting discoveries without doubt still await the keen-sighted and persistent observer.

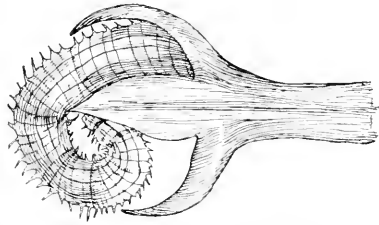


FIG. 170.—The pod of *Scorpiurus*, supposed to resemble a caterpillar.

To complete the subject of transport by animals we must mention the action of man, though his agency is of course incidental and not adaptational. Unintentionally he has spread weeds from country to country, until some occur all around the world, while deliberately he has carried the plants that are valuable to him to all parts of the earth. Indeed, upon this latter end he concentrates much effort and thought, reaching their culmination in the deliberate and systematic attempts of our national Department of Agriculture to gather useful plants from all parts

of the world, and to establish in this country every kind of plant which can possibly be of service to our people.

Before leaving dissemination it is desirable to note certain adaptations which are correlated therewith, though hardly a part of transport itself. Thus, some seeds



FIG. 171.—The fruit of *Stipa pinnata*, supposedly self-planting, as explained in the text.

seem to possess a certain power of planting themselves through the movements of a definite hygroscopic mechanism which is so built as to bore the seeds into the ground; the wild *Erodium*, and the grass *Stipa pinnata* (figure 171) are examples. In other cases the ripening fruit-stalk turns away from the light, and thus carries the seeds into clefts of the rocks or the cliffs on which the plants grow, thus ensuring their fall in a place conformable to the habits of the plant; this is true of the *Linaria Cymbalaria* of Europe, already described in another connection (figure 81). Some

plants place the seed pods in a protective position while ripening. This is common in water plants, which draw the fruit under water by a spiral coiling of the stem, and in the Peanut, which draws it underground. Others, which have seeds scattered by wind, greatly elongate the stalks of the seed pods during ripening, thus raising them to a position more exposed; it is thus in the Dandelion. Some seeds become attached firmly to moist ground by aid of a mucilaginous substance formed from their coats by contact with dampness, though the advantage thereof is not clear, unless the attachment aids the light weight of the seed in providing a resistance permitting the root to be forced more readily into the ground. Again, in some pods the seeds will not all germinate the same year, even under perfect conditions, but some require a year longer than others,—thus ensuring the perpetuation of the plants even if all the seedlings of one year are destroyed by any

calanity. Some seed pods, by action of hygroscopic mechanisms, open only when the weather is favorable for the particular mode of dissemination of their seeds, whether this requires wetness or dryness. And there are yet other disseminational adaptations, some real, some accidental, some imaginary, described in the works of Kerner and of others already referred to in the foregoing pages.*

When we view as a whole the results attained through these modes of dissemination, and note how wide is the spread some plants have secured through the world, it becomes plain that in the long run the sum total of the accomplishments of the non-locomotive plants in this regard, is no whit inferior to that of the highly-locomotive animals, if not indeed markedly superior thereto. This shows the efficiency of the dissemination methods,

* Dissemination, dealing with prominent and highly developed adaptations, has always been one of the favorite topics of ecological study; and it affords valuable material alike for amateur investigation, for student themes, and for popular scientific articles in the illustrated magazines. In the hope that the reader may wish to follow this subject more deeply than my limits allow, I add here the titles of the principal accessible works upon it. The foundation work is Hildebrand's *Die Verbreitungsmittel der Pflanzen* (Leipzig, 1873), an admirable, but all too brief a treatise, which, unfortunately, has never been translated. There is a wonderfully clear and well-illustrated account in Kerner's *Natural History of Plants* (translated by Oliver, New York, Henry Holt & Co., 1895). One of the best synopses, illustrating the striking cases, is Beals' excellent little book, *Seed Dispersal* (Boston, Ginn & Co., 1898), while much briefer though good are Weed's *Seed Travellers* (Boston, Ginn & Co., 1898) and a chapter in Lubbock's *Flowers, Fruits, and Leaves* (London, The Macmillan Co., 1886). Of articles accessible in magazines the best are Folsom's *Adaptations of Seeds and Fruits*, in *Popular Science Monthly*, 1893, 218, and especially Ridley's *Dispersal of Seeds by Birds*, in *Natural Science*, Vol. 8, 1896, 186, one of the very best discussions of this subject anywhere in print. And of course, there is a host of special papers of all degrees of technicality in the various scientific magazines. Considering the attractiveness of the subject, it is very remarkable that nobody has yet undertaken to prepare a modern encyclopedic work upon it, something comparable with the books we possess for cross pollination; and I commend this subject to any ambitious young naturalist among my readers, warning him that the task is vast and will take him nearly a lifetime, but assuring him that it offers an opportunity for just such a distinctive and useful piece of work as most men find the greatest satisfaction in doing. There is not in science any kind of a book that is so lasting in value as this, excepting only the one which presents material wholly new.

while illustrating with new force the fact that the race is not always to the swift.

Finally, it is important to note that the ways in which plants thus secure transport for their seeds, are closely analogous, if not identical, in principle with those by which man supplements his own feeble powers of locomotion. He cannot swim far, but he can provide suitable appliances to make the winds carry him over the broad ocean; he cannot fly at all, but he can place suitable appliances in front of certain explosive forces and make these drive him triumphantly through the air. The difference between the Dandelion plume and the ship's sail, or between the explosive capsules of Witch Hazel and the aëroplane engine, is merely one of detail and degree. Man and plant are doing the same thing in essentially the same way, the chief difference being that man knows what he is doing while the plant does not. The belief that seed-wing and ship-sail have been developed in ways that are fundamentally the same helps to explain what I meant in the chapter on Protoplasm when I said that all protoplasm can think.

CHAPTER XVI

THE METHOD OF ORIGIN OF NEW SPECIES AND STRUCTURES, AND THE CAUSES OF THEIR FITNESS TO THE PLACES THEY LIVE IN

Evolution and Adaptation



F the various aspects which Nature presents to the intellect of man, there are two of particular prominence,—facts and explanations. Of these the greatest by far are facts,—naked, stark, primitive, elemental, cosmical facts. They are the raw material of science, and nothing can replace them. But when one has made himself master of a goodly number thereof, and has arranged them in some kind of preliminary classification, he soon comes to crave explanation of the remarkable relations they are sure to exhibit. Explanation is the office of Philosophy, and there is a Philosophy of Nature. The phases thereof most important to the student of animals and plants concern the origins of their multifarious kinds, of their elaborate structures, and of their remarkable fitness to their surroundings. There was a time when none of these were; now they all are; when and how, in the interval have they arisen? This is the great present problem of philosophical biology, and one which the reader, fresh from his contemplation of the facts and relationships set forth in the preceding pages, is now prepared, and I hope eager, to attack.

There are two great explanations, logically and historically, of the origin of species, structures, and adaptations,—viz., Special Creation and Evolution. The doctrine of Special Creation, held almost universally down to a half century ago, maintained that

every kind of plant and of animal, with every one of its manifold parts, was created substantially as it now exists at some definite time in the past by the act of an omnipotent and omniscient Creator. On the other hand, the doctrine of Evolution, now held by all biologists and most other thinkers as well, maintains that each species of plant, and each one of its structures, has been derived by gradual modification from preëxistent and simpler kinds, which in turn were derived from yet other and still simpler kinds, and so on, in an unbroken chain of descent back to very ancient and very simply-organized ancestors, whose exact mode of origin is still quite unknown.

It is now a long time since it was thought needful to present in biological courses or books the evidence for Evolution against Special Creation, but our present-day acceptance of Evolution as almost an axiomatic truth involves some danger of leaving our learners in ignorance of the nature and force of the evidence which has compelled its acceptance. I would dearly like to present this evidence to the reader as I do to my students, but the callous incompressibility of paper and type forbid; and it must suffice to say that it is drawn from these several sources:— from the *analogy of plant and animal improvement by man* (soon to be considered in a separate chapter on Plant Breeding), whereby from simple wild forms of both animals and plants, new kinds, most diverse and most wonderful, have been produced; from the results of *classification*, which show that the kinds of plants and animals fall naturally into an arrangement similar to that established by relationship based upon descent among mankind, some of the very same terms indeed (race, tribe, family) being used in both cases; from *morphology*, which shows that the diverse forms of special structures,—spines, tendrils, pitchers and so forth,—are all modifications of simpler preëxistent structures, usually leaves, stems or roots; from the existence of *gradations*, all the way up in regular steps from the very simplest kinds of plants to the most complicated, with no notable gaps or missing links in

the series; from *fossils*, those relics of ancient plants converted to stone and preserved in the rocks, which show that the earliest plants to flourish in the earth's history were the simpler kinds, while those which came later were progressively more complex, and the very highest of all appeared last; from *geographical distribution*, which is such that in general the kinds of plants most closely related are found nearest together, while those which are farthest apart are most distantly connected; from the existence of *rudimentary structures*, such as the imperfect stamens in irregular flowers, or the appendix in man, which are useless to their present possessors, but are useful to the near relatives, and hence presumably to the ancestors, of the kinds; from *embryology*, or the course of development of the individual from the egg, which often exhibits some temporary stages quite useless to the developing individual but useful in those ancestors which the form must have had if evolution is a fact; and from yet other sources which need not here be particularized. In all of these directions the phenomena are perfectly explained by evolution, but present well-nigh insuperable logical difficulties to an explanation by special creation. Or, the case can be stated in this way,—if evolution be assumed, then the facts are intelligible, but if special creation be assumed, then they are enshrouded with inconsistency and mystery.

I may venture at this point to remind the reader, though probably the caution is needless, that the question as to whether evolution is or is not a fact is a purely scientific one, to be judged by purely scientific evidence, tested by inexorable scientific logic. It is fatal to a correct judgment upon such a subject to approach it with preconceptions or prejudices of any kind, metaphysical, personal, or religious; for the mind of man is so organized that whenever it seeks evidence for some favorite belief, it has no trouble at all to find it. To him who puts on colored glasses, all things look of that color; but evolution is something to be viewed only in the purest white light of the truth.

But while evolution is accepted as a fact by the consensus of

present biological opinion, biologists differ much in their opinions as to the method by which it has been effected,—for of course the fact or non-fact of evolution is one thing, and the method whereby it has been brought about is another. Evolution may be true and yet every one of the explanations of the method thereof, given heretofore by scientific men, may be false. These explanations, however, are so important in many ways that we must now proceed to consider them.

Of all the explanations of the method of evolution, the greatest and best known is Darwin's, embodied in his principle of Natural Selection. It was, indeed, the first logically-satisfactory explanation ever given of the way in which evolution may have been brought about; and, because it was logical, it enabled thoughtful men for the first time to believe in evolution as a fact,—for they could not believe in its reality so long as they could not understand how it might have been effected. Herein consists Darwin's greatest service to science; and this, moreover, is the reason why his name is associated with evolution so closely that most people regard the two words as practically synonymous. And the case is not at all affected by the fact that Natural Selection may yet prove not to be the real explanation of evolution. It is a possible and a logically-adequate explanation, but not necessarily on that account the correct one.

So important is this principle of Natural Selection, historically as well as scientifically, that we must now consider it sufficiently to make its significance clear; and this is the more needful because it is commonly misunderstood even by many of those who talk much about it. I shall try first to present the subject as I think that Darwin conceived it, giving later the modifications introduced by subsequent investigation.

In essence Natural Selection is a deduction from the inter-operation of five factors, all of which are familiar to observation,—viz., variation, overproduction, struggle for existence, survival of the fittest, heredity.

Variation.—It is a matter of familiar knowledge that all living things, or the structures they produce, even the most closely-related, are different from one another,—to such a degree, indeed, as to justify the common saying that no living thing is exactly like any other living thing. The differences, or *variations*, affect every possible feature,—size, form, color, texture, etc., and occur in every possible direction; and some of them at least are inherited from the parents and transmissible to offspring.

Over-production.—All living beings possess a power of reproduction not only sufficient to replace the individuals which die, but also to increase greatly their numbers. Moreover, the rate of increase, in even the slowest breeding forms, is surprisingly rapid, while with most kinds it is enormously so. Thus, a plant which produces only ten seeds a year (and few produce so very small a number), would have one billion descendants within ten years, and would soon cover the earth to the exclusion of all others could its increase proceed without hindrance.

Struggle for Existence.—Although every kind of plant and of animal is thus tending to increase enormously in numbers, nevertheless in a broad way those numbers remain stationary from one generation to another. Local fluctuations do of course occur, for some kinds of plants or animals are on the way to extinction, while others, such as weeds or insect pests, have periods of rapid expansion; but in general it is true that there are no more of any particular kinds,—lichens, goldenrods, thrushes or squirrels,—in a given region one year than another. The reason thereof is obvious enough,—the world is already as full of animals and plants as there is food or room for, and new ones can find a place only as the old ones die out. This, then, is the situation;—that while great numbers of plants and animals are born into the world in each generation, there is only room or food for an occasional one of the number. But as each and every one of the individuals thus born has an equal right and impulse to survive and possess

itself of the scanty room and food, there results among them a constant struggle for existence.

Survival of the Fittest.—In this struggle for existence among a great many individuals of which few can survive, what determines which those few are to be? If the young individuals were born all alike the survival would obviously be determined by nothing but chance; but in fact they are all born unlike, and among the differences, or variations, which they exhibit, there must happen to be some which fit their possessors better for the conditions of the particular struggle in hand than do others; and such better-fitted forms will naturally be the ones to succeed. This is the survival of the fittest. Where the seedlings of spruce trees spring up of themselves in fields that are abandoned, it comes finally to pass that a few tower upward in full vigor, while the shade underneath them is almost like night from the profusion of dead stems of the unsuccessful,—the ones which did not possess the variation of most rapid upward growth to possession of the indispensable light.

Heredity.—In reproduction, as everybody knows, the main features of the parents are repeated in their offspring, or are hereditary. Now this is true also of at least a part of the variations. Hence, when a plant or an animal survives by virtue of some particular advantageous variation, that variation is likely to be repeated in its offspring. Meantime, of course, the unfit have perished, and left no descendants. The whole tendency, therefore, is towards the production of a race in which the valuable variation is universal.

