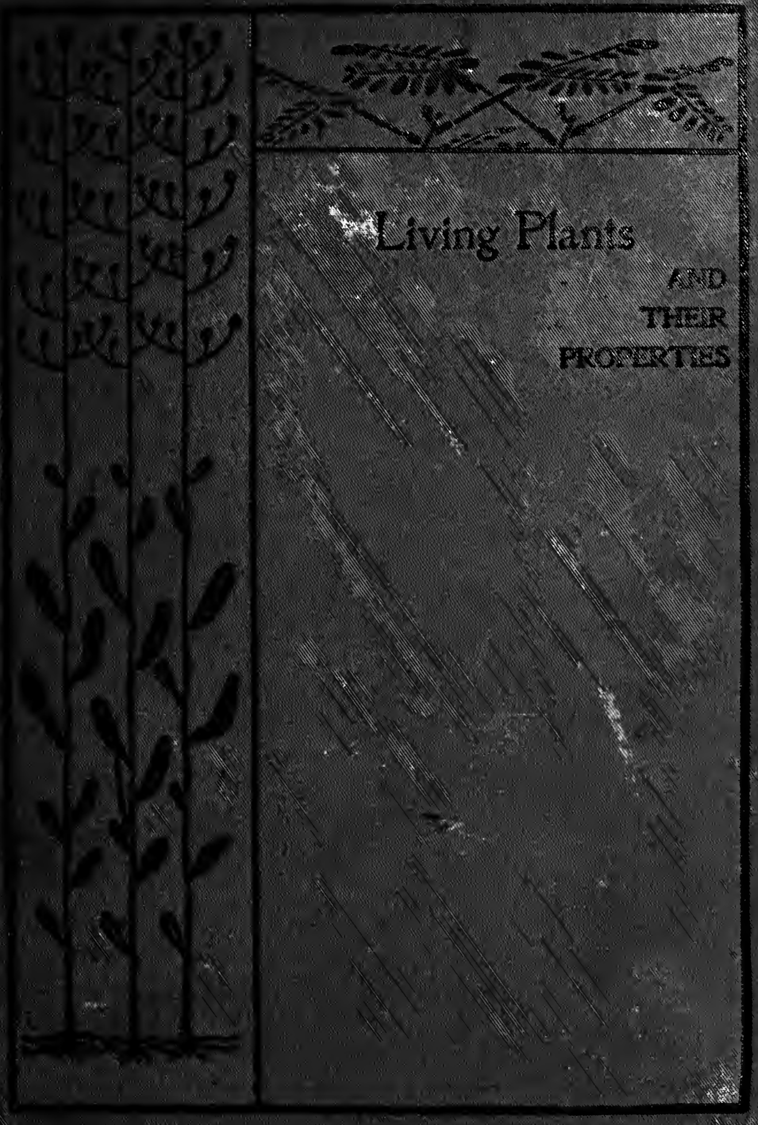
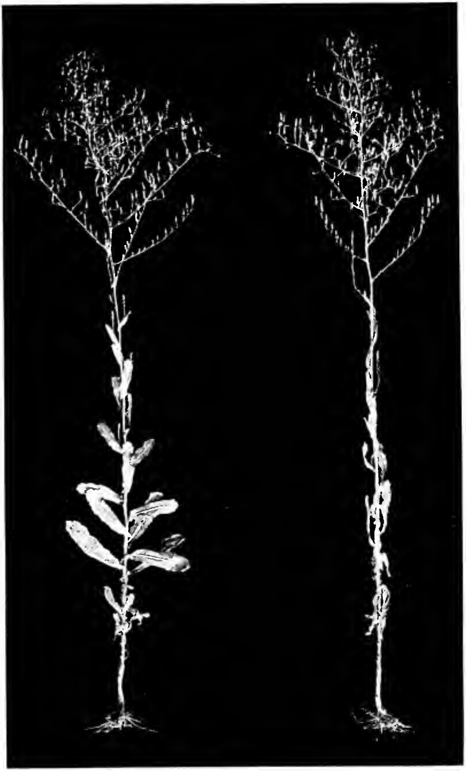


Living Plants

AND THEIR PROPERTIES

Dye

LIVING PLANTS AND THEIR PROPERTIES



PLANT OF WILD LETTUCE

The left hand figure as seen from the east, the other figure as seen from the south, showing the compass-like habit of adjusting the leaves in the meridional plane.

LIVING PLANTS AND THEIR PROPERTIES

A COLLECTION OF ESSAYS

BY

JOSEPH CHARLES ARTHUR Sc. D.
PROFESSOR OF VEGETABLE PHYSIOLOGY AND PATHOLOGY
IN PURDUE UNIVERSITY

AND

DANIEL TREMBLY MAC DOUGAL PH. D.
ASSISTANT PROFESSOR OF BOTANY IN CHARGE OF PLANT
PHYSIOLOGY IN THE UNIVERSITY OF MINNESOTA

NEW YORK
BAKER AND TAYLOR
MINNEAPOLIS: MORRIS AND WILSON
1898

UNIVERSITY PRESS OF MINNESOTA
MINNEAPOLIS

PREFACE

The essays comprised in this book are selected from popular addresses and articles presented by the authors within the last five years. The unequal conditions of the original preparation have made it necessary to revise and rewrite certain articles in order to meet the requirements of their juxtaposed position. The occasion has been seized to omit portions less relevant in the present connection, and to amplify others to meet the demands of continuity, clearness, and harmony with current botanical thought. The original presentation of each subject is denoted by a foot-note under the title. The authors are separately responsible for the chapters to which their names are signed in the table of contents.

The publication of this volume, it is believed, is justified by the appreciation accorded the essays, upon their first appearance; and it is the hope of the authors that it may stimulate an interest in the phases of botany covered, both among general readers and also among workers in the co-ordinate branches of animal biology.

March, 1898. THE AUTHORS.

TABLE OF CONTENTS

I

THE SPECIAL SENSES OF PLANTS.*

Aside from the tales of travelers, the varied plant myths, and the inventions of story writers, there have been fancies and beliefs held by learned men in past ages, which invested plants with specific powers differing from those of animals only in clearness of manifestation. Not until the middle of the present century, however, did the commonly observed movements of plants receive any genuine interpretation. Aristotle and his followers to the time of Cesalpino (1583), vaguely ascribed a soul to plants which directed their vital operations and distinguished them from lifeless nature. Jung, a contemporary of Kepler, Galileo and Descartes, who dominated botanical thought in Germany during the seventeenth century, expressed his

---

*Condensed from a presidential address before the Indiana Academy of Sciences, December 27, 1893.

view in the sentence: "*Planta est corpus vivens non sentiens.*" A hundred years later Linnæus gave his famous definition of the three kingdoms of nature: "Minerals grow, plants grow and live, animals grow, live and feel." These great leaders of scientific thought inclined to deny sentience to plants as a matter of definition, but did not wholly discountenance some of the vagaries of their predecessors.

Eighteenth century opinions

At the beginning of the present century general students of plant life were inclined to admit greater range of the plant's powers. Sir J. E. Smith, in his "Introduction to Botany," a work which met with such favor as to pass through seven editions within twenty-six years, has voiced the uncertainty of the period regarding the plant's status in the form of a query: "As they possess *life*, *irritability* and *motion*, spontaneously directing their organs to what is natural and beneficial to them, and flourishing according to their success in gratifying their wants, may not the exercise of their vital functions be attended with some degree of sensation, however low, and some consequent share of happiness?" Erasmus Darwin, a few years before, and J. E. Tupper, a few years later, expressed similar sentiments in works that met with popular recognition and approval.

Application of terms

The passing of the present century has seen an increasing tendency toward the serious use of terms for plant activity borrowed from the volitional and neural manifestations of animals. These, in part, are suggested by purely superficial analogy, and intended solely to lend greater attractiveness to the narrative, as in Charles Darwin's description of a twining plant, whose horizontal extremity repeatedly slid past the support which temporarily arrested its progress as it swung slowly around in a circle. "This movement of the shoot had a very odd appearance," he says, "as if it were disgusted with its failure, but was resolved to try again." Yet in part there is implied an obscure but real analogy, as when the same author in another work sums up his studies of the root tip with the assertion that in its power to direct movement in the adjoining parts it "acts like the brain of one of the lower animals."

Knowledge of mechanism

So long as the comparison of animal and vegetable activities rested largely upon external appearances, with very limited understanding of the changes within the organism by which they are brought about, no considerable advance was possible. At first the interpretation was necessarily based upon human and animal analogies. As Julius Sachs has admirably said in his "History of

Botany," "from our own vital motions we argue to those of the higher animals, which we comprehend immediately and instinctively from their conduct; by aid of these the motions of the lower animals also become intelligible to us, and further conclusions from analogy lead us finally to plants, whose vitality is only in this way made known to us."

An illustration of such reasoning is admirably set forth by G. H. Lewes, the eminent English psychologist, in his volume on the object, scope and method in the study of psychology. He says: "Touch the eye of a frog, and there is at once the response of a reflex closure of the eyelid. Touch the hairs of a venus fly-trap (*Dionœa muscipula*), and there is at once the response of a reflex closure of the leaf. Confine the frog and the dionœa under a glass shade, and place there a sponge, over which ether has been sprinkled. Both plant and animal breathe this air in which there is vapor of ether, and as this vapor penetrates to their tissues we observe a gradual cessation of all sensibility; first the reflex actions cease, then the irritability of the particular tissues ceases. Stupor has supervened for both. Now remove the glass shade; the vapor dissipates, the fresh air penetrates to the tissues in exchange for the vitiated air, and both frog and dionœa slowly recover their sensibility." From this experiment he justly concludes "that the animal and plant organisms have with their common structure common properties, and if we call one of these properties sensibility in the animal, we must call it thus in the plant."

Primary unity with great diversity

Modern investigations have more and more confirmed the fundamental unity of the primary functions of animals and plants, but at the same time have increasingly emphasized the great divergence they have obtained in developing along lines of specific adaption to the needs of the energy-liberating animal on the one hand, and of the energy-conserving plant on the other hand. Until recently the difficulty of interpreting the movements of plants without recourse to the assumption of a structural device in some way comparable to the neuro-muscular mechanism of animals has seemed very great. But the wonderful advance in studying the plant's minute structure and general physiology during the last few decades has revealed unsuspected and ample vegetal methods of bringing about movement as the result of stimulation, which bear no analogy and no counterpart to those of animals, but have been developed with a trend as different as the physical basis of tissues in the plant is different from that in the animal.

What constitute special senses

If we ask ourselves what could properly be considered as constituting special senses in plants, it will be necessary to remember that in the broadest ecological import the special senses of animals are the conspicuous ways in which they respond to particular kinds of external stimuli in promoting their well-being, and that the same must be true of plants. Knowing that irritability is a fundamental property of all living matter, let us see what advantages the animal and the plant could secure by its special development.

It is unquestionable that the paramount necessity of every organism is self-preservation. To secure food, to avoid injury, and to obtain the requisite supply of light, heat, moisture and air, may be considered the fundamental necessities of every living being, whether man or monad, tree or microbe. It is in these directions, therefore, that we must look for special senses.

Sense of contact

The animal has developed a quick response to contact. This is probably the most universal of all the senses, and in its lowest forms is little removed from simple irritability. It primarily contributes to the animal's safety, as it gives warning of the proximity of uncongenial or dangerous objects, and is also an important factor in the operation of securing food, and in many minor operations. It is a characteristic sense in well nigh every animal, and in the larger number is especially developed and intensified in certain organs that may be appropriately termed organs of touch.

If we return to plants, we find this simplest and most generalized of senses, with some notable exceptions, practically absent. In a few instances, as in the tendrils of certain plants, there is a marked, sometimes a marvelous sensitiveness to touch, but it is connected neither with the attainment of safety nor of food. Only in the very few and exceptional cases of insectivorous plants, like the sundews, has the plant acquired a sense of touch to aid it in detecting and grasping food. But sensitiveness to contact is not a common property of plants.

Trend of sense development

An inquiry into the conspicuous difference between the attitude of the animal and the plant toward objects external to itself must reveal some of the reasons underlying the trend of sense development. And first of all it must be noted, that when the animal detects something inimical to its safety, it moves away from the offending object, a procedure impossible to the plant with its anchorage of roots. Were the aspen quaking through fear of impending calamity, it could not escape by flight, or by the displacement of its body by so much as an inch. In another, and even more important particular, does the animal with its power of locomotion show the need of a different set of senses from those of the plant. The ingestion of a large amount of solid food requires the animal to search for a suitable supply; while the plant, partaking only of food in solution and in comparatively small quantities, is enabled to secure it by slender feeders extending into the surrounding medium. In securing food and protecting itself from injury the animal makes use of three important senses: smell, hearing and sight. The plant with its fixed position and simpler requirements does not need these senses; they would be useless to it, and have not been developed.

Free and fixed organisms

We may safely conclude that in so far as animals and plants respond in a marked manner to stimulation, it is along two distinct lines, to correspond with the necessities of free organisms on the one hand, and of fixed organisms on the other.

For a fixed organism orientation is of prime necessity. The roots of a plant must penetrate the soil and its foliage be spread to the air.

Yet the root or shoot has no power to deviate from extension in a straight line unless it is acted on by some external force, no more than a cannon ball or other moving body has power to vary from a straight line. If a seed in germinating lies in such a position that the roots point upwards and the stem downwards, some method is needed by which the plantlet may readjust itself, either by turning over bodily, or changing the direction of its growing parts. As every one knows, the latter alternative is adopted, and the roots bend down and penetrate the earth, while the stem bends up and lifts its foliage into the air. It is so apparently a matter of course that stems grow up and roots grow down, that we may never have given a thought to an explanation of the process. Even botanists have only recently felt the full necessity for an explanation of the fact, as it has been less than two decades since Vöchting announced his theory of rectipetality, or the inherent

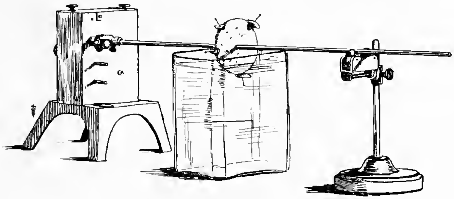


FIG. 1.—A clinostat. Germinating seeds are pinned on the cork disc, and are kept moist by dipping into water as they revolve. One revolution is made in about twenty minutes. Under these conditions the primary root and stem grow straight in whatever position they are fastened.

tendency of growing organs to extend in a straight line unless acted upon by outside force.

Discovery of gravity sense

There is only one force known that acts uniformly in the direction of the center of the earth, that is gravity; and it was the genius of Andrew Knight, an Englishman, to demonstrate as long ago as 1806, that this force does furnish the directive influence in securing verticality to plants. He grew plants on revolving wheels, and found that they responded to centrifugal force, and that when the wheel was placed horizontally and revolved at a speed that made the centrifugal force equal to that of gravity, both roots and stems grew obliquely, taking the position of a resultant of the two forces, that is, of forty-five degrees to the vertical.

But this discovery by Knight was not immediately fruitful, for no one could tell how gravity produced the effect ascribed to it. If it pulled the root down, why did it push the stem up? The stem is as heavy as the root, why are not both attracted toward the center of the earth? It was a curious paradox to say the same force acted now one way and now exactly the reverse on different parts of the same plant; as if pulling and pushing were the same thing. It was supposed that gravity acted upon the root as it does upon a mass of taffy candy, drawing it downward.

But Sachs showed in 1873 that the root of a bean fixed horizontally over mercury could penetrate the mercury in assuming a vertical position. As mercury is about thirteen times as heavy as the tissues of a young root, it is evident that far more force was expended in penetrating the mercury than could have been derived from the physical action of gravity, that is, from the simple weight of the root. The experiment has since been tried in another and more obvious way by harnessing a root tip lying horizontal to a weight suspended over a pulley, the weight being raised as the root bends downward in response to gravity. From these experiments we must conclude that gravity does not act physically but physiologically to induce the curvature, that is, it acts as a stimulus. It is a small spark that fires the gun. The spark will fire a pistol or a cannon, the result depending solely upon the amount and arrangement of the explosive material. So in the root, if there is the proper mechanism and storage of force, gravity will release this force and cause the bending, the amount of work done being enormously out of proportion to the initial expenditure of energy.

But when the bending takes place, will it be upward or downward? If it were a purely mechanical device, it is evident that by knowing the structure of the organ, one could predict the direction of movement under stimulation. But we shall have to look beyond and above simply mechanical laws for an explanation, for the living organism acquires specific powers of adaptation and heredity.

Movement connected with growth

Although the force which a plant can exert amounts to several atmospheres, it is only in the young tender portions, usually at the ends of the branches of the stem and root, that this force can be successfully applied to secure movement of the whole organ. It therefore comes about that movement in plants is oftenest associated with growth. This arrangement permits each root tip and growing stem to have its own kind and degree of sensitiveness. Thus we find by experiment that while the first root which starts from a seed, the tap root, is sensitive to gravity in such a way that it places itself parallel to the direction of the impinging force and points directly downward, the secondary roots, which branch from it, are sensitive after a different fashion, and instead of growing parallel to the force, grow at an angle to it, the exact angle being different for different kinds of plants. The tertiary roots, or next set of branches, are usually very little sensitive to gravity, or if they are sensitive they assume a nearly horizontal position. The stems react in a similar way, except that the general direction is upward instead of downward, and in consequence of the diversity of sensitiveness of the primary and secondary shoots, the branches are spread out to the air and light, imparting to each species of tree and herb its characteristic appearance.

Transmission of impulse

But if there is no nerve-like communication between one root tip and another, or between one stem and another, there is sometimes a distinct transmission of impulse from the cells receiving the stimulation to the cells a short distance away where the movement is consummated. Thus, in the tip of the primary root Darwin found that only the cells at the very tip were sensitive. If so small a piece as one millimeter be removed from the end of the root by cutting or burning, all power of movement is lost. This remarkable localization has been denied by Sachs and Detlefsen, who characterize Darwin's claim as sensational, but the fact has been fully verified by Wiesner, who found that if the root is weakly sensitive, the seat of irritability coincides with the zone of most rapid growth, but if highly sensitive, it will be at a distance.

To sum up the characteristics of the gravity sense: It is localized in or near the ends of growing roots, stems and other organs of the plant; it is developed in varying strength in different organs; it sets up movement of the organ in response to stimulation; the direction of movement will depend upon the specific kind of sensibility acquired by that organ; the direction of the movement will always bear some definite relation to the vertical without regard to the position of the plant.

Sensitiveness to light

But, what other senses have plants? Next to a proper position, most plants need a suitable exposure to light. I shall not attempt to show the numerous and interesting ways in which plants respond to light. Everyone knows how plants lighted from one side, as when placed before a window, bend toward the light. This is a true sensitiveness, for it results in bringing about definite movement. The stems place themselves parallel to the direction of the incident rays—that is, point toward the window, while the leaves place themselves at right angles to the direction of the

FIG. 2.—Charlock seedlings growing in a glass of water before a window. The stems bend toward the light and the roots away from it.

light—that is, with their upper surfaces to the window. Leaves and stems, therefore, show

Fig. 3.—Day and night positions of the leaves of redbud Cercis Canadensis).

sensitiveness characteristic of each. Some stems, however, like those of the Virginia creeper, turn away from light, enabling them to cling to dark walls. Roots which are generally buried in the soil, rarely exhibit sensitiveness to light, and when they do, it is usually to turn from it. If light comes to the organ from two directions, it will bend toward the source of the stronger light, and differences which will affect the plant are far more minute than can be detected by the eye.

As in the case of roots, certain stems place themselves not parallel with the direction of the light, but at some particular angle to it, in accordance with some inherent necessity. Not as large a part of the plant, as a rule, is as sensitive to light as to gravity, but the degree of sensitiveness is often greater.

Chemical sense

Plants also possess a chemical sense, a kind of taste, by which they detect certain substances in solution fitted for their nutrition. By this means parasitic fungi starting to grow upon the surface of other plants find their way into the stomata from which the acid juices of the tissues diffuse, and thus gain entrance into the host. Roots exhibit sensitiveness to many nutritive substances, although not as a rule to the same extent that fungi do. It enables them to turn and grow in the direction of the best food supply, and accounts for the popular notion that roots seek rich soil.

Moisture also exerts a directive influence upon roots, and sometimes upon other parts of the higher plants, as well as upon the organs of many lower plants. Usually the movement is toward the moister side. It is evidently beneficial to the plant in keeping its absorbing organs bathed in the greatest available supply of fluid.

Moisture sense

Plants are thus seen to react sensitively to gravity, light, solutions, moisture and contact. Each is a special kind of sensitiveness, having its own method of reaction. Two or more kinds of sensitiveness may reside in the same organ, when its position will be a resultant of the several forces. There are no exclusive organs of sense in plants, although there is more or less localization in certain parts; and there are no nerves although the motor impulse may be transmitted some distance, even as far as seventy centimeters or more in very vigorous sensitive plants, for example in mimosa. To complete the comparison I should say there are no muscles in plants, although they execute movements of very considerable amplitude. Their motor mechanism is operated by devices having no counterpart in the animal organization, but is the outcome of specific adaptation.

Aristotle's notion, which is still too prevalent, of an ascending complexity in vital phenomena from plants to man, should be wholly abandoned. The only way of viewing organic nature, to secure proper interpretation, is that of two diverging lines of development, one through motile forms, and the other through fixed forms. Each line of development has worked out peculiarities of its own. If the special senses of animals show wonderful adaptations, the special senses of plants, although very dissimilar, will, when better known, appear quite as remarkable.

The observation of Sachs, the learned professor of Würzburg, and one of the most farseeing of physiological botanists, is particularly pertinent in this connection. "We have no necessity," he says, "to refer to the physiology of nerves in order to obtain greater clearness as to the phenomena of irritability in plants; it will, perhaps, on the contrary, eventually result that we shall obtain from the process of irritability in plants data for the explanation of the physiology of nerves, and this, although it is as yet a distant hope, gives a special attraction to the study of the irritable phenomena of plants."

II

THE DEVELOPMENT OF IRRITABILITY[*]

The economical acquisition of nutritive substance in proper amount is a fundamental necessity of every organism, and to the conditions attendant upon the performance of the nutritive functions must be ascribed the chief causes underlying the development of the plant body. The chlorophyll processes have, therefore, been the paramount factors in the development of the shoot, and the absorptive processes have ruled the differentiation of the root system.

Derivation o existing forms

In an early stage of the existence of the ancestors of our present plant population they were doubtless thalloid organisms, unicellular or multicellular, floating in the water, and were perhaps in many instances endowed with

---

[*] Given in an address before the Botanical Club of the University of Chicago, Jan. 18, 1897.

the power of locomotion. All of the cells contained chlorophyll and shared in the work of food formation, and since more or less of the surface of each cell was bathed by the fluid in which it lived, all absorbed the mineral salts in solution in the surrounding medium, and all of the cells participated in the reproductive processes.

It will not be profitable here to follow the direction or possibilities of morphological differentiation into detail, except to say that the organism soon found it more economical to be attached to a fixed point rather than to float at random or swim through the water which contained the mineral salts in equal diffusion, and in which the necessary intensity of light bore a direct relation to the distance from the surface. Then in consequence of this newly acquired habit of fixation, and the recession of the water from the substratum occupied, some distinct and important physiological changes ensued to meet the new conditions attendant upon the nutritive processes.

Chlorophyll and sunlight

The sunlight impinging upon the portion of the plant containing chlorophyll no longer came filtering down through layers of water of varying depth, but beat upon it from all points in an arc of one hundred and eighty degrees. The greater amount of energy thus available to the aerial shoot could only be made of use to the plant by the arrangement and division of its chlorophyll areas, and the morphological necessities will account for the method of differentiation of the shoot, and the very great degree of segmentation and branching which it has attained. The segmentation of the shoot has made possible not only the profitable display of ever-increasing areas of chlorophyll-bearing tissues, the proper elevation, orientation and isolation of the reproductive organs, but also a separation of the minor functions and the differentiation of special organs for their performance. The separation of nutritive, reproductive and other functions has been accompanied by a contemporaneous separation and development of the special forms of irritability which are concerned with the forces dealt with by each organ. Thus, for example, the most important factor in the processes carried on by the leaf is the radiant energy derived from the sun. As a necessary concomitant of the advantageous use of this energy, the leaf has developed a strongly marked irritability to light and heat rays.

By these special powers it is enabled to move its chlorophyll-bearing areas in the leaves into such position that the exact intensity of light and heat rays suitable to its specific constitution will be received and as a result of the relations of the organ to the horizon in response to its heliotropism and thermotropism, it has also acquired in some instances a trace of geotropism. The elimination of all but nutritive functions from the leaves has made it possible for these organs to perform such functions with greater economy, and made superfluous also the presence of any other forms of irritability which would direct the position of the leaf.

Pollination

In the accomplishment of the reproductive process, an incidental condition is the transferance of the pollen from its place of formation to the surface of the stigma in the same or other flowers. In a great majority of instances the relation of the line adjoining the anther and the stigma to the vertical or horizon, is of the utmost importance, whether the pollination is accomplished automatically, by air currents, or by insects, and a well marked geotropic reaction is therefore generally exhibited by flowers with the motor zone located in the peduncle. These organs also show minor heliotropic reactions.

Organization of shoot

The same process of analysis may be applied to the entire shoot, with the general result that each organ will be found to respond to a number of forces generally limited to two or three, though of course, instances are not lacking where a greater number of forms of irritability are found to reside in the same organ, as for example, in tendrils. In such instances, however, the excessive number of the forms of irritability have beeen developed to meet special ecological conditions, bearing upon both the nutritive and reproductive processes either directly or indirectly. Furthermore, the organs of the shoot may also acquire the power of special reactions to internal forces or stimuli, such for example, as the carpotropic movements.

Distribution of nutritive factors

In a consideration of the localization and distribution of the property of irritability, attention is to be called to the fact, that the conditions concerned in the nutritive processes of the shoot show an invariably wide diffusion. Carbon dioxide exists everywhere in the atmosphere in uniform proportions and bathes every part of the shoot. Sunlight is bounded only by the horizon line and may reach any surface of the shoot in diffuse form. The chlorophyll processes may then be carried on by the sub-epidermal tissues in any portion of the shoot, and as a consequence, a greater proportion of the peripheral protoplasm of the shoot has developed an irritability to sunlight, although it may not always be manifested by organic or external movement, or other response.

The researches of Rothert have shown that a large part of the surface of the leaf of Avena and Phalaris exhibits a heliotropic sensibility, and that the laminæ of dicotyledonous leaves exhibit an equal distribution of sensitiveness over their entire surface, and that the leaflets in a compound organ are strictly coordinate and equal with respect to their irritability. Those branches of the shoot that have developed special, or ecological adaptations exhibit an extension of the irritable surface corresponding to the limited diffusion or occurrence of possible stimuli, modified to some extent by the character and inclusiveness of the reaction.

Sensory and motor zones

Before further progress is made in the discussion, the chief facts in the organization of the irritability of leaves should be recalled. The portion of a leaf which is capable of receiving light and converting it into some other force which will set up a reaction is termed the *sensory zone*. The portion of the organ in which motion ensues is termed the *motor zone*. Now as may be seen by the preceding paragraph the sensory zone is located in the blade of the leaf, and if the movements of the leaves of the bean or mimosa are observed, the motor zones will be found at the base of the petioles. Light striking the blade of the leaf sets in action a second force, which is transmitted to the motor zone where a third force causes the movement. The leaf then is a living machine the movements of which are directed by two forces—light and heat (sometimes gravity), while the root is directed by many forces.

Although the motor zones of the shoots do not include as large proportions of the plant as the sensory zones, yet the distribution is fairly general throughout growing regions. It is possible to induce curvatures in some stems in which growth has almost entirely ceased. The curvature is accompanied by a revival of the growth activity, however.

