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CONTRIBUTIONS TO PLANT PHYSIOLOGY

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CONTENTS

CONTRIBUTIONS TO PLANT PHYSIOLOGY

THE DEPARTMENT OF PLANT PHYSIOLOGY

By Burton E. Livingston

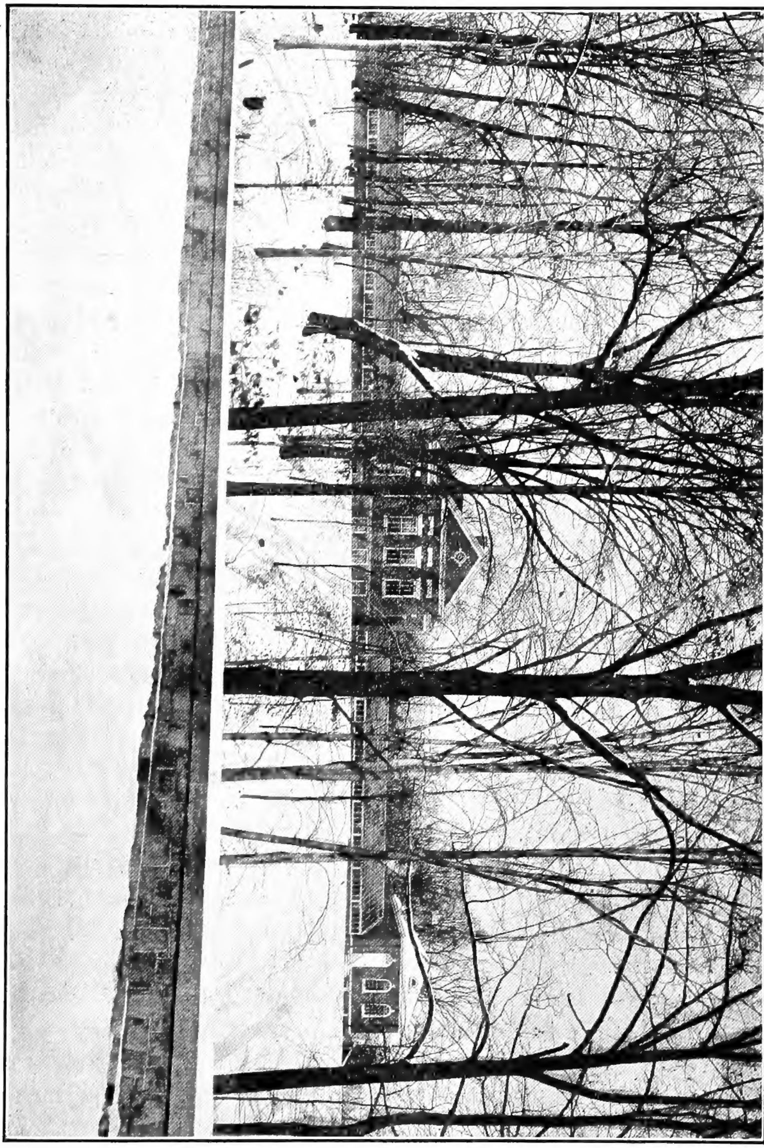
The Department of Plant Physiology, established in the autumn of 1909, has experienced a very satisfactory growth during the seven and one-half years of its existence. It entered the present Laboratory of Plant Physiology as soon as the building was completed, in the winter of 1911-12. The laboratory building has been described, with photographs and plans, in the *Johns Hopkins University Circular* for December, 1916. The present paper is offered as a preface to the following preliminary reports of plant physiological work now in progress or recently completed, and deals with two topics, the general aims of the department and the nature of the work so far accomplished or in progress.