It will now be evident to the reader that these five factors acting together must tend to cause a natural selection, and hereditary fixation in each generation, of the fittest, or most advantageous variations, of whatsoever kind. It remains to consider, and this is a point too often overlooked, how a variation can accumulate and become intensified, generation after generation, until it forms a well-marked character of the species. This, also, is easily under-

stood on reflection. For not only do the offspring of the parents preserved by possessing a fit variation inherit that variation, but they vary in regard to that variation itself. Therefore in any generation, while some of the individuals will inherit the variation about like the parents, a few will vary towards a greater intensity thereof; and in the struggle for existence in this generation, these more extreme individuals will survive. Their offspring, in turn, will tend to resemble them in possessing the greater degree of the variation, but the offspring will include some that vary towards an even higher degree, and these will survive, and so on. Thus a variation, by its continued selection in one direction generation after generation, can pile up until it produces a large and visible change in that feature of the plant. But the different features of the organism are so closely tied together that a change in any one always involves some others, while, moreover, selection may be operating upon more than one feature of a plant at a time. Thus the accumulation of variations gradually make their possessor look distinctly different from the original ancestors; and when that point is reached we call it a new species, especially if, as usually but not invariably happens, the intermediate and less well adapted forms have died out in competition with the better. The process is represented in operation, with increase in size assumed as the advantageous variation, in the accompanying diagram (figure 172). This process of progressive adaptation would continue until the species theoretically has become as perfectly adapted as possible to the selective conditions; but in fact such stability would never be reached since the conditions themselves, like all the rest of the world, are in continual alteration. And such is THE ORIGIN OF SPECIES BY MEANS OF NATURAL SELECTION, OR THE PRESERVATION OF FAVORED RACES IN THE STRUGGLE FOR LIFE, in the words of the title-page of Darwin's greatest book.

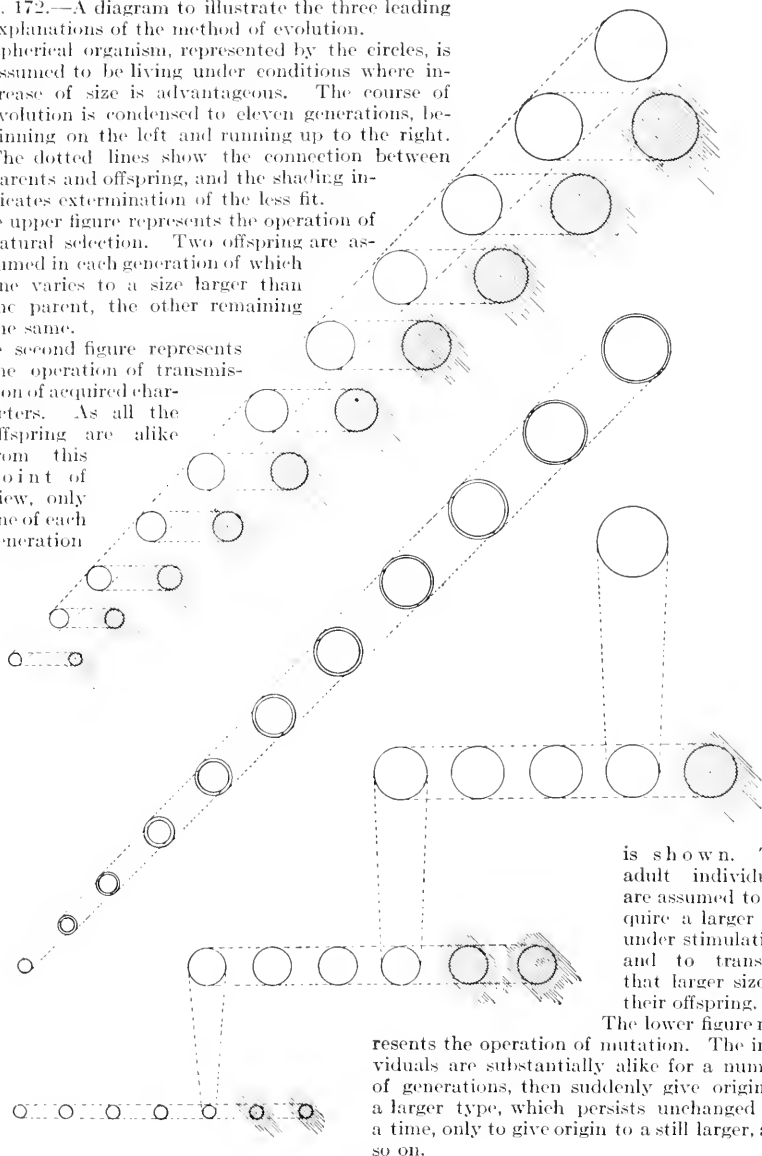
The theory of Natural Selection explains very perfectly not only the origin of new structures and new species, but also the

FIG. 172.—A diagram to illustrate the three leading explanations of the method of evolution.

A spherical organism, represented by the circles, is assumed to be living under conditions where increase of size is advantageous. The course of evolution is condensed to eleven generations, beginning on the left and running up to the right. The dotted lines show the connection between parents and offspring, and the shading indicates extermination of the less fit.

The upper figure represents the operation of natural selection. Two offspring are assumed in each generation of which one varies to a size larger than the parent, the other remaining the same.

The second figure represents the operation of transmission of acquired characters. As all the offspring are alike from this point of view, only one of each generation



is shown. The adult individuals are assumed to acquire a larger size under stimulation, and to transmit that larger size to their offspring.

The lower figure represents the operation of mutation. The individuals are substantially alike for a number of generations, then suddenly give origin to a larger type, which persists unchanged for a time, only to give origin to a still larger, and so on.

cause of their adaptations to their surroundings. It will be evident to the reader that the principle, while logically strong, is highly

hypothetical; and, needless to say; mankind has not yet seen the natural evolution of a species by this process. It has a weakness in the fact that all of its reasoning is on the assumption "other things being equal," whereas in fact the innumerable other things rarely are equal. It has a strength, on the other hand, in the fact that the kind of artificial evolution effected by man in the production of new kinds of animals and plants, uses precisely and solely the same method of selection and preservation of variations. There is, however, this notable difference between the products of artificial and natural selection, that the former tend always to revert back towards their former condition, while apparently the latter do not; and to many observers this difference seems fatal to any support of natural by artificial evolution. It may be, however, that the time element in the process is important, and that the comparative rapidity with which man makes his new kinds does not allow the new characters enough time to "set." If one keeps a band of rubber stretched only a brief time it springs back to its old shape; if longer, only partly; if long enough, not at all!

It is difficult for anyone, and impossible for me, to think at much length about Natural Selection without recalling its great author. Science hath her heroes no less than war, and Darwin was one of our noblest. An Englishman, born in 1809 to singular good fortune in material things, and fortunate in the influences which molded his intellectual life, he came slowly to his great conception, which he first published when he was fifty years old. This was in his book *The Origin of Species*, which by common consent is agreed to have exercised a more profound effect than any other secular book upon human thought. It is difficult for us in these more liberal days to comprehend the bitterness of the opposition which his support of evolution aroused, partly among the older naturalists but chiefly among those who imagined that the foundations of religion were endangered. But through all the storm he stood steadfast,—calm, just, and magnanimous, even

though to his other great provocations was added the torment of chronic ill-health. Of him his friend Huxley has said,—“The more one knew of him, the more he seemed the incorporated ideal of a man of science.” Possessing vast speculative powers, he nevertheless kept his imagination in touch with the truth by incessant and laborious observation and experiment. Yet this greatest of all naturalists was no demi-god, much less a person abnormal to his kind, but a warm-hearted, humanly-interested, honorable-souled gentleman. He lived to see the complete triumph of his life-work, and died in high honor in 1882 at the age of seventy-three.*

The second in importance, though first in time, of the great explanations of evolution was Lamarck's principle of the “transmission of acquired characters.” It is almost the exact logical opposite of natural selection, and the life of its author contrasts almost as greatly with that of Darwin. A Frenchman, born in 1744, he was at the height of his career about fifty years before Darwin, as Darwin was fifty years before our own time; and it is a coincidence of no little interest that the work in which he most fully expounded his views was published in 1809, exactly fifty years before the *Origin of Species*. But Lamarck, unlike Darwin, failed to keep his imagination checked by investigation, and his theories in close touch with the facts. Therefore he had the mortification to see his favorite work ignored by his contemporaries; and he died, in 1829, in disappointment, infirmity and

* The reader will wish to know more about Darwin, and will find great satisfaction in a study of his *Life and Letters* (one of the great biographies of literature) by his son Francis. In that work, his own autobiography, and his son's reminiscences, are of first interest, but the most charming glimpses of his character are given by his letters,—for example, that written to his wife from Moor Park, in April, 1858, and that written to his friend Asa Gray, on August 9, 1862. And the reader should not fail to read the remarkable obituary of Darwin by Huxley in *Nature* for April 27, 1882,—doubtless the noblest tribute ever paid by one scientific man to another. The *Origin of Species* is not an easy book to read, nor can it be really appreciated by anyone until he has acquired a considerable background in biological knowledge; but after that the reasons for its real greatness become clearly apparent.

poverty. Yet though his labors were seemingly without immediate fruit, they were of great service, nevertheless, in awakening men's minds to the problems and possibilities of evolution, and thereby making the way easier for Darwin.

Lamarck's theory is founded on two factors,—the alterability of individuals, and the hereditary transmission of the results thereof.

The Alterability of Individuals.—This is not theory, but familiar fact. Everybody knows that our own muscles, with their associated blood vessels, nerves, and bones, can be improved in size and strength by exercise, as can our minds, and other features of our being; and likewise these can all degenerate through disuse. And so it is throughout the animal kingdom. The process is well understood: the use of the part serves as a stimulus which leads the organism to throw more material and energy into those parts, precisely in the manner which we have studied already in the chapter on Irritability. In the same chapter we have seen also how plants can alter their structure under stimulation. Thus some kinds of plants can develop a thicker epidermis under the stimulus of dry air; some trees can apparently build stronger stems under stimulation of bending by the wind; and indeed there seems to be no limit to the directions and degrees in which plants can respond structurally, and adjustively, to stimulation. The structural alterations thus produced in individuals, are called *acquired characters*.

Transmission of Acquired Characters.—This is the crucial point in the theory of Lamarck. He held that characters acquired during the life of the individual, as described above, are transmitted to their later offspring, which, therefore, exhibit larger muscles, or finer minds, or thicker epidermis, or stronger stems, than would have been the case had the parents not developed those features. Lamarck actually uses the illustration of the blacksmith's arm, powerfully developed in the practice of his trade; and he maintains that the later-born sons of the smith will

have more powerful arms than would have been the case had their father adopted some less strenuous trade. Most of our popular beliefs tend to the same end, especially as to moral and intellectual qualities; for it is commonly supposed that the finer mind developed in an individual by high education, or the degeneracy produced by submission to vice, are somehow transmitted to the offspring. If a feature is hereditary for one generation, however, it is hereditary for more; and thus, according to Lamarck, a character can go on piling up generation after generation until it reaches a degree of development sufficient, along with associated changes, to make its possessor rank as a new species. Of course, on this principle, all individuals born into the world have an equal chance for survival, and mere chance would determine success. This method of evolution is illustrated in comparison with that by natural selection on the accompanying diagram (figure 172).

The Lamarckian explanation of evolution has a great merit in its simplicity, but has the fatal defect that the crucial transmission of acquired characters is not confirmed either by ordinary observation, or by any experiment which has been devised to test it. Moreover, that gigantic system of experiment always in progress in plant and animal improvement by man has failed to yield one fact in its support. Furthermore, the phenomena which apparently are the strongest in its favor can be explained more simply in other ways. Thus, the blacksmith's sons, it is true, tend to have stronger arms than ordinary men; but this need not mean that they inherited the stronger arm acquired by the father, but only that they inherited the same robust protoplasm which enabled the father to become a successful smith. So the children of highly educated parents are apt to be bright, not because they inherited the educated minds of the parents, but because they inherited the finer quality of mind-protoplasm which made high education in the parents a possibility; and so with the children of tuberculous parents, who inherit not the

tuberculosis, but the weak lungs which render tuberculosis possible. Taken as a whole, therefore, the evidence we possess upon the subject does not tend to support the Lamarekian theory.