Development of root functions

Having followed the shoot to its ultimate and present form we may retrace our steps to the beginnings of the root-system. The primitive function of the root of the plant emerging from an aquatic habit was of course purely mechanical and consisted in holding the organism in place. With the recession of the water the plant no longer found solutions of mineral salts bathing its surface. Its rudimentary anchoring organs were, it is true, left in contact with small quantities of fluid, but the amount of surface was by no means adequate or proportional to the now rapidly enlarging shoot. Under such circumstances it might do but one thing—extend the root-system and thereby increase its absorbing surface.

The functions of the root are not so numerous as those of the shoot, and while the efficient performance of the necessary amount of absorption, to keep pace with the increase in mass and surface of the shoot, has demanded a repeated branching, yet no segmentation like that of the shoot has occurred. The less important function of the root, fixation, is purely mechanical, and the separation of the two functions has not been effected by a localization of the functions in different organs, but is an incident to the stage or degree of development of these organs. Physiologically the basal portion of roots sustains a relation to the absorptive system similar to that of the basal portions of typical stems to the chlorophyll-bearing and reproductive organs.

In the earlier stages of growth any given portion of the root is purely directive, next absorptive and in the later periods, is exclusively fixative. Only in certain special classes of aerial and other plants does a separation or isolation occur. The stem, on the other hand, is at first directive, and then fixative, and does not in any stage of its existence assume the relative importance which is to be ascribed to every portion of the root in one period of its development.

In explanation of this method of development, so widely different from that of the shoot, it is to be said that roots have taken on fewer functions, and have always been surrounded by much more uniform conditions than the shoot, and in consequence have met the necessity of a much narrower range of adaptive modifications. But, while the rapidity of variation of outward conditions affecting roots has been much less than that of the shoot, yet the greater number of the factors concerned and the inequalities of diffusion and distribution of the nutritive substances are much greater than those affecting the shoot. Water and food substances lie below the surface of the substratum and the root has developed a highly marked form of geotropism, which enables it to penetrate the soil. Water and food substances are by no means so uniformly distributed as sunlight and carbon dioxide, however. While water exhibits a fairly horizontal distribution in quantity, yet so far as its actual availability is concerned, differences corresponding to the physical characteristics of the soil are to be found. The vertical distribution is modified in the same manner. The mineral food substances present no system or uniformity of distribution whatever. As a matter of fact the masses of food substances may and do lie in all possible directions from the absorbent zone of the apical

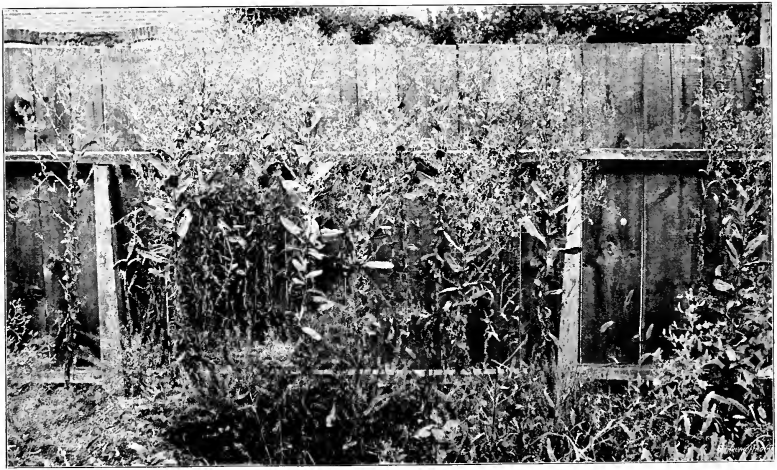
Nutritive factors in soil

portion of the root. In order to reach such irregularly distributed masses of nutritive substances, it is evidently necessary that the root should develop an irritability to a much greater number of forces than any member of the shoot, and furthermore it is evident that all the forms of irritability thus acquired must be located in the apical portion of the root, the proper directive activity of which only can result in facilitating the absorptive processes. The coincidence of several forms of irritability within such narrow limits has necessitated differentiations in another direction from that offered by the shoot. The differentiation of the shoot resulted in a tendency to separate the different forms of irritability with their attendant mechanisms. The increase of the efficiency of the root has resulted in the acquisition of a constantly increasing number of forms of which the mechanism must necessarily be identical. Still further, this has resulted, of course, in the differentiation of the separate parts of the mechanism, and increase of its delicacy of reaction. This may be held to apply to all similar arrangements, especially in the ecological adaptations exhibited by certain members of the shoot.

Organization of roots

Thus if an examination of the mechanism of irritability of the root is made, it will be found that only an extremely small portion of the organ may receive a stimulus from gravity, light, temperature, moisture, running water, chemicals, electricity, contact or injury. This sensory zone consists of a mass of cells in the shape of a cylinder beginning immediately back of the growing point and not more than one millimeter in length. The portion of the root in which curvature ensues lies immediately back of the sensory zone.

The root is a generalized type of the mechanisms by which plants respond to external directive stimuli, and the shoot is a specialized type. The same mechanism in the root is capable of response to eight different classes of stimuli, while in the shoot but two or three may act upon any given organ, in such manner as to secure a responsive movement.



WEEDS IN A NEGLECTED YARD

The fence is six feet high, and the wild lettuce stands fully six inches higher
Photographed in September

III.

WILD LETTUCE AS WEED AND COMPASS PLANT*

Likeness to cultivated lettuce

The prickly lettuce is a plant closely resembling the common garden lettuce, especially the narrow leaved Cos varieties. The similarity is more striking if we compare them after the flower stalks have begun to appear. There are in fact good grounds for believing that the garden forms were derived from the wild lettuce: a view held at one time by Bischoff, DeCandolle, and other authorities, who wrote the Latin name of the garden forms *Lactuca Scariola* var. *sativa*, instead of *L. sativa*, as adopted by Linnæus and adhered to by most of recent writers.

The plant is an annual, coming from seed each year. Occasionally the seed germinates in the fall, the plant making some growth be-

---

*A portion of Bulletin No. 52 of the Indiana Experiment Station, issued November 10, 1894.

fore the cold weather. In this form it passes the winter, thus becoming a winter annual. The term is applied to distinguish such plants from true biennials. It is in flower from July to September.

General characters and habits

The height of the plant is from a few inches in poor soil up to five or six feet, or more, in rich soil. As seen along fence rows and in meadows it stands as a rule about three or four feet high. In general the plant possesses a central straight shaft, branched only above. The lower half or two-thirds of the stalk is clothed with leaves of quite uniform width, four to six inches long by one to two inches wide, while the upper half or third of the stalk sends out spreading, rather bare branches, much subdivided, and ultimately bearing inconspicuous yellow flowers. Each flower (capitulum) gives rise to about a dozen dark brown (so-called) seeds of similar shape to those of the garden lettuce, but somewhat shorter. Each seed (in reality a fruit, consisting of a dry capsule inclosing the solitary small seed, like all members of the composite family) bears a slender rigid stalk as long as itself, in turn supporting a white, filmy parachute, like that of the dandelion seed, only smaller, which serves to buoy up the ripe seed and waft it long distances on currents of air.

The whole plant has a pale, pea-green color.

Its specially characteristic feature is the presence of a row of soft prickles along the edges of the leaf and a row down the midrib beneath. There are also a few prickles scattered over the stem, particularly the lower portion. With these exceptions the plant is smooth. These prickles are from an eighth to a quarter inch long, and although scarcely stiff enough to penetrate the flesh, yet give the plant a rough and disagreeable character when handled. The juice of the plant is milky.

The prickly lettuce is a native of southern Europe, northern Africa, and the temperate part of middle Asia. At the present time it occurs as a weed in nearly all arable parts of Europe and Asia, except the colder regions. In England and northern Europe it is only an occasional weed along roadsides and in waste places, and is not troublesome to the cultivator.

Prickly lettuce made its advent in this country not far from thirty-five years ago; the exact date and place have not yet been ascertained. It is supposed to have come in with packing, ballast and other wastage. So far as can be inferred from available data, the plant gained a foothold in some Atlantic port. After having become established it was carried to the larger cities of the West, and from them scattered in all directions by the railroads. To be more specific, it appears to have first been seen in Cambridge, Mass., about 1863, and about fifteen or twenty years later to have appeared in several of the larger cities along the great lakes and the Mississippi river. It is probable that the fact that these cities are upon water-ways had little to do with the matter, but being great railway centers must have been an important factor.

First appearance in America

The earliest record in American literature is in the edition of Gray's Manual of Botany issued in the year 1867, where the plant is said to occur in waste ground and along roadsides in Cambridge, Mass. In the editions of 1866 and earlier it is not mentioned. It was, however, to be found in Cambridge at least four years earlier than the published record, as specimens exist in the Gray Herbarium of Harvard University, collected by Mr. D. Murray, in both 1863 and 1864. It was found upon ballast ground near New York City in 1879, but not seen in previous years. The ballast grounds of Philadelphia, which have received much attention from local botanists, do not appear to have yielded a specimen of the plant until 1883. Along the Atlantic seaboard the plant is still comparatively uncommon, and does not become an abundant weed anywhere in the region east of the Alleghany mountains.

Although the plant did not find an especially congenial soil and climate when it landed upon our shores in its emigration venture, yet it was able to maintain itself and to spread. In the course of fifteen years it had penetrated into the Mississippi valley, probably making the longer distances as the hobo travels, by clinging to freight trains, for it is first recorded as seen in St. Louis in 1877. It was afterward detected in Toledo, Chicago, St. Paul and other cities. In three or four years it was an abundant weed in almost every large city of the central west. At the

Fifteen years of conquest

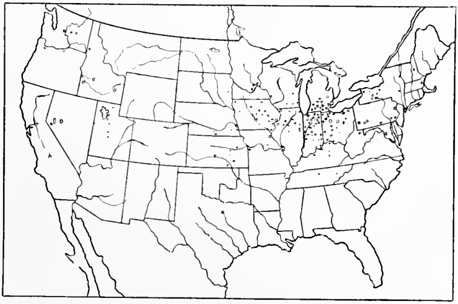


FIG. 4.—Map of the distribution of wild lettuce, as reported to the U. S. Department of Agriculture up to October, 1895. The comparative rarity of the weed in the Atlantic states, where first introduced, and its abundance in the central states, are conspicuously shown. (After Dewey.)

present time it is especially abundant in this part of the country, not only in cities and towns, but on farm lands and along highways.

The inference appears well founded that the plant has found its most congenial domain between the Alleghany and Rocky mountains, and between the fortieth and forty-third parallels. The region in which it has become so well established and so abundant as to take on the character of a prominent weed embraces the northern half of the states of Ohio, Indiana, Illinois, the southern parts of Michigan and Wisconsin, and part of Iowa. Outside of this region it occurs locally in every direction so that its distribution may now be said in general to extend throughout the United States.

Probably no one thing about this plant impresses the observer more that the appearance of having "come to stay," an expression used by many of those who have recorded their first acquaintance with it. It is a weed not only because it is a "plant out of place," but because it possesses certain attributes that enable it to maintain itself wherever a seed finds moisture and soil enough for the forthcoming plantlet to gain a foothold.

Before discussing this pre-eminent trait of the plant, however, it will be well to mention some lesser features that go to help it in its conquest of the land. In this connection the number and ease of distribution of its seeds is an important item. Each small head of flowers ripens about twelve seeds (*i. e.* seed-like fruits), and a plant of medium size, according to an estimate made by Miss Freda Detmers, bears 688 heads, or 8,526 seeds. Each seed is well constructed and protected to enable it to withstand a siege of the elements, and is likely to reach the succeeding springtime in good germinating condition, unless devoured by the birds. This contingency is not, however, of much moment, for the seeds are enclosed by a close wrapping of green scales until entirely ripe; they are then fully exposed only a short time, being carried away by the first breeze; and when they drop to the ground, after a longer or shorter sail through the air, they become almost invisible, their color being that of dry soil.

Seeds and their distribution

Each seed, as it leaves the mother plant, is supported from a white, feathery parachute, about half an inch across, which enables it to keep afloat upon currents of air for a long time, and ensures the plant a wide and rapid dissemination.

The flowers, which are yellow and small, only open a short time on clear days, and then close until the seed is ripe, and in the meantime look almost like young, unopened buds. This deceptive appearance may lead the cultivator to think he is cutting the weed in the bud before it has blossomed, when in reality it is loaded with young seeds, which will ripen as the plant dies, and be discharged to start another crop, almost as effectively as if the plant had been left standing.

The plant finds protection from herbivorous animals and boring insects through its bitter milky juice. For although like the garden lettuce, it is tender and palatable when young, it becomes exceedingly disagreeable to the taste after the flower stalks start up.

The prickles also, although weak and not very abundant, have a protective value to the plant by restraining animals from eating it.

How to be a successful weed

Although the plant, by its milky and bitter juice, and by its prickles, renders itself distasteful and unattractive as food for animals, and by prodigality of seeds, with their ample means for distribution and self-protection, insures a rapid and wide dissemination, thereby securing great advantages as a dominant and ever-present member of every area of vegetation, yet it is the possessor of another attribute belonging to a successful weed of even more importance, and that is its ability to grow and seed whatever the character of the soil and surroundings. Stone heaps, weedchoked corners of fences and yards, alongside gutters and roadways, a crevice in the pavement, beaten paths, all are acceptable places in which to flourish. But such poverty and ill usage are by no means essential factors in its success, for it also springs up in meadows, gardens and cultivated fields. Still the power to extract sufficient moisture and food from compacted and sun-beaten earth, and thus to overtop competitors, and in the less favorable spots to grow where few plants could live, place it in the first rank of noxious annual weeds.

Where it can maintain life, seed will be formed, even when conditions are unfavorable for full development. Thus one will often find in very dry soil plants only a few inches high bearing a number of flower heads and fully formed seeds. If by any accident the upper part of the plant is removed, branches at once start from below, and bear leaves and flowers.

The tenacious hold upon life which the wild lettuce exhibits is remarkable. It may be broken down, trod upon, cut off, and yet it puts out new shoots from below and flourishes again; its roots may be in the driest gravel, the most compact clay, or squeezed into the crevices of walls or pavements where moisture almost fails, and yet it grows. But all this tenacity of life is only displayed as long as the roots remain undisturbed. A plant of wild lettuce once pulled up dies as quickly as any other plant. When mowed, the top that is cut off dies as soon as ragweed, cocklebur, horseweed or thistles do; it possesses none of the live-for-ever quality of purslane. Neither has the root any recuperative force in itself. If the stem be cut away well down into the root, the whole plant dies, no shoots ever starting up from the roots in the soil.

The various characteristics enumerated largely explain the success of the plant as an introduced weed. In the central west, it is a formidable rival of ragweed, horseweed, cocklebur, jimsonweed, pigweed and other tall-growing annual weeds, especially during dry seasons. In July and August the plant becomes most obnoxious, for then it sends up the seed stalks. The heat and dryness which are likely to occur at this season and retard the growth of other plants, killing the small and weak ones, give the conditions which enable wild lettuce to gain the mastery and flourish in disheartening luxuriance.

Not only has the plant the properties of a weed, but it has the appearance of one. It looks weedy. There is nothing about it that will ever give it an æsthetic value. To city-bred and country-bred observers alike it will be only a weed, and nothing of the nature of the transformation of ox-eye daisies into marguerites will ever befall it.

Even a weed may be interesting

Although wild lettuce is an uncompromising weed, with no beauty of flower or leaf, yet it possesses some points of much interest to the student of plant life. "A garden in which nothing thrives has charms that soothe the rich possessor," asserts Cowper; and if we turn in such a spirit of expectancy to this weed tramp, although annoying us by its unwelcome presence in our yards and fields, we will find it to have characteristics worthy of study.

The mechanical and biological causes which determine the time and manner of opening and closing of the flower heads must be a fertile subject of inquiry. The construction and expansion of the airy parachute also deserves attention. Numerous other things about the plant may well engage the scrutiny of the careful student.

Only one of these features need occupy us at the present time, however. The species is characterized in the various manuals as possessing vertical leaves. As nearly all plants hold their leaves horizontal, *i. e.*, with the edges right and left, this peculiarity of the edges of the leaves being presented up and down, that is, at right angles to the customary position, may repay closer examination. A little scrutiny shows that the leaf is set upon the stem in the normal manner, and the vertical position attained by a quarter turn near the base. Some leaves turn one way, and some the opposite way, to gain the desired uprightness.

The habit of polarity

This in itself is odd enough, but a further examination shows all the leaves on a plant to stand for the most part in one plane. If the plant is looked at from a certain point of view, one sees the flat surfaces of the leaves, partly upper and partly under surfaces, while seen at right angles to the former direction the leaves present their edges only. The leaves of each plant, in fact, lie approximately in a single plane.

Even stranger yet, the plane in which the leaves lie is that of the meridian, that is, the leaves of the prickly lettuce present their edges north and south. The species, in fact, is a so-called compass plant, and exhibits one of the most curious and interesting cases of physiological adaptation to be met with in plants. Its polarity was first observed by Dr. Stahl, professor of botany at Jena, who published a very full account of the matter in 1881.

There are two species known which are preeminently entitled to be called compass plants:

one is the subject of this article, the prickly lettuce, a native of the old world, the other is the rosin weed, which is indigenous to the new world. The latter (*Silphium lacinatum* L.) occurs on the western prairies from Ohio to the Rocky mountains. It is a large, coarse plant, but yet an attractive one, with sunflower-like heads. It is usually known as rosin weed, from the resinous exudation, which children gather and convert into a white palatable chewing-gum.

Another compass plant

So strong is the polarity of the leaves of this plant that it has repeatedly served a very useful purpose in providing travelers with their bearings when lost on the prairies during dark nights or cloudy days. This characteristic was familiar to pioneers long before Gen. Alvord of the U. S. Army made it known to the scientific world in 1842. Longfellow, upon hearing of the plant and its service to travelers, made it the basis of some lines in Evangeline:

> "Look at this vigorous plant that lifts its head from the meadow,
> See how its leaves are turned to the north, as true as the magnet;
> This is the compass flower, that the finger of God has planted
> Here in the houseless wild, to direct the traveler's journey
> Over the sea-like, pathless, limitless waste of the desert."

Unfortunately the poet at first misapprehended the real character of the plant, with its coarse, rigid stem, and wrote, "Look at this *delicate flower* * * * that the finger of God has *suspended* here *on its fragile stalk*," but in later editions of the poem changed the wording as above.

The compass plant of the prairies and the compass plant of the highways differ, in that the former exhibits polarity chiefly in the radical leaves (large, coarse leaves, a foot or two long), and the latter in the stem leaves. Otherwise the phenomenon in the two plants is practically identical.

Explanation of the peculiar trait

There was much conjecture for a long time as to the cause of this unique behavior. It was suggested that the magnetic currents of the earth acted upon iron oxide in the leaves, or that the abundant resin in the plant brought about electrical disturbances. But both theories failed when put to the test, and others stood no better until the relation to light was observed. It was found that plants grown in boxes, if turned one quarter round, readjusted their leaves to again point north and south. This occurred when the plants were grown in bright light, but not when grown in darkness. It was also found that the number of stomata (breathing pores) was essentially the same on both surfaces of the leaf, while ordinarily there are very many more below than above. Further uniformity of structure between the two sides of the leaf was also found to exist.

It is unnecessary to point out all the reasons for the conclusion finally reached, that compass plants are endowed with an organization which enables the leaves, as the midday sun becomes unpleasantly bright, to turn part way around and present less surface to the action of its rays. Figuratively, one might say the plant turns a cold shoulder to the sun, when he becomes too ardent.

Ordinary leaves permit the sun to shine upon the upper surface only, having that side constructed to bear the light and heat without injury, while the under side, having a more delicate organization, is turned from the sun. When the compass plant adjusts its leaves in the only position possible by which equal illumination is secured for the two sides during the middle of the day, the under side of the leaf is evidently in danger of injury unless reorganized. Such a change does in fact come about. As the palm of the hand is calloused by repeated rough usage, so the lower surface of the leaf is inured to the sun's action by exposure, the change consisting of a profound alteration of the underlying tissues as well as of the superficial portion. Physiologically there is no longer an upper and a lower surface to the meridional leaf, but simply a right and a left surface; both sides function alike.

Some time ago the writer made the observation that the garden lettuce also shows polarity of the stem leaves, although not so marked as in the wild plant. It is stronger in the plain narrow leaves of the Cos and Deer-tongue varieties than in the curled leaves of the more common varieties.

Both the wild and garden forms show no vertical adjustments of the basal or so-called root leaves, the edible part of the cultivated plant. In feral plants these leaves are not called upon to endure the hot sun of July and August, having already performed their office during spring and early summer, and died. The compass plant of the prairies (*Silphium*), on the contrary, retains its root leaves throughout the torrid season. It is evident that the device is primarily a midsummer adjustment, only developed in such foliar organs as are destined to endure the fiercest insolation.

There are eight or nine species of wild lettuce indigenous to North America, but none of them has yet been observed to show polarity. The species that are most at home in the western prairie regions, such as *Lactuca Ludoviciana*, are most likely to show tendency toward the habit.

IV.

MIMOSA: A TYPICAL SENSITIVE PLANT.*

Uses of movement

Movement as an adjustment to variations in temperature and light is one of the most necessary and most highly useful adaptations made by leaves. The species that can accomplish the movements most economically will have a great advantage in the struggle for existence where the solar factors are most intense. In fact it is to be said that no plant in the tropics exposes its leaves to the perpendicular rays of the noonday sun. In the species incapable of producing the movement, the adjustment is secured less perfectly by the passive drooping of the leaves. In the temperate zone active movements of leaves are exhibited by species of Leguminosæ, Oxalidæ, Malvaceæ, Tiliaceæ and Marsiliaceæ only, but in the tropics the number is enormously mul-

---

*Adapted from a lecture on "Movements of Plants" given before the Institute of Jamaica, June 19, 1897.

tiplied and includes among other families the Euphorbiaceæ and Marantaceæ. The groups mentioned have shown a peculiar fitness for tropical environment. One genus alone, Cassia, includes four hundred and fifty species, nearly all of which are at home in countries near the equator. One of the northern representatives, *Cassia chamæcrista*, has acquired the name of the "Wild Sensitive Plant" throughout the middle and northern states, while *Cassia nictitans* is similarly designated in New England. Southward the number of species increases with that of the other leguminous plants until near the equator, representatives of the group form a very large proportion of the total mass of vegetation.

Power of movement

Mimosa pudica the "Sensitive Plant" or "Shameweed" of the West Indies is one of the most attractive members of this group, since in addition to the typical adjustments of the leaves, which it performs with great rapidity and delicacy, it also exhibits reactions to other and unusual stimuli. The movements of plants are generally so slowly made as to be incapable of detection except by repeated or long continued observation. Mimosa, however, is one of the small number which is capable of rapid movement of large organs. This fact, and the great degree of irritability shown, drew the attention of the

Characteristics of mimosa

earlier botanists, and it has been the object of a succession of investigations for more than a century. The plant has become a classical illustration in botanical literature, and a drawing showing positions taken by the leaves after movement, made by Duchartre many years ago, is still reproduced in text books.

The equatorial zone is the home of an enormous number of species. The island of Jamaica, with an area of about 6,000 square miles, about that of Connecticut, furnishes approximately four-fifths as many species of flowering plants as are to be found in the United States east of the Mississippi river. The advent of modern man into the teeming tropical areas, and the facilities he afforded intentionally and unintentionally for distribution has led to a wholesale emigration and intermingling of tropical forms.

Mimosa pudica was originally an inhabitant of the plains of Brazil and Venezuela, but it has accompanied man in his journeys around the world in the equatorial regions. It has become a virile pest in fields, gardens and pastures in warm countries, and is cultivated in greenhouses in latitudes as high as 55° N.

It is a low, spreading, prostrate, woody plant in the tropics. The forms seen in northern greenhouses show an erect stem because of insufficient light and are "drawn" in the language of the gardener. The scattered leaves consist of a long petiole bearing two or four leaflets, which are divided into eight to twelve pairs of small ovate pinnules. The bases of the stalks of the pinnules, the leaflets and the petiole are developed in the form of thick cylindrical swellings (pulvini). The woody, mechanical tissue in the stalks is in the form of a hollow cylinder, but in passing through the pulvinus to join the stem it comes together forming a solid rod. The central cylinder of mechanical tissue is surrounded by a thick layer of thin walled motile cells which are capable of rapid changes in form. Such alterations are due to variations in the hydrostatic pressure in the cells. When the cells of one side of the pulvinus give off water which passes into the spaces between the cells, a curvature toward this side results from the unchanged pressure of the turgid cells of the opposite side. The sinking of a leaf upon its petiole is due to the relaxation of the cells of the lower side of the pulvinus. When these cells reabsorb the water from the intercellular spaces, their former size and shape is slowly regained and the leaf is returned to its former position.

Organization

The continuous observation of half a dozen healthy plants through the course of a midsummer's day will reveal the greater number of reactions exhibited by this plant.

Day positions of leaves

Early in the morning the pinnules are seen to occupy a horizontal position with the blades fully exposed to the light. The petioles are slightly elevated above the horizontal. As the sun mounts toward the noonday position its rays increase in intensity, and their effect on horizontal leaf-blades will increase correspondingly. At sometime, however, before the rays strike the surface perpendicularly, the regulatory mechanism of the plant sets up movements in the pinnules by which their surfaces are directed upward at an acute angle. The angle increases as the sun nears and passes the zenith until the edges of the blades are directed almost exactly toward the sun, and its rays exercise an actual effect on the leaf not much greater than in the early forenoon. If this adaptation were not made, the fierce rays would strike through the leaf-blades so strongly as to injure the chlorophyll and evaporate more water than could be supplied by the roots, thus causing wilting.

Night positions of leaves

As the sun declines toward the west, the blades return once more to the horizontal position, but the approach of night brings

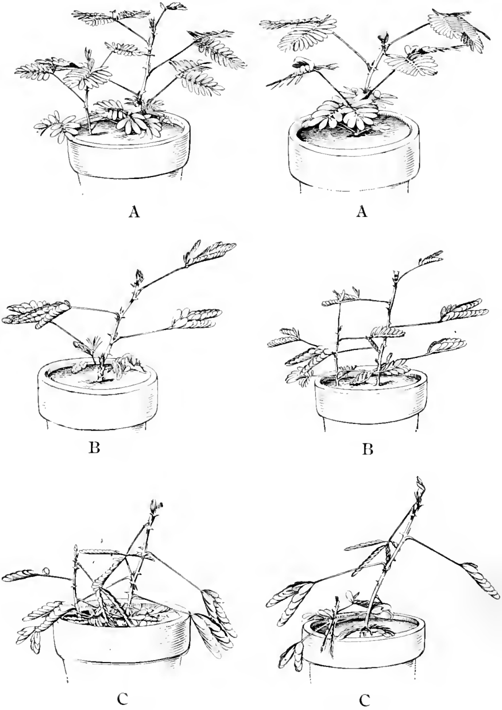


FIG. 5:—Mimosa: *AA*, normal position; *BB*, night position; *CC*, position after shock.

another danger to the plant, consisting in an extremely rapid radiation of heat and accompanying loss of water. This threatened injury is again avoided by deflection of the blades from the horizontal to the perpendicular. The movement begins at or near sunset and the laminæ slowly rise until their upper surfaces are appressed. The evaporating surface is thus reduced exactly one-half, while the radiation of heat is much less from a vertical plane than a horizontal one. Reference to the accompanying illustrations will show that minor movements have occurred. A movement of the pulvinus at the base of the petiole results in placing that member horizontally.

Reaction to shock, etc.