Aims of the Department

Nature of the Science—Plant physiology occupies a somewhat uncommon position among the natural sciences, having many of the characteristics of a young science, although it is not really such. Notwithstanding the fact that people have been interested in the physiology of plants for many generations, the subject has hardly yet become generally regarded as a separate science, and it has usually been included under the general designation of botany. Animal physiology, which is, of course, the corresponding subdivision of zoology, has long been considered as distinct. The simplest way to make the content of plant physiology clear to one not acquainted with it is to point out that it deals with plants in exactly the same way as animal physiology deals with animals. Thus it has to do with all the processes that go on in plants, and it considers these processes just as physics and chemistry consider the processes that go on in inanimate things. Indeed, the close relation between the physiology of animals and that of plants is becoming so well appreciated in recent years that a science of *general physiology* (dealing with the physics and chemistry of all living things) appears to be rapidly developing. It is seldom possible to treat any physiological topic adequately without reference to both plants and animals. Some of the topics dealt with in plant physiology may be mentioned as examples. Such are: water requirement; nutrition by inorganic materials; nutrition by organic materials; the exchange of energy between the organism and its surroundings; the chlorophyll function; respiration, with and without free oxygen; enzymes, activators, hormones, and the general phenomena of catalysis; the control of growth and development, including reproduction; the physiology of movement and its control, and the physics and chemistry of protoplasm.

The non-physiological aspects of biology may be grouped together as *morphology,* which deals with the structures of organisms. Perhaps one of the most noticeable aspects of physiological endeavor, and one in which it differs remarkably from morphological study at the present time, is this, that it has little to do with the general problem of evolution and phylogeny. Evolutionary philosophy has been built up largely from morphological observations, and it is only recently that it has become possible to relate different organisms to each other with reference to their physical and chemical processes. The evolution of animals and plants has never yet been one of the main topics of physiology.

The sciences of mycology, bacteriology, pathology, ecology, etc., all have their morphological and physiological aspects, and their subject-matter may be treated from the standpoint of static description or from that of process dynamics. Thus, that branch of pathology which deals with the identification of parasitic organisms is mainly morphological in its point of view, while the sciences of toxicology and immunology are clearly branches of physiology. It is not without significance that many of the characters by which the bacteria



LABORATORY OF PLANT PHYSIOLOGY (CENTER), EXPERIMENT GREENHOUSE (LEFT), AND PART OF BOTANICAL LABORATORY AND GREENHOUSE (RIGHT).

(From the south,—Wyman Parkway.)

are classified and identified are physiological, since the processes induced by these minute organisms happen to be more easily observed than are their structural differences.

Application of Physiological Science—Just as physics, chemistry, climatology and biological morphology become applied in physiology, so does physiology become applied in many other lines of human activity. As with other sciences, there are, in general, two groups of applications that are possible. First, there is the general application of physiological knowledge and principle to the formation of what has been called a "philosophy of the universe." This is perhaps its application as "pure science," and for this application plant physiology is almost, if not quite, as valuable as is animal physiology. Such application is not usually called an application at all, not being primarily practical for the physical aspects of human life, in the sense of "buttering bread." But there are still men who do not live by bread alone, and a commercial age has not yet proved that a general appreciation of the relations of the things about us may not be ultimately as valuable to the human world as are those things which money buys directly. It is in this direction of application that modern natural science claims at least an equality with philology, history and the other humanities.

The second group of applications possible for physiological science includes those commonly called practical, by which food and clothing and dwellings may become more readily available to human beings, and by which human health and comfort may be enhanced. Just as animal physiology finds its most numerous applications of this sort in the fields of medicine, surgery, hygiene, animal husbandry, etc., so plant physiology contributes most to human physical welfare in the fields of agriculture, forestry, fermentation operations, bacteriology, etc. These applications are more interesting to more persons than are those of the first group and their importance is not to be minimized. Indeed, the more a science may be practically applicable the more opportunity it may have for becoming philosophically applicable. The two kinds of application advance hand in hand, but the great majority of individuals may remain generally careless of the philosophical kind. For the growth of plant physiology and for its best service to the world, it is clear that most of its devotees must give much attention to the practical problems of plant production and plant culture, and such is indeed the case.