The contrast between the theories of Darwin and of Lamarek is given the sharpest definition by the work of Weismann, an eminent German zoölogist still living. Darwin himself, while convinced that natural selection was the leading factor in effecting evolution, was inclined, especially in later life, to admit some transmission of acquired characters; and indeed he actually invented a special theory (called *pangensis*, a flow of tiny solid particles from all parts of the body to the germ cells), to explain a possible mode of its operation; but his follower Weismann stood for Natural Selection, pure and simple, as against the rival theory, and even invented an ingenious conception to explain the naturalness of the operation of the one and the impossibility of the other. In brief, he held that there are two kinds of protoplasm in each animal,—one reproductive, the *germ plasm*, confined to the eggs and the sperm cells, and the other the *body plasm*, making up all the rest of the organism. Now the fertilized egg-cell, from which the new individual grows, is obviously germ plasm. As it grows and develops, a part of the resultant cells keep on being germ plasm, which, however, remains latent until the animal is adult, while the remainder of the cells develop into body plasm, which grows immensely and comes ultimately to surround, protect and nourish the embedded germ plasm. Then when the time for reproduction has arrived, it is always the latent germ plasm, never the body plasm, which builds the new egg-cells and sperm cells, whose union starts another individual in the same way as before. Thus germ plasm produces body plasm, but body plasm never produces germ plasm. Hence the germ plasm is potentially immortal, keeping on as one continuous line of tissue from generation to generation, while the body plasm is mortal, made anew in each generation and perishing utterly therewith. The matter can be expressed also in this manner,—that the germ plasm forms a

kind of continuous axial thread upon which the body plasm is strung at intervals like beads on a string, except that we have to imagine the beads as growths from the string! On this theory the germ plasm is the essential protoplasmic basis of the race, and the body is simply an organ which it builds to secure its own nutrition and protection. Now it is obvious that any variation which originates in the germ plasm can show itself in all of the succeeding germ plasm, and also in all of the bodies which grow out therefrom; on the contrary, any variation, or other feature, *including an acquired character*, which originates in the body plasm, must perish with that body and cannot affect the bodies which come after, unless it can go round through the germ plasm, for which no mechanism is known to exist, excepting possibly that mentioned in a paragraph to follow. This theory of Weismann's explains very perfectly an evolution by natural selection of innate (in-born or germ-plasmic) variations, and also supplies a reason for the non-transmissibility of acquired characters. It shows how children can exhibit cultured minds or large muscles like their parents without inheriting the results of their parents' culture or exercise, for while the results of culture or exercise are confined to the body plasm, and perish when it does, the capacity to develop the results depends on the constitution of the germ plasm which parents and children share alike. The bodies of children resemble the bodies of their parents, therefore, not because the former are derived from the latter, but because both are derived from the same source. This ingenious theory of Weismann's has not been confirmed by further research so far as its physical basis in the two kinds of protoplasm is concerned, and it never applied well to plants, which seem very clearly at times to create germ plasm out of body plasm; but I give it this much of our attention because all recent research is tending to confirm the correctness of its central principle, which stands perfectly when expressed in this way,—that body characters are derived from germinal determinants, which in turn are derived from preceding

germinal determinants in a continuous line, but never from body characters. And the fallacious physical basis given his theory by Weismann has been replaced by a secure one supplied by Mendelian studies, presently to be considered. Indeed, the modern conceptions of heredity, based on Mendelian results, is a veritable reincarnation of the central feature of Weismannism.

Before leaving this part of the subject it is needful to say that such evidence as does seem to favor a transmission of acquired characters is found in connection with certain diseases. The cases seem to hinge upon chemical changes produced in the blood, which, circulating and diffusing throughout the whole body, can thus reach the germ cells and through them the next generation. On this basis, any acquired character which affects the chemistry of the blood could, theoretically, be transmitted to the germ plasma and the next generation, although changes which are simply of a physical or mechanical nature could not. We have a close analogy in the relation of scion characters to stock characters in grafting, already considered (page 350); for it appears to be generally true that characters which are dependent upon the sap can be extended or "transmitted" from the scion to the stock, and vice versa, while characters which are dependent upon the protoplasm are confined, on the contrary, strictly to scion or stock respectively. This principle of chemical transmission may yet prove to be important in evolution, and may rehabilitate Darwin's theory of pangenesis on a new basis; and it accords with the tendency of all modern research to reduce natural phenomena to a chemical foundation. Indeed, some students of the subject have suggested that the chromosomes, those carriers of heredity in the nuclei of cells, are simply collections of enzymes, each of which controls some single process of development in the new individual.

The study of the problems of evolution exhibits three separate epochs. The first was that of *speculation from impressions*, culminating in the theories of Lamarck. The second was that of *induction from observation*, inaugurated and carried to highest

perfection by Darwin. The third is that of *test through experiment*, of which we are witnessing the very beginning. Its great leader is de Vries, an eminent Hollander still active in scientific service.

Some twenty years ago de Vries noticed in Holland a certain weed,—an American Evening Primrose, called *Œnothera Lamarckiana* (note the coincidence of name!),—which showed such remarkable phenomena of variation that he brought some of the plants into his botanical garden where he could study their behavior with exactness. The result was remarkable indeed, for he saw new kinds originating before his eyes, not by any slow process, but the fastest that is physically possible,—viz., in one step from parent to offspring. When seeds were taken from the ripe pods of *Œnothera Lamarckiana*, and planted with precautions which precluded all possibility of error, most of the seeds grew into plants like the parents; but some grew into a much smaller kind, others into a much larger kind, and yet others into other kinds, differing in other respects (figure 173). Thus from the parent species several daughter kinds were produced, and not once alone but regularly generation after generation. The new kinds do not differ much from the parent, but enough to enable trained botanists to distinguish them with certainty; and moreover they differ not in one but in a great many features. The individuals of any one of these new kinds exhibit minor, or fluctuating, variations among themselves it is true; but they preserve throughout a sufficiency of definite characters in common. Furthermore, and this is a matter of the very greatest importance, when seeds of each of the daughter kinds were planted by themselves, they reproduced each their own kind, and that not alone for one generation, but for several, and indeed for as many as time has allowed since their discovery. Finally, the same experiments have been repeated elsewhere, and with identical results. There seems no doubt, therefore, that this species of Evening Primrose is actually giving off several new kinds year after year, and kinds which reproduce themselves permanently.

Such new kinds were supposed by de Vries to be species, of an ultimate or elementary sort, and, in reference to their mode of origin he designated them *mutants*, while the parent species he described as being *in mutation*. As to the exact relation of mutation to evolution, that was supposed by de Vries to be this,—that mutants, or elementary species, and not single variations, are

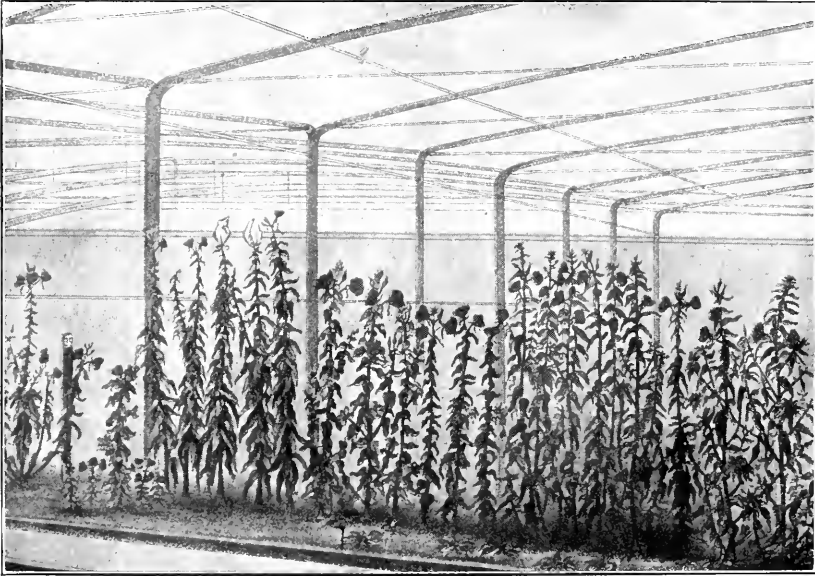


FIG. 173.—Groups of the mutants of *Enothera*, growing in de Vries' experimental garden at Amsterdam. The parent species, *E. Lamarckiana*, is the single one on the extreme left. In one group two flowers are covered with bags for experimental purposes. Observe the distinctness of the groups from one another, in conjunction with a certain amount of variability within each group. (Photographed from a colored picture in de Vries' book, *The Mutation Theory*, Vol. II.)

the material upon which selection works. Darwin thought the basal variations were mostly single, finely-graded, and more or less unstable, while de Vries offers instead collections of variations large, definite and permanent; but otherwise their views are in full harmony, both agreeing that natural selection is the final factor which determines survival. Like variations, the mutations

which happen to be adaptive would be preserved in the struggle for existence, while the unadapted would perish. Then, according to the theory, after a time the surviving species would mutate again, and the fittest of its mutants would survive, and so on. Thus would the species be kept adapted approximately to environments, while evolution would take place in a series of short abrupt steps separated by long pauses,—a condition illustrated in the lower part of our diagram (figure 172). De Vries' view of evolution has, moreover, one marked advantage over Darwin's in explaining the existence of species and structures which bear no adaptive relations to the environment, such for example as the wonderfully diverse forms and markings of the Diatoms; for such features can originate and reach a considerable degree of development by mutation, if not cut off by natural selection, while on Darwin's view only those things which were adaptive had any chance of a considerable development.

The great interest of de Vries' work at once stimulated a wide search for other examples of mutation in both animals and plants; and a very few other cases have been discovered. Attempts have also been made to set species into mutation experimentally, but with only dubious success. It is thus plain that species in mutation are very few,—which fact is explained by de Vries on the supposition that species display short periods of mutation separated by long periods of quiescence.

But though species in mutation are undoubtedly rare, species apparently identical with mutants have been found to be common, though there is no evidence as to how they have arisen. The more intensive studies of the past few years have shown that species formerly considered single are in reality aggregates of dozens or hundreds of these mutant-like species, which have now become so prominent in scientific literature that they have attained to a distinctive designation of their own, viz., *elementary species* or *biotypes*. Thus the little "Ladies Tobacco" of our earliest spring fields, thought by the acutest observers of the last generation to

represent but one species (viz., *Antennaria plantaginifolia*), has been found to include a dozen, all perfectly distinct, permanent, and recognizable by good observation; the Brambles and some Grasses have been claimed to include not dozens of species but hundreds; and the Hawthorns of America have already been described to the number of over a thousand, with no end to the trouble as yet. The same thing is true also of cultivated plants, and strikingly so of the grains. A field of Indian Corn, for example, has been found to consist not of one species, as we used to suppose, but of dozens of biotypes, or elementary species, crossing and hybridizing greatly it is true, but capable of separation and ultimate pure breeding each by itself. It is important to remember, however, that the fact of the existence of these elementary species is quite independent of the question as to their origin; and many of those who have had most to do with their discovery doubt whether they have arisen by mutation, though de Vries, of course, believes that they did.

There is one other great name associated with evolution, even though somewhat indirectly, and that is Mendel, whose discoveries in the particular field of heredity are exerting a profound influence upon present-day evolutionary thought. We have already discussed his work in our chapter on Reproduction, and need only summarize here the points of importance to our immediate subject. They are these:—

First, each individual organism, animal or plant, is an aggregate, or mosaic, as it were, of a definite number of characters each of which is represented by a determiner or unit in the germ cells from which it has developed. These characters are thousands in number in the higher organisms, fewer in the simpler, and include all kinds of features of structure, form, size, color, etc. Thus eye-color in man, and the number of rows of grains on an ear in Corn, are such unit characters.

Second, every germ cell, whether egg-cell or sperm-cell, contains one complete set of units capable of reproducing all the

characters of the organism, but never any duplicate units. On the other hand, the fertilized egg-cell, and every cell of the body subsequently arising therefrom, contains a duplicate or double set, one from each parent, from which selection has to be made during the development of the organism; and this double set prevails until the new formation of the germ cells, each of which in the "reduction division" receives but a single set.

Third, while each one of these newly-formed germ cells contains a complete set of units, these are partly derived from one of the parents, and partly from the other. Moreover, in any given germ cell, the paternal and maternal units are mixed in the most complicated manner, and, furthermore, hardly any two germ cells can be found with the same combination. Consequently when the unions of these germ cells in reproduction are left wholly to chance, as Mendel's results prove that they are, then the most diverse possible combinations of paternal and maternal characters must result, even among close-fertilized kinds such as many plants are, while the complications are proportionally greater among cross-fertilized beings, like mankind. We have thus the explanation of the very familiar fact that no brothers or sisters are ever found who exhibit the same combination of characters of father and mother,—even the case of identical twins being no real exception, since these are known to arise from the splitting of one fertilized egg-cell.

We have now brought our subject quite down to our own days, which are distinguished by extreme activity in experiment. It is not possible, however, to estimate as yet the value of the results that seem to be accruing therefrom. We lack perspective, of course; and moreover the conclusions have not yet received the thorough critical testing which is essential to establish that "impersonal validity," without which they cannot rank as scientific knowledge. But I shall add here a synopsis of the principal matters which seem to be crystallizing out from these studies.

First, exact studies on variation seem to show that the fortuitous variations of Darwin are of two distinct kinds or classes. One class, now called *fluctuating variations*, includes those caused by the immediate environment acting either forcibly (producing injury, &c.), or through stimuli calling out irritable responses; they are not hereditary, and therefore have no influence in evolution. They are variations of the body plasm only, in Weismann's sense. The reader will find good examples of variations of this type in the differences between the individuals within each of the mutation groups shown in figure 173. The other class includes those that are inborn, and hereditarily transmitted from generation to generation,—variations of the germ plasm, in Weismann's sense. These are variations upon which natural selection works. Their origin is unknown, but they are related if not identical with mutations, and with permutations and combinations of Mendelian unit characters. The two classes of course, are indistinguishable by the eye, and only determinable by experiment.

Second, the very newest studies, announced during the writing of this book, appear to be demonstrating that the mutants of Evening Primrose discovered by de Vries, are simply in large part the separation or segregation out of original elementary species which hybridized together to form the original *Oenothera Lamarckiana*. This case of mutation, therefore, is not an instance of the appearance of new species, but simply of the reappearance of old ones temporarily obscured in a combination; and it leaves unsolved the question of the origin of elementary species.

Third, all the recent work is confirming the reality of the existence of elementary species or biotypes, though it is throwing very little light on their origin. Moreover, and here is a most important point, it is showing that these biotypes, though apparently homogeneous (and therefore forming a single *phenotype*), are in reality composite, since they embrace a good many Mendelian combinations (or *genotypes*). But it is not worth while to follow these matters further at present, since we now verge close to the firing

line, where issues are doubtful. It must suffice to say that our knowledge of these subjects is in process of active extension at this moment.