The "night," "sleep" or *nyctitropic* movements occur daily while those to avoid the effects of the hot sun are exhibited only when a certain intensity is attained. The regular daily recurrence of the conditions which cause the nyctitropic movements has fixed them so firmly in the plant that they occur at rhythmic intervals re-

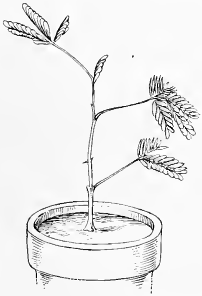


FIG. 6.—Hot sun position of Mimosa.

gardless of the surroundings of the plant. The "sleep" of the plant on any given night is not the direct result of the absence of light at that time but of the darkness of previous nights. If a healthy individual is placed in continuous light or darkness, it continues to "go to sleep" at regular intervals for several days, but finally sickens or adjusts itself to the new conditions imposed upon it. The habit is regained on restoration to normal conditions.

The sleep position may be produced in the middle of the day by suddenly excluding the sun's rays, but the normal position will soon be regained unless the temperature is greatly reduced. Mimosa is one of the plants in which the night position is wholly a response to low temperatures.

If a screened plant is suddenly exposed to the sun's glare in the middle of the day, the leaves sink and the pinnules close as if struck or jarred. Many interesting deviations from these typical reactions have been observed. Thus, if a healthy plant is placed in a dry room at 15° Centigrade the blades will be found extended in the morning, while the petioles have assumed and retained a depressed position. The reactions described above are not especially characteristic of mimosa, since they are exhibited by many hundreds of species and may be easily observed in the bean, oxalis, locust, cassia, and other leguminous species.

It has other forms of irritability, not at all common or widely distributed. Thus if one should lightly touch, or blow the breath upon, the expanded leaflets of mimosa at ordinary temperatures, the pinnules or ultimate divisions of the leaf would rise up above the midribs upon which they are borne, closing in pairs. If the shock were given with sufficient force or if a blow of the pencil be given upon the stem all the leaves will erect the pinnules and sink on the petioles. A flame held near the leaflet, or the fumes of acid, ammonia, or chloroform, will cause the movement also, while an electric current applied to almost any part of the plant has a similar effect. More correctly speaking, the breaking of the current is the true stimulus. The plant responds to chemical, mechanical, thermal and electrical stimuli. An interesting difference between the reactions of mimosa and those of the tendrils of climbing plants is that the latter move when pressed by a solid body, but not when struck. Mimosa, on the other hand, responds to a blow or shock, but not to a steady pressure, as the leaves may be given a steady pressure by the thumb and finger without results.

FIG. 7.—Successive positions of mimosa after stimulation at the tip of a leaflet. *a*, position a few seconds after a flame is applied at *f*. *b*, the impulse has reached the base of the leaf. *c*, the impulse has traversed nearly the entire shoot and is nearing the leaf-tips of the last leaf reached.

A careful analysis of the above reactions will yield many interesting results. If a quick snip is given with scissors to the terminal pair of pinnules in one of the upper leaves, the pinnules disturbed will close rapidly and then the other pairs will react in succession until the base of the leaflet is reached. After a short interval the basal pairs of pinnules of the neighboring leaflets close and thepairs toward the apices in succession. Before the motion has been taken up by all of the leaflets the pulvinus at the base of the main leaf-stalk acts, and the entire leaf sinks. If the stimulus has been given with sufficient force, or by means of a match flame instead of the forceps or scissors, the movement will be taken up in turn by the leaves above and below the one treated. The reaction of the plant is most rapid in specimens growing vigorously, and standing in moist air at a temperature of 30–35° centigrade.

Transmission of stimuli

It may be noticed that a short time elapses between the action of the stimulus from the scissors or flame and the reaction of the leaflet. This is termed the *latent period* and amounts to slightly less or more than a second according to conditions. The experiments also have demonstrated that the effects of a force applied to one part of the plant may be transmitted over its entire body, which is often a yard or a meter in length. If careful note of the time is made between the application of the stimulus to the plant and the reactions in different portions of the plant, together with accurate measurements, it will be found that the *impulse* or force set in motion by the stimulus travels at the rate of eight to twenty-five millimeters (⅓ to 1 inch) per second under favorable circumstances.

As the plant stands in the quiet atmosphere on a warm morning, a breath of air or the smallest drops of water striking the blades will cause reactions. If the movement of the air is continuous and freshens to a breeze, or the drops of water are followed by a steady rain, the plant finally replaces the pinnules in the original position, though blown about or beaten by the rain. The plant is enabled to do this by its great power of accommodation to any force acting upon it. The real stimulus is not the force in itself but consists in changes in the forces acting upon the plant. This may be demonstrated if a specimen is subjected to a spray of water forming an artificial rainstorm in a greenhouse. After a time it becomes accustomed to the falling water and resumes the normal position. If now the force of the spray is suddenly increased, a reaction is shown, and the pinnules are closed. After exposure to the heavier spray for a time it once more resumes the normal attitude and the experiment may be repeated with similar results. A specimen of mimosa grown in a pot may be carried on a journey in a wagon or railroad train, and may be seen to resume the normal position after it has become accustomed to the jarring from the vehicle, if the temperature and light are favorable. While an individual may thus accommodate itself to an unusual intensity of any force, it is as delicately sensitive to other stimuli as usual. Thus one may stand some distance from a

Repetition of stimuli

plant exposed to an artificial rainfall and cause a reaction by a puff of the breath.

When a plant has become accustomed to a continuously acting force, the amount of increase necessary to secure a reaction is a definite and fixed proportion of the continuously acting force. The formula which expresses this proportion has been found to apply to the reactions of both plants and animals.

Method of transmission

The manner in which impulses are transmitted from one part of a plant to another forms a problem, the solution of which has baffled investigation for more than a century. Many interesting experiments looking toward a determination of the question have been made.

It has been found that when a section of a stem has been girdled by the removal of the bark and cambium the transmission of an impulse is in nowise hindered, thus proving that the path lies through the wood, which in this plant is composed of cells which die on attaining normal size. The fact is proven more positively by the removal of the wood from another section, the living tissues and bark being allowed to remain. In this instance no transmission occurs.

If a short section of a stem is killed by means of a bandage of cloth kept saturated with boiling water for several minutes, transmission is not hindered and a stem may be so treated as to consist of alternate dead and living portions and still transmit the effects of stimulation. This set of experiments disposes of the idea that the transmission of impulses is in any sense a function of living matter in mimosa.

The presence of a system of elongated cylindrical cells in the outer part of the woody tissue, containing glucosides and water under pressure, led to the formulation of the theory that these tubes were the paths of transmission and that impulses consisted of simple hydrostatic disturbances traversing the system, as the pulsations of the forcing engines are transmitted through the mains and pipes of a city water system.

The mere presence of these tubes can have no especial significance, because they are found in hundreds of species of Leguminosæ in which transmission does not occur. It is to be admitted of course that the tubes might serve such use in mimosa, though not in any other plant. When sudden disturbances are induced in the contents of the tubes by means of powerful pumps, abrupt pressure, the application of heated rods to the stem or strong chemical solutions to cut surfaces, no reactions follow, and it is difficult in face of such results to maintain that an impulse is a hydrostatic disturbance. As a matter of fact impulses have been conducted through air-dry wood of the stem in which hydrostatic transmission would be impossible, and the only pathway would be the water of imbibition in the cell wall. Information as to the condition of water in the wall is not sufficient to make the formulation of any reasonable theory based on this assumption possible.

Purpose of reaction to shock, etc.

The reaction of mimosa to impact and injury is supposed to be a protection against drouth and damage from grazing animals. A recent writer says: "When a browsing animal approaches a clump of mimosa and agitates any part of it at all strongly the green appearance disappears at once, and only an apparently withered clump in which the hard and prickly stems are most conspicuous remains; the consequence being that the animal either turns away or passes through the clump to less bewildering pasturage."

As the plant has not been studied in its habitat in Venezuela and Brazil it is not definitely known whether it is ravaged by grazing animals or not. The theory was once proposed and widely reiterated that the contact irritability of mimosa was developed as a protection against hailstorms, regardless of the fact that the plant never encounters such dangers in the torrid zone. As has been shown it is not a protection against rain, because the plant soon becomes accustomed to the falling drops, and opens. The fact that many plants of the temperate zone, among which is the ordinary locust (*Robinia pseudacacia*), exhibit irritability to impact leads to the suggestion that the plant must be very delicately poised to be able to avoid the dangers of changes in temperature, and that any shock sets the protoplasmic machinery in motion.

The movements of mimosa in response to the action of ether, chloroform and other anesthetics, as well as electricity, is due to the direct action of these agents on the motor tissues. A similar instance is afforded by the action of changes in temperature upon tendrils.

Equipped with an irritable organization of such a high degree of complexity, mimosa can easily hold its own in the swarm of competing organisms in tropical climates. A similar organization would be highly disadvantageous as well as impossible in high latitudes.

V.

UNIVERSALITY OF CONSCIOUSNESS AND PAIN*

"It is my faith that every flower that blows
Enjoys the air it breathes!"

Wordsworth.

It is the glory of modern science to have shown that the phenomena of the universe are capable of being grouped into classes and sub-classes, and that through all the ramifications runs an essential nexus, or genetic association. In the organic world the development of plants and animals has been shown to be governed by similar laws for both, and their special ways of maintaining the fundermental characteristics of their existence is being found more and more to be based upon like properties.

Unity in nature

In the following pages the writer hopes to present a generalization that throws a somewhat different light upon the life of plants

---

*Read before the Parlor Club, an organization devoted to literary and scientific culture; Lafayette, Ind., Sept. 20, 1896.

from that usually entertained, and yet he does not wish to claim more than well-established facts and reasonable analogy will uphold.

Superstition of the mandrake

An old superstition ascribed to the mandrake, a common plant of the Mediterranean region, a supersensitiveness that caused it to utter such cries of pain when drawn from the earth "that living mortals, hearing them, go mad." This marvelous anthropomorphic exhibition was associated, so it was said, with an equally marvelous resemblance of the plant to a human body wherein lay the reasonableness of the plant's behavior.

Can a mandrake feel?

By logical extension of modern deductions regarding the nature of the physical basis of life and the unity of ecological methods in its expression, it is not too much to claim that a more genuine agreement exists between mandrakes and man than the superficial one of form that appealed so powerfully to the ancients; in fact, as is well known at present, the representatives of both kingdoms not only grow, breath and require food, but they respond to changes in environment by being irritable. On the one hand the irritability rises, especially among the higher animals, to a clear exhibition of feeling, capable of inducing suffering; what is there in the logic of the situation that prevents us from assuming that plants also feel? I venture to say that they do feel, and that the mandrake, or any other plant, is really hurt when pulled forcibly from the ground, suffering its modicum of pain, although unaccompanied by signs that make the fact patent to our senses. If a plant can feel a bodily hurt, it must necessarily possess consciousness, for pain without consciousness is inconceivable. Hence the thesis: all living organisms, whether animal or plant, are capable of conscious pain to a degree commensurate with the requirements of their nature.

Meaning of consciousness

At the outset it must be clearly recognized that the word consciousness, as used in this connection, contains no reference to self-consciousness, which implies introspection. Self-consciousness, it may be said in passing, is necessary that the individual may, for instance, be aware of its own identity, or may reflect upon a given sensation, which powers belong, undoubtedly, not to all classes of beings, but only to the more highly organized, and especially to those with a centralized nervous system.

General consciousness, on the other hand, implies a recognition of the impact of stimuli; the individual knows that the uniformity of the conditions of its existence is disturbed, sometimes pleasurably, sometimes painfully.

Recognition does not come, however, with all changes in external conditions, they must reach a certain violence, or intensity, before consciousness is aroused; and the degree required for efficiency will vary with the organism.

Examples of consciousness

The state of consciousness and the usual accompanying reaction of the organism can be illustrated by the well known effects of a thrust. Let us suppose that the organism in question is a man, and the thrust is received from the proboscis of a mosquito. The man may be especially sensitive to mosquito bites and retaliate with a violent blow of the hand. However, being a rational being, he may first reflect upon the probability of getting the greatest satisfaction from his effort, and take certain precautionary measures to secure deadly aim. If the same invasion of personal rights be attempted with the man's canine companion, the reactionary effects are similar in every essential; but being a far less rational being than his master, the dog will give little or no thought to the manner of the removal of the offending insect. As we go down the scale of organized life the mosquito bite will continue to meet with counteraction, taking on more and more the character of a simple sensitive response to an irritation.

In order to carry our observation further and have the trials under better control, suppose a splinter of wood, or a feather, be used as the irritating object. If now this awakener of consciousness be cautiously applied to the back of the neck of an unsuspecting person, it will arouse reaction, provided the friction has been sufficient to be felt. Suppose we tickle the nose of a dog, who is taking a siesta with his eyes shut; there is not sufficient difference in the results to require comment. If the back of a caterpillar or worm next be tested, a wriggling of disapproval takes place. Now touch the mantle of the lazy clam, and make sure that your fingers are not too near to be caught between the jaws of the shell as it springs together. Try a sea-anemone and watch the speedy infolding and packing away of its whole garniture of brilliant fringes. Proceed, if you choose, to the bell-animalcule, the amœba, and others of lowest and simplest animals.

But we need not stop with animals. Try the same test on the leaf of the Venus' fly-trap, and note the astonishingly quick interlocking of the rat-trap edges of the leaf-blade, a movement that has brought mortal surprise to many a fly. Brush the inner surface of a tendril of the wild cucumber and notice how it begins in a moment to slowly coil up.

Touch the leaf of a sensitive plant and see it shrink away into the smallest compass attainable.

What do all these animal and plant movements mean, except it be that the individual has *felt* something and acts responsively, according to its ability. And yet it may be objected that while man and some of the higher animals may possess genuine feeling, that is, to be more explicit, may experience conscious pain, yet the lower animals and all plants only react mechanically upon stimulation, such as frictional contact, shock, light, heat, electricity, etc. To illustrate: when a dog howls upon being hit with a stone, it will generally be admitted that it is because he suffers pain; but when an earthworm struggles as the angler threads it upon the hook, a question arises whether the movement is indicative of pain or whether it is simply reactionary, like the quivering of a mass of jelly when struck; and when a twig is pulled from a tree no more thought of pain is connected with the act than in the breaking of a stone.

Definition of terms

In discussing a subject like this considerable difficulty is found in using terms in such a way that they will convey an exact and uniform meaning. In the task I have essayed, nothing is easier than to upset the whole argument by employing the words feeling, pleasure, pain, etc., in some of their several legitimate meanings, which are not, however, those suitable for the topic, and ignoring the meanings which alone can lead to clear notions. To show the diversity of usage in employing the word "feeling" I will quote Ward in the Encyclopædia Britannica (xx, 40), who observes that "it is plain that further definition is requisite for a word that may mean (1) a touch, as *feeling* of roughness, (2) an organic sensation, as *feeling* of hunger, (3) an emotion, as *feeling* of anger, (4) *feeling* proper, as pleasure or pain." It is in this last sense only that I wish to employ it. And it is well to bear in mind in the same connection, that in simple organisms, feeling, like other functions, will have but a simple and feeble development, while in complex beings, it will take on a diversity commensurate with the degree of organic attainment, preserving, however, throughout the whole gamut of variation, the same fundamental quality of physical pain and pleasure.

No less diversity exists as to the use of the terms pain and pleasure. In a recent volume on the subject (Marshall: Pain, pleasure and æsthetics, 1894, p. 169) I find it stated that the "activity of the organ of any content if efficient is pleasurable, if inefficient is painful," which is nearly in accord with the philosophy of Lester F. Ward, who says that "the supply of tissue is attended with pleasure," and "the destruction of tissue results in pain" (Monist, v, 253). But both these observations, it seems to me, carry the analysis too far. I am inclined to agree with Paul Carus, who says that although "It is generally assumed that pleasure is an indication of growth and pain of decay, it has never been proven, and after a careful consideration of this theory I have come to the conclusion that it is based upon an error. Growth is rarely accompanied with pleasure and decay is mostly painless." He goes on to remark that the most optimistic philosophers look upon pleasure as positive and pain as negative, while the greatest pessimist, Schopenhauer, turns the tables and says pain is positive and pleasure is negative. He adds as his own opinion that "an impartial consideration of the subject will show that both pleasure and pain are positive. Pain is felt whenever disturbances take place, pleasure is felt whenever wants are satisfied" (Monist, i, 559). This definition accords so well with the usual mode of thinking and use of terms that I deem it unnecessary to elaborate it. If now it be admitted that pain results from a more or less violent interruption or alteration of the normal functional state of the organism, we shall only have to make sure that the organism knows that it is suffering the pain, and the basis of the argument will have been established. It must be remembered, however, that a sensation which would be called pain, if of sufficient intensity, when very slight might be called simply discomfort.

This leads us to a consideration of what is to be understood by consciousness. It is inadvisable to attempt an extended exposition of this much treated and intricate question, both for want of space and because metaphysical subjects are proverbially tedious. It seems to me sufficient in order to make my position intelligible, to say that when the organism is aware of a feeling of pleasure or pain, or of any other sensation, knowing that the same is located within its own organs, it is possessed of consciousness. This is what is usually known as simple sense-perception, the simplest type of consciousness. In the higher and more complex forms, memory plays a constantly increasing part; and judgment, the formation of concepts, and all the intricacies of mental activity finally enter into the problem.

It is usual to begin with man, and say with Noah Porter that consciousness is "the power by which the soul knows its own acts and states" ("Human Intellect," par. 67), or with Locke that it is "the perception of what passes in a man's own mind" ("Human Understanding," II, i., 19), and then to pass down the scale of being and admit the possession of consciousness in such animals as are thought to be endowed with a "soul" or "mind," according to the definition these words are permitted to bear. Anatomical structure is made to furnish considerable evidence in this connection. Perhaps Grant Allen's remarks about the earwig in his lucubration on "microscopic brains" present sufficiently well the attitude of most writers at the present time. "Of course most insects have no real brains," he says. "The nerve substance in their heads is a mere collection of ill-arranged ganglia directly connected with their organs of sense. Whatever man may be, an earwig at least is a conscious, or rather a semi-conscious automaton. He has just a few knots of nerve-cells in his little pate, each of which leads straight from his dim eye, or his vague ear, or his indefinite organs of taste; and his muscles obey the promptings of external sensations without possibility of hesitation or consideration, as mechanically as the vaive of a steam-engine obeys the governor-balls" ("Evolutionist at Large," 2). Again in speaking of slugs and snails he says:

"Their nerves are so rudely distributed in loose knots all over the body, instead of being closely bound into a single central system as with ourselves, that they can scarcely possess a consciousness of pain at all analogous to our own" (ibid, 12). Of course, if animals of as high an organization as insects and snails are thought to be meagerly endowed with sensibility, animals of still lower grade, and those especially that are without nerves must be quite outside the bounds of consideration, to say nothing of plants.

But there is another way in which to approach the matter; and one, it seems to me, that leads to results more in accord with our present understanding of the unity of nature and the evolution of organic forms. Living protoplasm is a very unstable substance. Living organisms of even the lowest type have but a fighting chance for continued existence. Life, asks the poet, what is it?

> "A frail and fickle tenement it is;
> Which, like the brittle glass which measures time,
> Is broke ere half its sands are run."
>
> —Notes and Queries, 1863.

General irritability

The smallest and most structureless being, as well as the largest and most intelligent, must guard itself against bodily accidents of all kinds, it must look out for its daily means of subsistence, and furthermore, it must maintain itself against the encroachments of fellow beings. The struggle for existence is by no means a fiction, even with an amœba. What is the provision, the device, the method by which the organism is enabled to successfully meet the destructive and levelling tendencies of the world outside itself? It is to be found, without question, in that general property of all living matter usually designated as irritability. If a bit of the leaf of waterweed, the hair from a pumpkin stem, an amœba, or any similar vegetable or animal structures be placed under the microscope and irritated in some manner, say by a light tap or shock, sudden change of temperature, an interrupted current of electricity, etc., the soft protoplasmic portion will shrink and change form in a characteristic way that thoroughly justifies us in saying that it makes a sensitive response to the stimulus. After a time the normal form and activity are regained, and another irritation will be followed by another visible response. If, however, the irritation be too severe—if the tap be too strong, the change of temperature too great, or the electric shock too intense—the convulsion which follows will be mortal, and no favorable environmental conditions or supply of energy will again restore the life that has disappeared. The protoplasm or animalcule is as genuinely dead as the man who has been knocked over with a mortal blow. Every organism, except when in a special state of repose—for instance, during the hibernation of some animals and the period of a plant's existence when enclosed in a seed—every organism of whatever grade of development is possessed of sensitiveness of essentially the same character as that of the simplest bit of protoplasm revealed by the microscope. As the organism rises in the scale of being, irritability takes on a correspondingly varied development. And it may be asserted that the recoil when I accidentally press my hand against a thorn is of the same essential nature as that of an amœba or slime-mold when pierced with a sharp point; or that the so-called instinct of the dog which urges him to follow up the scent of a rabbit when hungry, has its basis in the same fundamental property of living matter as that which causes the lively spores of the salmon-fungus (*Saprolegnia*) to swim toward the spot from which there is a slight emanation of decaying fish, or the leaf-mildew to turn and grow toward the breathing pore of a grape leaf, into which it desires to enter and find a congenial place of development, because it detects a slight escape of vegetable acids from that direction.

Irritability in its various forms must, there-

Welfare of the organism

fore, be considered the property of living beings by which they defend themselves against injury, secure food, and obtain the best conditions for existence. But there is no efficiency in irritability unless the organism is enabled to change its position or the position of some of its organs upon stimulation, that is, it must be capable of molar motion. How molar motion originated is a question into which I shall not enter, although a most important one in a full exposition of the subject; neither shall I touch upon the origin of organs and some other related matters of philosophical importance. It will suffice in this connection to point out that the preliminary to every vital movement, not automatic, is an effort. That all plant and animal movements, not accidental, are related to the welfare of the organism is a proposition that will be generally admitted; and such movements may consequently be classed as adaptive. That all movement having significance must at first have been adaptive seems to be sufficiently clear, and therefore automatic movements must necessarily have been derived from conscious ones. This, I am aware, is the reverse of the usual course of reasoning, and as the form in which I have stated it is too concise to be readily apprehended, it will be best to give a few lines to its elaboration.

Adaptive movements imply consciousness

That an adaptive movement requires effort, and that effort implies consciousness is the first step in the argument; that automatic movements must have been derived from conscious movements, in order to avoid the absurdity that actions can be directed toward an end by pure chance, is the second step in the argument. These steps can probably be illustrated by a concrete example better than by abstract statement; and I shall take a familiar example although the complexity of the conditions give many opportunities for being misunderstood, rather than select an illustration from the less familiar domain of simple organisms. The man who is being tormented by a mosquito, that is, receiving a stimulus giving rise to pain, must put forth an effort in order to move a hand to crush the offender. That effort must be a conscious effort, or else the blow would be aimless and futile and stand in no relation to the cause. But if the man were preoccupied, he might aim a well directed blow at the mosquito and yet not realize that any such thing had occurred. In this case it is evident enough that it was not the first time that he had performed a similar act. The first time such a movement was made, it must have been a conscious one, and for many times afterward, until it could be performed without conscious effort. All other automatic movements may be similarly explained. In reference to the involuntary movements of the heart and other viscera, Cope has suggested that they "were organized in primitive and simple animals in successive states of consciousness, which stimulated voluntary movements, which ultimately became rhythmic" (Organic Evolution, 511). He goes on to observe that "the structure of the infusoria offers the structural conditions for such a process," and proceeds to illustrate how the contractile vesicle might have thus arisen, and from it the mammalian heart. But we need not follow him.

Lester F. Ward has said that "pleasure and pain are the conditions to the existence of plastic organisms, pleasure leading to those acts which insure nutrition and reproduction, and pain to those which will insure safety" (Psychic Factors of Civilization). Cope has elaborated the idea into a well maintained hypothesis, which he calls archæsthetism. He defines it thus: "It maintains that consciousness, as well as life, preceded organism, and has been the *primum mobile* in the creation of organic structure. This conclusion also flows from a due consideration of the nature of life. I think it possible to show," he goes on to say, "that the true definition of life is *energy directed by sensibility, or by a mechan-*

ism which has orifiinated under the direction of sensibility" (l. c. 513). With this view of the role of consciousness the writer fully agrees.

Let us now stop and see where we are. I have tried to show that all organisms, even to the very simplest, whether plant or animal, from the very nature of life and the struggle for its maintenance, must be endowed with conscious feeling, pleasure and pain being its simplest expression. I have attempted to show that consciousness is not a function superimposed upon, or evolved from an advanced state of organic development, but is co-extensive with life.

Pain a factor in evolution

The hypothesis would likely meet with considerable adherence were it not for plants, which all writers seem to think present an insurmountable difficulty. Paul Carus, the learned editor of the *Monist* and author of many important philosophical treatises, asserts that "pleasure and pain are undoubtedly important factors in the evolution of the animal world, but the kingdom of plants demonstrates that the existence of plastic organisms with complex systems of nutrition and reproduction and also devices for safety is possible without pleasure and pain" (Monist, iv. 624). Cope has tried to get around the difficulty in his work on the primary factors of organic evolution by assuming that plants are wonderfully degenerate, having little cause for exertion, and behave in this respect like parasites. "We can understand," he says, "how by parasitism or other mode of getting a livelihood without exertion, the adoption of new and skillful movements would become unnecessary, and consciousness itself would be seldom aroused. Continued repose would be followed by subconsciousness, and later by unconsciousness. Such appears to be the history of the entire vegetable kingdom" (l. c. 509). The writer believes that such opinions as just quoted are the outcome of ignorance of the present status of botanical science; not the botany that teaches *about* plants—their names, and the ways of identifying the different kinds—but the botany that introduces the learner to a knowledge of their modes of living, their habits and their physiology. Plants are more difficult to study and understand than animals, because they are so much more unlike ourselves. Vegetable activities are very different from animal activities; they have been developed along different lines. It is only recently that we have begun to understand them at all. And yet already, the elucidation of plant movements is providing a key to the study of animal movements. Recently an investigator at the

Action of plants difficult to interpret

Zoölogical Station at Naples has shown that when a moth flies into a flame it is attracted in essentially the same way that the window plant is when it turns to the light. One must go to the tropics to see the highest development of movement in plants, on account of the high and uniform temperature, and possibly other environmental conditions. I have been told that in Java, as one walks through a tangle of sensitive plants, they will drop down in their deprecating way for yards on either side, as if suddenly aroused into life only to be again transformed into lifeless sticks by some unseen power.

It is because plant movements are so slow, as a rule, that we get the erroneous idea that they are rare. Have you ever noticed that beans and clover put their leaves into a different position at night, the same as a sensitive plant does; and that locusts, lindens, red-bud, and many other trees and shrubs do the same? Suppose a seed falls upon the ground and germinates: if it has no sensitiveness by which it feels the action of gravity, the chances are that it will speedily perish, for the root would not otherwise find its way into the soil, except through accident. There is one excellent reason why plants rarely respond visibly to bodily injury, and that lies in the fact that they are, for the most part, fixed objects. They have not been required to learn to move out of the way of danger, or to recoil when hurt, because the character of their structure makes movement difficult, their limbs and organs are not sufficiently plastic, and their attachment to the earth restrains them, like Prometheus bound.

This leads me to say, that as a rule we do not expect the right things of plants; we do not understand them. Our point of view is not well chosen. Animals are free moving beings, with their soft parts in considerable masses, while plants are fixed to one spot all their lives, and have their soft parts infinitely divided, each particle being encased in a rather rigid envelope. How can they act alike? And yet both are organized from the same character of living matter, which is obedient to the same general laws.

In another respect plants differ widely from animals. They have no nervous organization, and no co-ordinating centers for determining the character of movements. The movement that follows a stimulus is therefore confined usually to the near vicinity of the point of stimulation. If they experience pain, as I think they may, it can rarely extend to the whole organism, but the injured organ suffers without its fellows being affected.

