

PRESENT PROBLEMS OF PHYSIOLOGICAL PLANT ECOLOGY

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By physiological ecology is here meant merely the study of the factors which determine the occurrence and behavior of plants growing under uncontrolled conditions. Field physiology would be almost a synonym for the term here used. Pure physiology proceeds, as far as is possible, by controlling conditions. By varying known conditions and measuring the plant responses definite relations are established between stimulus and response. But ecology must perforce proceed without the known conditions, without the synthetically built-up environment of pure physiological research. Here it is necessary to measure and *analyze* natural conditions and to relate these to the behavior of the plants. The problem of measuring the plant phenomena, the determination of the number, size, form, structure, etc., of the plants involved, is essentially the same for both lines of study, but that of measuring environmental conditions is, of course, much more difficult where the latter are uncontrolled.

There is a principle of scientific research, that in an investigation which involves the measurement of a number of causal factors and the relation of these factors to resulting conditions, the various measurements should be of as nearly equal accuracy as possible. Where a number of complex factors are to be dealt with, as in ecology, progress must come, on the one hand, from a refinement of methods of measurement and, on the other, from better interpretations of the data resulting from these measurements. According to the principle just stated, we should ever seek to improve those of our methods which are the

least accurate, not those which are the most easily susceptible of improvement. It is, indeed, often a waste of energy to seek the highest possible accuracy in *all* of a series of measurements where one or more are at best of low accuracy. The accuracy of the resulting summation must be subject roughly to the error of the least accurate of the members.

It is not my purpose to submit any recommendations as to improvement in the general philosophy of ecology, although we must all realize that one of our greatest hindrances at present lies in the careless thinking which fills our literature with wrong or at least misleading imaginings, such as are suggested by the Jonah-like words, *adaptation*, *use*, *purpose*, etc. It is to certain lines along which improved methods of measurement seem desirable that I wish to call your attention at the present time. Our methods for dealing with the plant responses, with the *effects* of environment, already possess a general accuracy far surpassing that exhibited by the methods employed in measuring the environmental conditions which act as causes. I am unable to avoid mentioning, however, one phase of plant measurement which has so far received an almost insignificant minimum of attention, both from physiologists and ecologists. I refer to the subterranean portions of the plant. The relations existing between the environmental factors and the development and behavior of underground stems have been studied for some forms by Vöchting, Klebs and others. Roots have usually been studied in water or in air and only in the last few years has their behavior in the natural medium, the soil, been seriously taken up. A number of agriculturists have attacked the problem here suggested, but of course with reference to cultivated plants. Freidenfeld has made, as far as I am aware, the first attempt at a really broad study of the ecology of roots. The work of Dr. Cannon on the root systems of desert plants shows how extremely important subterranean competition may sometimes be. It would seem

that the underground portions of ordinary plants are well worthy of more attention than has heretofore been accorded them.

We turn now to the environmental factors. When it is sought to determine the causes influencing the behavior of plants growing under natural conditions, two very different methods may be resorted to, the observational and the experimental. By the experimental method we try to determine, on the one hand, the kind and amount of vegetation and, on the other, the magnitude of the various physical conditions which make up the environment. From these two series of observations are selected paired concomitant factors or groups of factors, and when the same concomitants appear in a number of such pairs the conclusion is drawn that the relation between the paired factors is a causal one. By the experimental method we seek to control the conditions to a greater or less degree, either synthesizing an artificial environment (experimental physiology), or growing the same plant forms under various natural environmental complexes. This sort of work may be termed experimental ecology. In so far as the environment is artificially synthesized, it is comparatively easy of measurement, but where natural conditions are allowed to obtain, the experimental and the observational methods both require the measurement of uncontrolled factors, and thus present great difficulties.

The complexity of natural conditions makes it necessary often to break them up into component parts and to measure the parts separately. For convenience in handling, these factors have been classified into climatic and edaphic, but I fail to see that such a classification has any relation to the activities of the plant. I shall, therefore, speak here merely of environmental factors, classifying them, for ease in discussion, into those which are active above the soil surface and those which are active below it. Each group must, of course, be further analyzed according to the purposes of the investigation. But it must be remembered that the data from separate com-

ponent factors usually need to be again summed in order to express the environment as a whole. For the great general problems of plant geography it seems inadvisable to attempt too extended an analysis, rather is it better to seek methods of measurement which will furnish integrated evaluations of groups of environmental conditions. With our present lack of knowledge, the pressing of the analysis too far often results in such a complex of data that an interpretation is impossible. A fairly satisfactory integration of the main air factors seems to be furnished by the atmometer; as to the soil factors, we have made hardly a beginning in this direction. In the following paragraphs I shall first consider the measurement of the air factors, denoting by this term all factors which are active above the soil surface, whether or not the air is actually involved.

Atmospheric Factors.—Atmospheric pressure can be easily measured by means of the barometer, curves are automatically constructed by the barograph. Considering the perfection of this instrument, it is rather unfortunate for ecology that the plant is so little influenced by the natural variations in atmospheric pressure.

