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SOME ENERGY RELATIONS OF PLANTS[1]

THE science of botany is about one hundred and fifty years old. Great changes have occurred during this time in the point of view from which botanists look at the plant.

The first scientific interest in plants was in merely naming them. In the latter part of the eighteenth century Linnæus extended the use of generic names which were already in use, added species names for greater convenience in handling his herbarium specimens, and thus established the binomial system, now in universal use in naming plants. Thus was laid the foundation of taxonomy as the earliest phase of the science of botany.

Linnæus clearly saw that the next step in the advance of botanical knowledge was to be classification. He himself made some crude attempts at arranging plants in classes. His system he well knew to be artificial. He clearly foresaw that more complete knowledge of the structure of plants, particularly of their buds, flowers and fruit, would ultimately lead to the classification of flowering plants in a natural system. His successors were busy with the attempt to learn enough of this structure of reproductive parts to enable them to put plants into a systematic classification according to their natural relationships.

This gave rise to morphology as the second great phase of the advance of botanical

[1] Address as retiring president of the University of Washington Chapter, Sigma Xi, Seattle, June 4, 1918.

science. It has gone a long way toward its goal of securing and interpreting data bearing on the order of the evolution of the various groups of plants and of thus putting classification on a natural basis. Morphology stands to-day with somewhat changed ideals as one of the big phases of modern botany. Contributing to evolution and working along with it, it offers a large field for investigation. A little later men began to interest themselves especially in the functions of plants—how they make their food, and from what raw materials it comes. This gave rise to plant physiology, the science which lies at the basis of the problems of plant production.

Following this, the destruction of growing crops by parasites led to a scientific study of the organisms that cause plant diseases. This interest in the mutual relation of host and parasites is the foundation of plant pathology, a subject having large possibilities in increasing food production as well as attractive from the standpoint of pure science.

In 1895 the publication of Warming's book focused interest on a new point of view in botany—that of plant societies living together as communities, limited as well as favored by a common environment, but not grouped at all according to their natural relationships in a morphological sense. This has given rise to ecology—a somewhat unorganized, but hopeful phase of modern botany.

We now have, then, four main lines of interest in modern botany—morphology and evolution, pathology, physiology and ecology. In the broadening of our knowledge of plants and of our interests in them, we have gotten far from the point of view of those who looked upon plants as merely things to be named—of those whose interest in plants was merely in the ear marks that might be useful for identification. In the shifting of interest from this mere naming of plants to their natural classification as based upon their structure and reproduction, and the broadening of this into interest in their functions, their health, their diseases, and even their mutual relations in plant societies, interest in the plant as a living thing has naturally developed.

In all of the modern phases of botany the tendency now is to look upon the plant as a living organism with work of its own to perform its own problems of existence to solve. In the very early stages of this interest it seemed to many persons that the mere statement that the plant was a living thing was a sufficient explanation of the phenomena shown in its activities. Perhaps this may still seem so to some.

The search for a "vital principle"[2] at first based on observation and speculation, but later professing to find some basis of support in the facts of modern experimental biology has proved unsatisfactory as not contributing to progress. Whether it is the "entelechy" of Driesch or the "x-entity" of Ganong it offers only slight help in getting anywhere. Neither the vitalist nor the neovitalist offers us a program for work.

During the years immediately preceding 1900 the tendency to postulate some sort of material particle as the ultimate basis of life was dominant. These particles or corpuscles were supposed to consist of more than one molecule and it was from them that the organism was built up in one way or another. They were also supposed to be the bearers of heredity.

In botany corpuscular theories resulted largely in research, the basic idea of which was that the chromosomes produced in the nucleus at the time of cell division are the bearers of heredity. Since these bodies are

[2] *Cf.* Child, Senescence and Rejuvenescence," Chap. 1.

plainly visible in a dividing cell under the microscope, attention was naturally focused upon them. However, even if any one succeeded in connecting up the transmission of some particular character to the offspring with some peculiar form of one of the chromosomes we still had the question of why that particular form was connected with that particular character. Thus little was accomplished so far as the fundamental problem was concerned. Although much knowledge was gained by investigations of this sort, they still furnished no means of direct attack upon the fundamental problem.