Plants not degenerates

Plants as a class are not degenerates. In their way they have reached a high state of development, but it is not the development of animals. As their movements are slow, and poorly co-ordinated, it must be assumed that their pains and pleasures are correspondingly feeble; not but that they are genuine, nevertheless, and to them mean as much as ours do to us. If another man who is inferior to ourselves, if a horse, a dog, a bird may be made to suffer, and in consequence ought to have considerate treatment, so may the simplest animals and so may all plants.

I will close with a quotation from Grant Allen, and a comment thereon. "Hoeing among the flower beds on my lawn this morning, for I am a bit of a gardener in my way," he writes, "I have had the ill luck to maim a poor yellow slug, who had hidden himself among the encroaching grass on the edge of my little parterre of sky-blue lobelias. This unavoidable wounding and hacking of worms and insects, despite all one's care, is no small drawback to the pleasures of gardening *in propria persona*. Vivisection for genuine scientific purposes in responsible hands, one can understand and tolerate, even though lacking the heart for it one's self; but the useless and causeless vivisection which can not be prevented in every ordinary piece of farm work, seems a gratuitous blot upon the face of beneficent nature. My only consolation lies in the half-formed belief that feeling among these lower creatures is indefinite and that pain appears to effect them far less acutely than it effects warm-blooded animals." To which I have to add that he should have embraced plants, and then concluded that in proportion to their degree of organization they are hurt, and to the same degree deserve consideration.

VI.

HOW COLD AFFECTS PLANTS.*

If one should carefully note the exit of his floral acquaintances in the autumn he would find that not all of them succumb to the rigors of the cold season at the same time. Some of the members of the plant communities peculiar to meadows, woods and slopes will give over activity at the first suggestion of frost, while others endure a long succession of freezing nights before they finally perish. Still others, the conifers and evergreens, the thick beds of mosses, and the thin green layers formed by the liverworts and the grayish coating formed by the lichens, live through arctic winters without great apparent change, except indeed that some grow and fruit in and under the snow. Between the groups which

---

*Given before the Botanical Seminar, University of Minnesota, Nov. 13th, 1897.

are killed by the winter, and the evergreens which withstand it without any great alterations in outward form, stand the deciduous trees, which cast their leaves, and herbaceous plants with thickened underground stems, which withdraw the living substance from the leaves and stems to the underground structures, leaving the entire shoot to perish in the winter storms.

Varying reaction to cold

The degree of cold necessary to ensure the death of any species depends entirely upon the specific constitution of the protoplasm and the stage of development, or stage of activity of the organism at the time it is subjected to the low temperature.

According to numerous tests made during the last half century, it has been found that many delicately leaved, rapidly growing species are killed by a temperature above the freezing point, others native to the Arctic zone are not injured when the air and the soil in which they grow fall to seventy degrees centigrade below the freezing point. Well matured and air dried seeds in the resting stage have been subjected without injury for prolonged periods to the extremest low temperatures that can be produced in the laboratory. In one series of experiments seeds were immersed in liquid air at a temperature of about two hundred degrees centigrade for several hours with no resulting damage. From this last series of tests, it may be safely said that the protoplasm of plants when in the proper resting stage is practically indestructible by cold. Not only have seeds great power of resistance to cold, but they are capable of carrying on growth at low temperatures. The seeds of several common cereals will germinate on blocks of ice at a temperature of one or even two degrees below the freezing point.

Appearance of frozen plants

If frozen leaves are taken in the hand and crushed or bent, they retain the form given them. During the crushing, the breaking of the ice can be heard distinctly. Frozen plants do not regain their elasticity upon thawing. Upon the contrary, they become limp, partly transparent, and exhibit changes of color chiefly due to the destruction of the chlorophyll. The entire body of the plant has lost its consistency, and the different tissues may be easily stripped apart. When exposed to the sun, the leaves shrivel and assume a rusty brown or black color. They entirely resemble charred leaves, and the farmer says that the frost has "burned them."

It is not to be taken for granted that all of the cells of a plant are equally resistant to cold. Thus it is known that hairs and the guard cells of stomata remain active when the remainder of the plant is frozen solidly. Without doubt other differences also exist.

To understand these appearances one must recall the salient features in the structure of the leaf: that it is composed of a mass of loosely-arranged, thin-walled, globular, cylindrical or irregular sacs lined with protoplasm and containing seventy to ninety per cent of their volume of water. The loosely-arranged cells are held in position by the strong mechanical tissue of the ribs or nerves, and the whole enclosed by the single layer of epidermal cells: that of the lower side has openings (stomata) which permit the escape of watery vapor accumulating in the spaces among the inner cells.

Ice in the tissues

If now a section is made of a frozen leaf, it will be found that the spaces between the cells usually containing air are filled almost solidly with ice crystals. From whence is this ice derived? It will be remembered that the cell contains a large proportion of water, some of which is in the form of a solution of acids, salts, etc., in the cavities of the cell, and some in the form of water of imbibition in the protoplasm and in the cell wall. The water of imbibition may be imagined as filling up the minute spaces between the groups of molecules in the cell wall and the protoplasm. Now it is a well known principle in physics that water in a solution and water in capillary spaces, or water of imbibition will not freeze until the temperature falls a certain amount below the freezing point; and it will be pertinent to state at this point that the temperature of small plant bodies is approximately the same as the surrounding air, with the exception of the flowers of certain aroids and other plants. Ice then may not be formed until the temperature of a plant has fallen more or less below the freezing point, amounting to two or even six degrees below in some instances. The exact point will vary with the specific constitution of the plant, as it does in solutions of different substances.

Relation of the cell to cold

Protoplasm even in its simplest forms is highly automatic, and self-regulating. When the cells of a leaf are subjected to a low temperature, they contract and a portion of the water contained is driven out into the intercellular spaces where it is frozen. By this provision the proportion of the water in the cells is reduced and the danger of ice formation and consequent destruction is averted. If now the temperature is again lowered an additional amount of water is forced into the intercellular spaces, rendering the cell solutions still more concentrated, and less easily crystallized into ice. This process may continue until the greater part of the water has been driven out of the cell sap, protoplasm and wall, and may be seen piled up in the spaces in the form of small pillars or discs, in many instances completely filling up the space between the cells and forcing them apart, but not injuring the protoplasm or the cell wall by the crystallization of water in their interstices. It is thus to be seen that the extrusion of water into the intercellular spaces is a protective device of the protoplasm. In many instances the amount of ice formed in the spaces among the cells may be so great as to split the tissues completely apart. This is especially noticeable in trees, and the sudden yielding of the firm wood to the pressure of the ice crystals within is accompanied by startling reports familiar to those who frequent the forests in the early days of winter. In many of the herbaceous plants the splitting of the stems is followed by the formation of very delicate and fantastically arranged sheets of ice crystals, which are commonly known as "frost flowers."

The excretive power of protoplasm is not always sufficient to enable it to reduce the percentage of water in the cell to such a degree as to escape freezing. In such instances, ice is formed inside the cell, and the withdrawal of practically all of the water in the protoplasm to form the crystals results in the architectural disintegration of the living substance. It is as if all of the mortar used in the construction of a building had been irregularly withdrawn, leaving only a toppling, ruinous pile of bricks.

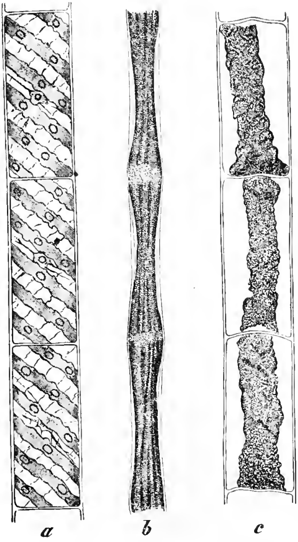


FIG. 8. Spirogyra magnified 300 times: a, intact; b, frozen in ice: the cells are shrunken but no ice is formed in the cells; c, thawed: the protoplasm is contracted upon the chlorophyll bands, and the nucleus is disorganized. After Molisch

Relation of the organism to cold

The formation of ice in the plant does not imply its death. If the temperature falls to a certain point characteristic of each species a disorganization of the protoplasm will ensue, and the plant dies regardless of subsequent treatment. On the other hand it is well known that many plants may be frozen and recover normal appearance, and that the death of others may be averted by practices known to the gardener. Thus some frozen plants, if submerged in water a few degrees above freezing and allowed to thaw, will entirely recover. If such plants are placed in warm air to recover, the ice in the intercellular spaces gradually melts and a large proportion of it evaporates into the air, while the protoplasm absorbs only a small amount. All of this ice was in the cell originally, and its return is necessary for the welfare of the cell and the plant. A frozen plant, thawed in the open air, therefore, is sometimes killed by loss of water which might be prevented if the plant were immersed in a vessel of the fluid. If ice be actually formed inside the cells, however, the plant dies whether thawed slowly or quickly, in dry or moist media.

Death above freezing point

The death of plants by low temperature above freezing point is due to related causes. Acanthus, coleus, basils, melons, tobacco plants, etc., blacken and die if exposed to a temperature of three or four degrees above freezing point for a single night. In such instances the death of the leaves is due to the fact that the chilling of the roots decreases their ability to absorb water from the soil as fast as it is needed by the leaves, which shrivel, blacken and dry up in consequence. If one of these plants is placed in a pot and the earth about the roots not allowed to approach within fourteen degrees of the freezing point, the shoot and leaves may be exposed to air near the freezing point without injury. As has been shown elsewhere the casting of autumn leaves is a provision of deciduous plants, whereby the leaves are cut away at the time when the absorbing capacity of the roots and the water supply is decreased.

Adaptations against cold

The power of excretion of water from the cells by protoplasm is the primary means of protection against death by cold, and is possessed by all plant protoplasm. It is evident, however, that this is a method designed primarily for the safety of each individual cell. The organism as a whole may be expected to exhibit adaptations to shield the cells from the extremes of low temperature. The most common device for escaping cold consists of a deeply penetrating root system and the development of underground stems. The roots are sent down to a depth at which the temperature does not reach the freezing point, or does so slowly, and rises again so gradually that no harm is done. The primary purpose of the roots is of course to penetrate the soil in such manner as to fix the plant and obtain a supply of mineral salts, and in so doing a region not subject to the rigors of low temperature is reached. Some lowly-growing plants avail themselves of the blanket-like coverings of leaves and snow which fall upon them before the extremest rigors of the winter are at hand. Many plants native in alpine regions are specially adapted to take advantage of this means of protection. Among them are some of the rhododendrons, dwarf junipers and pines.

The stem of *Pinus humilis* of the higher mountain slopes, although eight or ten inches in diameter and strong enough to stand erect and sustain the ample crown, grows almost parallel with the surface and a few inches above it. The branches which are ordinarily erect are very flexible and easily bent downward, and when weighted spread themselves along the ground. This is true of branches which stand up to the height of a yard or more. When the early storms set in, and the ever increasing layer of snow settles down over everything, the branches slowly bend under the constantly augmented weight, and finally are pressed against the soil under many feet of snow. In this position they are also secure from the shearing action of moving masses of ice and snow above them. When the snow melts in the spring the elastic branches return to the upright position, and the early climber may see the old leaves plastered over with earth, and small stones adhering to the twigs and branches. The gardener imitates the action of these pines when he bends rose bushes and small shrubs to the ground and covers them with earth and straw.

A very interesting method of avoiding death by cold is afforded by many aquatic plants. Species which float on the surface of water owe their buoyancy to small bubbles of gas in or between the cells. On the approach of winter, the gas is given off, and the plant sinks to the bottom, either in the form of spores or the entire vegetative body of the plant.

In such forms as the water lily, the leaves and flowers die down and the main stem of the plant, a bulky rhizome loaded with food, is securely imbedded in the mud below the freezing line. At the beginning of each season new leaves and flower-stalks are sent to the surface.

Perhaps the most interesting adaptation is that offered by such aquatic plants as the pondweeds, bladderworts and stoneworts which root in the mud at a few feet below the surface. With the approach of autumn the tips of the stems grow in the form of a thick shoot with short, crowded leaves which are termed *hibernacula.* The hibernacula finally break loose from the stem, which dies, and sink to the bottom before ice formation sets in, and lie quiescent during the winter. After the spring thaws, if one rows over the shallows near a lake shore, he may see the hibernacula resting on the bottom, and as soon as the sun's rays have warmed the water sufficiently to allow growth, a few rise to the surface, and all begin to send out roots from the lower end, and stems form at the upper

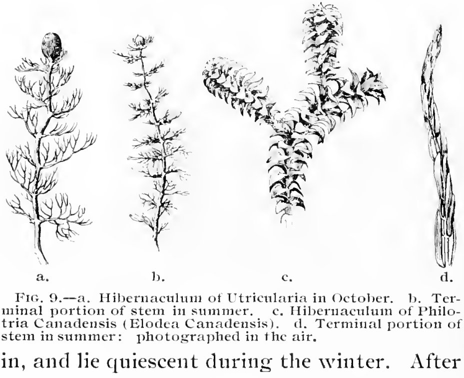


FIG. 9.—a. Hibernaculum of Utricularia in October. b. Terminal portion of stem in summer. c. Hibernaculum of Philotria Canadensis (Elodea Canadensis). d. Terminal portion of stem in summer: photographed in the air.

end, with the result that the entire plant is reproduced within a short period. Some species form a hibernaculum at the tip of each branch, with the result of multiplying the plant by this method.

Some plants as a whole avoid low temperatures by growing in such a manner as to be covered with a protecting blanket of leaves and snow; and others retire to a depth below the frost line in the medium in which they live.

Winter buds are of course devices for the protection of growing tips against sudden changes of temperature and moisture, as well as from mechanical injuries due to wind, sleet, snow or ice.

As a conclusion to be derived from the foregoing paragraphs it is to be seen that protoplasm seeks to avoid danger of disorganization from the formation of ice in its interstices by getting rid of a portion of its water when the temperature falls, and the death of a plant does not necessarily follow "freezing." Death by cold may be due to the direct action of cold, or to the consequent desiccation of the tissues. When due to the latter cause it may be brought about by temperatures above the freezing point.

That temperature has been a most important factor in the evolution of the vegetable kingdom, as well as in the distribution of the separate forms, is evident when one considers the vegetation of a mountain from its base with its warm breezes and soft sunshine to the bleak summit with icy winds, cold nights and ravines filled with snow.

VII.

TWO OPPOSING FACTORS OF INCREASE.*

Two sides to plants

The energies of the plant are used for two general purposes: the development and maintenance of the vegetative parts, and the formation of special reproductive bodies. In some respects the efforts of the plant in these two directions are antagonistic. The vegetative part consists of root, stem, foliage, etc., and at first, and sometimes for a long period in the life of the individual, the energies of the plant are wholly absorbed in increasing the size and promoting the functional activities of

---

*Condensed from two articles: one in collaboration with Miss Katherine E. Golden, entitled "Weight of the Seed in Relation to Production," published in *Agricultural Science*, May, 1891; and another entitled "A New Factor in the Improvement of Crops," read before the Society for the Promotion of Agricultural Science, August, 1893, and published in its *Proceedings* and in *Agricultural Science*, September, 1893.

these organs, all being connected with the welfare of the individual plant. After a time special reproductive structures are developed, consisting of seeds or spores and the accompanying parts that aid in their protection and dissemination. They find their use in continuing the race, that is, in providing for another generation of individuals.

The formation of the vegetative part and the formation of the fruiting part may be treated as separate tendencies in plant life. They rarely proceed *pari passu*, for usually if one is favored, the other is less favored. This is popularly expressed by saying that the plant runs to leaves, or runs to vine, or on the other hand that it runs to seed, or it overbears.

The portion of the plant having economic value for food belongs sometimes to the vegetative, sometimes to the reproductive side. Most fodders, and many culinary vegetables, such as cabbage, radish, lettuce and asparagus, belong to the vegetative part, while the grains, fruits and such vegetables as peas, beans, tomatoes and egg plant, belong to the reproductive side. The object of cultivation is to increase the size and quality of the part used, and it is evident, therefore, that one requirement of the husbandman must be to learn the conditions which promote the development of the particular side of the plant to which the crop in question belongs.

But it is not from the standpoint of the cultivator that the present article was written, but rather from that of the evolutionist, although the illustrations being drawn from cultivated plants make it easy to see practical applications of the conclusions.

Nutrition and development

It has been pointed out that among the lower animals, a sudden check to growth increases reproduction. I wish to expand that statement into the much broader and more widely applicable generalization that a *decrease in nutrition during the period of growth of an organism favors the development of the reproductive parts while abridging the vegetative parts.* The converse, that an increase in nutrition favors the vegetative parts while abridging the reproductive parts, is equally true.

Unimpeachable statistics are not abundant, for experiments bearing directly upon the problem have not been undertaken, and serviceable data culled from the supplementary records of other experiments are not very complete or numerous. Enough are obtainable, however, to lend very material aid toward establishing the generalization.

The cultivator employs no method so frequently for enhancing the value of his harvest

Effect of soil fertility

as increasing the fertility of the soil. It is a method of giving the plants a greater supply of nutriment, whereby they grow larger and yield more. If the principle just stated holds true, however, the increase will be greater proportionally for the stems, leaves and roots than for the seeds and fruits. The data provided by Latta from experiments conducted in Indiana bear this out. Wheat grown upon fertilized and unfertilized areas, averaging the results of three seasons, 1889–91, showed a decided gain in both straw and grain due to the richer soil; but upon examining into the relative increase of straw and grain, it is very evident that while the increase in yield of grain was considerable, it was by no means so great as the increase of straw, and that the proportion of straw to grain was, in spite of the increased yield, in reality lessened. (See table I., page 116.) Essentially the same results are evident in data obtained by Caldwell in Pennsylvania with corn, averaging the results of ten years, 1881–90, (omitting 1887, the crop being destroyed by insects). (See table II.)

A very different method of increasing yield is the treatment of seed grain before sowing to a short bath in hot water. It is especially interesting to find that this method develops the same reciprocal relations between the vegetative and reproductive parts of the harvest as in the preceding cases. In a crop of wheat (see table III) thus treated it was found, that while the total weight of straw and grain was both as a whole and separately increased by the hot water treatment, the yield of grain was lessened as compared with the yield of straw.

If we turn from the statistical method of demonstration and appeal to general observation, an overwhelming array of facts can be brought to bear.

It is a common observation that plants in too rich soil run to leaves instead of fruit. Every farmer knows that he can expect little or no grain from an excessively rich spot of ground, although the plants grow far taller and larger. The orchardist root-prunes his trees to bring them into bearing, when they prove to be unusually backward; the florist permits his plants to become pot bound to induce them to flower more freely; certain slow acting diseases, e. g., peach yellow, and cotton rust, increase and hasten the fruiting. A wide range of such general facts could be cited, familiar to every one having experience in such lines. In this connection Professor Atkinson, of Cornell University, has called attention to the longer time that elapses before spores are formed when certain bacteria are provided with more abundant food material. A customary culture gave a crop of spores in 15–20 hours, a culture with fewer germs (second dilution) in 36 hours, and one with still fewer germs (third dilution) in 48–72 hours.

The prolificacy of weeds in sterile soil is a matter of common observation. The great ragweed in poor soil produces a crop of seeds when but a few inches high, and the same is true of other weeds, especially noticeable in normally tall ones. Wild plants rooted in thin soil on rocks often bear single flowers as large as all the remainder of the plant. Analogous development may be seen in some alpine plants.

As a summary of the evidence already brought forward it is plain that the environmental conditions of plant existence have a disproportionate effect upon the two sides of plant life, the vegetative and the reproductive. An increase in available supply of food, as when the farmer fertilizes his fields, an earlier and stronger start in spring as in the case of wheat treated to a bath in hot water before sowing, the larger amount of food as when fewer and fewer bacteria are placed in same amount of culture media, all show a favoring action upon the vegetative part greater than obtains with the reproductive part. On the other hand, checking growth by root pruning or by keeping plants in undersized pots, reducing the general vitality by slow disease, and depriving the plant of sufficient soil and moisture, show a favoring action upon the reproductive part in hastening and multiplying the formation of flower and seed far in excess of the development attained by the vegetative part.

Provision for perpetuity

As a factor to insure perpetuity this law is evidently important in guarding against extermination, for the poorer the conditions for growth, the more effort the organism puts forth toward seed-bearing. One cannot fail to be impressed by the thought, however, that if this be a general law of nature, it would seem to imply that the weakest and least favored individuals, being most fruitful, are most likely to be perpetuated, which is in evident contradiction to the accepted theory of natural selection and to common observation.

There is, however, another factor which comes into play here, as a corrective of this tendency to deterioration of the race, and it is to this law that special attention will now be directed.

In all the methods of increase in rate of growth, so far brought forward, the change has been due in the main to external agencies, and the increased growth was found to be correlated with decrease in amount of reproduction. There are, however, methods of increase in rate of growth, arising from causes inherent within the organism, that tend in quite a different direction, in fact, are opposed to those already cited. The best illustration, and the only one to be given in this article, is that shown by the size of seeds. It may be stated as a general law that *large seeds produce stronger plants with a greater capacity for reproduction than small seeds of the same kind.*

Size of seeds

That larger seeds produce stronger plants, that is, plants possessing both heavier vegetative parts and larger yield of fruit, can be shown by abundant experimental data.

To be sure there is quite a common belief that the size of the seed has no material effect upon the product; that, provided a due regard be paid to vitality, any size of seed will answer the purpose of propagation. This belief is one of long standing, and is also held by some men of eminence. Sir Joseph Banks, one of the leaders in agriculture of a hundred years ago, advocated the use of small seed as answering the purpose of the farmer "as effectually as the largest." He had wheat especially in mind, and as the largest grains contain the most flour, the use of the large instead of the small seed for sowing seemed to him "unnecessary waste of human subsistence." In recent years the distinguished scientist, Haberlandt, has given expression to essentially the same opinion. He believes it is chiefly the strain and the favorable conditions for growth that influence the product, and not the weight of the seed. He doubtless represents the opinions of a large percentage of cultivators of the present time, inclusive of many good thinkers. Probably a fair statement of the general opinion would be that if a strain is to be kept up to its full vigor, or if improvement is desired, careful selection of the largest seed is indispensable, but that the difference between the use of the large and small seed will not be noticeable in the first year's crop. This view is not, however, borne out by experiment, as we will see.

Early growth

The amount and strength of the early growth from the seed has been studied by Marek, who experimented with beans and peas. The seeds were laid between moist blotting paper for seventeen days, and then measurements were taken of the length and diameter of the primary and lateral roots and of the stem. The figures all stood higher for the large seeds than for the small seeds, except for the length of the pea stem. Similar experiments were carried out by von Tautphöus, who used from two to four sizes each of wheat, barley, rye, oats, corn, beans and peas. He measured the lengths of the plumule and radicle from day to day for two weeks. His conclusion was that the larger and heavier the seed, the stronger the development. He found, however, an apparent exception in peas, as did Marek, in which the main root and stem are shorter the larger the seed. But in this case it was noted that the extra strength is expended in lateral growth, forming a thicker stem and more side rootlets, thus bringing the apparent anomaly into line. A subsequent experiment by Marek was carried somewhat further. Three sizes of English beans were planted April 24th, and their growth noted up to maturity, July 12th, with the result that the larger the seed the taller the stems and the more numerous and larger the leaves. It also occurred to him to test the force exerted by roots of seedlings in piercing the soil, and in this respect also the offspring of large seed showed marked superiority over those from small seed.

Final yield

Taking into account now the harvest, we find some excellent experiments with clear results. Trial of large and small seed roughly separated by sifting was made by Goff with onion, cauliflower, turnip and cabbage, with some gain in favor of the large seed in all but the last, and also made by Latta with wheat, who also obtained gain for the large seed.

Lehmann separated peas into three grades, large, medium and small, and planted 528 seeds of each. The germination showed that the larger seeds were possessed of greater inherent strength than the smaller, the number of seeds growing from each lot being 480, 478 and 423 respectively. The yield in peas, pods and vines, taken separately or together, and estimated per plant or as total weight, gave the largest figures for the product of the largest seed, and intermediate figures for the product of the medium seed. (See tables IV and VIII.)

An experiment in this line with corn was conducted by the writer in 1889. Thirty kernels from a single ear of white dent corn were separately weighed of which six grew that were over 400 milligrams each, and nine that were under 300 milligrams each. The product of these fifteen plants gave a greater average weight of ears for the large than for the small seed, which was also true of the cobs and kernels taken separately. (See table V).

The accompanying graphic illustration of these results brings out the differences in the weight of the kernels even more strikingly. The solid line indicates the product from large seed and the interrupted line from small seed.

The diagram as a whole shows the variation at different parts of the ear, the butt being to the left and the tip to the right.

Thus far we have given the results of experiments in all of which the seed was provided the same ground space without regard to size, and the data show that the large seeds give larger returns than the small seeds. It would be natural to suppose that if the small

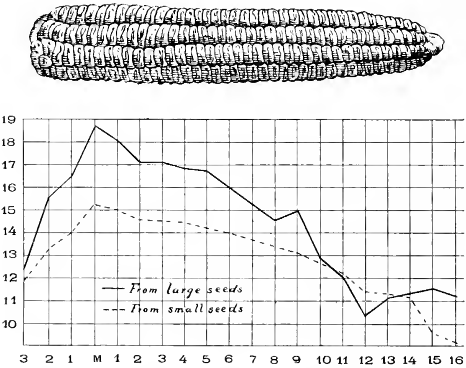


FIG. 10.—Illustrating the product from large and small seeds of corn. Data for the curves were obtained by weighing the kernels on each ear of the product by fifties from base to tip. The heaviest lot of fifty came not far from the base. These maxima were averaged and marked "M," and the next fifties right and left in succession were averaged in the same way. Figures along the bottom of the diagram show position of each fifty seeds, and along the side the average weight in grams. The position of the ear of corn above corresponds to the curves.

seeds were placed correspondingly closer together, or in other words, if the seeds were planted according to weight instead of number, the results might be reversed. For it is evident that the same weight or measure of seed will contain a much larger number in case of small seeds than of large, and in planting the small seeds will require less ground area for development, and consequently a greater number of plants can mature upon an equal space.

This phase of the question has been tested by Lehmann. He planted 188 grams each of large, medium and small peas upon equal sized plats of ground, and although there were more than twice as many small seeds as large, and nearly once and a half as many medium seeds as large, still the harvest was greatly in favor of the larger seeds, both per area and per plant. (Data in table VI., page 118).

A practical lesson is very pointedly brought out here, that in sowing farm seeds the amount of the harvest depends quite as much, and it may be more, upon the quality (size) of the individual seeds as upon the weight or measure sown per acre.

Superiority of large seeds

Is it not apparent that large seeds show great superiority over small seeds in numerous requirements that enter into successful plant life? In the first place, a larger proportion germinate, and this evidence of the possession of greater strength is followed up by more vigorous growth and the display of increased capacity for overcoming obstacles.

The resulting plants attain to greater development, as the size of leaf, length of stem and weight of any part or of the whole plant abundantly proves. It is especially noticeable that in this display of greater vigor both vegetative and reproductive parts are benefitted; and while the individual plants are making a more successful fight in promoting their present welfare, they are enabled to provide more abundantly for the next generation, by producing a better crop of seeds.

Although the proposition in relation to size of seed, with which we started, has been illustrated and established so far as present space permits, yet in order to compare more fully the tendency of the powers of the plant derived from the two sources, which for convenience we may call acquired and hereditary, the former coming from food, light, warmth, and other external conditions, and the latter from the energy stored in the seed, it is necessary to bring forward still other data. We may venture to formulate this proposed extension of the law relating to the size of seed thus: *large seeds give rise to plants with a greater deve-*

lopment of the reproductive parts, and less of vegetative parts, than small seeds do.