Fourth, exact study devoted to determining whether the selection of variations, in the Darwinian sense, can actually produce a new species have given very largely a negative result,—much evidence tending to show that selection simply isolates the biotypes, but cannot in any way alter them. If, however, biotypes originate from other biotypes, as it seems that surely they must, then the method of evolution would be substantially that imagined by de Vries for his mutants, and that represented in our comparative diagram (figure 172). Thus, selection would still rank as the great decisive, though not as an originating, factor in evolution. As to adaptation, that still stands as a corollary of any kind of evolution by selection, for selection imposes a step-by-step development in touch with the environment. The conception of biotypes is wholly consistent therewith, and indeed helps to explain some of the peculiarities of adaptation,—especially the somewhat loose, clumsy, or generic character that most adaptation displays in conjunction with the occasional existence of highly exact fitness. In general in Nature, structure fits function about as well as a man's physique fits his trade,—that is, always in a general way, and sometimes very exactly. We cannot expect rigid biotypes to fit intergrading environments any more than we can expect polygons to match circles,—though with some many-sided kinds, the correspondence can be appreciably close. But it is perfectly clear that the first great problem of present-day experimental evolution is the determination of the origin of biotypes, or, to be exact, of the variations or characters which constitute biotypes. I should not be surprised if it were to turn out that the origination of new characters or biotypes is a normal function of organisms, adaptively acquired by them precisely as any other physiological function has been, and represents their method of securing survival in changing environments. It

is a voluntary offering of material, so to speak, for selection to choose from.

Such is the present state of uncertainty in our knowledge of some of the most fundamental matters in evolution. The truth we shall learn later through intensive study and experiment. At many places the world over,—at the Desert Botanical Laboratory in Arizona, at the Station for Experimental Evolution on Long Island, at many Government and University Stations in Germany, England, and this country,—trained experts, under the best of conditions, are subjecting these problems to the test of rigid experiment. The results are sure to be important and may be revelational. It is one of the great privileges of living in this age that we may witness these advances, and may even have part in them. There is in store for us all, who are students of biological science, many a thrill of purest delight as we open the pages of our weekly scientific newspaper,—our *Nature* or our *Science*,—and find the first announcement of discoveries which will later illuminate one by one the dark problems of nature. Science has indeed good reason for her distinctive optimism.

CHAPTER XVII

THE REMARKABLE IMPROVEMENT MADE IN PLANTS BY MAN, AND THE WAY HE BRINGS IT ABOUT

Plant Breeding



IN all the wide range of relations existing between plants and mankind, there is not another single fact which compares in importance with this,—that plants can be altered by man to make them fit better his needs or his fancy. His accomplishments in this field, indeed, partake of the marvelous. Everybody knows the magnificent exhibition type of *Chrysanthemum*, with its superb great globular head of snowy incurving petals, well-nigh geometrical in the perfection of its symmetry. But does everyone know that it has been created by man out of two daisy-like plants smaller and humbler than the commonest weed of our hayfields? Likewise, all those strongly individualistic types of the same noble flower,—the prim little pompon, the star-like anemone, the stiffly-correct reflex, the shaggy Japanese, and a number of others, a few of which are shown clustered together upon the accompanying plate (figure 174), have all been differentiated from the same unpromising beginning. Again, the Bartlett Pear, huge and luscious, has been developed within three hundred years from a small stony fruit attractive to no one except vagabonds and omnivorous small boys. Indian Corn and Wheat, chief of the food plants of civilized man, have been improved so far from the simple wild grasses with which the first cultivators had to begin, that Botanists are hardly yet fully agreed as to what those wild ancestors were. Oranges,

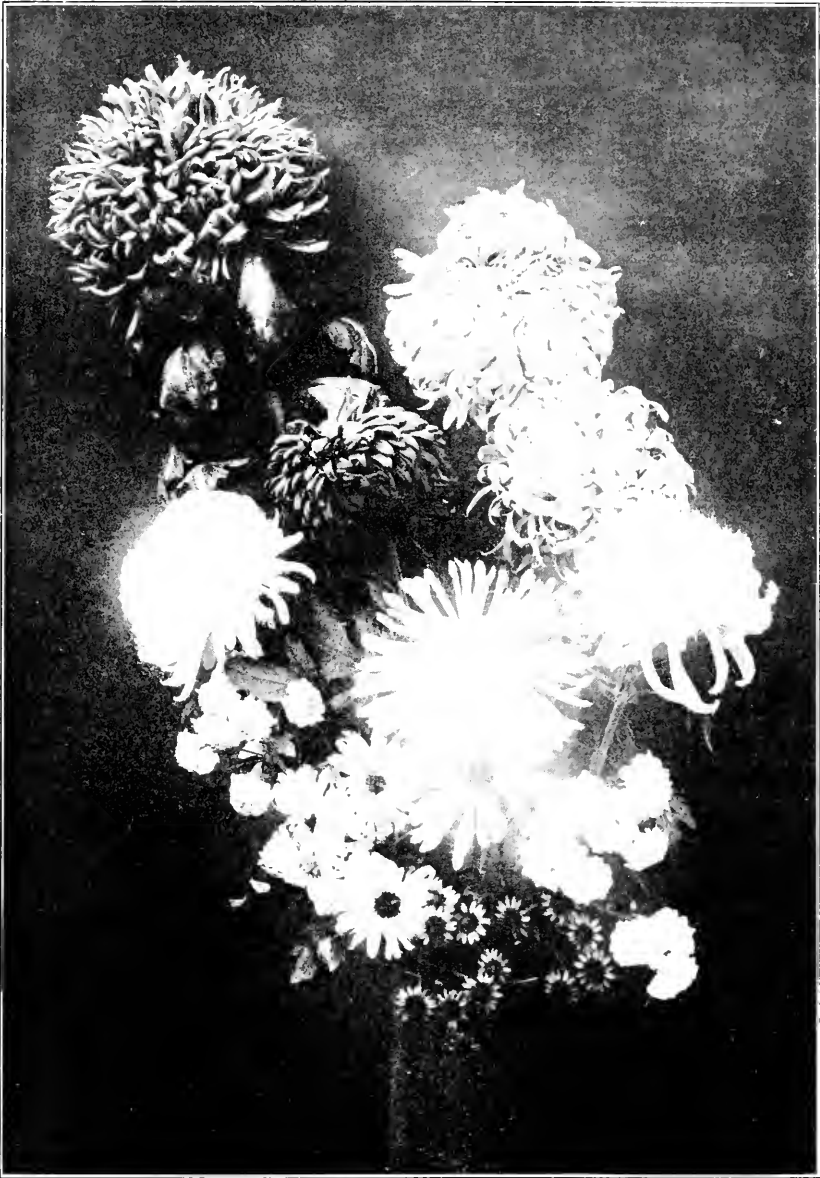


FIG. 174.—The leading types of *Chrysanthemum*, all developed by man from wild ancestors having a size and form very like the lowermost single flowers of the picture.

Bananas, Pineapples have been immensely enlarged, greatly improved in flavor, and actually rendered seedless. Brilliantly red foliage plants, including some trees, have been derived from green forbears. Invaluable vegetables, often imposing in size, have been made to spring from insignificant weeds, as in case of the familiar varieties represented in the accompanying picture

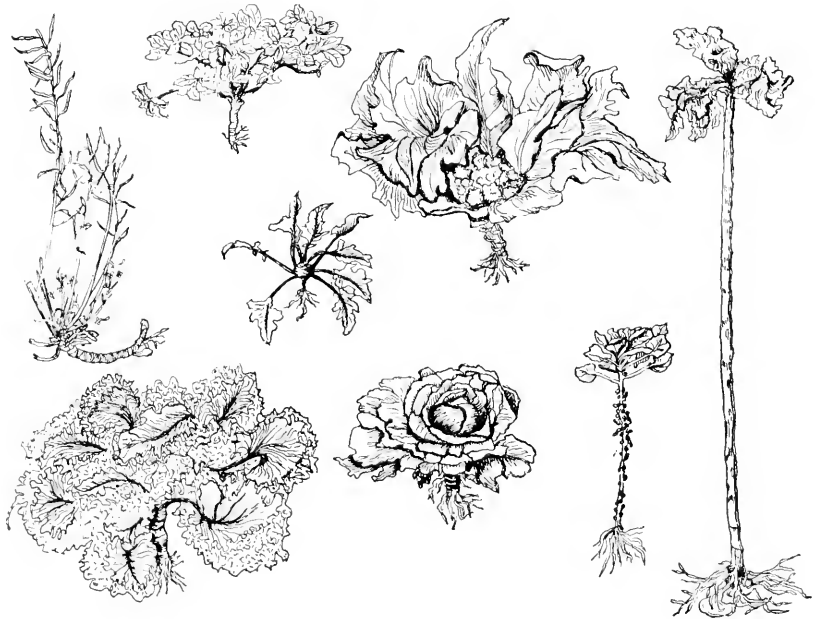


FIG. 175.—Representative forms of Cabbage, Kohl-rabi, Cauliflower, Brussels Sprouts, and Tree Cabbage, evolved by man from the wild shore plant, *Brassica oleracea*, of which two forms are shown in the upper left hand corner. The pictures are about one twenty-fourth of the natural size. (Redrawn from a colored wall-chart by Laurent and Errera.)

(figure 175). Not one of these remarkable productions, or any of the vast number of which they are typical, would exist to-day, were it not for the craft and the patience of man. It is now our particular task to inquire in exactly what way this indubitable miracle has been wrought.

The methods of plant improvement are few, old, simple, and

perfectly known. The earliest cultivators made use of them, and the most scientific of horticultural experts have no others to-day. For convenience of study we may consider them as three in number and distinct, though in fact they are interwoven inextricably. They are,—*Selection of Variations; Preservation of Sports; Crossing and Hybridization.* And perhaps the reader will here add in his mind “and also *Cultivation;*” but he would be wrong. Although cultivation can produce better individuals, it cannot produce of itself better races, for the two are not the same thing at all.

1. The Selection of Variations.—The reader will already have noticed the very close connection which exists between Evolution, considered in the preceding chapter, and the Improvement of Plants by man, or Plant Breeding, our immediate subject,—a connection which explains the juxtaposition of the two chapters, and is not badly expressed by calling Plant Breeding artificial evolution. Moreover, the two have precisely the same basis,—in Variation, which we must now consider rather more fully than was needful before.

If all the plants of one kind, or species, were born exactly like one another, as crystals are, then, so far as we can see, no improvement of plants by man would be possible. But plants of the same species are not born alike any more than are people of the same race or even the same blood. In a field of Corn, are all the plants of one height, or have they the same number of grains to the ear? Are the Elms in a meadow all cast in the same mold of grace? Are the flowers of any one annual precisely alike in their hue? There is an experiment which my students try every year, with a result that is always surprising to them, and a satisfaction to me. From a large lot of seeds of the same variety and crop, they select a definite number of grains just as similar as possible in size, form, weight, color and other features; these they plant at exactly equal distances apart, at the same depths and in the same positions, in a box of evenly-mixed earth, which is then

kept watered, warmed and lighted uniformly over its whole surface. This is something which the reader can readily try for himself, and I commend it to his favorable attention. As the plants come up, the differences they exhibit in rapidity of germination, in the rate of subsequent growth, and in every detail of their structure, are most striking, as the accompanying pictures, traced from photographs, to some extent illustrate (figure 176). In their main features, it is true,—those by which we distinguish

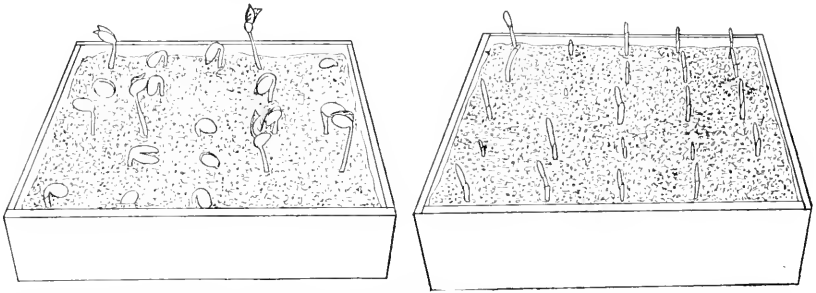


FIG. 176.—Young seedlings of String Bean and of Corn, grown from seeds as nearly alike in all visible features as possible, and planted exactly alike. Traced from a photograph.

them,—plants of the same species are alike, but in their details they are always different, and often conspicuously so. Plants of the same kind are, as it were, alike in general but different in particular. The matter is sometimes expressed in this way, that no living being is just like any other living being,—a statement impossible of logical proof, but shown by experience to be true for all practical purposes.

Turning now to a more exact examination of these differences, or variations, we find that they arise from diverse causes. A part of them are of purely mechanical origin, being forcibly imposed upon some individuals, but not others, by overcrowding, attacks of enemies, or lack of suitable nourishment. Thus, insufficiency of water causes the dwarfing of plants simply because they have not enough water with which to grow big; and man can make individual plants short-stemmed in this way if he wants to. Another part of the variations arise from the remarkable power

which individuals have of adjusting their parts to peculiarities in the distribution of light, moisture, minerals or other essential conditions of their immediate surroundings,—a power which we have studied with some care in the chapter on Irritability. An example thereof is the greater lengthening of stems (which are “drawn,” in the language of gardeners) when exposed to insufficient light, and of which the very longshoots formed by potatoes in cellars are an extreme example. Upon these stems the deficiency of light acts as a stimulus, making them lengthen out as if in the effort to carry their leaves into full brightness; and man can make plants long-stemmed in this way if he wants to. But when all of the differences due to mechanical causes or to irritability are eliminated, as can largely be done by careful experiment, there remains always a great residue of differences for which there is no conceivable origin except that they are innate or inborn in the plants themselves. Thus, when all external conditions of water-supply, light, &c., are carefully made the same for all the plants under our experiment above described, the stems of the plants nevertheless differ in length, some being shorter and some longer. And man can also obtain long-stemmed plants in this way if he wants to. It is thus plain that the differences between individual plants of the same species arise in at least three different ways, which we may summarize in an order the reverse of that of their treatment above, by saying,—that in some of their features plants are born different, others of their differences are achieved, while some of their differences are thrust upon them.

Of the three kinds of differences, the inborn variations are the only ones important in the improvement of plants, as in natural evolution, and for the same reason, that they are the only kind which can be transmitted to descendants. Although man is able by regulation of the water or light supply to make individual plants short-stemmed or long-stemmed, he cannot by this means make a short-stemmed or long-stemmed race which will reproduce itself generation after generation. The only known way in which

he can obtain such a race is by watching for plants which naturally exhibit an inborn short-stemmed or long-stemmed variation, respectively, selecting them out and propagating them; the short- or long-stemmed character will appear in their descendants, and by consistent repetition of selection of the same variation for some generations, a race capable of perpetuating the short- or long-stemmed character can be obtained. The fact, then, that innate variations are *hereditary* is the most important fact about them from the point of view of plant improvement.