Investigations of the sort just mentioned illustrate the first fundamental defect of all corpuscular theories, considered as a means of advancing our knowledge of biology, viz., the corpuscles are hypothetical and thus merely serve to put biological problems beyond the reach of scientific investigation.

A second defect of corpuscular theories is that they provide no adequate mechanism for the correlation of the various organs making up a complex organism. Means of securing dominance of one part and subordination of another are lacking.

With the advance of knowledge of physics and chemistry and the growing interest in experimental plant physiology, the point of view in regard to plant functions shifted and we were chiefly concerned for a time with what may be called the chemical point of view in considering the phenomena involved in the activities of living organisms. It is of course, evident that chemical reactions play a large part in the life processes. It is also well known that life is closely associated with the substance which we call proteins. This gave rise to the idea that certain complex protein molecules are the "producers of life."

Though the molecule itself according to this conception is not alive, its constitution is the basis of life and life results from the chemical transformations which its lability makes possible. The living substance, then, says the explanation of life, is a substance in which some of the labile molecules are continually undergoing transformation. Life itself would then consist in chemical change, not merely in chemical constitution. Death must then be regarded as a change from lability to stability. The dead proteins, which the chemist might analyze could not of course, show the properties of the living substance, and the fundamental problems of life were thus again placed outside the realm of experimental science.

About 1900 questions began to be heard as to the existence of a "living substance" of more or less definite chemical structure. We are indebted largely to Höber's book published in 1911 for crystallizing our ideas as to the hopelessness of the purely chemical point of view and pointing the way to the physico-chemical, for starting us away from the idea that protoplasm is merely a complex chemical substance, toward the conception of protoplasm as composed of many chemical substances existing as a complex physical system. This assuming a colloid substratum for the organism, is the physico-chemical theory of life which represents the prevailing point of view in the biology of to-day.

This leads us to look upon the plant as a living physical system, receiving energy from its environment and doing work that is more or less useful to itself and to mankind. It points the way to a definite program for work and is then a source of gratification to the modern experimental botanist.

"The situation at present," says Dr. Briggs,[3] "may perhaps be fairly summar-

[3] *Jour. Wash. Acad. Sci.*, 7: 89, 1917.

ized as follows: The mechanism of plant processes not at present explainable on a physico-chemical basis would be termed by the vitalistic school as 'vital,' by the physico-chemical school 'unknown.'" This well expresses the current thought of experimental biologists.

When we have once recognized our ignorance and have found a means of learning, the situation looks more hopeful. Having arrived at this physico-chemical conception of the organization and activities of the living plant, the energy point of view furnishes the best means now available of making the experimental attack on the nature of the processes involved in plant metabolism. Change in the physical system must always be conditioned by the energy available. Since we look upon the living plant as a physical system we must be concerned with its energy transformations. We have until very recently considered the activities of the plant largely from the view point of the materials received by it from the outer world and the products formed from these materials. Now we are turning our attention toward the question of what forms of energy the plant may be able to use in these various transformations, or rather, we are broadening our vision to include both the materials and the energy.

In our consideration of the energy relations of plants we are largely concerned with four questions: (1) From what sources does the plant receive its energy? (2) What work does it accomplish by means of the energy received? (3) How effectively does it use this energy? (4) In what classes of plant problems does the energy point of view suggest a hopeful means of attack in research.

Under certain conditions the plant may absorb heat from the surrounding air. It also commonly takes in from the soil solution and perhaps even from the air certain energy containing compounds. Still the plant receives much of its energy directly from the sun in the form of light rays. What we know of its reception and use by the plant is largely confined to that portion lying within the visible spectrum, though some scientific excursions have been made into the realms of the ultra-violet and the infra-red rays.

The leaf is the most useful portion of the plant for receiving and utilizing this radiant energy of the sun. Being by nature a surface-exposing organ, the leaf brings its green cells into such a situation that they advantageously receive light energy from the sun's rays.