It is intended here to directly compare the reciprocal relations of the two sides of the plant as influenced by the parent seeds. The data may be taken by weighing the fruiting portion and comparing it with the weight of all the remainder of the plant, both done when at their best development; or other methods may be used.

Vegetative and fruiting parts compared

Excellent data are supplied from the researches of Lehmann (see table VIII). He grew large, medium and small peas, over 400 of each lot, and obtained plants that were heavier for the larger seed in both their vegetative and their reproductive parts, *i. e.*, the leaves and stalks for the vegetative part and the peas and pods for the reproductive part. And yet when the weight of the vegetative portion is compared with that of the reproductive portion of each lot, it is clear that the fruiting part has attained a stronger development in comparison to the remainder of the plant in the lots from larger seeds. To state the facts in another way, the larger seeds not only grow larger plants, but those which have fruiting parts more strongly developed than the associated vegetative parts.

Interesting data are furnished by Birner and Troschke using oats and peas, and by Marek with peas. The last investigator found that the weight of peas of first quality was nearly three-fourths of the whole harvest raised from large seeds, and only about one-third of that from small seeds. (See table VII.) In this case, therefore, the large seeds not only gave a much better total yield, but far more seed material of high grade with which to continue the strain.

Marek, in Germany, experimenting with wheat (see table IX), and Plumb, in the United States, with oats (see table X), have demonstrated the same fact. Both have provided data which show that the amount of grain in comparison with the straw was greater in case of large seeds than of small ones.

Statistical evidence of this kind might be greatly extended, although observations have rarely, if ever, been instituted with this particular end in view. Casual observations give no aid to this part of the inquiry, as the differences are obscured by other factors which stand out more prominently. What the eye cannot detect, however, is readily and unmistakably revealed by the rule and balance.

So far as data can be marshalled at present, there appears good reason to believe that large seeds, besides giving rise to larger and more fruitful plants, also possess an inherent tendency to accentuate the reproductive side of the resulting development. If peas are sown, the largest seeds not only give rise to the largest plants, with the greatest weight of pods and of seeds, but to an excess of fruitage when compared with the remainder of the plant; and in a similar way with other kinds of plants, the largest parent seeds give the greatest returns of fruit and daughter seeds, both absolutely and also in comparison with the growth of leaf, stem and root. It is to be understood, of course, that we are not attempting to deal with single plants, but with sufficiently large numbers to neutralize individuality and small accidents, which sometimes produce most unaccountable variations.

External and internal factors

If we consider the bearing of all the data now brought forward, it seems reasonable to assume that in the ultimate analysis we are dealing with acquired and inherited tendencies. In the one case the impulse or stimulus to development comes from without; it is environmental, and acts more strongly upon the somatogenic portion of the plant, while in the other case it is inherent in the organization of the seed and derived from the parent plant. Whatever the explanation of the origin may be, however, it seems certain that these two opposing factors of increase play an important role in the economy of nature. As the food supply is lessened, a greater effort is made on the part of the parent plant to enhance the chances for perpetuity; but at the same time the largest seeds, having the greatest potentiality, stand the best chance in the future struggle; and although the best nourished plants produce the fewest seeds, their greater size gives them decided advantages over seeds from starved plants. The two laws acting together, therefore, aid in maintaining the perpetuity of the species and its full measure of vigor.

TABLES.

I. Yield of Wheat on Fertilized and Unfertilized Ground.

(Weights calculated to the acre.)

Treatment.	Weight of straw in pounds.	Weight of grain in pounds.	Proportion of straw to grain.
Unfertilized	2813	1602	1:0.56
Commercial Fertilizer	4279 3971	1938 1884	1:0.45 1:0.47
Unfertilized	2727	1506	1:0.55
Stable manure	3699 3361	1818 1728	1:0.49 1:0.51
Unfertilized	2894	1512	1:0.52
Average unfertilized	2811	1540	1:0.55
Average fertilized	3880	1842	1:0.48

II. YIELD OF CORN AND WHEAT ON FERTILIZED AND UNFERTILIZED GROUND.

(Weights calculated to the acre.)

Crop.	Treatment.	Weight of stalks in pounds.	Weight of grain in pounds.	Proportion of stalks to grain.
Wheat......	Unfertilized ...	1367	958	1:0.70
	Fertilized	2119	1246	1:0.59
Corn	Unfertilized ...	2430	3498	1:1.44
	Fertilized	3144	3966	1:1.26

III. YIELD OF WHEAT WITH AND WITHOUT HOT WATER TREATMENT.

(Weights calculated to the acre.)

Treatment.	Weight of straw.	Weight of grain.	Proportion of straw to grain.
Untreated........................	3737	1716	1:0.46
Hot water bath.............	4555	1908	1:0.42

IV. PRODUCT FROM LARGE AND SMALL PEAS.

SIZE.	Wt. in grams of 100 seeds.	No. of seeds planted.	No. of plants grown	Wt. of harvest in grams.			
				Peas.	Pods.	Vine.	Total.
Large......	273	528	480	1814	437	3170	5421
Medium..	221	528	478	1495	357	2630	4482
Small	160	528	423	998	280	2010	3288

V. YIELD OF INDIAN CORN FROM LARGE AND SMALL SEED.

SIZE.	Av. Wt. of kernels in milligrams.	Av. Wt. of cobs in grams.
Large..	312	53
Small..	268	47

VI. PRODUCT FROM LARGE AND SMALL PEAS.

SIZE.	No. of peas in 188 grms	No. of plants grown.	Peas harvested in grams.	
			Per area.	Per plant.
Large	384	360	2307	6.40
Medium............	530	505	2224	4.40
Small...............	780	680	1590	2.34

VII. PRODUCT OF LARGE AND SMALL PEAS.

Size of Seed.	Wt. of peas in grams		Wt. of pods in grams	Wt. of vine in grams	Proportion of vine to fruit
	1st quality.	2d quality.			
Large	1375	554	1519	4185	1:0.83
Small	540	1045	1405	4074	1:0.76

VIII. PRODUCT OF LARGE AND SMALL PEAS.

Size of seed	Aver. wt. of single seeds in grams	No. of plants	Wt. of vine per plant in grams	Wt. of peas and pods per plant in grams	Proportion of vine to fruit
Large	2.73	480	6.60	4.69	1:0.71
Medium	2.21	478	5.50	3.87	1:0.70
Small	1.60	423	4.75	3.02	1:0.64

IX. YIELD OF WHEAT FROM LARGE AND SMALL SEED.

Size of seed	Weight of straw in grams	Weight of grain in grams	Proportion of straw to grain
Large	2411	3039	1:1.26
Small	2211	2456	1:1.11

X. YIELD OF OATS FROM LARGE AND SMALL SEED.

Size of seed	Wt. of seeds sown pr. 1000 in grams	Weight of straw in ounces	Weight of grain in ounces	Proportion of straw to grain
Large	35.4	556	190	1:0.34
Small	15.9	518	143	1:0:28

VIII.

CHLOROPHYLL AND GROWTH.*

The adult leaf manufactures about ninety-seven per cent of the food of the plant from water and carbon dioxide of the air. In the study of its functions and development it is of the greatest importance to know whether the plant can build up a leaf from food stored within its body, or the products of other leaves, or whether the products of the maturing leaf itself are necessary to enable it to complete growth.

Historical

In recognition of this fact it was one of the earlier questions taken up in the study of the physiology of the plant, and it has engaged the attention of a number of authors of the first rank. It would not be possible to recount

---

*Adapted from a lecture on "The Relation of the Growth of Leaves and the Chlorophyll Function" before the Linnean Society of London, June 18, 1896.

here the exact results attained by each one, except to note that the first investigation of the subject was made by de Saussure in 1804, and from his experiments upon leafy shoots of woody plants he was led to assert that leaves may not carry out full development, or maintain normal existence when the food-forming processes were inhibited. Subsequently in dealing with various phases of the question Boehm, Kraus, Rauwenhoff, Stebler and Vöchting arrived at results in harmony with those of de Saussure. On the other hand Batalin, Vines, and Jost have reached results quite to the contrary. Corenwinder made two series of experiments, one series resulting positively, the other negatively.

The experiments which would be of value in the decision of this question consist in allowing young leaves of many species of plants to develop under such conditions that no food can be formed.

Methods of experimentation

To place leaves under such conditions that the chlorophyll-bearing cells may not carry on the formation of food, and that all growth must be carried on by means of food brought from a distant portion of the plant, several methods may be used, viz.: the leaf may be enclosed in a dark chamber consisting of a small box which will exclude all rays of light from the leaf, without which the chlorophyll is inactive, or one side of this box may consist of a sheet of blue glass which would permit only the blue-violet rays to pass and thus allow but a small amount of food to be formed; the plant may be grown in a substratum, or nutritive solution, from which iron salts have been omitted, and as a consequence no chlorophyll would be formed in the leaves; the shoot or the entire plant may be placed in atmosphere made free from carbon dioxide by means of chemical reagents. Of these methods chief reliance is to be placed upon those in which light is excluded from the plant, and in which carbon dioxide is excluded from the leaves.

The former method induces such profound disturbances of the chemical processes and regulatory mechanism as to place the plant under highly pathological conditions. The more conclusive experiments are those by which branches, or entire plants are introduced into a sealed chamber, which is kept free from carbon dioxide by means of solutions of potassium hydrate, and the ventilating openings were guarded with tubulures similarly provided. The exact method of dealing with the plant may be illustrated by the following description of the treatment of *Arisæma triphyllum*.

The large tuberous corms were gathered

from the soil in woods in October, and placed in a cold house until February 1st, when they were placed in a temperate room, beginning growth two weeks later. Ordinarily the plant sends up one or two leaf-stalks thirty to fifty centimeters in height bearing the trifoliate lamina, with an area of one hundred to two hundred and fifty square centimeters and a scape twenty to forty centimeters in height, bearing a spadix enclosed by a hooded spathe. The hood contains a large proportion of chlorophyll and sustains in greater part the functional activity of the leaf, and exhibits similar reactions to light and modified atmospheres. The correlation of growth is such that the scape and inflorescence attain full size within ten days from the opening of the bud, and the greater part of the leaf-expansion follows in the next ten days. During the first ten days the starch stored in the corm is drawn upon to furnish an increasing amount of material for the growth of the aerial organs; during the next ten days a decreasing amount is drawn from the corm, and usually after that time a stream of plastic material sets in the opposite direction from the laminæ, which is in part stored in the corm and in part used in the development of the lateral offshoots, which begin development at this time.

Buds which had attained the height of ten cm. were brought through an opening in a glass plate allowed to rest upon the top of the pot in which the plant was grown. The opening around the bud was securely sealed by means of wax, molding clay, or the following device: A cork stopper was perforated with an opening larger than the ultimate size of the sheathing petioles, and the upper part of the opening was enlarged to form a cup-shaped cavity. After the cork had been saturated with paraffin it was placed in the glass plate and enclosing the bud, the bottom of the cup-shaped cavity covered with a loose layer of asbestos or glass-wool, and over this was poured a layer of mercury five millimeters in thickness, which was covered with water to prevent injurious action of the metal.

This method of sealing exerted no harmful pressure on the plant and allowed it to expand in a normal manner—a very important consideration in experiment where soft-stemmed herbaceous plants were used. The plants were covered with a bell-jar of a capacity of four to eight liters sealed to the glass plate, and provided with two tubulures. To one tubulure was fitted a series of potassium tubes or vessels containing potassium hydrate in solid form, and saturating a mass of asbestos fiber. The second tubulure was con-

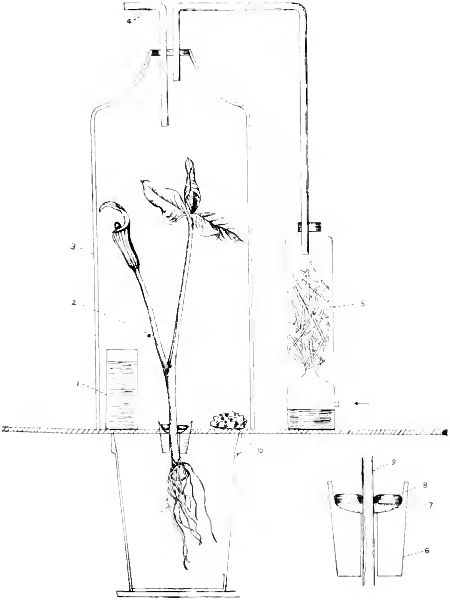


FIG. 12.—Apparatus for growing plants in an atmosphere free from carbon dioxide: 1. Dish containing solution of potassium hydrate. 2. Specimen of *Arisæma triphyllum* 10 days after opening of bud. 3. Receiver of 10 liters capacity. 4. Outlet-tube connected with aspirator. 5. Sticks of potassium hydrate and moist asbestos fiber. 6–9. Detail of method for sealing plant in receiver. 6. Cork. 7. Asbestos fiber. 8. Mercury. 9. Stem of plant. 10. Sponge saturated with water.

nected with an aspirator, by which the air was occasionally renewed. Several vessels containing two to five grams of solid potassium hydrate were placed inside of the bell-jar. The potassium absorbed water rapidly and soon dissolved. To provide against the dryness of the inclosed air thus induced a large sponge saturated with water was placed near the plant. These precautions furnish normal conditions except in the composition of the air, from which almost all of the carbon dioxide is taken. It is of course understood that the plant is constantly giving off this substance as a result of its oxidation processes, and it may be imagined as forming a diffuse stream from the plant to the vessels containing the potassium solutions. The amount actually present in the bell-jar at any time however must have been quite small. The potassium solutions were renewed once each week.

Growth in the absence of carbon dioxide

Plants of Arisæma grown in the apparatus described above exhibited a normal development during the opening of the bud, and the preliminary stages of the unfolding of the leaves, which are crumpled in the bud during a period of two to four days. The development process was arrested, however, at a very early stage, and the laminæ were unfolded only so far as to expose the ventral surface, and the crumpled appearance was not lost. In ten to fourteen days after the beginning of the experiment, the laminæ assumed a yellowish color, as a result of the decomposition of the chlorophyll, and other signs of deterioration appeared ending in the death of the organ a few days later.

The structure and arrangement of the tissues had undergone but little differentiation from the forms present in the folded condition, and differed from the normal forms by the size of the single layer of palisade cells and the globular form of the spongy parenchyma, and seemed moreover to be in a state of hunger. It is to be noted that the sheathing spathe also undergoes similar abnormalities, but since it is never folded, and since its development consists principally of a longitudinal expansion of the cylindrical sheath and hooded tip, the more apparent deviation is one of size. The thickness is such as to prevent crumpling. It is to be noted moreover that the development of the spathe is usually accomplished before the leaves have begun maximal growth under normal conditions. If mature leaves were sealed into an apparatus similar to the above, no changes were discernible until fifteen to twenty days later. At this time the starch, and other carbohydrates with which they were richly loaded, having been used, a shrinkage was noticeable and the leaf was found to be in a state of hunger. On restor-

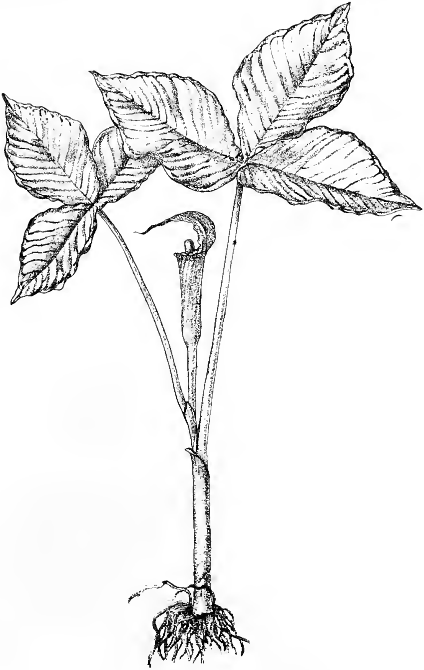


Fig. 13.—Arisæma triphyllum grown in open air.

ation to a normal atmosphere before decay had begun they were restored to a normal condition.

In order to cultivate plants in darkness but under otherwise approximately equal conditions, a bottomless chamber of galvanized iron was constructed, and allowed to rest on a metal bench covered with a layer of moist sand. This dark chamber was placed in such position that the sun's rays did not strike it, and was attached to a simple pulley, by which it might be raised and lowered to allow an occasional examination of the plants.

Effect of darkness

Awakening plants with corms five centimeters long, when placed in this chamber, showed a greatly exaggerated development of the bud scales, a rapid elongation of the scapes and petioles attaining a length nearly double the normal in five to eight days. The daily increase of these organs in some instances amounted to twelve centimeters. The laminæ sometimes were carried completely or almost completely through the unfolding stage, but were rarely able to attain a full extension, or area, much in excess of the folded condition, and owing to the absence of the directive influence of light, assumed various positions with respect to the horizontal. The process of decay did not begin until fifteen to twenty days after the beginning of the experiments, and if the plants, after unfolding, were brought into diffuse light with gradually increasing intensity, the normal appearance was finally resumed. The color of the etiolated leaves was of the customary waxy yellow, upon which the reddish purple color areas characteristic of the external tissue were boldly apparent. The spathe exhibited great variety of reaction, but in general it did not attain full development. This was the invariable result if this member alone was enclosed in a covering excluding light. And although not responsive to the directive action of light or gravity, it assumed an upright or outwardly recurved position in darkness.

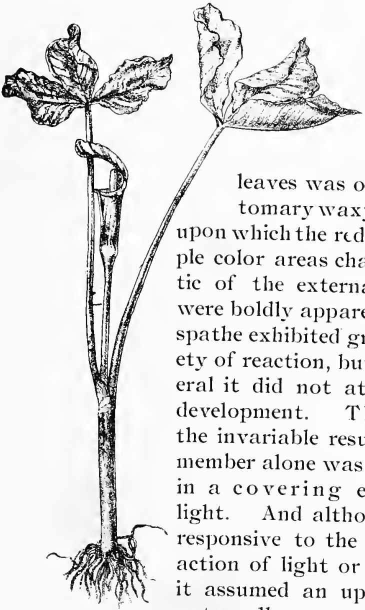


FIG. 14.—Arisæma triphyllum grown in an atmosphere free from carbon dioxide.

If plants with mature leaves were placed in the dark chamber a renewed activity of the petioles occurred, lasting two to three days, and in four or five days the laminæ began to bleach and decay.

Plants grown in a diffuse light exhibited features of development in general analogous to those shown in darkness. Elongation of the petioles, and scape, and dwarfing of the spathe especially of the overarching hood occurred. Still more marked, however, was the restriction of the area of the laminæ, corresponding to the intensity of the light.

In order to determine how far the diversion of food from certain members, and its concentration in one might affect its development, recourse was had to the removal of two of the three aerial members of plants grown in a dark chamber. If the leaves were removed no changes resulted in the development of the scape or spathe. The latter organ was dwarfed, although not more than thirty centimeters from the stored food in the corm. If the scape and one leaf were removed from a plant emerging from the bud in a dark chamber, the remaining leaf exhibited a development quite similar to those of entire plants under similar circumstances, except that the petiole reached a length much in excess of those on an entire plant. The laminæ were extended in such manner as to cause the disappearance of the angles of the leaf-folding in

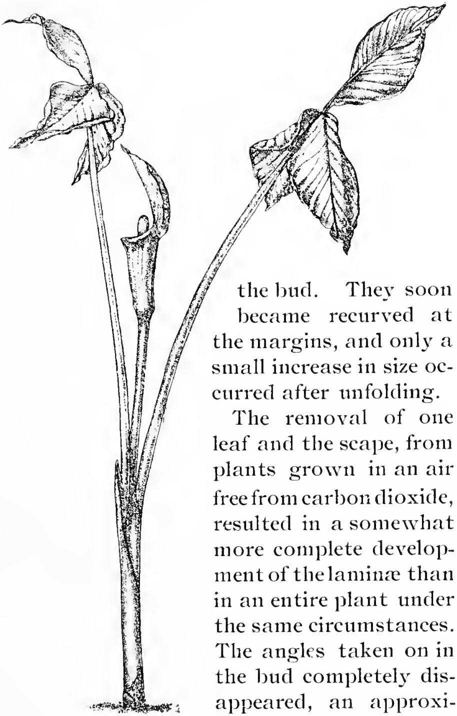


FIG. 15.—Arisæma triphyllum grown in darkness.

the bud. They soon became recurved at the margins, and only a small increase in size occurred after unfolding.

The removal of one leaf and the scape, from plants grown in an air free from carbon dioxide, resulted in a somewhat more complete development of the laminæ than in an entire plant under the same circumstances. The angles taken on in the bud completely disappeared, an approximately normal green color, and a position quite

Total results with Arisaema

similar to that of plants in free air was assumed. The amount of food available for development must have been two or three times as great as that usually afforded a single leaf. In twelve to fourteen days, however, the laminæ began to exhibit signs of deterioration; but if at this time they were removed from the apparatus and placed in the open air the normal condition was regained and development proceeded in the usual manner.

It is to be seen as the result of the foregoing experiments that the leaves on an entire plant of Arisæma are incapable of development, beyond the unfolding stage in an atmosphere free from carbon dioxide. If two of the three aerial members are removed, the remaining one may attain a more advanced stage of development. In darkness the petioles are greatly elongated, and the laminæ unfold, but no expan-

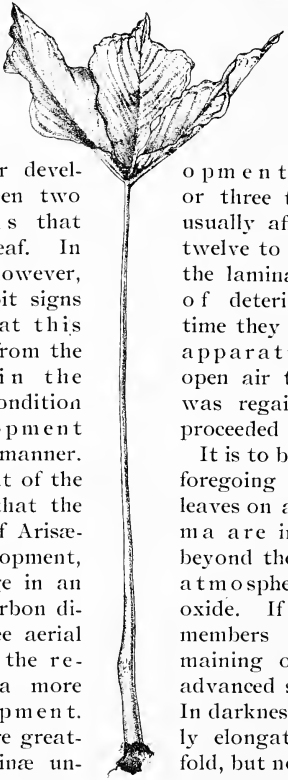


Fig. 16.—Arisæma triphyllum with flower stalk and one leaf cut away, in an atmosphere free from carbon dioxide.

sion of their area ensues. The removal of concurrent members results in an exaggerated extension of the petiole, but has no effect on the laminæ. A similar result is obtained with the spathe under both conditions. It is to be noted that in light the removal of concurrent organs results in an increased development of the laminæ, and in darkness of the petiole.

Calla palustris is a plant consisting of a creeping rhizome one to two centimeters in thickness, from the apex of which arise a few cordate leaves with petioles fifteen to twenty centimeters long and one or more solitary scapes eight to fifteen centimeters high. The relatively large rhizomes are filled with stored food.

Plants brought into a warm house and placed under the apparatus described above exhibited a development of the petioles and laminæ during a period of ten to twelve days that resulted in the formation of perfect leaves. The continued existence of the plant, however, under such conditions was impossible because of the destruction of the stored food by fermentation.

Results with Calla

In the dark chamber the slight extension of the petioles occurred while the laminæ attained a size equal to those in the open air, although they were recurved at the margins. No effects were obtained by the removal of the concurrent members.

Seedlings of Zea mais, with the shoot emerging from the cotyledon, were placed entirely inside of the apparatus, where they remained for a period of eight to twelve days without carbon dioxide. In such experiments the plant evidently could carry on the extension of the shoot only so long as food could be obtained from the seed. To determine the actual constructive value of the stored food in the seed, plants were allowed to remain in the apparatus until the leaves exhibited indications of deterioration, which was eleven to fourteen days after the beginning of the experiment. The plants were more slender and the leaves narrower than in control plants. A small amount of starch was still to be observed in the seeds, both in the plants grown in the air free from carbon dioxide and in normally grown plants of the same age.

Results with Zea

In darkness the stems are elongated and the etiolated leaves are much narrower than in normal plants.

Specimens of Phoenix dactylifera were obtained by the germination of the seeds of the commercial date, a process requiring from twenty to thirty days. The seed consists largely of reserve cellulose, and according to Haberlandt is sufficient to allow the formation of a primary root more than a meter in length, before the unfolding of the first foliage leaf in the natural habitat of the plant. In planting the seeds in moist soil this excessive development of the roots was useless, and foliage leaves began to unfold when the root had attained a length of a few centimeters.

Results with Phoenix

The seedlings grown in small pots were placed inside the apparatus and kept free from carbon dioxide for a period of thirty to forty days. The leaves, which at the beginning of the experiment were emerging from the sheathing scale, exposing a tip one to two centimeters in length, attained a length of fifteen centimeters and a complete normal expansion corresponding to that of organs grown in the open air. Such leaves usually attain a length of twenty to thirty centimeters by a slow process of growth lasting several months, and my experiment, therefore, covers only the earlier stages of development.

Specimens placed in a dark chamber during a period of thirty to forty days exhibited an exaggerated elongation of the cotyledonary and leaf scales, as well as the leaf itself, which retained its lamina in the plicately folded position. The increase in length amounted to twenty to thirty per cent more than in control plants.

It is safe to conclude that the development of seedlings of corn and date may proceed so long as the necessary amount of plastic material is available.

In such manner many specimens each of *Arisæma triphyllum*, *Calla palustris*, *Lilium splendidum*, *Trillium erectum* and *T. erythrocarpum*, *Isopyrum biternatum*, *Oxalis floribunda* and *O. vespertilionis*, *Justitia sp.*, *Hibiscus rosa-sinensis*, *Zea mais* and *Phœnix dactylifera* were grown. Of these it was found that leaves of Arisæma perish in an air free from carbon dioxide at the beginning of the unfolding stage; leaves of Calla, Lilium and Trillium attain normal stature but are incapable of further existence. Leaves of Zea carry on normal development during a period of ten to twelve days, but in this time attain each a stature inferior to that of control plants, and then begin to deteriorate. Leaves of Oxalis, Isopyrum, Hibiscus, and Justitia attained normal stature, and were capable of continued existence at the expense of food derived from storage tracts, or active chlorophyll-bearing tissues.

In the ordinary course of leaf development growth is carried from the rudimentary stage to the unfolding of the lamina at the expense of food derived from storage organs or from the main axis. Ordinarily the supply of food transported to the developing leaf is supple-

Ordinary course of growth

mented early in the unfolding stage, by food formed by the young lamina. In a short time the supplementary amount from the leaf is entirely sufficient for its own needs for constructive purposes; and at this time the reserve food transported to the leaf has undergone great diminution. When a leaf is placed under such conditions that the lamina is inactive, the amount of reserve material which can be transported to the leaf will, in many instances, be found insufficient for its needs. This will be best understood when it is stated that the amount used at this time is many times greater than that needed in the earlier stages, and moreover, that the difficulties of translocation have vastly increased. Thus by the elongation of the petioles—amounting from two to ten centimeters daily in Arisæma—the distance between the stored food in the corm and the point of consumption in the leaf-blade has been greatly exaggerated. Then again the amount of stored food has been materially reduced by consumption and the intervention of destructive fermentations.

It is apparent without recourse to a further recital of the detail of the experiments, that, if at a time when the available food supply is diminishing to a minimum, and the difficulties attendant on translocation are becoming greater, the needs of the leaf should suddenly mount to a maximum, the supply may be found insufficient, unless supplanted by the food-forming activity of the lamina, and deterioration of the tissues, due to starvation, must ensue.

Growth with insufficient nutrition

The stage in which the translocated food becomes inadequate is not identical in all species. Thus it appears from my experiments that relatively small leaves, or those with less rapid development, or with a readily available supply of food material, may attain a much more advanced stage than those in which the contrary conditions prevail. The conditions may be so favorably disposed as to allow not only of the complete development of the leaf, but also of its continued maintenance under conditions of functional inactivity with respect to the chlorophyll.