There is one other point about the heredibility of variations which we must note at this place. It was Darwin's view that variations rise and fall, or flash, as it were, across several generations, and, unless preserved by selection, sooner or later die out. But modern studies are showing that variations appear linked several together in those mutants, biotypes, or elementary species which we have already considered in the preceding chapter, while, once in existence, they persist indefinitely. What then, on the newer view, is the gardener doing when selecting variations for the improvement of plants? Simply this,—he is isolating the desirable biotypes from among the less desirable kinds making up the great mixture of which any crop consists. Thus a field of Corn or Wheat consists of a great number of biotypes, and hybrids thereof, from which the best kinds can be selected and propagated. But, on the newer view, once the best biotypes are isolated, no further improvement is possible, while the selection of variations should permit an indefinite, or at least much larger improvement. Experience is certainly showing the truth of the modern view in many cases, though the accumulation of single small variations seems equally clear in other instances.

A second great fact about variation is this,—it is *spontaneous*, which means that it appears without any determinable reference to any features of the surroundings. But while the surroundings do not in any known way determine the nature of variations, they certainly do promote them, both in number and intensity, as

shown by the fact that variations become more active when the external conditions are changed. This happens when plants are taken to new countries; or are brought out of forest or field into garden or greenhouse; or are subjected to high cultivation, through which are provided better conditions for nourishment and comparative freedom from natural enemies; or are given different soils, fertilizers and exposures; or are crossed in reproduction,—a matter which we shall consider more fully in a moment. There are, of course, limits to the change of conditions that plants can endure, but within those limits all changes in external conditions are followed by more rapid, diverse, and extreme variation. Variation in organisms may be symbolized by the gentle trembling of the surface of water held in a full dish at arm's length; if the hands are deliberately shaken a little, the trembling increases, though the shaking must be kept within limits, else the water is spilled from the dish. The cultivators of plants, realizing well that variation is the basis of the possibility of improving plants, and observing that change in conditions promotes it, have from the earliest times made use of these methods for rendering more variable those forms which they wish to improve, but which naturally exhibit little variation. This is precisely what they mean by their expression "break the type."

A third vital fact about variation is this: it is *fortuitous*, which means that it takes place in any possible part, feature, or direction, indifferently, according to chance, and shows no tendency to follow any particular lines, excepting in so far as structural conditions may make it easier to vary one way than another. Stems do not vary towards shortness alone nor longness alone, but towards shortness, longness, thickness, thinness, roundness, angularity, flexibility, stiffness, and any other peculiarities which the construction of stems makes it possible for them to exhibit. Moreover, these variations insist, so to speak, upon originating and directing themselves, and all the ingenuity of man has not yet enabled him either to originate or to determine the direction

of any desired variation in any given plant. Therefore his only resource is to wait until the desired variation appears, which will be the sooner the larger the number of plants that he deals with, and the more actively he employs the devices for "breaking the type." Under these conditions, it is only a question of time when any desired variation that is mechanically, physically, or chemically possible will appear, after which it can be selected and intensified by the methods already described.

Let us now illustrate, by a suppositional case, the way in which man makes use of variation in improving some particular kind of plant. Let us suppose that out of a race of white-flowered plants, the breeder desires to develop a red-flowered variety. He knows it is useless to try to turn the flowers red directly, by chemicals in the soil, regulation of the light, or anything of that kind, for although white flowers might conceivably be made red by such methods, the redness would not be transmitted, and the next generation would be just as white as ever. He knows that his only chance of success lies in the spontaneous appearance of a strain of red color, and accordingly he grows just as many plants as he can possibly find space for, giving them diverse conditions of soil, fertilizers, situation and cultivation, in an effort to break the white type. Inevitably, sooner or later, unless, indeed, as sometimes happens, there is some chemical obstacle in the constitution of the plant, some redness will appear, faintly perhaps but unmistakably, in some of the white blossoms. He then isolates those plants, remorselessly destroying all the remainder, and breeds them together if possible, though this is by no means indispensable. From the seeds of the selected plants he raises as many as he can, and amongst their flowers though some revert back to whiteness, the majority are likely to show the red strain of the parents, while a few (though perhaps not for another generation or two) will exhibit a still redder strain. The latter, of course, are then selected, and bred together, and their seeds are sown as before. In the resulting generation will appear fewer white

flowers than before, a larger proportion of red like the parents, and perhaps a still redder strain, though again this may not appear for a number of generations. Thus, gradually, generation after generation, the quality of redness becomes extended and intensified, while whiteness diminishes to final disappearance; so that finally a permanently red-flowering race has been secured. Whether, however, this process depends chiefly upon the selection and accumulation of red variations in the Darwinian sense, or upon the isolation of successively-appearing new biotypes, I do not know, but expect the near future to decide.

In any case, the improvement of plants by the selection of variations is a slow process, and it is fortunate that a far more rapid, even though rather spasmodic method exists, viz., the preservation of sports.

2. The Preservation of Sports.—The most of my readers, I fancy, know something about sports among plants. The most typical ones originate like this. On some ordinary plant a single bud, differing visibly in no wise from its neighbors, grows out to a branch which bears leaves, fruits or flowers conspicuously different from all others on that plant. About five years ago, in a greenhouse where I teach, a certain Pompon Chrysanthemum bearing pretty pink flowers put forth a single branch on which all of the flowers were entirely different, being a striking bronze brown. For that season the plant was a wonder to visitors, who delighted to represent that they could hardly believe their eyesight; a pride to the students, who accepted its appearance as a delicate compliment to themselves; and a treasure to me, who made the best of this unusual educational opportunity. From both the sporting and the ordinary branches we took cuttings, and from these the next season we grew two plants of the respective colors, which we have propagated continuously to this day. On an ordinary green beech tree in Scotland somewhat less than a century ago, a single one of the innumerable buds grew into a branch on which every leaf was dark red. That

branch was propagated by grafting and these plants by grafting again; and such was the origin of all those favorite lawn trees which we call copper beeches. On an ordinary orange tree, not so many years ago, a single bud produced a branch which bore only seedless fruit, the seedlessness being correlated with the presence of a tiny accessory orange embedded almost wholly in the larger; that branch was grafted, as were the resulting branches; and this is the origin of the thousands of trees now bearing the navel orange. Nectarines are bud sports from peach trees, and most of our finest varieties of apples, of pears, and of many other fruits have originated in just such a manner. Hawthorns, Azaleas, Pelargoniums ("Geraniums"), Roses, Carnations, and many other plants sport greatly in the color of their flowers; and many of our choicest varieties of these charming plants, including double-flowered forms, came thus into existence, as did many of our cut-leaved trees, variegated plants, and crested oddities. Sometimes the sports take curious directions, as in the case of branches which bear leaves that unfold in the spring several days in advance of any others on the tree. I know a tulip bulb which, year after year, produces flowers highly doubled and accompanied by a colored peduncular bract. This latter case is interesting as marking a transition over to those peculiar structures called monstrosities, which are largely, though not always, sports. Indeed a monstrosity is usually but a sport which strikes us as somewhat abnormal or "queer," such for example as green roses, crested plants, and other "freaks," all of which can be propagated regularly by cuttings. And other sports are known in great number as recorded in the books devoted to horticulture. But as to this, one must not forget that only those sports which appeal to man as useful, attractive, or curious, are likely to receive mention in such books, while innumerable others, which make their appearance but have no interest to man, are left in oblivion.

Concerning the causes of bud sports we know as little as we do

concerning the causes of variation, the two, indeed, being doubtless identical in nature. Like variations, bud sports are spontaneous and fortuitous and can be rendered more frequent by cultivation; and they are hereditary through the new buds they produce, though never by seeds. Everybody knows that a Bartlett Pear or a Baldwin Apple can be propagated by grafting, but not by the seeds, which do not produce those fruits, but just plain ordinary mongrel pears and apples. Were it not for the fact that most of the plants which produce bud sports can be propagated by slips, or cuttings, or else by grafting (which is merely a process of giving ready formed roots to slips unable to make roots for themselves), it would not be possible to preserve bud sports, and they would perish with the plants which produce them. But those methods of propagation do permit man to preserve them, to his very great advantage.

Sports from buds, however, are not the only kind, for seed sports also occur, though upon the whole they are less conspicuous and important than bud sports. Among brilliantly red cardinal flowers, some plants occasionally occur with pure white flowers; when seeds from the white flowers are planted, they produce white-flowering plants. The white cardinal flowers are typical seed sports, and the fact that they propagate by seed is typical. Some cut-leaved trees (e. g. Wier's cut-leaf Maple), and some fine varieties of fruits have also originated as seed sports. Whether these trees come true to seed I do not know, and the matter is not practically important, since they can be propagated far more speedily and easily by grafting. It is obvious that seed sports which propagate their characters through seeds differ in no essential particular, except perhaps that of degree, from the mutants, or biotypes, described in the chapter on Evolution.

3. Crossing and Hybridization.—The reader will recall that seed-formation must be preceded by fertilization, which in turn requires that the pollen-grain containing a male cell shall be transferred from anthers where it is made, to a stigma giving access

to the female cell in the ovule. Now in nature this transfer is effected by the agency of wind, water, or insects, but in cultivation man can transfer the pollen himself if he pleases, and can thus to some extent control the parentage of the new individuals formed in the ovules. And these are the various combinations he can make:—

(1) He can pollinate a given stigma by pollen from the same flower. This is called *close pollination* in Botany and *in-breeding* in Horticulture. With many plants, perhaps the majority, no result follows, for the seed does not set, the ovule being sterile to the pollen of the same flower; while in many kinds of flowers such pollination is impossible, because the pollen and ovules in each single flower ripen at different times, or because of other impediments. It is thus obvious that nature takes trouble, so to speak, to prevent such in-breeding; and the implication that such breeding is in general not advantageous is confirmed by such evidence from experiment as we possess, which shows that the offspring of close in-breeding are generally inferior in variability if not in vigor to those more widely bred. But in the very fact that in-breeding does not favor variability is found its chief horticultural importance, for it can be used to keep a race true to its type when that is desirable. In practice, however, such use is very limited because the same result can be attained much more easily in most plants by propagation through cuttings or grafting, and by the systematic weeding out of all plants (horticulturally called “rogues”) which show individual variations.

(2) He can pollinate a given stigma by pollen from another flower on the same plant. This also is in-breeding, and experiments have shown that the results are little if any better than in the case of the first method.

(3) He can pollinate a given stigma by pollen from a different plant of the same kind. This is called *cross pollination* in Botany, and *crossing* in Horticulture, and is that to which most of the cross-pollinating mechanisms and methods in flowers are adapted.

It is both known from experience, and also has been shown by experiment, that crossing yields more vigorous, abundant, and variable offspring than in-breeding, in which fact lies the reason, doubtless, why nature promotes it. In crossing, not only is variability promoted by the introduction of the peculiarities of two lines of ancestry, but the very commingling of the two strains of protoplasm seems to favor the appearance of wholly new variations, somewhat after the analogy of these liquids in chemistry, which are perfectly clear by themselves but turbid when commingled. It appears also to be a fact that the offspring are more vigorous, prolific, and variable yet, if the two plants between which the cross is made are not raised side by side under the same conditions, but apart and under somewhat different conditions. Cross pollination between plants thus grown is something which nature cannot provide for, but man can, and sometimes does, as when he plants seeds in alternate rows treated somewhat differently in cultivation. By this method man can intensify variation, and thus provide a wider and better basis for selection.

(4) He can pollinate a given stigma by pollen from a plant of another variety of the same species. This is called *hybridization* in both Botany and Horticulture, though by some it is also designated crossing. Occasionally no result follows, but usually seed sets and will grow into new plants which breed freely together. The first generation of such hybrid progeny exhibit characters derived from both of the original parents, and are likely to be more vigorous than those parents; but (and this will be news to many of my readers), these characters are not combined in the same way in all of the descendants of those hybrids, though the ways are very definite. This very important matter, which involves a notable natural law discovered by Mendel and known by his name, has already been considered in the chapter on Reproduction, and it will suffice to recall here that the characters of the original parents are inherited by the descendants of hybrids as definite entities in definite mathematical proportions. This fundamental

fact has a practical consequence of the first importance, since it is thus made possible for a breeder so to breed the hybrids together as, on the one hand, to eliminate utterly out of the hybrid race any given undesirable quality inherited from either of the original parents, and, on the other, to combine and fix permanently in the race any two given desirable qualities originally occurring in separate parent races. Thus, it has been possible to produce hybrid races of wheat in which the superior flour-producing quality of one variety has been united with the superior frost-resisting quality of another, the inferior frost-resisting quality of the former, and the inferior flour-producing qualities of the latter having been eliminated permanently out of the hybrid race. Moreover, it is possible, theoretically at least, thus to combine in one race any number of good qualities from any number of different varieties of a species, though in practice, as we shall see in a moment, the matter is attended with immense practical difficulties. It is, however, in this possibility of combining in one race the desirable qualities from different races while eliminating the opposite qualities, that the highest utility of hybridization in connection with the improvement of plants consists.

(5) He can pollinate a given stigma by pollen from a plant of another, but allied, species. This also is called hybridization, in both Botany and Horticulture. In the vast majority of such pollinations no result follows, but in the few cases where seed is formed, the derived specific hybrids, like the varietal hybrids just considered, exhibit characters derived from both parents, as also new characters not traceable to either. Like the first generation of varietal hybrids, also, they are often larger and more vigorous than either parent; but on the other hand they are almost invariably defective in reproductive power, and can hardly ever reproduce by seeds. A famous example of a species hybrid is *Lilium Parkmanni*, a magnificent Lily even finer than either of its superb parents, but it is rarely seen in gardens because it does not

reproduce at all by seeds and only badly by bulbs. Such of these species hybrids, however, as can be reproduced by cuttings or grafting can be preserved indefinitely, and this is the case with hybrid trees, because the seedling can be grafted into either of the parent trees, or into some allied kind, and thereafter can be multiplied with rapidity and certainty. It is obvious from these considerations that specific hybrids can only rarely be made the foundation of a race, and equally plain that they can play no appreciable part in the natural evolution of plants.