It is in the green cells of the leaf that those transformations of energy take place, which are most significant to the plant in its own problems of existence as well as to man in his.

The radiant energy falling upon the leaf of the plant may be disposed of in several ways. Some of it is reflected from the leaf surface and is then lost so far as its immediate effect upon the plant is concerned. This is a very small amount, but still it can not be entirely neglected.

Some of the sun's energy passes entirely through the leaf and is then also lost. Direct measurements of both the intensity and the wave-length of the light thus passing through the leaf have been made. Some of the energy retained by the leaf is used in evaporating water from the surface of the leaf. This is a much larger amount than both of the preceding combined. The amount of water thus evaporated from the aerial portion of a plant is large relative to the weight of the plant itself. Grass plants often give off in the form of vapor in every twenty-four hours of dry hot summer weather, a quantity of water equal to their own weight. The grass of an ordinary city lot 50×125 feet would give off under these conditions about 125 gallons of water in every twenty-four hours. If this is raised an average of 1 foot, it means the expenditure of 1,100 foot pounds of energy per day through the medium of the grass on the city lot.

A birch tree standing in the open has been found to give off over 800 pounds of water per day. A man equipped with two ordinary water pails would have to make thirty-two trips in order to carry this amount of water. If he had steps up to the top of the tree and could make a round trip very ten minutes he would work over five hours per day to carry this amount of water.

This evaporation is a large factor in raising water to the tops of plants. Recent investigation indicates that this molecular diffusion which we call transpiration exerts suction throughout the whole vascular system of the plant—leaves, branches, stem and roots. The contained water seems to be under tension even to the tips of the roots.

Transpiration operates through osmosis in leaf cells and through the tensile strength of the water column in the conductive tubes of the plant to accomplish this. While the actual vaporization of this water is dependent solely upon the evaporation power of the air (*i. e.*, temperature and relative humidity of the air actually in contact with the leaf cells) it is very probable that other forces arising from the presence of energy containing compounds in the plant are largely responsible for placing this water on the surface of the cells where the evaporating power of the air can act.

I have now mentioned two ways in which the plant allows radiant energy to escape without making use of it, and one way in which it uses it. The fourth possible fate for this energy is in food synthesis by the plant. A very large amount of the radiant energy received by the leaf is used in making compounds of high energy content from compounds of low energy content. The basic process in this group of synthesis is the manufacture of sugar and starch from carbon dioxide and water. This process depends upon the catalytic action of chlorophyll, the green coloring matter of plants.

This is a reduction process resulting in the storing of energy in such a form that it may be released by oxidations, such as occur in respiration, for the use of the plant. If not thus freed for the direct use of the plant this energy may remain stored in the form of coal or of hydrocarbon oils, and even ages after its capture by the plant may furnish heat for our homes or power to drive our railway trains or autos. More immediately it furnishes us through our food, all of which comes directly or indirectly from plants, the energy to perform work with our hands and our brains. The activities of the world are based on photosynthesis—the reduction of carbon dioxide by the plant resulting in the formation of carbohydrates.

This series of syntheses started in the formation of carbohydrates by the plant is important in the more direct production of mechanical energy, as well as in the matters just discussed. It is perhaps looking far into the future to consider a time when the world's supply of coal and of hydrocarbon oils may be exhausted, but such a time may come. If we keep up our present rate of stripping the earth of its clothing of forest trees, the supply of wood will not last forever and a constantly increasing portion of it will be necessary for structural purposes. The situation tends to turn our attention toward those sources of energy, which are not destroyed in the using and those that are capable of renewal within a brief time by growing plants.

The utilization of water falls and the employment of solar engines come under the first head. Here in the West we are utilizing, in electrical form, a considerable amount of energy from water falls and rapids, and have only just begun on the development of the possible power sites of the region. While many other localities can develop considerable amounts of energy in this way, not all portions of the earth are so well favored. Solar engines are reported to be in successful operation in a few places where the total annual amount of sunshine is unusual. Even with the full use of hydroelectric power and of solar engines, the situation, while not appearing serious for the immediate future, is such as to cause us to look with interest at the possibility of alcohol and other plant products as a source of energy.