Temperature is very important in plant activities, and we have practically perfect instruments for its measurement and for the construction of its curve. Unfortunately we have as yet no well-tested method by which temperature can be interpreted in regard to its effect. A beginning which promises much has been made by Dr. MacDougal with his integration of the thermograph record and Professor Lloyd has told me of a new method devised by him for interpreting maxima and minima. Here lies one of the best fields for the scientific ecologist with a mathematical turn of mind.

Wind velocity can be measured and recorded by means of the ordinary forms of anemometer, but the instruments are not well suited to field work, largely on account of their expense. Perhaps improvement may be forthcoming along this line.

The conditions of humidity, which appear to be so important to plant life, can best be measured directly by means of the dew-point apparatus, but the instrument is not as satisfactory in the operation as could be desired. The whirled psychrometer and the wet and dry bulb thermometer are more easily operated and are quite satisfactory as regards results, especially where the humidities dealt with are not too low. Attention may be called here, however, to the inadequacy of the wet and dry bulb thermometer without a strong current of air. The current should be so strong that any increase in its velocity would produce no further lowering of the temperature of the wet bulb. The hair hygrometer is unreliable unless often standardized by some other instrument. Especially is this so in regions where the humidity is usually low or where its fluctuations are very great. Much improvement is surely possible in connection with this factor.

The evaporating power of the air, an integration of the effects of temperature, wind velocity, relative humidity, and, to some extent, of light intensity, is at least not as difficult of measurement as formerly. The porous cup atmometer can be made to give data for a curve as well as a final integration for a long period. It seems that we may expect much from this or some similar instrument.

Precipitation data are easy to obtain with amply sufficient accuracy, but the factors of superficial and subterranean run-off as well as that of evaporation from the soil surface (all of which are almost hopelessly difficult to measure) make these data very hard to interpret, except for particular localities. Their final interpretation will probably go hand in hand with that of evaporation and soil moisture.

For the measurement of light intensity—a factor which has been shown conclusively to be of prime importance in many ecological problems—we have at present no reliable and practical instrument. The delicate bolometer

would doubtless give the data needed, but it is not well suited to field work and is at best too expensive. The so-called photometers (such as those used in photography) are unsatisfactory in the extreme, both theoretically and practically. They are, of course, not photometers at all, but actinometers, and for our purpose it is to be remembered that the shorter light waves are at least not the most important in plant activity. Here again is a field that should prove wonderfully fertile to him who has the courage and patience to cultivate it.

The determination of the composition of the atmosphere is important in certain lines of investigation and in the solution of general ecological problems in certain regions. For this purpose the methods already at hand are perhaps satisfactory enough, though we are unable to obtain automatic records of fluctuations in these conditions.

Soil Factors.—If the factors active above the soil surface present great difficulties, those active in the soil present greater ones. What knowledge has been gained by the agriculturists is seldom at the disposal of the ecologist, perhaps partly from the nature of the agricultural literature, and partly from a too common feeling that agriculture and ecology are far apart. (It appears to me that ecology is the legitimate and necessary meeting-place for scientific botany and scientific and practical agriculture.) But the agriculturists have not made any very great progress in this field. Their measurements of soil conditions are too often merely determinations of the various amounts of inorganic salts which can be extracted from the soil by one or another cleverly chosen solvent. In some cases determinations are made of the total amount of organic matter in the soil, but it appears that these chemical results lack much in ease of interpretation, so much that they are of little value to the ecologist.

Soils have been classified by various workers according to the size of the component particles, but I have not

found any adequate method of interpretation by which the data of the physical analysis may be made to aid in the explanation of vegetational conditions. There is no doubt that these data contain much valuable information, if we but knew how to interpret them.

A beginning has been made in the important and fundamental inquiry into the attraction of the soil for water and the ability of the soil to conduct water to plant roots, but our ignorance in this regard is even more dense than that concerning the normal physiology of the roots themselves.

The geological origin of soils (a subject which makes up a large portion of the text-books on soils) is of no possible importance in either agriculture or ecology. Mitscherlich—the author of the most scientific book on soils which I have come upon—says in his preface,

For our cultivated plants the geological origin of the soil in which they grow is in no way important; the growth of the plants must always depend upon the *present* physical and chemical constitution of the soil.

Of course this is just as true of uncultivated forms. But attention needs to be called here to the principle already mentioned, namely, that in the pioneer work in such a field as this it is often not well to analyze the great general factors to too great an extent. Great general vegetational features may be compared with great general soil features, and wonderfully enlightening results have come from such comparisons, as, for example, those obtained by Dr. Cowles and his associates in this field.

The possible importance of small amounts of organic chemical substances in the soil has been strongly emphasized by the work of the Bureau of Soils and by that of Dr. Dachnowski and others, and evidence in this regard is rapidly accumulating from all parts of the world. There is now little reason to doubt that bog soils and others which are poorly drained owe the character of their vegetation in great part to the presence in the soil of toxic bodies. There is evidence that many well-

drained soils contain similar substances. The ecologist can not afford to neglect this important line of advance.