(6) He can pollinate a given stigma by pollen from a plant of another but allied genus. Though some such generic hybrids have been made as a matter of scientific experiment, this has only been possible with genera extremely closely related, and moreover the hybrids are unstable and of no horticultural importance. Nor have any attempts at hybridization over wider limits ever succeeded; and the occasional newspaper accounts of crosses between members of different plant families are lies, when they are not obvious jokes.

It is evident from this discussion that plant-breeders make use of in-breeding, crossing, and hybridization for various purposes in accordance with the results which they wish to attain. By suitable combinations it is possible to keep races close to their type and thus preserve desirable characteristics; to break the type and thus provide a basis for the development of new characteristics through selection; to eliminate undesirable features out of a race; to combine the desirable features of two or more races into one; and in general to promote vigor and productivity. I think it will now be evident why crossing and hybridization are so prominent in plant improvement.

It will interest the reader, at this point, to learn in what way crossing and hybridization are effected in practice. It is no trouble at all to transfer the pollen from any ripe stamens to any ripe stigma. It is only necessary to pick the fine pollen dust from the opened anthers by some dry utensil to which it will cling (for

which purpose a common camelshair paint brush is admirable and usually employed), and then press it against the desired stigma, which is sticky and to which therefore the pollen adheres. The difficulty in the process comes from the fact that undesired pollen may also reach the stigma, and effect a wrong fertilization. It is therefore necessary to prevent access of any pollen except that deliberately placed upon the stigma by the experimenter. Close pollination is prevented, in those plants which allow it, by snipping off the stamens before the anthers are ripe; while undesired cross pollination is prevented by use of a gauze, or thin paper bag kept closely tied over the flower except at the moment when the desired pollen is applied to the ripe stigma. The sight of such bagged plants must be familiar to all those who have visited agricultural experiment stations, and they are shown in figure 173.

The reader will no doubt be surprised that in this discussion I have laid no more stress upon cultivation, which surely, he will say, does much improve plants. Cultivation consists in giving to plants such conditions of space, nourishment, and freedom from enemies as will permit them to develop to the highest degree that their internal capacities allow. It produces, therefore, better individuals and crops. But it does not produce better races, because, as we know, the good effects of cultivation are chiefly irritable responses whose results are never transmitted to the next generation. Indirectly, however, cultivation does help in racial improvement, for on the one hand all offspring are benefited by greater physical health in their parents, and, on the other, with greater physical vigor goes greater variability and tendency to production of sports,—those foundations of the improvement of races. Just as the best nourished animals play more vigorously than the ill-nourished, so the best cultivated plants vary and sport the most actively,—from very excess of physical vigor, no doubt.

In my discussion of this subject thus far, I have made it an aim, as elsewhere through this book, to exhibit the theory, so to speak, of the subject. For this purpose I have had to separate

out the constituent methods and discuss each by itself. But thereby I have given the matter an aspect of simplicity which it is far from deserving, for not only are the methods inextricably interconnected, but practical difficulties of innumerable sorts interpose large obstacles to their successful operation. Thus, I have spoken of plant breeding as it would be conducted when a matter of deliberate intention on the part of a worker with a definite idea in his mind. This, however, it rarely is except in the case of modern scientific plant-breeders, wealthy amateurs, or a few far-sighted commercial dealers in horticultural novelties, of whom the most conspicuous by far is Luther Burbank, well known of late to the readers of periodical literature. As a matter of fact, most plant improvement has been made on the spur of the moment, by the selection of something which happened to please the fancy, or appeal to the sense of profit, of gardener or farmer, who of course has always sought to propagate from the plants he considers his "best." But the art of horticulture is long, and the life of man is short, and fancies change, and things that are profitable vary; wherefore improvement has been spasmodic, and along most devious courses. Nor are horticultural productions wholly stable when once secured, for varieties, even when true to their good character for a time, tend strongly to revert or merge off or "wear out" to less desirable kinds, though there is perhaps a difference between mutations which are permanently stable, and the results of the selection of small variations, which are unstable. Furthermore, hybridization, especially for the combining of features from different races into one, is by no means so simple as its theory implies, but a process distinguished by innumerable failures, and requiring a persistence and skill that few breeders command. The potentialities of improvement, indeed, have a vast burden of practical troubles to carry; and it is this which makes its progress so halting and laborious.

It is evident that in his improvement of plants, man never creates, except by a figure of speech, but only directs. He cannot

compel plants to go as he wishes, but he can lead them in any direction they are capable of going. The forces of improvement lie deep inside of the plants themselves, seething and smoldering ready for an outbreak; all that man can do is to suppress or bank them in places where they are doing no good, and give them free vent where they can produce beneficent results. The method of effecting desired results through the guidance of internal forces is not, however, confined to plant breeding, but is that by which all great organizers of large enterprises, and all great leaders of men, effect their successes. By this method they succeed when those who try to force the improvement from without meet only with failure.

CHAPTER XVIII

THE PRINCIPAL GROUPS INTO WHICH PLANTS NATURALLY FALL, WHETHER BY RELATIONSHIP OR HABIT

Classification



ONE does not go far with the study of plants before he perceives that they fall into groups, and groups within groups, according to the degrees of their likenesses and differences. Some kinds are so closely alike that botanical experts dispute as to whether they really are different or merely two forms of the same, while others are so very unlike that they offer not the least point of resemblance; and there is every gradation between. The arrangements of plants in their groups, and of these in relation to one another, is Classification, which we must now proceed to consider in so far as it has connection with the particular theme of this book. And we naturally begin with the groups which are largest and best defined, of which there are five,—Algae, Fungi, Moss-Plants, Fern-Plants, and Seed-Plants.

The Algæ.—These are the distinctive plants of the waters, comprising especially the Seaweeds, but also many kinds that dwell in rivers and lakes, and a few that live out in the air. In size they range widely, from kinds too small for the eye to detect up to the great *Macrocystis* of the Pacific, whose thousand feet (pretty nearly) of length surpasses anything that land plants can offer. In shape they are bewilderingly multifarious,—spheres, cylinders, hairs, plates, tufts, fronds, and even leafy stems, which

latter bear a striking, albeit superficial, resemblance to those parts in the higher land plants. Whatever their shapes, they exhibit a wide prevalence of minuteness, thinness, or fine division of structure, these features being correlated with the comparative scarcity of the indispensable gases, which they, like the fishes, must take from solution in the water. In color they are typically green from the presence of chlorophyll, by aid of which they make their own food precisely in the manner of the familiar green land plants; but in a good many kinds, including most of the larger and best-known, the green is mixed up with red or brown pigments which aid in a better utilization of the light under the conditions prevailing where those kinds make their homes. Their anatomical structure is cellular, as in land plants, but much simpler, with far less division of labor among the various cells, and only unimportant structural differences between the several tissues. Their reproduction is partly by fission, but chiefly by spores, which are simple one-celled bodies various in aspect and mode of formation,—some of them actively free-swimming, and others passively floated by currents of water; in addition, fertilization occurs, in all grades of complexity from the accidental fusion of two precisely-similar free-swimming cells up to the union of a tiny, free-swimming, chemotropically-attracted, male cell with a sessile food-filled female cell.

The best-known kinds of the Algae are these. Among the GREEN (AND BLUE-GREEN) ALGAE are the *Diatoms*,—found in all waters, with microscopical flinty shells of wonderful beauty and marvelous variety; the *Blue-green* kinds, forming unhealthy-looking scums of that color in unpleasant damp places; *Pleurococcus*, which makes up the familiar green coating upon the shaded sides of standing tree-trunks; *Vaucheria*, the darker-green coating on damp earth in warm shaded places; *Uroglana*, hardly visible to sight, which gives the bad odors and taste to the water of reservoirs, from which, fortunately, it can be driven by traces of compounds of copper; *Spirogyra*, which composes the very bright green

felted mats, buoyed up by entangled bubbles of gas on the surface of still waters; *Cladophora*, and its relatives, often mistaken for Mosses, those hair-like, net-like, brush-like, fringe-like forms which sway and wave from their moorings on stones in the bottoms of slow-moving brooks; and certain of the simpler kinds which are enslaved in the meshes of some Fungi to make up the remarkable Lichens. The curious Red Snow, reported by Arctic and Alpine expeditions, and the redness of the Red Sea, famed in geography and biblical history, owe their characteristic colors to certain red stages in the development of simple Green, or Blue-green, Algae.

Of the BROWN ALGAE the most familiar are the *Rockweeds*, whose tough branching fronds cover rocks of the beaches where exposed to the swing of the tides; the great leathery *Kelps*, known to the sailors as "Devil's Aprons," abounding in the seas of the north; and the leafy-stemmed kinds, including the *Sargassum* which gives name to a Sea, more plenty towards the south. These Brown Algae are the only marine kinds which are exposed with regularity to the air, either between tides on the beaches or during flotation on the surface; and this better access to gas-supply helps to explain their larger and stouter forms.

Of the RED ALGAE, the best known are the dark-red, almost purple *Irish Moss* and *Dulse*, familiar to all persons who have had the good fortune to grow up in a sea-port; the *Corallines*, those reddish-chalky-warty incrustations upon stones near low-tide mark, often mistaken for corals which they aid materially in the building of coral reefs, though also extending far north of the range of those much misunderstood animals; and the beautiful rose-red, soft-foliaged *Sea-mosses*, most plenty towards the south, where they often arouse the collecting instinct in persons who never have been moved to collect anything else.

Such are some of the principal ones of the fourteen thousand or more different kinds of Algae which botanists have named and described.

As one might expect, there are plants supposed to be Algae which really are not. Thus the Eel-grasses, the Pond-weeds, the Duck-weeds, and many other Water-weeds, are Flowering Plants which have adopted a life in the water, and therefore an Alga-like aspect. They can be told by their flowers which they bear in their season, and which separate them sharply from the spore-bearing Algae.

We turn now to consider the origin and evolution of these Algae, together with their classification. If evolution is a fact, and all evidence appears to agree that it is, then classification must be an expression of genealogical descent, and expressible in a genealogical tree, comparable with the kind which some people are fond of constructing to show the genealogical ramifications of human families. Such a tree, for the great primary groups and their principal subdivisions, is presented in our accompanying diagram (figure 177), and the mode of its construction is as follows.

First as to its most ancient, or lowermost, part. We have good reason for believing, as the chapter on Protoplasm suggested, that our present green plants were preceded in time by a colorless kind, which, though without chlorophyll and of the utmost simplicity, could yet make their own food from carbon dioxide and water by using the energy of chemical oxidation of soil minerals in place of that of the sunlight. We have precisely such chemosynthetic organisms, a kind of soil Bacteria, still living on the earth at this day; and they are doubtless the lineal descendants of the ancient forms, which probably lived in the mud of shallow seas that may be full of them yet. These ancient chemosynthetic organisms were neither animal nor plant but both and between,—the dawn of the kind of plant-animal forms sometimes called Protista; and therefore I suggest that we call them Eoprotista. These Eoprotista, therefore, form the base of the genealogical tree. Then, like all later groups, they must have expanded, developed, varied, evolved, thus originating a great many branches, of which the greater number perished, and only

four survived; (a) the *Chemosynthetic Bacteria*, whose persistence to this day is shown by the continuous line sweeping up and off to the outer rim of the tree where lies the vegetation of this, our own,

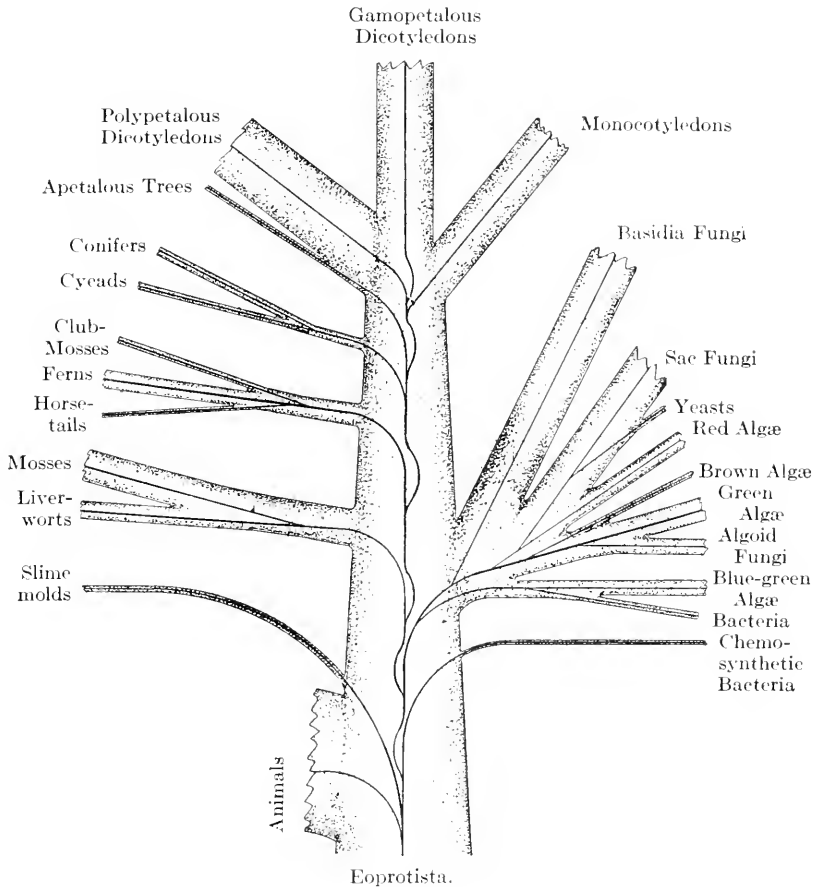


FIG. 177.—A genealogical tree of the principal groups of plants. The axial lines show the supposed relations of the groups at the time of their original evolution from one another, while the solid trunks show their present numbers and connections.

day; (b) the *Animals*, a vast group, shown on the left by an unfinished stump which it is some zoölogist's business to finish if he wants it; (c) the *Slime-molds*, well described by their name, a group of very simple organisms which creep as white films over

damp rotting wood in dark places, in a way so like to some animals that zoölogists lay even stronger claim than do botanists to their possession, and, (d) the most important of all, the *Algae*.