In addition to the uses above mentioned for this energy, it may also function in other processes going on within the plant and necessary for its life and growth, and thus for its continuing to function in making possible the existence of human life on the earth. The intake of water by the plant from the soil solution seems to be mainly through the process of osmosis, although there seems to be much reason now for believing that we have been placing entirely too low an estimate on the part played by imbibition. In either case, the energy for the intake of the enormous quantities of water evaporated from the plant as well as the considerable amount used in the synthesis of food substance resides in the substances elaborated by the plant from the raw materials taken in from air and from soil solution.

Osmosis and imbibition are processes whose energy is largely traceable ultimately to the photosynthetic activity of the plant itself or of other plants either recently or in the remote past. Among the important results of this intake of water is the maintenance of form in the softer parts of plants, due to the fact that their cells are so full of water as to be turgid. Everyone is familiar with the loss of form by the leaves and young stems in wilting, *i. e.*, a loss of the turgidity of its cells.

Considerable amounts of work are done by plants in their mechanical effect on obstacles that come in the way of their growth. Striking evidence of this was seen on the campus in the spring of 1910 where the large ferns buried under the asphalt put down on the campus roadway during the preparation for the exposition of 1909, burst through these roadways at numerous points and continued healthy growth until trodden down by the increasing number of students and faculty of the university. By the further expenditure of energy the plant increases the extent of its own tissue by cell division and by the thickness of the walls of these cells, resulting in rigid tissue which are the main factor in the mechanical strength of older woody portions of plants. This energy comes to the aid of man in supplying wood and coal for fuel and for the various uses which wood finds in the structures incident to modern civilization.

There are other minor uses for the radiant energy received by the plant from the sun. Under certain conditions a limited amount of it may go to keep up the temperature of the leaf to that of the surrounding air. A certain amount of the sun's energy finds its use in the locomotion of the adult form of a few lower plants and of minute reproductive bodies in many higher plants. A small amount through oxidation results in the production of luminosity in a limited number of plants.

The plant uses this energy inefficiently. The potential energy stored up in the plant, as measured by determining the heat of combustion, is only 1 per cent. to 5 per cent. of the total energy received from the sun. Thus 95 per cent. to 99 per cent. of the energy received is dissipated by the plant.

The energy point of view has helped greatly in clarifying our methods of thinking on biological problems. As a result we are now experimenting along lines that give great hope for future success.

Luminosity in plants was for a long time an intangible will-o-the-wisp—a foundation for belief in ghosts. It was not until it was studied as an oxidation that the facts were established and the mystery cleaned up.

Our study of the intake of water by plants from the soil solution has in the past consisted too much in the substitution of the word "osmosis," for any clear notion of the nature of the processes that really take place. A good deal of thought unfortunately not so far resulting in much experimentation is now being directed toward the nature of the energy involved in the two processes for which we use the names "osmosis" and "imbibition."

Considerable more thought and experimentation have gone into attempts to understand the kinds and magnitude of the energy involved in the raising of water to the tops of plants. The chief progress in this field during recent years has been the result of thinking in terms of energy.

Among the many important economic contributions made by botanists during the last few years, a piece of work by Briggs and Shantz[4] on crop plants for arid regions well illustrates the usefulness of thought along energy lines. Plants that flourish without irrigation in these arid regions must, of course, be able to get along with very little water. They found that the efficiency with which these plants use radiant energy is inversely proportional to their water requirement. Hence, instead of introducing from more humid regions the plants of high water requirement and trying to supply to their roots all of the water that they can use, a more profitable line of endeavor seems to be that of the reduction of the water requirement of varieties of crop plants that are to be grown in these regions. There are two lines of endeavor that seem hopeful in this—the selection of varieties having low water requirements and the lowering of the evaporation rate by artificial means, thus lowering the water requirement of the plant.

[4] *J. Agr. Res.*, 3: 1–63, 1914.