The water conditions of the soil have not received the attention which their importance justifies. For determining the amount of soil moisture our methods are confessedly crude and unsatisfactory, yet they have not been employed as extensively as their accuracy seems to justify. Graphs of the fluctuations in the water content have yet to be constructed, although their construction is comparatively simple and their value for our purpose must be very great. Such curves should replace the bare and almost useless data of precipitation and run-off. Improved methods of measuring soil moisture will of course be of great value, if such can be devised.

As to the rate at which the soil can supply water to the plant—quite a different question from that dealing with the amount of soil moisture—we know almost nothing. This rate of possible supply, or the resistance offered by the soil to water absorption by roots, is, I think, perhaps at present the most important problem in all ecology, and it has hardly been touched upon. But the problems here suggested seem to be as difficult as they are important.

We know almost nothing in a quantitative way about the relations between the oxygen of the soil and plant development. If this field should be developed we should undoubtedly be placed in condition to explain many dark and complicated points. The capillary power of the soil apparently determines, other things being equal, both the rate of water supply and that of oxygen supply, and perhaps the best that can be done here, in the absence of more perfect methods, is to study plant behavior with reference to capillary power and water content. But ecologists have hardly even attempted to relate the easily determined capillary power (which is constant in any given soil) to the vegetation, and it is difficult to foresee what important results might be forthcoming from such a simple study.

The temperature of the soil can be measured and recorded with about as great ease as can that of the air. But we meet here the same difficulties in regard to interpretation.

Finally, for a goodly number of ecological investigations, the bacterial flora of the soil must be investigated. The agriculturists have made good progress here and we may do well to follow them. The possibilities are very great.

In conclusion I should like to call attention to what appears to me to be the one great general need of ecological work, namely, the need of quantitative studies. It is only through such studies that the science of the relation of the plant to its environment can make real progress.

DISCUSSION OF DR. LIVINGSTON'S PAPER.

DR. BURNS: I am heartily in accord with all Dr. Livingston has said, and I have a lot of records of light readings, that I think I have had for the past six or seven years, that I don't know what to do with. An ecological work, for instance, will dilate on rain force, and then leave that alone, and presently suggest something entirely different. It seems to me that we could work on something in the line of the determination of the maximum and minimum of light, and along this line I have been trying to work out the amount of shade that these plants can endure before they will die out and be succeeded by some other plant, but I have not got on very far.

DR. POND: It would be very valuable if we had some work bearing upon an analysis of a given factor in a given case, and it may be interesting to know that a recent article really attempts it. I refer to the article of Ball's on "Temperature and Growth." Of course, temperature is an external condition. Its effect on growth may be either unseen or apparent in some outward manifestation. This article shows, by a careful analysis, that the temperature factor in the specific case which he was working on, namely, a fungus,—the temperature factor as applied produced a substance which inhibited growth of that fungus and finally stopped its growth.

PROFESSOR BARNES: May I take this opportunity to say that I hope very much some of the reforms will be adopted, not only by ecologists, but also by some other members of the botanical fraternity. Mr. Harshberger's quotation that our ideas never keep pace with the growth of our language, and our language never with our ideas, has more truth in it than we imagine. Our ideas have not always kept pace with the growth of our language (laughter). It is greatly to be hoped that the language will not be strained any farther. We need no extensive growth of that, and while far be it from a mere editor to suggest to any ecologist that a page of tabular matter not only costs three times as much to set up, but seems

actually useless and trifling, yet I hope that these suggested reforms will become actualities.

DR. LIVINGSTON: In that very connection it occurs to me that perhaps there is another line of ecological work which goes a step farther in clearing up, that is analysis of conditions. What is found out about physical conditions—then comes the question, how do these conditions come into existence? That is, perhaps, a part of the study of ecology. Very often we have to take the analysis back in order to explain how conditions arise; for instance, this plant grows less because of light, heat and moisture conditions. Now I might enquire how these conditions are brought about? By a tree growing alongside or the absence of vegetation—so we see how ecology leads ever to other fields!

DR. GRIFFITHS: I recall, in connection with the gentleman's statement regarding light and heat, a surprising experience I learned of by talking to a commercial gentleman in Arizona—a commercial man but a scientific one at the same time, a gentleman connected with the solar motor industry, of which you have heard a great deal, and I was surprised at the results of his measurement of light and heat, the measurement of heat particularly. He measured heat, of course, in direct relation to his machine—the reflecting surface of his machine—by a thermometer placed in a black box, with its face to the sun, the box simply being an open one, with the open side to the sun. Much to my surprise he informed me positively that an hour's sunlight on the Atlantic Coast was more efficient than an hour's sunlight on the desert of Arizona. Now, that may be an obvious fact to botanists, but it was not to me at the time. I subsequently thought of the matter, and thought possibly I could see reasons for it, but it had never occurred to me before. The result mentioned is possibly due to the presence of a smaller amount of dust in the atmosphere upon the Atlantic Coast. With a heavier rainfall the atmosphere is clearer. The transmission of heat is more certain and undoubtedly his statement was true. He has demonstrated it with his machine. I presume it is due to the presence of a large amount of foreign material in the atmosphere.