It is to be noted that the phrase, "functional inactivity," is used in a relative, not an absolute sense. The portion of the plant enclosed in the apparatus is constantly emitting carbon dioxide; which is rapidly absorbed by the potassium solutions. Under such circumstances the carbon dioxide may be imagined as forming a diffuse stream from the plant to the potassium, and the amount actually available by the chlorophyll-bearing cells at any one time must be extremely small. Some doubt still exists as to the cause of the rapid deterioration of inactive leaves. It is held by some that it is due to the harmful substances set free in the decomposition of chlorophyll, while it is asserted on the other hand that the breaking up of the chlorophyll is a result of starvation and functional inactivity.

Finally it may be said that in order to account for the reactions of inactive leaves in light and in darkness it is necessary to predicate the intervention of the regulatory mechanism in a manner almost entirely specific. Such action has been described in Arisæma, which on the removal of concurrent members, develops laminæ in the light and petioles in darkness. That is to say, it should not be taken for granted that all of the changes described in the above plants are due simply to disturbances of the nutritive processes, but represent to some extent an irritable response of the plant to the unusual conditions under which it is placed and from which it attempts to free itself. Thus the excessive elongation of the stems and petioles in darkness seems very clearly an adaptive modification for lifting the leaf-blades and chlorophyll out of obscurity and into sunlight, and may not be accounted for on any other grounds. (This theory of elongation as an adaptive modification was originally proposed by Godlewski in 1873.) The results of the foregoing discussion may be briefly summarized in the following paragraphs.

Conclusions

The relation of the growth of leaves to their food-forming power, is such that some are able to carry development no further than the beginning of the unfolding stage of the laminæ; others are able to carry the development to an approximately normal stature; and others are capable not only of the development to normal stature but also of continued maintenance under conditions of enforced inactivity.

This varying reaction of leaves is dependent upon a series of conditions which may be included in the phrase "availability of the food supply."

The deterioration of certain leaves under conditions of forced inactivity is due to insufficient nutrition and is accompanied by the disintegration of the chlorophyll.

The behavior of inactive leaves in light exhibits no similarities or correspondence, in simple growth or upon the intervention of correlation processes, to their behavior in darkness.

Material constructed in active chlorophyll areas and stored in special organs may be transported to inactive chlorophyll-bearing organs in some plants in light and in darkness, and be used in such manner as to allow of the perfect development of these organs.

The removal of concurrent members in darkness may have no effect, may cause an exaggerated development of the petioles, or may result in the perfect development of the entire leaf. The nature of the regulatory mechanism in each instance is entirely specific.

It is possible for some plants to form perfect leaves in darkness, when some of the branches only are darkened, and for others when the entire plant is etiolated. It is thus shown that no invariable connection exists between the phototonic condition and leaf-development.

Placing a leaf under such conditions that it cannot construct food sets in motion the specific regulatory mechanism of the organism in such a manner that the plastic material may be withdrawn, and the organ cast off. An exaggerated development of the petioles may be induced in darkness by this mechanism.

The excessive elongation of the stems and petioles in darkness is to be regarded as a phenomenon of adaptation by which the leaf surfaces would be placed beyond any object intervening between them and the light.

IX

LEAVES IN SPRING, SUMMER AND AUTUMN.*

The yearly miracle of the appearance of innumerable shades and hues of green in awakening vegetation, exerts a mysterious influence amounting to fascination over the human race. A fascination made strong by the inherited experience of untold generations of forest-dwelling ancestors, reaching backward the entire present geologic period, and which grows in intensity as we creep from the creation to millenium.

Our vague and emotional inherited interest in the annual revivification of the vegetable world becomes vividly intense and direct, however, when it is learned that the universal blush of green is due to the most important coloring substance in the world—chlorophyll.

---

*Adapted from "Green Color of Plants," *Harper's Magazine*, April, 1897, and "Autumn Leaves," same journal, October, 1897.

It is literally true that the existence of every living thing is ultimately dependent upon the activity of plant-green.

The actual conditions are as follows: the elements which enter into the construction of protoplasm are carbon, nitrogen, oxygen, hydrogen and phosphorus. These elements are found in the form of free gases or simple compounds in the soil and atmosphere, and cannot be used by protoplasm until built up into the form of complex compounds. The construction of compounds indispensable for the nutrition of plants and animals does not result from mere proximity of the elements, since those most highly desirable are chemically inactive to one another, and will unite only under the influence of energy from without. The substances are selected and absorbed in their elemental condition by the plants, and in the crucible of the cell, glowing with potentiality absorbed from sunlight, are fused together and made ready for assimilation by protoplasm.

Importance of chlorophyll

The most important synthetic process is that which results in the formation of carbon hydrates from carbon dioxide and water. If this process were carried on by means of energy furnished by the activity of the protoplasm, the expenditure entailed would overbalance the benefits gained by the assimilation of the substances formed. It is clearly apparent, therefore, that the organism must receive energy from some external source and must be able to convert this energy into the forms necessary to promote chemical synthesis. Sunlight is a universal source of energy and green plants are the only organism capable of converting its rays into available energy. The transformation is effected by means of chlorophyll.

It is true that a few lower forms, inclusive of the "sulphur" and "iron" bacteria among plants and some of the lower forms among animals, are able to accomplish the construction of carbohydrates, but the total result of their activity is indefinitely unimportant, and is doubtless at the cost of energy furnished by complex compounds derived from other plants and animals.

Animals and non-green plants are therefore dependent, directly or indirectly, upon the substances formed by the green plants for food. This physiological characteristic has led a recent German writer to classify the fungi (mushrooms, toadstools, molds, etc.) among animals. A classification that would work privation to the vegetarian if seriously accepted.

The action of chlorophyll may best be understood when its physical properties are demonstrated. In order to do this a solution of the substance is obtained by placing a gram of chopped leaves of grass or geranium in a few cubic centimeters of alcohol for an hour. The solution will be a bright, clear green color, and when the vessel containing it is held in such a manner that the sunlight is reflected from the surface of the liquid it will appear blood-red, due to its property of *fluorescence*, that of changing the wave lengths of the violet end of the spectrum in such a manner as to make them coincide with those of the red end. It is by examination of light which has passed through a solution of chlorophyll, however, that the greatest insight into its physical properties may be obtained. If such a ray is passed through a prism and spread upon a screen, it may be seen that there are several intervals of dark bands in the spectrum. The rays which would have occupied these spaces have been absorbed by the chlorophyll and converted into heat and other forms of energy. This energy is directly available to the protoplasm containing the chlorophyll. As a necessary concomitant of its physical properties, chlorophyll is usually only to be found in organs exposed to the light. It would not only be useless but dangerous elsewhere, as it disintegrates in darkness into substances hurtful to the organism.

Properties of chlorophyll

It is found in greatest quantity in leaves in layers of special cells beneath the epidermis. It is not distributed throughout the entire cell, but occurs in the masses of protoplasm which the botanist terms *chloroplasts*. The chloroplasts are sponge-like structures, and the chlorophyll is to be found in solution in an oil in the interstices of the protoplasmic sponge.

Chlorophyll is an extremely complex substance and correspondingly unstable. Hence as soon as the chemist extracts it from the plant in the attempt to make an analysis, disintegration sets in and he is no longer dealing with chlorophyll, but with the substances derived from it by decomposition. Investigation upon the nature and activity of plant-green has been in progress more than a century, yet its exact chemical composition is unknown. It contains carbon, oxygen, hydrogen, nitrogen, magnesium and phosphorus, but the proportions and arrangement of the atoms of each element in the molecule of chlorophyll have not been exactly ascertained.

The beautiful and striking colors of autumnal foliage are due in greater part to substances formed by the disintegration of chlorophyll. The many thousands of tints of green leaves are due to a number of causes.

In some cases the outer layers of cells of the the leaf, or merely the walls of the cells, may contain coloring matter. The number and size of the chloroplasts, and consequently the amount of the chlorophyll, may be greater in some leaves than in others. Besides, the chloroplasts may be moved about in the cell and their distance from the surface of the leaf altered, or they may be placed in lines perpendicular or parallel to the surface. In this manner the infinite and elusive variations of color, so fascinating to the lover of nature, are produced in vegetation. The color of a leaf may vary momentarily throughout the day, as indeed does that of the entire landscape to the puzzled artist.

Varying tints

The cell sap which bathes the chloroplast in the leaves contains carbon dioxide absorbed from the air. When the sun shines upon a leaf the rays pass through the epidermis and penetrate the cells containing the chloroplasts. The chlorophyll converts a large proportion of the light into heat and other forms of energy. With this energy as a motive power the protoplasm of the chloroplast withdraws water and carbon dioxide from the surrounding cell sap and combines them in such manner that a substance known as formic aldehyde is formed and oxygen is liberated. In a second stage the atoms of carbon, hy-

Synthesis of food

drogen and oxygen in six molecules of formic aldehyde are rearranged in one complex molecule forming sugar, from which the other carbohydrates are easily derived. Protoplasm may not be formed from sugar alone, since nitrogen is a very important constituent of living substance. It is probable that nitrogenous substances are sometimes formed by a variation in the earlier stages of the process described above, by which nitrogen is substituted for oxygen in the molecule of formic aldehyde. Such a substitution would result in the formation of hydrocyanic acid. The recent discovery of this deadly acid in the leaves of a tropical palm lends favor to the hypothesis. It may be formed in many green leaves, but, like the earlier substances in the synthesis of sugar may undergo instant transformation and thus escape detection.

The absorption of carbon dioxide from the air, and the excretion of oxygen by vegetation is sufficient to balance the opposite process in animals, and hence the composition of the atmosphere remains unchanged. It is a notable fact that plants thrive in an atmosphere containing a much larger proportion of carbon dioxide than is found in the atmosphere at the present time. Normal air contains but one-twenty-fifth of one per cent of this gas, and the food-forming power of the plant is greatest in an atmosphere containing two hundred times as much, seven to ten per cent by volume. The power of using larger proportions of carbon dioxide was doubtless acquired in an earlier geologic period, and was adapted to the conditions then prevalent.

Acquisition of chlorophyll

The botanist finds himself lost in a maze of conjecture if he endeavors to trace backward the development of plants and determine the point at which they gained the power to form chlorophyll. It is quite certain that the simpler ancestral forms, which consisted of simple masses of protoplasm, were not able to construct and maintain a substance so complex and unstable as chlorophyll. The advent of this substance into the living world marked the attainment of a comparatively advanced stage of development. A tinge of probability lends itself to the theory that the protoplasm of all simple organisms which existed in a far distant age of the world's history were able to accomplish the synthesis of complex from simple compounds, and that the "sulphur" and "iron" bacteria are but remnants of this primitive physiological type.

Still another problem is to be found in the presence of chlorophyll in a number of the lower forms of animals. A fact which renders the task of making categorical distinction between plants and animals still more difficult.

The chlorophyll is not found in the organisms where the two kingdoms meet, but occurs in animals which have attained a high degree of development, such as the vorticella, and fresh-water sponges. It is supposed that the chloroplasts in these animals are descended from others derived from unicellular plants captured by the animals in an earlier stage of the development.

Autumnal leaf-fall

To a naturalist one of the striking and spectacular features in the history of living things is the manner in which vegetation puts on, wears, and discards its leafy coverings of green. The season begins with the assumption of an all prevalent, delicate green covering, composed of millions of irregular laminæ of every conceivable form, which hide the roughnesses of gnarled and crooked branches, the flinty soil and ragged moor. With the advancement of the leaves toward maturity, the earlier and more delicate tint deepens into a rich satisfying green that fills the eye, and then fades away in the long summer heat to dull gray and bluish greens, dust-colored and bearing the marks of many subduing struggles with wind and storm. The first breath of frost is the signal for a change on slopes, valleys, forests and meadows, by which the dull monotones are at once converted into a harmonious magnificence of color, as if by magic.

The splendor of the colored markings of the plants and animals of the tropics is a well worn theme with amateurs, but it does not stand comparison with the beauty of the autumnal tints of foliage of the north temperate zone. either in variety or richness of tone. Furthermore it may be said that the display offered by the forests east, west and south of the Great Lakes in North America is not duplicated on any part of the globe. The vegetation of the valleys and mountain slopes of the basins of the Rhine and Danube gives an exhibit which is only less beautiful because of the smaller number of species, and which is less remarked because of its shorter duration.

On some portions of the earth's surface within the tropics, where no great or sharply defined alterations in seasons occur, vegetation pursues a fairly even course all the year round. Each leaf retains its place on the stem until the full limit of its usefulness or endurance has been reached, and then withered and woody it falls to the ground in company with such of its fellows as may have reached a similar stage at the same time. Of the myriads of leaves borne by any tree, not so many are cast at one time, as to bare the branches or make any apparent diminution of their number, and many plants exhibit flowers and fruit as well during the year. Such favorable conditions for growth are found only in certain circumscribed areas, as a large proportion of the earth's surface within the tropics has a supply of moisture during one part of the year wholly insufficient for the needs of growing vegetation, and on the approach of this dry season the plants in rich regions discard all or a greater part of their leaf surfaces. This shedding of leaves is not attended by many of the more prominent features of autumnal leaves, however.

A portion of the year in the temperate zone is characterized by a protracted low temperature which is unfavorable to even the simpler forms of activity of protoplasm, and renders the presence of a great expanse of leaf surface not only useless but dangerous to plants growing in those zones, and provision is made for the economical disposition of the foliage.

Yearly rhythm

Plants growing in regions with this alternation of seasons have modified the primitive rhythm of protoplasm in such manner that they manifest annual periods of rest and activity. While this yearly period has been acquired in somewhat recent time perhaps, yet it is most firmly fixed in the constitution of the plant as may be demonstrated if an attempt is made to grow a deciduous tree or shrub in a conservatory after removal from its native forest.

The full significance and real causes of the phenomena attendant upon the fall of leaves in autumn may only be comprehended, when the uses subserved by the leaf, and the forms of activity carried on underneath its surfaces are recalled.

Activity of leaf

All the summer long the green surfaces have been lifted to the sunlight and by the magic of its potent touch have taken in carbon dioxide from the air and combined it with water in such manner as to form highly plastic substances, which flowing steadily to distant portions of the plant have by the subtle alchemy of protoplasm become converted into wood, fiber, and cork, hard, firm and light as such things only may be.

The scene of activity in the leaf is laid in the columnar and variously distorted cells containing the green color bodies (chloroplasts) and these cells are rich in protoplasm, albuminoids and sugar. A steady stream of water is sucked up by the minute hairs on the rootlets, and containing mineral salts in solution, has poured upward into these cells during the entire season. A small amount of the water has been used in combination with carbon dioxide in forming food, but by far the greater proportion has been evaporated through the membranous walls into the air-spaces, and passes outward through the breathing pores (stomata) into the open air in the form of vapor. The quantity of water poured into a thirsty sky in the heat of a midsummer day is by no means inconsiderable, even in smaller plants, and in a full-grown poplar tree may amount to a barrel. As the water enters the roots it contains from one-ten-thousandth to a thousandth part of its weight of potassium, calcium, and magnesium salts in solution, and it evaporates into the air leaving the mineral compounds in the plant. The minerals serve important uses in building up protoplasm, and facilitating the diffusion of food substances from one part of the plant to another. Eventually a large proportion of these substances accumulate in layers on or in the cell wall, or as crystals in the cell cavity, particularly in the leaf, in such condition as to be of but little use to the organism, and it would be benefited by being freed from this superfluous matter. Besides the inward condition of the leaf, changes in the environmental conditions make it highly important that the plant should dispense with its leafy extensions.

With the approach of the close of the growing season, the outward conditions have undergone a gradual and thorough change and the tree finds its enormous leaf surface throwing water into the surrounding dry atmosphere much faster than it may be taken from the soil by the delicate absorbing organs.

Cause of leaf-fall

The approach of autumn brings cool nights and a consequent great radiation of heat from the soil. The chilled root hairs in the soil are unable to take the necessary supply of water, and whenever the supply of moisture coursing upward through the sinuous roots and tall stems becomes less than that evaporated, adjustment must be made or damage will ensue. The plant is a most delicately self-regulating organism. It cannot increase the water supply, but it may and does decrease the evaporating surface by casting or shedding the leaves, a reaction which it exhibits to other conditions as well. Like the true seaman, however, the plant does not shorten sail by cutting away its canvas, but by a deliberate and well-timed series of processes, withdraws all of the substances from the leaf which may be useful to it, back into its body before it discards the empty sheets of cells and woody fibers of the petiole and lamina.

Before proceeding to a description of the mechanism of leaf-fall, it may be well to call attention to the popular and erroneous idea that the coloring and casting of autumnal leaves is due to the action of frost. It is true that the phenomena of autumnal leaf-fall are due to low temperatures, but as may be seen from the above, the defoliation of the plant is not a reaction to the cold, but is an adjustment to the limited water supply furnished by the chilled roots. The reduction of the water supply and the beginning of the processes leading to defoliation occur a long time before the temperature of the air is depressed to the freezing point, or the formation of frost. The influence of low temperatures upon the plant is illustrated by the manner in which leaves of tobacco and melon plants blacken and die as the result of cool nights before the occurrence of frost. These plants transpire a relatively large amount of water from the broad leaves, and if the temperature of the soil descends to forty degrees Fahrenheit, the roots are unable to take up the necessary supply of water, and the leaves are literally dried out, though they are incorrectly described as frozen or frosted by gardeners.

Withdrawal of leaf-substance

The casting of the leaf is not a sudden and quick response to any single depression of the temperature, but is brought about by a complex interplay of processes begun days or perhaps weeks before any external changes are to be seen. The leaf is rich in two classes of substances, one of which is of no further benefit to it, and another which it has constructed at great expense of energy, and which is in a form of the highest possible usefulness to the plant. To this class belong the compounds in the protoplasm, the green color bodies, and whatever surplus food may not have been previously conveyed away. The substances which the plant must needs discard are in the form of nearly insoluble crystals, and, by remaining in position in the leaf, drop with it to the ground and pass into that great complex laboratory of the soil where by slow methods of disintegration, useful elements are set free and once again may be taken up by the tree and travel their devious course through root hairs along the sinuous roots and up through million-celled columns of the trunk out through the twigs to the leaves.

The plastic substances within the leaf which would be a loss to the plant if thrown away, undergo quite a different series of changes. These substances are in the extremest parts of the leaf, and to pass into the plant body, must penetrate many hundreds of membranes by diffusion into the long conducting cells around the ribs or nerves, and then down into the twigs and stems. The successful retreat of this great mass of valuable matter is not a simple problem. These substances contain nitrogen as a part of their compounds and as a consequence are very readily broken down when exposed to the sunlight. In the living normal leaf the green color forms a most effectual shield from the effects of the rays, but when the retreat is begun, one of the first steps results in the disintegration of the chlorophyll. This would allow the fierce rays of the September sun to strike directly through the broad expanses of the leaf, destroying all within, were not other means provided for protection. In the first place, when the chlorophyll breaks down, cyanophyll (blue-green) is formed, anthocyan (blue-red) is constructed by the protoplasm, and at the same time the yellow lipochromes present in the cells, chiefly xanthophyll, become visible and take a share in protecting the plastic substances, which absorb the sun's rays in the same manner as the chlorophyll, so that the leaf exhibits outwardly a gorgeous panoply of color in reds, yellow, and bronzes that makes up the autumnal display. From the wild riot of tints shown by a clump of trees or shrubs, the erroneous impression might be gained that the colors are accidental in their occurrence. This is far from the case, however. The key-note of color in any species is constant, with minor and local variations. The birches are a golden yellow, oaks vary through yellow-orange to reddish brown, the red maple

Color as a protecting screen

a dark red, the tulip tree a light yellow, hawthorn and poison oak become violet, while the sumacs and vines take on a flaming scarlet. These colors exhibit some variation in accord with the character of the soil on which the plants stand.

From the above it is to be seen that the color of autumnal leaves is a screen under cover of which the protoplasm retreats into the main stem, carrying with it such other substances as may be of use to the plant. With the coming of spring the advance of living matter in the form of leaves and shoots is protected in the same manner by layers of reddish violet, or reddish brown coloring matter, which disappears on the appearance of the green coloring matter.

It is of special interest to learn in this connection that leaves which are covered with a dense growth of silky, woolly or branching hairs do not usually exhibit any marked autumnal colors. The presence of the screen is unnecessary in such instances because of the protection afforded by the matted or felted hairs on the surfaces.

At a time previous to the beginning of the withdrawal of the contents of the leaf, or the formation of the autumnal colors, preparations had been steadily in progress for cutting away the leaf when the proper time should arrive. At some point near the base of the leaf stalk, the formation of a layer of special tissue had begun between the woody cylinder in the center and the thin epidermis. When the time for the casting of the leaf arrives this special tissue grows rapidly, pushing apart or cutting the cells which have held the leaf rigidly in position, in such manner that finally the leaf stalk consists of the brittle cylinder of wood surrounded by the loosely adherent cells of this newly formed layer of separation. The merest touch or breath of air will split the layer of separation, break the wood, and allow the leaf to fall to the ground. After the layer of separation has been formed, a frost or freeze would help to break away the fragile strand holding the leaf in place, but exercises no other direct influence on the process.

Separation layer

Many plants make provision for cutting away the leaf at more than one point. The vine forms two layers of separation, one at the base of the leaf-stalk, and the other at the upper end below the blade. Layers of separation are formed at the base of the main leaf-stalk and at the base of the separate leaflets in such compound leaves as those of the Virginia creeper, horse chestnut and Ailanthus.

It is to be remembered, of course, that all plants do not discard their leaves on the approach of the inclement season. The leaves of evergreens are so organized that they may withstand the periods of drought or frost through several years. Before such leaves enter upon a period of inactivity, alterations are carried on in the cells, among which are the reduction of the proportion of water present, and chemical changes which result in the formation of substances not affected by low temperatures. The changes of color are not so marked as to attract general attention, and they are brought about by the withdrawal of the chlorophyll bodies toward the inner ends of the cells, and the formation of small proportions of yellowish or reddish coloring substances. The retention of the foliage is made possible by adaptations in form and structure, and is a result of the morphological nature of the plants involved.

Evergreen leaves

X

THE SIGNIFICANCE OF COLOR.*

The colors exhibited by the roots, stems, leaves and flowers of plants must have been used by man as distinguishing marks in the selection of food at quite an early stage in his development. Doubtless masses and combinations of the cruder colors afforded gratification to his dawning sense of the beautiful in these earlier times. Later he became imbued with the idea that man was the center of the universe and that everything, plants included, was meant to bear a good or evil relation to the human race. In the determination of the aspect of any plant, color and form were taken into account, and were held to be indicative of magical curative or poisonous properties.

Early views

---

* Adapted from "The Physiology of Color in Plants," *Popular Science Monthly*, May, 1896.

The last-named aspect of plant colors received its greatest attention during the prevalence of the practices of the Grecian Rhizotomoi and Pharmakopoli, and later in the "doctrine of signatures." The doctrine of signatures supposed that the color and form of plants indicated their relations, good or evil, to the human race, in reference to which they were especially created. This crude superstition attained greatest favor in the sixteenth century, and is still prevalent in obscure form among the lower classes in certain portions of Europe. The use of colors as a distinguishing mark between species, families, and groups began quite early in the history of attempts at classification, and still forms a minor character in modern systems.

Sprengel's discoveries

A consideration of the plant as an independent organism, and of colors with respect to the possible uses to the species forming them was first given by Konrad Sprengel near the close of the eighteenth century. In his wonderful book, *Das Entdeckte Geheimniss der Natur im Bau und der Befruchtung der Blumen*, published in 1793, he brought out the view that the colors of flowers are for the purpose of attracting animals which would carry pollen from one individual to another.

The facts involved interest many classes of naturalists, and observations have been extended in every direction by trained and untrained workers until the aggregate mass of results is nothing short of colossal. The conclusions advanced by Sprengel have been extended until effort has been made to show, that not only does the plant use color to attract useful insects to flowers, but that it also displays luring areas of color and stores of nectar on distant bracts and stems to lead unwelcome and harmful visitors away from the neighborhood of the reproductive members. Still further, many plants are supposed to exhibit colors in mimicry of some dangerous animal, or which would serve as a signal of warning to the ravaging animal of the presence of weapons or chemicals hurtful to it. In the highly speculative consideration given the subject the general principal has been drawn upon to furnish solutions to complicated or unusual arrangements of color, in a manner highly improbable and unscientific, and in many instances verging upon the impossible and ridiculous. That it can not be assumed *a priori* that the colors exhibited by the flowers or any other organ of the plant are devices to attract and guide or repel animal visitors is becoming more and more apparent.

Ecological considerations

Recent researches have demonstrated that a color sense is almost wholly lacking except among the higher insects, and that the form and odor of the flower are the features most effective in securing the attention of pollen-carrying animals.

It is of course undeniably proven that some colors do attract insects to flowers, and that pollination is accomplished as a result of the visit. If, however, the color is supposed to be developed as an adaptation, guided by the selective agency of the animal, some difficulties arise. In the first place, it is to be said that the selective power of the insect has been exercised only in comparatively recent times—since it developed the sense of color. Secondly the red, yellow, and white floral markings of leaves and flowers, as well as of other members, are due to katabolic or breaking down processes, and originate as well in injured or deteriorated organs in which the food-forming capacity has suffered diminution. In some instances, as in the screen of colored leaves, the formation of the pigments is due to the regulatory action of the plant, and serves the purpose of checking the diminution of the food-forming power, and hinders the disintegration of plastic substances, to which it owes its origin.

With all of the probabilities taken into account it can only be said that the selective power of animals toward plant colors may have accentuated the development of these substances in certain directions in lines determined by inherent physiological properties, the origin as well as the continuation of which are entirely independent of the preferences of the animal. If insects and birds do, in certain instances, show a preference for any color or color scheme it merely converts an indifferent to a useful property. This is true of attractive as well as of warning colors. By a recent series of experiments with a number of tropical plants which have a color scheme resembling that of a poisonous snake, which has been supposed to shield them from attack by animals, it has been found that the degree of hunger of the animals—snails, rabbits, antelopes, etc.—chiefly determines the choice of food, and that warning devices serve no actual use so far as has been actually demonstrated.

Enumeration of colors

It will be found most convenient to discuss the chemical nature and physiological uses of the more prominent coloring substances, under the heads of chlorophyll, etiolin, lipochromes, anthocyan or erythrophyll, and various special colors both red and yellow, to be found within the limits of families, or ecological groups. The manner of occurrence and their universal unstability are such that it has been impossible to determine their exact chemical composition.

Chlorophyll

Chlorophyll is perhaps the most important coloring substance in the world, for upon this substance depends the characteristic activity of plants, the synthesis of complex compounds from carbon dioxide and water—a process upon which the existence of all living things is ultimately conditioned. Only in a very few unimportant forms devoid of chlorophyll can the synthesis of complex from simple compounds, or from the elements, be accomplished. The function of chlorophyll may only be comprehended when its chief physical properties are understood. These may be best illustrated if a solution of the substance is obtained by placing a gram of chopped leaves of grass or geranium in a few cubic centimeters of strong alcohol for an hour. Such a solution will be of a bright, clear green color, and when the vessel containing it is held in such a manner that the sunlight is reflected from the surface of the liquid it will appear blood-red, due to its property of *fluorescence*, that of changing the wave length of the rays of light of the violet end of the spectrum in such manner as to make them coincide with those of the red end. It is by examination of light which has passed through a solution of chlorophyll, however, that the greatest insight into

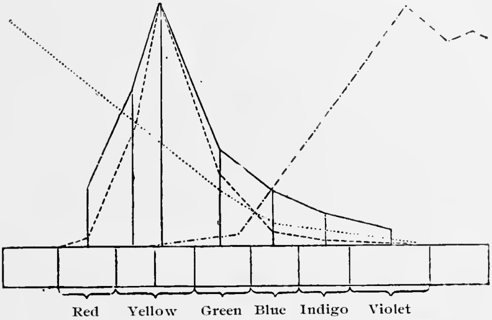


FIG. 17.—CURVES SHOWING SYNTHETIC, THERMAL AND DISINTEGRATING EFFECTS OF THE REGIONS OF THE SOLAR SPECTRUM. After Pfeffer.