So, the *Algae* evolved probably from Eoprotista, and by a method which was somewhat like this. Among the variations or mutations (or whatsoever else it is that our chapter on Evolution concluded does originate innovations in living Nature) arising in the Eoprotista, must have been many new chemical compounds, among which, in time, appeared chlorophyll. This substance happening to possess such properties that sunlight falling upon it dissociates carbon dioxide, enabled its possessors to make their food far more rapidly and easily than by the old chemosynthetic method; and therefore those plants were enabled to grow, increase, develop, and expand immensely until they filled the lighted seas of the world. Thus the little chlorophyll-bearing branch of our tree, the one that happened to be thus fruitful among so many that were barren, expanded so greatly that gradually it became the main trunk of the tree, which fact we may express by swinging it around into the main line of ascent as has been done in our diagram. Thus arose the *Algae*, the characteristic group of the waters, in which they have persisted right down to the present, giving origin in time to Red and Brown branches as the tree represents. It is interesting to know that our living *Algae* have an ancestry so ancient, so ancient indeed that they have doubtless had time to evolve everything of which they are capable, and have consequently reached a condition of comparative evolutionary stability.

The Fungi.—These are, so to speak, the degraded and criminal classes of plants, which prey upon good plant society, or eke out an unenviable existence as scavengers of its offal. Expressed more precisely, in the manner of science, they are *parasites* which take all their food ready-made from living green plants or from animals, causing, incidentally, damage, disease, or death; or else they are *saprophytes* which consume and destroy dead animal or

plant remains, thus turning them back into the general circulation of nature and rendering a service to the remainder of living things. This dependence upon other organisms for their food, with the correlated absence of chlorophyll, is their one great distinctive feature.

The principal kinds of Fungi are these:—*Bacteria*, commonly called “germs,” or “microbes,” tiniest of living things, some of them harmless, others useful, and others the causes of deadly diseases; *Yeasts*,—but the reader knows what they do; *Molds*, which spring up on moist bread, preserved fruits, and other good materials, spoiling them quickly for use; *Mycorhiza*, which form caps of closely-felted threads over the ends of some roots, and aid them to absorb materials from the soil; *Water-molds*, which form the white haloes round dead insects or small fish in the water; *Blight*s and *Mildew*s, showing as powdery or woolly white fuzzes on grape leaves and others; *Rots*, which soften, discolor, and ruin potatoes and other vegetables and fruits; *Spots*, which darken round areas on various leaves; *Smuts*, which convert ears of grain to an unctuous black powder; *Rust*s, the ragged red spots which appear on the leaves of the wheat in over-wet seasons, and on other grains also, to their infinite damage, but which are dear to the botanical teacher because of their heterogeneously polymorphic ontogeny; *Mushrooms*, which are good to eat, and *Toadstools*, which are not; *Puff-balls*, whose names sufficiently describe them; *Black-knot*s, which form swellings on branches of Cherries, with many destructive diseases of Chestnuts and other large trees; *Bracket-fungi*, which appear on the outside of tree-trunks as a kind of crude hemispherical bracket, unfortunately, however, with the flattened side down; the *Lichens*, gray, crisp, brittle, and crusted, living on rocks, fences and tree-trunks, and deriving their food from certain kinds of small Algae which they hold enslaved in their meshes; and a great many others not familiar to the public but well known to botanical students.

In shapes the Fungi are even more diversified than the Algae,

but they show, for the most part, a double structure imposed by their habit of life. First, they possess a feeding body, called a *mycelium*, consisting as a rule of innumerable fine, slender, white threads ramifying and radiating everywhere throughout the accessible tissues of the living plants, or amongst the decaying materials upon which they live; and second, they possess a compact spore-forming body which comes to the surface, and thus carries the spores to a position where they can be scattered by the wind. Most of the Fungi familiar to us, such as Rusts, Bracket-fungi, or Mushrooms, are simply the spore-forming bodies of feeding mycelia which branch profusely, though invisibly, through green tissues, tree-trunks, or earth. And it is an interesting speculation, by the way, whether kinds like the Bacteria, whose structure and habit do not permit them to bring their spores thus to the surface for dissemination, may not cause the death of their hosts as an adaptive measure in order that their spores may be set free by the decomposition of their victims. The cellular anatomy of the Fungi differs in a curious particular from that of the Algae and other kinds of plants, for the habit of forming the thread-like feeding mycelium persists in the spore-forming body, which is simply a collection of compacted and parallel cellular threads; and this explains why it is that Mushrooms, for instance, break apart in the fibrous-grained way that they do. In size the Fungi are all rather small, ranging from minute-microscopic up to the Toadstools and the Bracket-fungi, which never exceed some two feet across, though to the size of the spore-forming bodies must be added that of the radiating mycelium, which may range, albeit tenuously, over a diameter of several feet. In color the Fungi are not green, at least of the chlorophyll shade, for their most distinctive feature is the total lack of that substance; but they are typically white, verging to gray shades or brown. The spore-forming bodies, however, are brilliantly colored in yellows, purples, and reds in some kinds, notably the Rusts and the Smuts, and especially some of the poisonous Toad-

stools, though it is not yet certainly known what the significance of these colors may be. The reproduction of the Fungi is multifarious, but most commonly by tiny spores; and these are spread by the wind with the dust, of which they make up no inconsiderable part. These dust-like spores can be seen en masse by the reader if he will place a fresh mushroom, gills down, on some paper; for after a few hours a striking spore-print of the gills will appear. Spores, furthermore, are often of a thick-walled "resting" sort, which can endure dryness, heat, light, and other unfavorable conditions for months or even years; and this fact helps to explain why those particular plants are so ubiquitous and irrepressible. But they also reproduce sexually, at least some of them do, and usually by methods so closely like those of the Algae as to suggest a relationship between these two groups. This, indeed, is a conclusion sustained by abundance of evidence; and it all goes to show that the Fungi are really nothing other than Algae which have taken to a parasitic habit of life.

With the Fungi are commonly reckoned some plants which are fungus-like, but not Fungi. Thus the Dodder, and the Indian Pipe are Flowering Plants, though they have no chlorophyll or leaves, and present a markedly fungus-like aspect in correlation with the parasitic or saprophytic habit they have assumed. And there are many other flowering parasites in all degrees of development of the habit,—as witness the Mistletoe, which is only a part-parasite, a kind of a natural graft which takes water and minerals from its host, but makes its own food by means of its own chlorophyll. Such plants can always be told by their flowers, which they bear at some time in their lives, and which, of course, are wholly absent from the Fungi.

However ignoble the habit of the Fungi may appear from the view-point of green plants at whose expense they exist, their manner of life has been a success; for it has enabled them to develop no less than some sixty-six thousand different kinds already known and described by Botanists (between four and five

times as many as of Algae), while there doubtless remain a great number still to be discovered.

We turn now to consider the place of the Fungi in our tree of descent (figure 177). It seems perfectly clear that they all are derived, either immediately or remotely, from the Algae. We can imagine that as the Algae became large and abundant, some kinds took to growing upon others, at first merely as a convenient situation, but later making use of the decaying remains. But in nature, as in human affairs, it is only the first step which counts, and the transitions from a dead to a dying, then to a sickly, and finally to a healthy host are easy, giving origin in turn to an epiphytic, saprophytic and, finally, parasitic mode of life. Then, as the Green Algae evolved into the higher and air-living forms and came out to live on the land, they were accompanied by these parasitic Algae, which gradually became more and more altered in adaptation to the new conditions of their existence. And there you have the Fungi, which are nothing but parasitic Algae, although in some cases with an ancestry so ancient that we can hardly trace a sign of their primitive origin. The various principal sub-groups of the Fungi,—the Basidia division to which the Mushrooms belong, most ancient and specialized of them all, the Sae Fungi, which include the Lichens, the Algoïd Fungi, which comprise the water forms and others that are most like the Algae,—are shown in our tree in conjunction with their most probable ancestral branches of the Algae.

The Moss-plants, or Bryophytes.—These are typically the carpet plants of the land, especially the woods, where they form the fine close covering over ground, boulders, and prostrate tree-trunks; but they also extend out beyond into places that are open, particularly where wet. They comprise two well-marked divisions. First are the *Liverworts*, which mostly lie flat on the ground outspread in small thin fronds suggestive strongly of some kinds of Algae, though others bear delicate leaves. Second are the true *Mosses*, much more familiar, which have upright, slender,

fine-leafy, low stems growing densely-compacted together, with slender-stalked spore cases standing out from their tops. Most striking of them all are the Peat-mosses (*Sphagnum*), which form in wet northern climates the great bogs such as, doubtless, long ago, played a part in the origination of the coal beds. In size, the Moss-plants are all low, not over a few inches in height, and they have no parts underground excepting some water-absorbing hairs,—which fact explains why all Mosses are so easily stripped from the ground. Their cellular anatomy in the best developed forms includes a waterproof epidermis with stomata, and intercellular spaces,—features correlated with their air-living habit; but otherwise the tissues are little more specialized than in Algae, and their lack of a particular strengthening and conducting system explains why they never can rise much above the ground. In color they are typically green, often intense in its shade, from the presence of chlorophyll with which they all make their own food, though the greenness is often obscured, especially in those of exposed places, by screens of red or brown pigments which are doubtless a protection to the protoplasm against the injurious action of untempered light. Their reproduction is partly by dust-like spores, scattered from exposed spore cases by the wind, and partly by fertilization, effected by the fusion of a free-swimming male cell with a well-enclosed and protected egg-cell. And it is a fact of great interest to Botanists that fertilization and the production of spores alternate regularly with one another in two separate generations, whereby hangs a remarkable tale, too special for relation in this place, and of which, moreover, the exact point is still tantalizingly elusive. As to the numbers of the Moss-plants, some seventeen thousand kinds have been described, and doubtless a good many are still to be found.

Of course there are plants which look like this group, but are not. Thus there is a “Liverwort” which is a Flowering Plant (the *Hepatica*), while the “Spanish Moss,” of the Oaks in the

south, is also a Flowering Plant (belonging to the Pineapple Family); but the somewhat similar tree moss, or "Long Moss" of the northern woods ("The murmuring pines and the hemlocks, bearded with moss . . . stand like Druids of old") is a Lichen, as is the "Reindeer Moss" of the far northern plains. The "Sea-mosses" are Algae, as we have seen, and so are a lot of the moss-like little plants of fresh waters. Then the creeping Ground Pine of our woods, known even botanically as a "Club-moss," is not a Moss at all but a Fern-plant, of the group next to be studied. Furthermore, even Flowering Plants, especially in open mountainous regions, but including some kinds nearer home, like the Pyxie, assume often the moss habit, and therefore the moss aspect, to a degree often completely deceptive were it not for their tell-tale flowers which appear at some season.

We turn now to the place of the Moss-plants in our tree of descent (figure 177). There is no question as to their origin from the Algae, which, among a great number of branches, must have given rise to one with a structure permitting the absorption of gases from the air instead of the water. Thus was opened up to those plants an immense new field not then possessed by any other plants whatsoever,—all the surface of still waters and the moister parts of the land,—which latter were then, it is likely, far more extensive than now. Over the land, accordingly, these plants proceeded to expand as a dense living carpet, then the most conspicuous part of the earth's vegetation. So, our diagram shows their particular branch swinging into the main trunk, thereby displacing the Algae to a lateral limb; and from that time to the present these Moss-plants have persisted supreme in their own situation, giving off, however, from the simpler Liverworts the more complicated Mosses.

The Fern-plants, or Pteridophytes.—These are typical undergrowth plants, most at home in the shade of the woods, where they occupy a place above the carpet of Moss-plants, and beneath the canopy of the forest, though like all other groups they reach far

out beyond their own particular situation. They exhibit three main divisions. First are the true *Ferns*, whose gracefully-cut fronds and general habit of life are too familiar to need any description, though the reader should remember that in the tropics they grow into trees, among the most beautiful, though not the largest, that there are. Second are the *Horsetails*, which are stiff, green, rush-like plants, with terminal spore-cones, distinguished from the true rushes by their little leaf scales. They are no taller than two or three feet, and grow mostly in shoal water, or wet places, but sometimes on open sandy banks. Third are the *Club-mosses*, creeping, leafy, and not unlike their namesakes, the true Mosses, but much coarser, as the common Ground Pine well illustrates, or the decorative Selaginella of our greenhouses; while they are further distinguished by their little terminal cone-like masses of spore cases. In size all three divisions of the Fern-plants are now greatly degenerate from a former high estate, for, along with others now extinct, they once grew into the trees prominent in the earlier geological periods. In color all are green from the chlorophyll with which they make their own food, and no other color occurs, save an occasional red blush in young leaves, and the brown of their spore-cases or stems. Their cellular anatomy is well differentiated into tissues of different functions, including a highly-efficient system of water-carrying ducts together with strengthening fibers; and it was the possession of this fibrovascular system, no doubt, which permitted these plants to carry their foliage high above earth upon lofty stems from deeply-anchored roots, thus giving the world its first forests. Their reproduction is by spores spread afar by the wind from the upright plant, and this spore-formation alternates with fertilization which occurs in a way and a place not suspected by most persons. Thus in the true Ferns, and the process is substantially the same in principle in the Horsetails and Club-mosses, the little brown spores from the under sides of the fronds do not grow into plants like those which produce them, but into small (a quarter-inch in

diameter) thin, filmy, green, *prothallia*, lying flat on the ground in wet places and strongly suggesting either Liverworts or Algae. On their under sides are well-protected egg-cells fertilized by male cells which swim freely through water caught under the prothallium. Then from this fertilized egg-cell arises the familiar Fern-plant; and we have here a very perfect example of that alternation of generations which is of such great botanical interest. But it is evident that the Fern-plants are dependent for their fertilization upon the presence of standing water, though this can be supplied by a flooding during rain-storms; and this is the reason why those plants are confined for the most part to shaded or moist places. As to their numbers, some three thousand five hundred different kinds are known, with doubtless not a great many more to be found.