The field of photosynthesis is an extremely important one for the use of the energy point of view. All of the probable steps in the synthesis of carbohydrate from inorganic nature have now been repeated in the laboratory. In the main, however, this has been accomplished by employing forms of energy probably not available in the plant. The search for the energy that may be available for this synthesis should engage much of the attention that is now going merely to a consideration of the materials involved.

Some confusion on the energy involved in the process has resulted in the past from the fact that a few of the earlier workers had differences in intensity when they thought they had only differences in wave length. However, clearer thinking and better apparatus are already pointing to definite progress in this field. The photoelectric cell has already been employed in plant physiology as a means of measuring the light intensity under which the plant is carrying on its life processes and important data will undoubtedly be obtained through its use by future investigators.

The energy point of view has already helped greatly in our understanding of carbohydrate synthesis in plants and promises still more in the future for progress in our understanding of this process so fundamental to our well being and happiness and even to existence itself. The energy point of view is the keynote of modern investigations in plant physiology.

This method of thinking is proving beneficial not only in those biological problems upon which direct experimentation is possible but also in giving clearer notions of some processes that have taken place in the past and appear to be at the present time outside the realm of possible experimentation.

Thought as to the possible steps involved in the early stages of organic evolution furnishes a good example of this. We are now getting away from a consideration of merely the form of the possible organisms which represented the first stages in the evolution of higher plants and animals and are now considering what forms of energy they could have utilized. Since we can hardly suppose that the first step from the non living to the living involved the presence of chlorophyll we think about them in terms of the possible forms of energy that they could have found available. Progress is being made by this kind of thinking. The suggestion that it at present offers is that sulphur and iron bacteria being able to oxidize inorganic compounds and being thus free from the necessity of the presence of chlorophyll on the earth, probably represent very early stages in organic evolution.

The usefulness of the energy point of view is thus apparent. It is not profitable to think longer in terms of vital force, of corpuscular responsibility for inheritance, nor alone in terms of the chemical compounds involved. We think rather of the energy transformations as related to both physical and chemical conditions. Does it not seem evident that the line of future progress in many fields of botanical investigation will be largely along the paths seen from the view point of energy transformations in the plant?

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EDUCATIONAL EVENTS

THE DEATH OF THORILD WULFF

A letter from Peter Freuchen, the Danish factor at Knud Rasmussen's Station at North Star Bay, Northwest Greenland, written in late February, gives a direct and definite account of the death of Dr. Thorild Wulff, Swedish botanist and ethnologist, who accompanied Knud Rasmussen on his recent trip to Peary Land and return across the Greenland ice-cap. Translated from the Danish, part of the letter is as follows:

The party, composed of Knud Rasmussen, leader; Lauge Koch, geologist and cartographer, and Dr. Thorild Wulff, botanist and ethnologist, left North Star Bay, as you probably know, early in April, 1917. They were accompanied by four Eskimo—Hendrik Olse, Inukitsok (''Harrigan''), Ajago (''Pingasut'') and Boatsman.

They traveled without mishap as far as St. George Fjord, where difficulties began—no game at all, with the exception of a few hares and a seal or two; scarcely a trace of muskoxen. Hence they could go no farther than De Long's Fjord. Here they started homeward, exhausted, and much depressed by the loss of Hendrik, who was devoured by wolves while out hunting. Weak from lack of food, he had apparently lain down to sleep, and before he could defend himself, the wolves had overcome him.

The others talk of the return journey over the ice-cap as a bad dream. After incredible difficulties, they finally attained the west coast at Cape Agassiz near the Humboldt Glacier, just a short time after they had eaten their last dog.

Knud Rasmussen and Ajago at once started on a forced march to Etah to get aid. The others were to rest a little, and then follow slowly after, trying to kill enough game to sustain them. After a few days slow travel without any food, Dr. Wulff could go no farther, and laid himself down to die. He wrote messages to his children and his parents, and dictated to Koch a brief survey of the vegetation about Peabody Bay, for he had continued his observations to the last. He was so weak and ex-