———Synthesis. ·········Heat. —·—·—Disintegration.

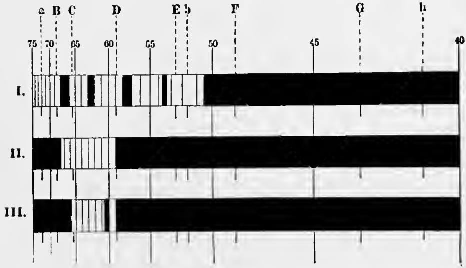


FIG. 18.—I. SPECTRUM OF CHLOROPHYLL WITH SEVEN ABSORPTION BANDS. The two in the red-yellow between B and D, and the three in the blue-violet, beyond F, blended in the diagram, are the most important and characteristic.

II. SPECTRUM OF AMARANTH-RED. All the rays except those falling between B and D have been absorbed.

III. SPECTRUM OF AUTUMNAL COLOR OF LEAVES OF AMPELOPSIS. All the rays except a part of those falling between C and D have been absorbed.

its physical properties may be gained. If such a ray of light is passed through a prism and spread out on a screen, it may be seen that there are several large intervals or dark bands in the spectrum. The rays of light which would have occupied these spaces have been absorbed by the chlorophyll, and converted into heat and other forms of energy. This energy is directly available to the protoplasm containing the chlorophyll, and by means of it the synthesis of complex substances may be accomplished. Moreover, the amount of synthesis accomplished by plants exposed to separate portions of the spectrum will be directly proportional to the amount of that portion which can be absorbed and converted into useful forms of energy. The amount of synthesis is shown to be greatest in the red rays between B and C, where the most complete absorption takes place.

Chlorophyll is a very complex and highly unstable substance, and during the absorption of light it is slowly broken down, but ordinarily it is rebuilt by the protoplasm as fast as it is decomposed. If, however, the chlorophyll and the leaf containing it are exposed to a light of such intensity that the chlorophyll is decomposed faster than it can be rebuilt, then damage must ensue, which if sufficiently extensive will result in the death of the entire leaf. The intensity of the light which induces a maximum of activity in any plant, and which it may receive without damage, is determined by its specific constitution.

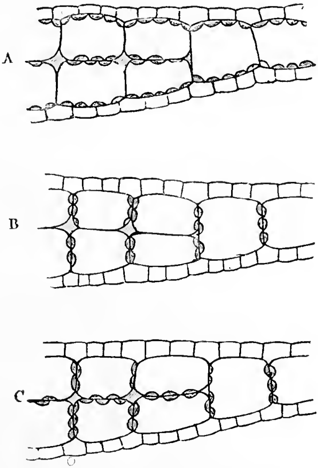


Fig. 19.—Transverse Sections through the Frond of Lemna trisulca (Duckweed), Showing Different Positions of Chlorophyll Bodies. A, position in diffuse light; B, in strong light striking the surface perpendicularly; C, in darkness. After Stahl.

In the greater majority of plants the efficiency of the chlorophyll increases in temperatures up to 35° centigrade, varies from 35 to

40C, and steadily decreases from 40 to 50°C. where activity wholly ceases. The intensity of light falling on a plant in an open plain during twenty-four hours ranges from almost total darkness to the blaze of the noonday sun, and varies almost momentarily. As an adjustment to this condition the intensity of the light impinging on the chlorophyll-bearing masses of protoplasm is varied by altering the position of the surfaces of the leaves by active and passive movements. In others in which this movement is not possible—such, for example, as the leaflike duckweeds which float on the surface of the water—the intensity of the light received is regulated by alterations in the position and distance of the chlorophyll from the surface of the organ.

In many plants growing in the bright glare of the sun a thickened cuticle or a heavy coat of hairs serves to protect the chlorophyll against the more intense action of the rays. Then, as will be shown later, other colors are often developed in the external layers of the leaf as a protection against intense illumination.

Chlorophyll is generally formed in special sponge-like masses of protoplasm (chloroplasts) in the peripheral layers in the cell, and is most abundant in leaves.

As a rule the chloroplasts may form chlorophyll only in sunlight, though several instances are known in which the green color is to be found in tissues in complete darkness. The presence of iron in the cell is necessary for the formation of chlorophyll, although it does not enter into the composition of the pigment.

When a plant is grown in complete darkness it assumes a pale waxy yellow color, the organs are usually abnormal in size and form, and are said to be *etiolated*. The yellow color of etiolated plants is *etiolin* which resembles chlorophyll in general chemical composition and physical properties. Many writers believe that etiolin is formed in the earlier stages of the construction of the chlorophyll molecules. In support of this view it has been noticed that plants grown in darkness and containing large quantities of etiolin turn green on exposure to light much more rapidly than those in which but little etiolin was found. Etiolin is not to be confused with the yellow colors of fruits and flowers, which are due to an entirely different class of pigments next to be considered.

Etiolin

The lipochromes are a series of substances varying through yellow and red, devoid of nitrogen, and which absorb certain blue violet rays of sunlight. These substances occur in company with chlorophyll in leaves and elsewhere in bacteria, algæ, fungi, as well as in

The lipochromes

the flowers and fruits of the seedforming plants. The lipochromes constitute the pigments of many animals also. Examples in the two groups are offered by the yellow color of the yolk of a hen's egg, and by the reddish yellow of the carrot, or the sulphur yellows of certain fungi. These substances occur in various forms, in oily drops in the fungi, in a diffused state throughout the plasma in bacteria, and in crystalloids in the carrot and in flowers. In leaves the lipochromes are supposed to occur in the chloroplasts. If an equal amount of kerosene or benzole is added to a solution of chlorophyll in alcohol and the mixture is shaken and allowed to stand for a few hours, the alcohol containing a yellowish lipochrome, xanthophyll, will separate from the kerosene or benzole solution. The yellow and yellow-red tints of autumn leaves are due to the lipochromes which become visible after the decomposition of the chlorophyll.

In leaves the lipochromes are supposed to act as a screen in preventing the disintegrating action of light on nitrogenous substances. Since the lipochromes disappear during the germination of the spores of fungi it is suggested that a function as reserve substance is also subserved. Colored bacteria in which the pigment is a lipochrome of which, *Bacillus brunneus*, *B. cinnbareus*, *Micrococcus agilis* and *Sarcina rosea* offer examples, have the power of occluding oxygen from the air, which may be given off under partial pressure. The pigment is the oxygen carrier and may act in a similar manner after it has been extracted from the organism. The green and purple bacteria of which *Bacterium viride* and *B. photometricum* are examples, contain two pigments one of which resembles chlorophyll and the other the red coloring matter of the algæ.

Anthocyans

The anthocyans comprise a series of substances soluble in water varying from red to blue and violet according to the acid or alkaline nature of the cell sap in which they are always found in solution. Thus a portion of a plant of a blue color from the presence of anthocyan may be changed to a red by immersion in an acid solution and the operation may be reversed. Similar changes are often brought about in the petals of flowers by chemical processes set up within the cell. Examples of changes of this character are shown by Pulmonaria, Mertensia, Symphytum and willows.

The anthocyans occur in stems, petioles, flowers, leaves, unfolding shoots, organs exposed to low temperatures, and in injured regions. It is quite generally accepted that the pigments embraced in this group are derived from the tannins. The colors which attract animals belong chiefly to this group.

Relation of anthocyan to light

Several theories have been proposed in the last decade to account for the functions of anthocyan. Engelmann found that red pigment permits 90 per cent of the orange rays, 10 to 30 per cent of the green and yellow, 50 per cent of the blue and 80 per cent of the violet to be transmitted unchanged. Müller has plotted the absorption spectrum of a large number of anthocyans, with the result that while Engelmann's results hold good in the main, some also absorb the lower red rays. As a natural result of such physical characteristics it is found that anthocyan converts light into heat, a portion of the converted light being the disintegrating rays of the blue violet end of the spectrum. That the anthocyan does partially retard the disintegration of chlorophyll by light may be seen if two vessels containing solutions of chlorophyll are so arranged that the light which strikes on one of them shall first pass through a parallel-walled vessel containing water, and that which strikes the other through a similar vessel containing a solution of anthocyan. The chlorophyll in the first will soon become much more discolored than in the second, which has received light transmitted through anthocyan. That the disintegrating rays may be converted into heat is demonstrated by the following ingenious experiment designed by Kny. Three similar glass vessels with parallel walls are filled with distilled water. In one vessel a number of green leaves of canna are placed, and in another such number as to offer the same amount of surface as those in the first, but which contain a large amount of anthocyan. The third vessel is left unchanged, and all are placed in sunlight of equal intensity. A certain rise in temperature naturally ensues in the water in the third vessel; a greater rise occurs in the first, showing that chlorophyll converts a portion of the light into heat, while the greatest increase takes place in the second, where, in addition to the action of the chlorophyll, the converting power of the anthocyan is exerted. The difference between the temperature of the vessels containing the green and red leaves often amounts to 4° C., which is due entirely to the action of the anthocyan.

The screen theory

The "screen theory" supposes that the chief purpose of anthocyan is to protect chlorophyll and other nitrogenous and unstable substances in transit and in situ from being broken down by the too intense action of light rays. A second theory holds that the development of heat and energy from a layer of anthocyan is an aid to the translocation of carbohydrates and other substances from one part of the plant to another, notably starch, from the leaves to the stem. The third theory consists of the idea that the heat developed by anthocyan serves chiefly as an aid in promoting transpiration. Many facts are at hand supporting both the first and last named speculations, though the argument in either case has not advanced to the stage of absolute proof. As for the second, many plants growing in cold situations are undoubtedly able to carry on metabolism to better advantage because of the heat derived from light by layers of anthocyan present.

The "screen" theory receives support from the fact that the upper layers of leaves of plants growing in intense sunlight and in exposed Alpine situations are furnished with layers of color on the upper or illuminated surfaces of the leaves, as are also the leaves of many shade-loving plants when grown in free sunlight. It is likewise asserted that plants devoid of color growing in the lowlands will develop anthocyan in the leaves when transplanted to Alpine elevations. Kerner transplanted the summer savory (Satureja hortensis) from lowland to a height of 3,200 meters and found that it developed a very strong layer of anthocyan. Ewart found that the plants on the summit of the mountain Geddeh, 4500-6500 feet, in Java, with a very moist air have but little anthocyan while on Pangerango, at a height of 10,000 feet, with a dry atmosphere the presence of red coloring matter was very marked. The power of absorbing the photochemical rays possessed by moist air would preclude the need of a protective coloring in the first instance. The writer has noticed that the young and pendant leaves of the mango (Mangifera) are but slightly colored in the lowland habitats of the tree in Jamaica but on the mountain sides, near 1000 feet, the young bunches show a perfect blaze of color especially in dry regions. Here, as in the highly colored young leaves of the maple, oak, grape, sumac, alder and others, the red coloring matter doubtless serves as a protection against the penetrating rays of the sun. At the same time it is to be borne in mind that the low temperatures of the elevations mentioned, or of the spring season may be the direct cause of the formation of the anthocyan.

The most satisfactory proofs of the formation of anthocyan as a screen are given by the exposure to daylight of plants growing in darkness. Under such circumstances the pearly white rhizomes of *Dentaria bulbifera* become violet. Plants of *Philotria canadensis* (*Elodea*) and *Utricularia vulgaris* grown in weak sugar solutions in strong light formed anthocyan, while other specimens in water and exposed to diffuse light did not, showing that the color is formed when needed only, and not accidentally, although its occurrence as in underground organs or in the center of massive tissues must be accidental and not useful.

Anthocyan as a screen is not always confined to the upper layers of the leaf. The leaves of the banana (Musa) are vertical and rolled up with the ventral surfaces outermost when young. One species develops color on the under side, which disappears as the leaf unrolls and comes down to a horizontal position. Uncaria, Alpina, Belemcanda, and other plants afford similar instances. The pinnules of Mimosa pudica are provided with a reddish coloring matter in the surfaces of the lower sides which are exposed when closed together in the "hot sun" position.

The coloring matter in the pistils of anemophilous plants such as Populus, Salix, Platanus, Ulmus, Ostrya, Carpinus, Corylus, Alnus, Acer, Fraxinus, Rumex, and others in which it can have no possible significance for animals, also serves as a screen against the effects of light. The growth of the pollen tube down through the pistil would be very much hindered by the action of light, which is prevented by the screening anthocyan.

Promotion of metabolism

The demonstrations of the useful properties of anthocyan as a developer of heat for promoting the chemical processes are not nearly so numerous. The opening of the flowers of some of the alpine grasses is brought about by the rapid elongation of the colored anthers under the influence of sunlight. It is suggested that the energy for the rapid growth is derived from the sunlight by the coloring matter. It is quite true that the heat from any source will cause these flowers to open quickly. The red color of certain gymnospermous flowers may accelerate their opening in the same manner.

Promotion of transpiration

The presence of layers of color in the lower sides of rosettes, and in leaves and rapidly growing organs in the deep recesses of jungles and swamps, admits of no interpretation except that such arrangements are useful in promoting transpiration by means of the heat developed. If a red and green leaf of the same species are placed with their bases in sunlight with the bases of the petioles placed in calibrated cylinders full of water it will be found that the transpiration is most rapid from the colored leaf since it absorbs the greatest amount of water. A very obvious demonstration may also be made if the base of the petiole of a leaf containing patches or spots of color is placed in an aniline solution. The dye will pass most quickly and rapidly to the regions containing anthocyan, indicating that the loss of water has been greatest from these areas.

The maintenance of a transpiration stream, laden with mineral salts, to leaves and rapidly growing shoots in an already moist and warm atmosphere is a matter of some difficulty and importance. If the temperature of a plant is higher than the surrounding atmosphere it may continue to carry on transpiration because of the greater tension of the aqueous vapor in the heated air of the intercellular spaces than in the surrounding medium. The presence of anthocyan would be almost a necessity to leaves under such circumstances.

In connection with the heat producing properties of anthocyan it is to be said that it may increase the amount of odorous substances volatilized from fragrant flowers, and thus indirectly aid pollination. It is also possible that the actual warmth of organs containing anthocyan may serve as a lure to animals.

A number of pigments of limited distribution occur in the citrus fruits, colored algæ and bacteria, which are but little known so far as composition and use are taken into account.

Red sea-weeds

The color of the red seaweed is due to the presence of phyco-erythrophyll which is present in the protoplasm associated with chlorophyll. It is to be noted here that the anthocyans are dissolved in the cell sap of the plants in which they occur. The gradation of the amount of phyco-erythrophyll at different depths suggests that the color serves the purpose of converting light into heat useful in promoting metabolism. The presence of a red pigment in Hæmatococcus and the resting spores of many algæ is doubtless a protection against the disintegrating effect of light on chlorophyll and protoplasm.

Markings not due to color

Effects quite as marked as those produced by colors may be brought about by the presence or mechanical arrangement of certain cells. The shade of green presented by a leaf will be determined by the number and position of the chlorophyll bodies with respect to the surface. Coatings of wax, mineral salts, and hairs also, bring about modifications. The silvery or silver gray or whitish appearance of surfaces is due to the loose arrangement of the sub-epidermal cells forming great intercellular spaces. The multifold refractions offered by the numerous free walls of the cells prevents the penetration of the leaf by light.

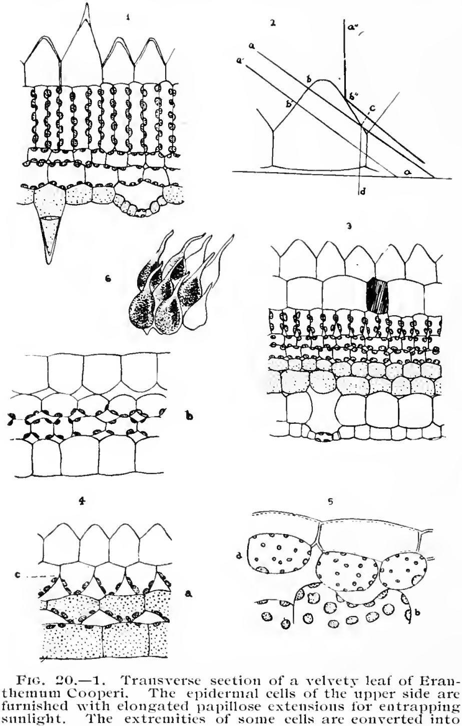


FIG. 20.—1. Transverse section of a velvety leaf of Eranthemum Cooperi. The epidermal cells of the upper side are furnished with elongated papillose extensions for entrapping sunlight. The extremities of some cells are converted into hairs. The epidermis of the lower side contains anthocyan.
2. Diagram showing the manner in which light enters the epidermal cells of velvety surfaces.

The tissues underneath such regions are usually free from chlorophyll. The leaf might be compared to a sheet of tinted glass which permits the passage of the greater part of the light which falls upon it while intact. When crushed into fragments the mass of minute fragments reflects back the rays at thousands of points.

Silvery areas

Plants such as the aloe, growing in the fierce light of a tropical desert, avoid burning and drying of the tissues by such arrangements. The silvery areas warm up much more slowly than a typical leaf. At the same time this feature is also of use to plants growing in moist, tropical climates, in the promotion of transpiration at night.

The silvery areas not only warm up slowly but they also radiate heat less rapidly than a typical leaf, and the higher temperature of these areas after sunset promotes transpira-

---

3. Transverse section of a velvety leaf of Piper porphyraceum. A layer of aqueous tissue lies next the epidermis of the upper and lower sides. The anthocyan is in the lower half of the leaf.

4. Mottled leaf of Begonia falcata. a. Transverse section of a brownish green velvety shining portion of lamina. The epidermal cells of the upper side are furnished with papillose extensions. The epidermal and sub-epidermal layers are joined without intercellular spaces. The epidermis of the lower side and the spongy parenchyma contain anthocyan. b. Transverse section through a silvery portion. The outer walls of the epidermis are plane. Large air spaces are present between the epidermis and the cells containing chlorophyll.

5. Transverse section of a bright spot on the leaf of Ranunculus ficarioides. The sub-epidermal cells, *a*, contain a few small chloroplasts, and are separated from the layer beneath by large air-spaces.

6. Papillose epidermal cells of Begonia imperialis, var. smaragdina, seen from above by refracted light. After Stahl.

tion at a time when it is at a minimum in normal leaves. This is an adaptation of great importance in certain regions as is indicated by the great number of species in which it is found. Begonia, Anthurium, Dracæna, Tradescantia, and Geranium offer examples of this arrangement.

The relation of silvery areas to light may be demonstrated if the lower side of a mottled leaf of Begonia or Anthurium is coated with cocoa butter or lard and allowed to cool. If the upper side is exposed to sunlight, the oily substance will melt under the green areas before that beneath the silvery regions is effected. If the experiment is continued until all of the substance is melted and then taken into a shaded place to cool it will be found that the butter opposite the silvery areas remains melted after that on the green portions has solidified. The silvery areas of the leaves carry on food-formation less rapidly than the green regions because of the great obstruction to penetration by light.

Velvety surfaces

Many leaves exhibit a rich velvety surface that is also due to structural modifications; when combined with underlying layers of color as in Cissus, the effect is very striking. The velvety appearance is due chiefly to the papillose extension of the outer walls of the epidermal cells. The conical and convex outer walls act as lenses in directing all rays of light, which strike the surface at any angle, into the interior, and in some instances actually focusses them upon the chloroplasts. Such an arrangement is to be found chiefly in plants native to moist climates, and generally growing in diffuse light. *Oxalis acetosella, Cissus discolor, Fucshia triphylla, Maranta zevlina*, and some begonias are examples showing this adaptation.

A plant or even a single leaf may exhibit colors due to several causes. Thus the leaf of *Begonia falcata* has silvery areas of the usual structure, brownish green patches in which the epidermal cells of the upper side are outwardly convex, and those of the lower side contain anthocyan. Arrangements of this character are most frequent in the foliage of tropical plants. The contents of the foregoing paper may be briefly summarized in the following paragraphs.

Conclusions

Colors may serve as an attractive or guiding device to lure animals to flowers or away from them. Physiological causes have played the principal part in the development of pigmented regions, and this development may have been modified by the selective power of animals to some extent. The color sense is lacking in some pollen carrying insects, and when present has been acquired in a comparatively recent period in the history of plants. Form and odor are much more efficient agents than color in the attraction of animals.

Chlorophyll converts light into energy by the aid of which the protoplasm which contains it is able to build up complex foods.

The lipochromes are found in leaves and other organs, associated with chlorophyll under the name of xanthophyll, in citrus fruits, in some underground members and in fungi and bacteria. The yellow tints of autumn leaves are due to lipochromes. These substances may occur in solid crystalloids in the cell or diffused throughout the protoplasm or suspended in oily drops. The lipochromes probably serve as reserve substances in some plants and in others as a screen against intense illumination. Bacteria furnished with a lipochrome pigment are able to occlude comparatively large quantities of oxygen which may be given off under partial pressure. Certain green and red bacteria are able to carry on food formation by means of a pigment resembling chlorophyll in physical and chemical properties. A second pigment which has some of the characteristics of the red color of the algæ is also present in these forms. The pigments of the bacteria have been the subject of but little investigation.

Anthocyan is the most widely distributed coloring substance. It occurs in solution in cell sap, varies from red to blue and violet and may be present in any part of the plant. It may serve as a screen against the disintegrating action of light on chlorophyll and other nitrogenous substances. By its heat-developing power metabolism and transpiration may be promoted.

The coloring matter in marine algæ may act as a screen against light and promote metabolism and growth by the development of heat.

The silvery or white appearance of organs is due to the loose arrangement of the cells. This arrangement serves as a protection against intense sunlight and is found in plants growing in heated deserts. The same arrangement may promote transpiration in plants growing in moist shady situations with cool nights or frequent rains.

The velvety appearance of surfaces is due to the papillose extensions of the outer walls of the epidermis. The extended walls serve as lenses to entrap sunlight and focus it upon the chloroplasts. This adaptation is most useful to plants growing in diffuse light.

Besides all of the occurrences of pigments noted above, colored substances often are found in the walls of dead cells, as in the wood of Hæmatoxylon (logwood) and other plants, in excretions and elsewhere in such manner as to have no physiological significance. The color in such instances is to be regarded as a by-product in the necessary chemical processes of the organism.

XI.

THE RIGHT TO LIVE.*

When we come to think of it, it is strikingly patent that the world was not fashioned to especially promote the convenience and happiness of individuals. Should we assume such an hypothesis what explanation could be offered for the prevalence of parasitism, by which the individuals of one species of animal or plant live upon, and at the expense of the individuals of another species, or what could be said in extenuation of the carnivorous habit, or even of the herbivorous habit? We find that plants as well as animals are no respecters of personal liberty. The glittering tentacles of the sundews encompass the struggling fly, and reduce the exquisitely developed body to a reeking paste, and bring to nought its enjoy-

Aggressiveness of plants

---

*Read before the Parlor Club, an organization devoted to literary and scientific culture, Lafayette, Ind., Sept. 17, 1897.

ment of air and light and fragrance. And there is a travesty upon human cruelty enacted by those curious swamp plants of North Carolina, when they clasp their bristling leaves together over the incautious insect with the same blasting results to the mortal life of the prisoner as befell the unfortunate victims of inquisitorial times who succumbed to the deadly embrace of the *eiserne Jungfrau*. When standing in the castle tower at Nuremberg, viewing this torture weapon of mediæval ingenuity, one can not but feel that here the God-like powers of man dropped perilously near the blind forces of lower nature.

Likeness of plants and animals

In all the essentials that go to constitute a living organism of whatever degree of complexity, that is, the ability to take food, to grow, to respond to stimulation and to exhibit spontaneous and directive energies, the plant is the Ishmaelitic branch of the same great world's family in which the animal has acquired a higher standing by superior awareness. In other words, the plant and the animal, in ultimate essentials are of like constitution. It is evident, therefore, that the argument for natural rights may be supported from either branch of the organic phylon; bearing in mind, however, that in shifting from the animal to the plant, or from the plant to the animal, the alluring quicksands of bare analogy must be sedulously avoided.

Turning from the dramatically tragic phases of plant life, let us look at the everyday conditions of existence. Two prominent factors in plant as well as in animal life, are the rate of increase and the supply of food. In regard to these some simple calculations will be helpful, although they may prove a cabala that will disenchant and spread before us a different panorama from the quiet, pastoral repose, which we confidently anticipate when we

> "Go forth under the open sky, and list
> To Nature's teachings."

Possible rate of increase

Linnæus computed the progeny of an annual plant, from which only two seeds grew into plants the second year, and from each of these two plants two others sprung up the third year, and so on for twenty years. This is a very low rate of increase, yet at the end of the second decade the one original plant would be represented by a million offspring. A computation made by Huxley gives a somewhat clearer illustration of the real tendency of plant life. By the terms of his supposition fifty seeds are able to make a successful growth from each plant of the preceding year, and a plant for full development is permitted to have one square foot of ground. Now estimating that the whole land area of the world in round numbers is fifty-one million square miles, and supposing for the sake of the illustration, that every foot of this ground is free from all encumbrance and equally capable of supporting plant life, we shall arrive at the astounding result that a single parent plant by the tenth year will have given rise to enough plants to occupy every foot of this great area, and over five hundred thousand billions besides. This means that an annual plant, increasing at a fifty-fold rate. has the capacity to supply a plant for every eight square inches of land surface of the whole globe within one decade.

Weeds as examples

Such marvelous results of fecundity are almost past belief, and it is worth while to inquire if any facts exist that give countenance to such deductions. The ubiquity and prolificacy of weeds are proverbial, but upon closer acquaintance even the popular fancy seems scarcely to reach the reality, to judge from the records. Sturtevant found that a plant of shepherd's purse, one of the most common and most insignificant of weeds, bore fully 12,000 seeds, that a plant of burdock had 40,000 seeds, and that a number of other common weeds were equally fertile. But the list that he examined reached its climax in the purslane, a plant which by its obtrusiveness and pertinacity has become the symbol of offensiveness—"as mean as pusley," the saying goes. A single plant of this species bore over two million seeds, surely a marvelous prodigality. And yet even these great numbers are certainly not the full measure of the plant's capacity, for some seeds may have dropped off before the time of counting, and many more might still have ripened if the interests of science, or other untoward circumstances, had not cut short a flourishing career.

Prolificacy of other plants

But weeds are not the only plants to show a superfluity of seeds. How many seeds do you think, are borne on a single beech tree, or even an oak? Certainly many hundreds more than ever grow into trees. And the grasses, and climbers, and shrubs, and the numerous wayside plants that individually affect our lives so little that we do not know them by name, does it not seem safe to assume that they are potentially capable, to be conservative, of a fifty-fold annual increase, rising in not a few instances to many thousand-fold, and sometimes to a million-fold? But the productive spots are already occupied, and outside of cultivated lands largely with perennial plants, so that there is little chance of even one out of the large number of offspring finding conditions for average development. What becomes of the other 49, or 999, or 999,999? Many never find the opportunity for germination and perish without feeling conscious life; but many others do start and attain some size only to be starved and smothered out of existence.