With the Fern-plants are commonly reckoned a good many others which do not belong there. Indeed, to most people, any plant with finely-cut foliage is thereby made a Fern, though many such plants will be found to flower at intervals. The little Japanese "Air-plant," graceful, feathery and deceptively Fern-like, is in fact an animal production, the tough horny skeleton of a little marine Hydroid, so naturally stained and arranged that not a few people declare they have witnessed it grow!

We turn now to the place of the Fern-plants in our tree of descent (figure 177). All evolutionary analogy would show that the Moss-plants like all other groups, gave off many branches, of which one in particular was a brilliant success. It was the branch which developed a vascular system permitting the ready conduction of water; and this freed those plants from their old ground-clinging habit and opened to them the upper air for the spread of great masses of foliage to the sun. Thus arose the Fern-plants, the earliest trees, which spread over the moister earth as its dominant vegetation, a fact which our tree represents by the swinging of this branch into the main trunk, displacing the Moss-plants. And they have persisted to the present in their own

situations, though sadly diminished in number and size, and reduced to the position of undergrowth, by the insistent and successful competition of a still higher group, the Flowering Plants. The three divisions they have developed are also shown by the tree.

The Flowering Plants, called also **Seed-plants**, or **Spermatophytes**.—These are all the rest of the plants of the earth, comprising all of the loftiest trees, practically all of the shrubs, and the innumerable flower-bearing herbs no matter where found, whether in woods, fields, waters, plains, mountains, deserts, or sea-shores. In shapes they are manifold, though usually displaying the characteristic differentiation into root, stem, leaf, flower, and fruit, the functions of which are now well known to the reader; but these parts may be modified multifariously in form, size, and combinations in adaptation to particular conditions of life. In size they range from the Redwoods, over three hundred feet high and thirty feet through, down to some Duckweeds, hardly larger than the head of a pin. In color, since they make their own food, they are typically green from the presence of chlorophyll, though some have become parasites and lost it; but in some special parts, notably flowers and fruits, they have developed well-nigh all the shades of the rainbow in adaptation to the accomplishment of particular functions. In their cellular structure they are developed beyond all other groups in specialization and division of labor, which is a reason for their obvious and growing dominance in all situations. Their reproduction is chiefly through seed-formation (whence the name of the group), following upon the fertilization of an egg-cell in the ovule by a male cell brought by a pollen-tube, as already very fully described in our chapter on Reproduction.

This fertilization arrangement, whereby a male cell is carried by a tube from a pollen grain to an egg-cell borne high on a plant, seems at first sight to possess nothing in common with that in the Fern-plants, where the male cell swims freely to the egg-cell through water caught under a prothallium pressed close to the

ground. But in fact there is every gradation between them, and one answers morphologically to the other in a manner most striking and satisfactory, though it is not any part of my business at present to explain the matter more fully. But there is one thing about this pollen-tube arrangement that is of greatest evolutionary importance,—viz., it has rendered these plants independent of standing water and a prothallium on the ground for their fertilization, and has thus freed them from the restriction which limits the range of the Fern-plants. Hence the Flowering Plants are able to extend over places too dry for the Fern-plants, and indeed over all parts of the earth where plant-life is a possibility at all; and not only that, but through virtue of their higher organization in other respects they are able to compete with the lower groups,—the Undergrowth plants, the Carpet plants, the Parasitic plants, and the Water plants,—in their own peculiar situations, of which they are slowly but surely taking possession in the course of their evolution. And the best evidence of their success is found in their numbers, for they have been able to develop no less than some one hundred and thirty-three thousand distinct species already known and named,—many more, it will be noted, than of all the other groups put together.

The Flowering Plants include two very distinct groups. First are the *Gymnosperms*,—Pines, Spruces, Firs, and that sort,—which are trees and tall shrubs without any flowers, and bearing their seeds naked on the branches, or partly covered by cone-scales; and they are almost wholly wind-disseminated and wind-pollinated. Second are the *Angiosperms*, with their seeds enclosed always in an ovary which is part of a flower. Some of them,—the Oaks, Chestnuts, Beeches, Elms, Birches, Alders, and such kinds,—are trees or tall shrubs, wind-pollinated (and therefore without showiness in the flowers) and wind-disseminated. The remainder fall into two sub-groups, Dicotyledonous or Exogenous Plants, which appear to occupy the main line of advance, and Monocotyledonous or Endogenous Plants, which seem to

have been separated from the Dicotyledons through an early partial return to a water habit. Both of these sub-groups are distinguished for the most part by insect-pollination, with its correlated floral showiness; and so much more effective and economical is this insect-pollination than wind-pollination that the Flowering trees,—Locusts, Magnolias, and most Fruit trees,—are slowly driving the wind-pollinated kinds from the earth. This insect-pollination, moreover, with which naturally goes animal-dissemination, renders the plants independent of exposure to winds for both pollination and dissemination, and hence capable of growing in all kinds of retired and lowly situations. Therefore there exist not only Flowering shrubs, which can grow as undergrowth in successful competition with the Fern-plants, but also Flowering herbs, which can grow in all sorts of places, even in competition with the carpeting Moss-plants, with the Water-plants, and with the Parasites.

We turn now to the place of the Seed-plants in our tree of descent (figure 177). Among the branches produced by the Fern-plants must have been one with a wind-carried, tube-producing, pollen-grain,—a discovery, or invention, which rendered its possessors independent of the standing water needed by the Fern-plants for fertilization, thus enabling them to range far more freely over the earth. Such was the origin of the Seed-plants, which swung into the main line of dominance, where they persist to this day. The first kinds were undoubtedly trees,—Gymnosperms and wind-pollinated Angiosperms,—whose exact relations to one another are still very uncertain; but from the latter originated the insect-pollinated kinds, first trees, then shrubs, then herbs. These latter possess all of the advantages of the lower groups in addition to their own,—are the heirs of all the ages in fact; and their higher organization is permitting them to do precisely the same thing that the higher races of men are,—to take possession of the earth to the suppression and extinction of the lower races.

Such are the five primary groups, sometimes called Classes, of Plants. Each is divided into sub-groups called Orders, and those again into others called Families, and those again into others called Genera, and those into Species. It is theoretically possible to follow out the branches of our genealogical tree through smaller and smaller ramifications to the ultimate tips, representing the species, of which there would be some two hundred and fifty thousand; and the construction of such a tree is the aim of every student of classification. It is, however, no part of our present business to follow this matter any farther, for, while the primary groups are distinguished very largely by differences of habit, this becomes less and less true with the groups that are smaller, and hardly at all with the species, which are mostly marked off from one another by characters having little connection with adaptation.

The Flowering Plants are the highest yet developed within the Plant Kingdom. Are there then no higher possibilities in plant evolution? So far as concerns any new field for them to expand in, there seems to be none, unless they follow the example of man, and take to free flight in the air. But the world is not yet finished, nor are all the possibilities of variational experimentation exhausted; and until such times come, evolution is not likely to cease.

There remains one other aspect of classification to be mentioned before this chapter can be finished. Although the large genealogical groups we have been considering happen to be distinguished pretty well from one another in habit, and thus constitute also ecological groups, the correspondence between genealogy and ecology is by no means exact. Examples, indeed, of the ecological intrusion of the genealogical groups into one another have been given in the preceding pages; and further study only serves to increase the number of such cases. Every group is striving to expand to its utmost, and whenever it can find an unoccupied crevice in the territory of another, it is not deterred

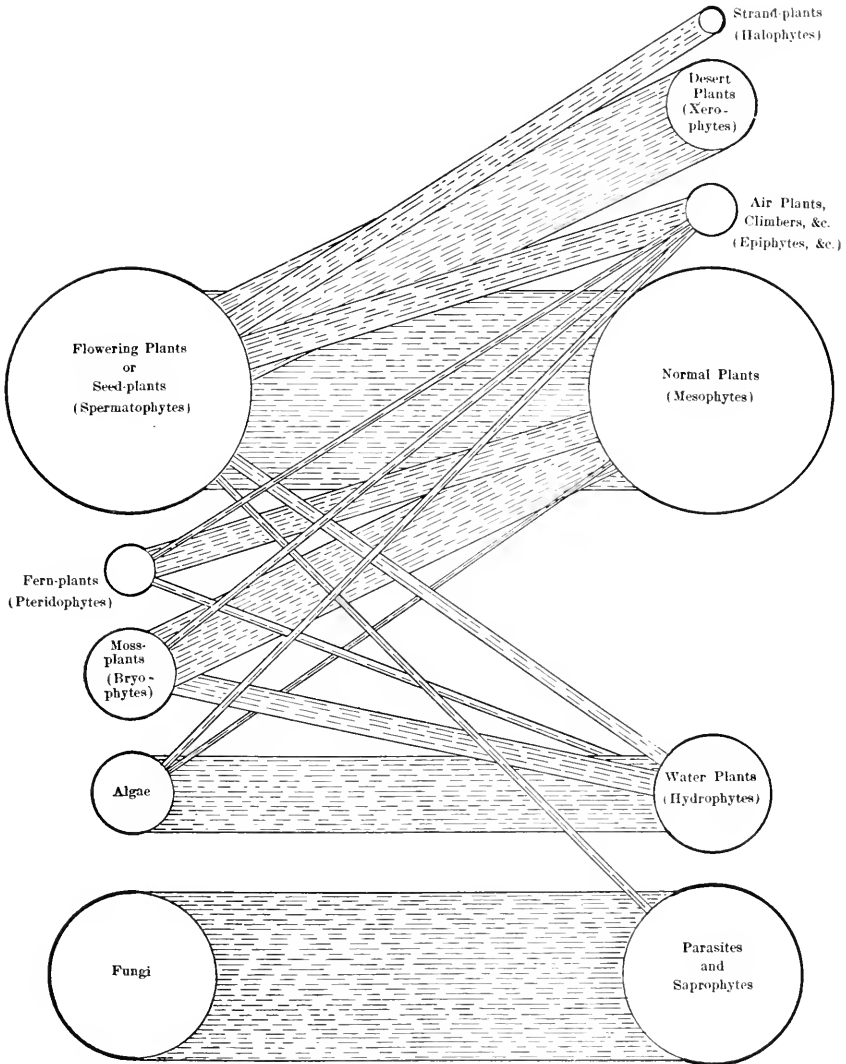


FIG. 178.—A diagram showing the mutual interrelations of the genealogical and ecological groups. The widths of the connecting bars show the approximate number of species involved.

by any genealogical courtesies from expanding to fill it. The result is this, that kinds of plants genealogically related have come to acquire very different habits, and hence to belong to very different ecological groups, while the different ecological groups include many kinds having the most different genealogical relationships, a matter which is brought out diagrammatically in the accompanying figure (figure 178). It is with plants as with men, who may be grouped by their blood relationships into families or clans on the one hand, or according to their occupations into trades, businesses, or professions on the other. Sometimes the two arrangements overlap, especially among primitive peoples, but often they do not, particularly in the higher civilizations. These ecological groups of plants have been characterized more or less fully in the preceding pages, and need only be summarized very briefly at this place.

A SYNOPSIS OF THE ECOLOGICAL GROUPS OF PLANTS

- I. INDEPENDENT PLANTS, or AUTOPHYTES, the highest and most distinctive plants, making their own food by aid of chlorophyll, and including:
 1. NORMAL PLANTS, or MESOPHYTES, living rooted in aerated soil supplying enough moisture to permit a wide spread of leaves and stems; mainly Flowering plants, but with many Fern-plants and Moss-plants, commonly massed together into forests which exhibit a canopy of trees, an undergrowth of shrubs, and a carpet of herbs.
 Furthermore, some kinds of Mesophytes are so strongly adapted to some particular condition of life as to rank as separate groups,—viz., Air plants, or EPIPHYTES, including members of all the genealogical groups, growing supported upon other plants, and highly adapted to that peculiar habit: CLIMBERS, mostly Flowering plants, whose very slender stems, lean, cling or twine by aid of others up to the light: TRAILERS, of all groups, which keep flat on the ground as a part of the carpet: INSECTIVOROUS Plants, wholly Flowering plants, which supplement the scantness of soil nitrogen in the places where they live by capturing and digesting insects through aid of remarkable adaptations: MYRMECOPHILOUS Plants, Flowering plants of the Tropics, supposed to attract ants for protection against other insect enemies, but of doubtful ecological status at present.
 2. WATER PLANTS, or HYDROPHYTES, living largely immersed in water from which they take their minerals and gases, and therefore mostly soft-bodied and finely divided; mainly Algae, but including some Moss-plants, Fern-plants, and Flowering plants.

3. STRAND PLANTS, or HALOPHYTES, living along the margin of salt water, and therefore condensed and otherwise adapted to the difficult absorption thereof; a few Flowering plants only.
 4. DESERT PLANTS, or XEROPHYTES, living in places excessively dry, and therefore condensed and protected for water conservation; mainly Flowering plants, with a few Lichens.
- II. DEPENDENT PLANTS, sometimes called HYSTEROPHYTES, including PARASITES and SAPROPHYTES, which take their food from other organisms, either living or dead, and lack chlorophyll and leaves; mainly Fungi, but including some Flowering plants.

Finally, there is one more way in which plants are classified ecologically. When considered en masse, plants constitute vegetation, and vegetation can be classified. A mass of vegetation which gives a distinctive aspect to a country, such as a Pine forest, or a natural meadow, is called a *Formation*; any group of plants commonly occurring together therein is called an *Association*; while the word *Society* is somewhat loosely used for any kind of vegetation group. This subject is one very much studied at present, and will ultimately give us a vivid method of describing causally the vegetation of any country.

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