Illustrative similes

The condition of the plant world may be likened to the American struggle for riches; a very few become millionaires, a small minority attain financial independence, but the great majority die without knowing the comforting security of a competence. It has become customary to speak of this overwhelming failure to attain a favorable position in the world as a warfare, and to some extent the term is applicable; it is an unorganized warfare, the fighting of a mob where there is no leadership, or to select a yet better simile, the frantic efforts of individuals under the excitement of a panic where action is controlled by the single desire to find personal safety. Darwin's striking phrase, "the struggle for existence," which has been so much used, and also greatly abused, seems applicable enough when we think that for each plant that attains normal development thousands perish. As in the panic, it is the strongest ones, or those having most advantageous positions, or who are most apt in adapting themselves to passing conditions, that survive; and in this sense Herbert Spencer's twin phrase, the "survival of the fittest" finds its application. It is the same in all essential particulars with animals as with plants, there is a constant struggle for a suitable portion of food and a comfortable amount of space, the fortunate few succeeding, while multitudes perish. To this general, coërcive law of the organic world man finds in himself no exemption, except in so far as the humanizing principle of altruism has effect. Thus throughout the world the truth in the refrain of Grant Allen's "Ballade of Evolution" finds confirmation:

> "For the fittest will always survive,
> While the weakliest go to the wall."

All are aware of the substantial use Darwin made of facts regarding nature's prodigality in animate forms, and the resulting competition between them, in establishing his theory of the origin of species. The logical result of the theory requires the subordination of the individual to the good of the race. As of all the myriad individuals only the fittest survive, the race is in consequence gradually improved. The battle is to the strong, and the weak are mercilessly shoved aside, oppressed, and annihilated. There seems no escape from the conclusion that the ethics of nature make right and might synonymous terms. Individuals not only crowd and overpower individuals of the same species, but they prey upon

A world of strife

those of other species to an extent scarcely conceivable. All the tribes of parasitic fungi draw their sustenance from the living host, and give rise to the long category of plant ills known as rusts, smuts, mildews, rots, molds and blights. The minutest vegetable parasites, the bacteria, attack and bring low the largest and most noble forms of both kingdoms, especially being man's most insidious and deadly enemies. With comparatively few exceptions animals of high and low degree, of all sizes, forms and habits, whether inhabiting water, earth or air, from the microscopic amœba to the bear and the elephant, seize upon and devour in part or in whole other living beings, in order to maintain their own existence. Not only does the lion kill other beasts of the jungle, the wolf seize the lamb, the owl eat the mouse, and the robin the earthworm, but the ox feeds upon the living grass, the sparrow gourmandizes upon myriads of young plants in the seed stage, and the caterpillar defoliates trees. With the exception of the carrion beetle, the house fly, the nectar-feeding humming bird, and some others, the animal world finds its daily food by destroying the life of other weaker beings, sometimes animal, sometimes plant life being preferred. In this wholesale destruction of life man lends a ready hand.

He has introduced the refinement of refraining from eating his fellow man, but he usually does not scruple to partake of any other kind of flesh that suits his palate, and never thinks of hesitating when plant life is in question. He has advanced so far as to cook much of his food, but he still enjoys a live oyster, and munches live celery, radishes and lettuce with a satisfaction that denotes utter absence of sensitiveness regarding the exercise of his rights. It occurred to me to notice how many individual lives were destroyed to furnish me a dinner to-day. The beef and the fowl required two animal lives. There were over a hundred lima beans, some six or seven hundred kernels of green corn, part of two or three Irish and sweet potatoes, many hundred grains of wheat for the bread, and still greater numbers of yeast cells to lighten it. I did not count the number of seeds in the sliced tomato, and do not know how many grains were required for the cup of coffee, neither can I well estimate the number of bacteria that took part in flavoring my piece of cheese, and which were smothered in the curing process. It was a simple repast, and yet to supply it required the sacrifice of a thousand or more individual lives, exclusive of the yeast and bacteria.

Destruction of life for a dinner

Was there anything wrong in this destruc-

Natural right to food

tion of life to furnish a meal for one individual? Would it have been any more or any less wrong to have eaten only animal food, or only vegetable food? Is there anything wrong in the owl eating a mouse or in the rabbit eating herbage? Evidently the answer is clear and direct. Every being is entitled by the very law of its nature, and by the constitution of the organic world, to the food needed for its sustenance, and animal life *per se* is no more sacred than vegetable life. This destruction of one being by another is in fact the only method by which the balance of life on the earth can be maintained; indeed, all existence is vicarious, many lives are sacrificed to maintain the few.

The evolutionary argument, which has now been illustrated, runs along two lines pointed out by Malthus nearly a century ago, neither favoring the individual. On the one hand excessive increase, and on the other, necessity for food, cause a dire struggle for existence, in which the race is benefited, but the individual is generally worsted. From this point of view the only right to live that an individual being can claim is vested in its chance possession of strength and opportunity; it lives merely through good fortune.

Logic of good fortune

If we inquire into the object of living, we shall find that the evolutionists, the pre-evolutionists and the creationists are essentially united in opinion. The chief end of existence is to bear offspring that the race may be perpetuated, they all say directly or indirectly. From the highest forms to the lowest, through both the plant and animal series, this is held to be sufficiently patent. Again the individual is sacrificed to the good of the race. In regard to plants this seems to have always been accepted as a matter of course. I might quote confirmatory statements without end, but will only give two. Cesalpino, one of the wisest of early botanists, said that "the final purpose of plants consists in that propagation which is effected by the seed," and it would be difficult to find any author who disagreed with him from that time to the present. It is so generally accepted that one should not be surprised that it is taught to children as an unquestioned fact. In one of Mrs. William Starr Dana's recent nature books for young readers, a whole chapter is devoted to the topic, "What a plant lives for," with the terse conclusion that "a plant lives to bear seed."

Object of living

Here is the philosophy of the ages regarding earthly existence in a nutshell; but to me it is a very unsatisfactory philosophy. I do not see why one may not argue that it is founded upon an absurdity, for it is equivalent to saying that the chief reason for living is to die that another may live, and that other must in turn do the same; thus true fruition, complete realization, is never attained, but is always in the unreachable future.

A misconception prevails, it appears to me, in regard to the place that death and reproduction hold in the economy of the world, which has thrown us upon a wrong track. We may safely assume that much of the diversity in the mode and form in which life is presented to us has resulted from the changeableness and uncertainty of external conditions. If moisture, warmth and food could be, and especially if they had always been, supplied to every organism in uniform and ample amount, the struggle for existence would present altogether another phase from its present day aspect.

If the moisture of air and soil were of approximately unvarying percentage from day to day, and year to year, and if warmth were maintained at the genial glow of a summer day without interruption, the provisions against drouth and cold, shown in seeds, tubers, bulbs, resting spores, sclerotia and similar protective devices, would be largely purposeless, and could not long persist, in fact might never have developed. Under such favorable conditions for continuous growth, without the necessity of providing for the interpolation of inhibiting periods of winter cold or summer dryness, the larger part of productive activity would doubtless disappear, and with it much of the fierce strife for place.

If added to other favorable conditions for existence an adequate supply of food were available, we can well believe that organisms might become potentially immortal, that is, they might live indefinitely unless killed by pure accident. Such a happy environment would be a true vale of Avalon:

> "Where falls not hail, or rain, or any snow,
> Nor ever wind blows loudly; but it lies
> Deep-meadow'd, happy, fair with orchard lawns
> And bowery hollows crown'd with summer sea."

It would, however, be a land of continuous youth, a Ponce de Leon realization, rather than a haven for effete King Arthurs.

Weismann finds an argument leading to the like conclusion in the fission reproduction of many unicellular animals, by which no part of the organism dies during the process of multiplication, but each part expands into the perfection of an individual. A not materially dissimilar process among higher members in the vegetable kingdom is the ready propagation by successive branching of such rhizomatous plants as certain ferns, iris and grasses. As the burrowing plant body pushes forward in its growth the living contents of the rear cells are gradually withdrawn, and the effete skeleton of cell-walls disintegrates; and in a similar way the appendages of leaf and root serve their purpose and are discarded, as a stag sheds his antlers. Although leaf and root and posterior part of stem repeatedly disappear the plant retains its identity as an individual. When the dropping away of the end of the rhizome has involved a branch, the two advancing ends become entirely separate individuals, a method of increase that some species find so efficient that they rarely or never produce seeds or even flowers. It is no fiction to say that such a plant never dies. It is compelled to drop its appendages and hibernate during the inclement season, but its physiognomy remains the same whatever age it may attain.

It has been shown in a previous essay (page 101), that increasing the food supply, or of other external factors favorable to growth, tends to prolong the life of the individual and to decrease the amount of reproduction. This is evidently moving, although but a step, in the direction of ideal conditions for the even display of vital energy.

These and other reasons which can not find place here lead us to think that both senility and excessive increase are not inherent characteristics of life, but have arisen to meet the demands of existence in a too changeable world, and that even death is a "concession to the outer conditions of life." Natural death may be regarded as a phylogenic incident, and accidental death as an ontogenic incident.

Death not essential to life

The argument here outlined, but which can not be adequately developed, is intended to show that reproduction is partly, and death wholly an adaptation, and that these can no more be said to be the purposes of living than can other adaptations, such as the annual production of winter buds on trees, and on such herbaceous plants as the tiger lily. Furthermore, the logic of excessive increase and consequent inadequacy of food does not warrant us in assuming that present forms of existence do not possess a natural right to the greatest longevity and fullest development which their individual opportunities permit them to secure. The individual is limited in the duration of its active period and in the expenditure of its energies by the inherited adaptations imposed by the conditions under which its ancestry has lived, and these limitations are necessarily passed on to its offspring, but its right to the full measure of its opportunities for self-development can not therefore be withheld. It must be true that

Plants are born to live

being, everyday existence, is an end in itself. "Plants are born to live, not to die," says L. H. Bailey in his work on the survival of the unlike, and the same is undoubtedly true of animals and of man.

Right to life should be respected

If I have made good my argument, the individual has a right to its life, it has a right to live, although under the present conditions it must maintain its position and its life by force. And if the individual has a right to its life, and if the purpose of that life is primarily to give enjoyment to the possessor, there is after all a sacredness about life that makes it wrong to destroy it needlessly. Not only the animal, but also the plant is entitled to consideration.

> "Life is not to be bought with heaps of gold,
> Not all Apollo's Pythian treasures hold,
> Or Troy once held, in peace and pride of sway,
> Can bribe the poor possession of a day."

XII.

THE DISTINCTION BETWEEN ANIMALS AND PLANTS.*

No classes of natural objects seem to the general apprehension more distinct and immiscible than animals and plants. The free moving intelligent animal appears immeasurably removed from the fixed insentient plant.

Yet, underlying this seeming distinctness, there usually lurks some vague feeling of analogy between the hidden springs of life in the two classes of beings. Strange flights of the imagination have imposed themselves upon belief in all ages, that are hard to account for unless we take this general feeling of a unity, or possibility of transference be-

---

*A paper read before the joint session of the sections of botany and zoology of the American Association for the Advancement of Science, at the Springfield meeting, September 2, 1895, and printed in the *American Naturalist*, November, 1895; somewhat revised and extended.

tween the essential natures of the two classes of objects, to be deep-seated and almost universal. Only two or three centuries ago there were even learned men who believed in the Scythian lamb, that grew on the top of a small tree-trunk in place of foliage, and in the wonderful tree of the British Isles, whose fruit turned to birds when it fell upon the ground, and to fishes when it fell into water. In still earlier times, even more astonishing vagaries were accepted as common knowledge, especially when vouched for by travelers.

Learned vagaries

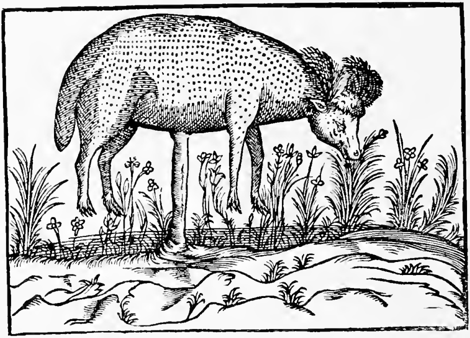


FIG. 21.—The Scythian lamb, that vegetated like a tree, but ate herbage. It was reputed to flourish on the salt plains west of the Volga. Cut reproduced from Claude Duret's "Historie des Plantes," 1605.

But naturalists and others, who withheld

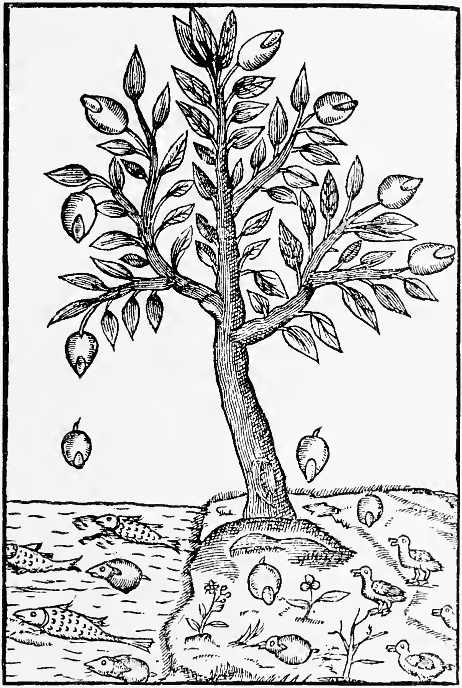


FIG. 22.—The tree of the British Isles, producing both fishes and birds. Gerarde and other eminent naturalists describe it with confidence. Cut reproduced from Duret's "Historie des Plantes," 1605.

belief in the fabulous tales about strange beings in far off lands, such as Pliny describes in his Natural History, and were able to keep their love of the marvelous within bounds, and to found their conceptions so far as possible upon verifiable observations, held more rational and clearer views of the two kingdoms. As a consequence of direct, although not extended, observation the separation of the higher animals and plants appeared to most persons of bygone times, as well as of today, simple enough. The free, independent movements of animals, well directed toward evident ends, and plainly originating from internal impulses, have from such a standpoint fully entitled them to be called animate objects; while plants, deprived of the power of moving about, seemingly without feeling, and to all appearance incapable of conscious re·action, could only be described as living, as animate, only by an extension of terms, and certainly not as sentient.

Ancient opinions

It does not take a very wide acquaintance with living nature, however, to become aware that freedom of movement and fixity of position are not distinctive characters of animals and plants respectively, and that even the possession of feeling does not wholly separate them. Many centuries ago, as we learn from

Aristotle and other ancient writers, it had been observed that sponges grow attached firmly to rocks by root-like extensions, yet possess some feeling. that sea-cucumbers (*Holothuria*) and sea-slugs (*Ctenophora*), although having freedom of movement, seem to lack feeling, and in this respect behave like plants, that sea-anemones are fixed objects, yet are sensitive like animals, and that many other living things have characteristics that make them in like manner uncertain of classification. Aristotle's conclusion from these facts, that "nature passes gradually from the insentient over to the sentient through forms that truly live but are not animals," only needs the substitution of *Mycetozoa* and some *Flagellata* for the *Po-*

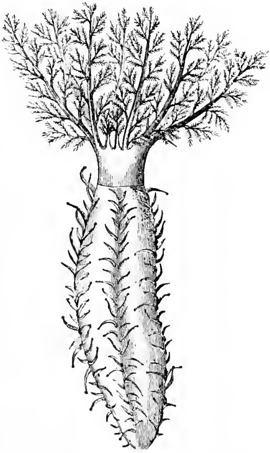


FIG. 23.—A sea-cucumber with extended branched tentacles. (After Claus.)

rifera and *Cœlenterates* as its foundation to make it acceptable to some students of the present day.

Modern opinions

The citation of a few opinions held by modern savants regarding the ultimate distinction between animals and plants, although necessarily brief and without the setting which the authors considered the justification for their conclusions, will indicate how numerous and vain have been the attempts to find some character of universal diagnostic value. To some minds the task of properly placing the animal-like plants and plant-like animals has been well enough disposed of by creating an intermediate kingdom. This was first done by the Englishman Wotton at the beginning of the active period that followed the intellectual stupor of the middle ages. In his work on the distinguishing characters of animals, "De differentiis animalium," pub-

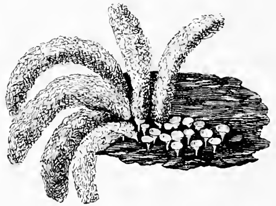


Fig. 24.—A mycetozoan (*Arcyria nutans*) in the resting state, attached to bark. Part of the spore masses removed, leaving their bases. Enlarged three diameters. (After Engler and Prantl.)

An intermediatz kingdom

lished in 1552, he established the group of plant-animals or zoophytes. These organisms were subsequently shown to possess but a superficial analogy to plants, being thoroughly animal in all important respects. Most zoologists and botanists since the time of Wotton have been content to share the problematical forms, either in common or by sufferance, permitting them to be carried into one camp or the other at the convenience or pleasure of the student. A few years ago, however, Hæckel advocated an arrangement that met with some favor. He proposed to place the simple intermediate forms together under the heading Protista, a plan that time shows has added nothing to clearness of conception or convenience of study.

Blending of the two kingdoms

Many writers believe that no characters can be found that are universally diagnostic. Dr. Asa Gray once said (1860) in connection with an argument in justification of Darwinian evolution, that in regard to the two classes of organisms, "no absolute distinction whatever is now known between them. It is quite possible that the same organism may be both vegetable and animal, or may be first the one and then the other." The learned Dr. Claus, in his prorectoral address before the University of Marburg in 1863 on the limits of animal and plant life, after carefully reviewing the whole subject, says in his concluding sentence that "a fast and absolute boundary between animals and plants does not exist." The last sentence of Professor Huxley's lecture, delivered in London in 1876 upon the border territory between the animal and the vegetable kingdoms, breathes the same sentiment. It was his opinion that "the difference between animal and plant is one of degree rather than of kind, and that the problem whether, in a given case, an organism is an animal or a plant, may be essentially insoluble."

The positive statements of such leaders of thought require no additional evidence to show that finding crucial tests to apply under all circumstances is well nigh hopeless. And yet the writer believes that the last word is not said, and that a clue will yet be found leading to a reasonably clear solution of the problem.

Characters from structure and function

It has long been recognized that characters drawn from structure are far more reliable in determining relationship than characters drawn from function. The latter respond more readily to changes in the environment, and therefore forms having little affinity may possess the same physiological adaptations.

Profound changes in the environment eventually bring about changes in structure; but they follow so slowly that rudimentary organs and various vestigial structures reveal the true affinities where all other characters fail.

In all serious attempts to fully distinguish the two kingdoms, so far as they have come to my notice, the characters selected have been essentially physiological, and not structural. Some of the most noted of these may be briefly mentioned. Linnæus leads with his classical aphorism: "*Lapides crescunt, vegetabilia crescunt et vivunt, animalia crescunt, vivunt et sentient*," with which he opened his work on philosophical botany in 1751. Cuvier, in the second edition of his "Regne animal," issued in 1828, elaborated four reasons for the "division of organized beings into animals and vegetables:" viz., the possession by animals of (1) organs for ingestion of food, (2) circulatory system, (3) nitrogenous structure and (4) true respiration, of which the first seemed to him most important, and did, indeed, survive the longest. The distinction advocated by Dangeard (1887), Minot (1895), and others, that only animals are capable of receiving solid food into the body, may be considered the latest phase of

Various physiological distinctions

Cuvier's first proposition. Sedgwick and Wilson in their "Biology" (1886), find the sole characteristic of animals to be dependence upon proteid food. Von Siebold in a dissertation upon this subject published in 1844, believed he had found a criterion in the contractility of tissues. Some have brought forward the chlorophyll function, or the production of starch, cellulose, etc. The latest suggestion is probably that of Conway MacMillan (1895), who sees a fundamental difference between animals and plants in the dynamic, energy-liberating nature of the former, expressed morphologically in cephalization, and in the static, energy-fixing nature of the latter, expressed morphologically in sporophytization.

Whatever the characters that are selected for our crucial test, it is evident that they must apply equally to the highest and most complex forms, to the simplest unicellular forms, and to all intermediate grades. What structure or structures are there so universal, so indispensable to the simplest and to the most complex, to animal and plant alike, from which characters can be drawn of universal application? The least complex organisms are likely to furnish most readily the clue to the answer. Setting aside physiological considerations, and having in mind the simplest organism, it is evident as soon as mentioned, that the first structure likely to be present, aside from the indispensable cytoplasm and nucleus, would be a cell wall. The cell wall is the shield, the armor, the enveloping cloak, that the organism throws about itself to protect the living, delicate protoplasm from the rough contact and harmful influence of the outer world. Some protection is well nigh indispensable upon the free surfaces. For the unicellular organisms it is a cell wall; for the multicellular organisms the walls about the cells of part or all of the tissues persist, or else only the general free surfaces develop walls. It is in the nature of this almost universal investment that it is proposed to point out a fundamental distinction between animals and plants.

The most universal structure

In attempting to distinguish animals and plants by means of definite characters, there is, however, another point that first needs attention. Diagnostic characters can only be drawn between like things, and in so far as the characters are also fundamental they must be based upon fundamental features. In searching for essential points of resemblance or dissimilarity, it cannot be denied that the normal individual in possession of its full

Characters to be taken from the active organism

powers is the real and genuine organism to which attention is to be directed. Secondary characters may be drawn from adaptive and more or less incidental structures, but not so the primary ones. Of all adaptive or ecological features of the organism the reproductive organs and processes are most prominent, and have naturally attracted great attention. Botany has been popularly styled the study of flowers, although flowers are only the decorated vestibule to the real sanctuary of the science. In trying to discover the innermost reasons for establishing a criterion between the two great classes of beings, only the normal vegetative state of organisms need, therefore, be considered, and the reproductive state, when the organism disports as a new-born entity of naked protoplasm, or is reduced to a spore or an egg, or hibernates in seed or cyst with protective and dispersive appendages, may be ignored. We are to keep in view only the vegetative organism, and not the mode in which a succession of individuals is maintained.

Reproductive states to be ignored

The fundamental characters of animals and plants may, in accordance with what has been said, be given as follows:

Animals and plants defined

PLANTS *are organisms possessing a carbohydrous investment.*

ANIMALS *are organisms possessing a nitrogenous investment.*

These characters hold good for the active individual only, and have no necessary application to reproductive stages. They are diagnostic characters and are not to be considered as in anywise defining the powers or functions of the two classes.

In cellular organisms the investment may extend to each protoplasmic unit, as is usual in plants, or to the units of certain tissues, as is usual in animals, or be developed only upon the general exterior, as is specially the case in cœnocytic organisms, like some of the common molds and sea-weeds (*Mucorinæ* and *Siphonaceæ*).

By designating the constitution of the protective investment, it is intended to cover only the original or basic substance of which it is composed, without reference to subsequent depositions or infiltrations, of whatever character they may be. Thus in the walls of grasses and Equiseti there is often a great amount of silica, in certain seaweeds (*Corallina*) much lime, in tunicates so much cellulose that it sometimes amounts to one-fourth of the dry weight, and yet, in the case of the plants named, the original and fundamental substance of the wall is carbohydrous, and in the animals nitrogenous.

Chemical features of cell walls

The carbohydrous investment of organisms, chemically considered, is probably always some form of cellulose. There are primary and compound celluloses, and various modifications of these. In some instances nitrogen seems to be associated with the cellulose, as Winterstein has recently claimed in the case of certain fungi, but of the nature of this association nothing is definitely known; the facts can have little bearing upon the fundamental proposition here laid down.

The nitrogenous investment is chemically always of the nature of a non-protoplasmic proteid, of very complex molecular structure, undoubtedly varying much in different organisms.

Both the carbohydrous and nitrogenous vestural substances are very likely chemically analogous, as maintained by Elsberg some fifteen years ago. Quite recently Cross and Bevan in their treatise on cellulose suggested that the substance of the proteid cell wall "may prove to be of similar carbon configuration to that of cellulose."

Physical features of cell walls

But in physical characters the two kinds of cell investiture are widely different, and especially so in their degree of elasticity. Carbohydrous membranes stretch but little, while nitrogenous membranes are highly extensible; and herein lies the basis of the wonderful divergence in mobility shown by animals and plants. The power of free movement, which characterizes the animal and has rendered possible its great and varied development, depends primarily upon the nature of the investment, just as the rigidity of plant bodies and their slow adjustments also depend by restriction upon the investment. It is no doubt possible in ultimate analysis to trace many of the prominent physiological characters of both kingdoms to this difference in structure.

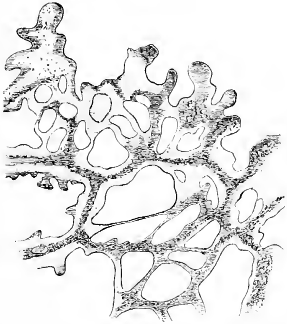


Fig. 25.—A mycetozoan in its vegetative or plasmodial state, much magnified. (After Cienkowski.)

The test applied

In applying the crucial test, some organisms present special difficulties. Some forms in their vegetative state consist of so-called naked protoplasm, of which the most con

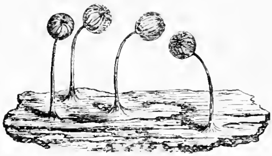


Fig. 26.—A mycetozoan (*Dictydium cernuum*) in its resting state, showing four fruiting stalks attached to a piece of bark. Enlarged ten diameters. (After Engler and Prantl.)

uous and well-known examples are the mycetozoans. Many species of these fungus-animals (*Pilzethiere*) possess a distinct nitrogenous envelope about the plasmodium, which by its chemical reaction is shown to be non-protoplasmic, and it may be inferred that careful examination will find it present in most of the species, and that it can be considered as potential or undeveloped in the others. They are, therefore, distinctly animal in their fundamental characteristic. Although usually treated in botanical text-books and studied by botanists, they were shown by DeBary, as long ago as 1864, to have more points of agreement with animals

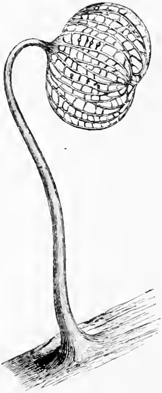


Fig. 27.—One fruiting stalk from above. Enlarged fifty diameters. (After Engler & Prantl.)

than with plants, and he believed them to be "outside the limits of the vegetable kingdom." This separation by DeBary was made without reference to a nitrogenous membrane, which may, however, be considered the crucial diagnostic character.

Another set of organisms, with apparently naked protoplasm during the vegetative stage, are the endophytic parasites belonging to the group of genera represented by Synchytrium, Woronina, Olpidiopsis, Rozella and Reesia. Whether they ever possess any demonstrable nitrogenous envelope has not been ascertained, but it is known with much certainty that they have no cellulose envelope; they are, therefore, not plants, and must, in consequence, be animals. This disposition of them has already been made by Zopf on the ground that a "plasmodial character of the vegetative condition is entirely foreign to the Eumycetes." The Chytridiaceæ, which are

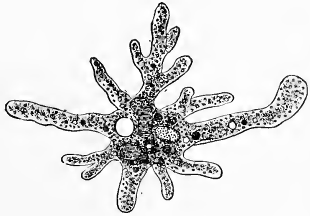


Fig. 28.—An amœba (*Amœba proteus*). The clear spot is a pulsating vacuole. Greatly enlarged. (After Leidy.)

usually associated with the Synchytria, have a much reduced but demonstrable mycelium formed of cellulose, and are, therefore, unmistakable plants.

Among the lowest forms, as generally classified, the Rhizopods, including Amœba, and the far simpler Monera, show no distinct envelope, either nitrogenous or carbohydrous, but as the other affinities appear to be with animals rather than with plants, they are doubtless rightly placed in the animal kingdom. It is reasonable to expect that more careful examination will, in some cases, show a simple or imperfectly formed nitrogenous envelope.

The crucial diagnostic character, which is here proposed, has in its favor the separation of plants and animals upon a line which accords well with the consensus of opinion of thoughtful students, both botanists and zoologists, an opinion which has been formed from a variety of structural, physiological and developmental data. Full relationship must necessarily be adduced from a study of the life-history of organisms; diagnostic characters only form points of departure.

INDEX TO PLANT NAMES

INDEX TO PLANT NAMES.