Both groups of applications have their philanthropic or altruistic and their personal or selfish aspects, using these adjectives in their usual sense. Thus, a world philosophy may be cultivated with the conscious aim of advancing human development in general, or with the aim of advancing certain individuals, groups or institutions, as by increased financial income. Of course, the two aspects overlap, but the broadly philanthropic aim seems to have been frequently more evident than the other among the great philosophers and religionists of the past. We are not told that a Buddha or a Christ or a Pasteur has given much attention to personal financial income or to the copyrighting or patenting of his ideas. Nevertheless, it is quite possible for a modern philosophical scientist to give attention to such personal things without detracting from the broader value of his work.

The practical applications of a science such as plant physiology may be carried forward for either altruistic or personal ends. The latter kind of activity is commonly called commercial. A plant physiologist may work for years in perfecting methods for the production of better or more abundant agricultural crops, and his main aim may be either to lower the cost of food to the multitude, or to gain for himself fame or financial profit. The work itself may be the same in both cases, and even the publication of his results and conclusions may not be markedly different. However, as in all such personal activities, the results eventually become free to the world, and may thus become just as important in general human advancement as though the work had been planned with that end in view. Personal interest can usually withhold results of this kind for only a limited time; patents and copyrights run their courses and commercial secrets are sooner or later divulged. As has been remarked above, the two points of view overlap, an individual's motives are seldom or never exclusively of the one or of the other kind, and they shift from time to time.

It has seemed desirable to give space to the discussion just presented, on account of the long-standing misapprehension that still exists between the exponents of "pure science" and those of the arts and commercial applications of science. The writer is convinced that all these various human motives for scientific work must exist side by side, even in the same individual, and that it is for a university department to present all of them to its students. But the outstanding fact seems to be that the work itself should be much the same in all cases, assuming of course, that actual dishonesty is ultimately as bad from the commercial point of view as it is from the altruistic, as bad in practical applications to human physical needs as it is in philosophical applications to what have been called human spiritual needs.

Training of Physiological Students—It should be appreciated that physiology articulates intimately both with biological morphology and with the physical sciences. It is obvious enough that the processes and reactions of living things are not to be understood without a certain amount of morphological or anatomical knowledge. Thus, anatomy and histology are, in this way at least, and otherwise to some extent, prerequisite to the study of physiology.

On the other hand, the changes of matter and energy that go on in living things cannot be seriously studied without a broad and rather detailed knowledge of the principles according to which such changes occur in dead matter. In this way the field of physiology furnishes opportunity for the application of physics and chemistry in the understanding of life. So important is this consideration that physiology may be defined as the physics and chemistry of living things. This consideration has not been so generally appreciated as seems desirable, and many of the present leaders in physiology have first approached the subject through the avenues of morphological study. Perhaps it is because of this that beginners are often led to devote several years to academic work in morphological pursuits before they are allowed to become acquainted with the physiological aspect of biology, so that they discover the need of an intimate knowledge of physics and chemistry only at a rather late stage in their development. It is a significant fact that very few of the present workers in plant physiology have been led to their interest in the subject from an introductory study of the physical sciences, although physiology offers some of the most important physical and chemical problems.

Considering the general applicability of physical as well as morphological knowledge to physiological study, it is becoming more and more evident that a tyro in physiology should be encouraged to devote much more attention to physics and chemistry, in the earlier years of his preparation, than is now generally the case—which necessarily means that he should not be encouraged to devote so much time to biological morphology as he does in most institutions where young natural scientists receive their training.

The considerations just set forth have been given prominence in planning the training leading to the doctorate from this department, and, while no formal prerequisites are stated, the need of as much knowledge of chemistry and physics as the student can obtain is constantly emphasized. At the same time he is urged to become well acquainted with the main facts and general principles of animal physiology and with those of the comparative anatomy and histology of plants, as thus far available. Since climatic conditions exert such controlling influences upon the behavior of plants, that physical branch which is termed climatology must also receive much emphasis.

It is the general plan of the department to erect no artificial barriers before the prospective student; the work is so organized that any person who understands elementary physics and chemistry can enter our physiological work. If his morphological or physical knowledge is inadequate this may be corrected as his work goes on. In short, an interest in, and a serious desire to become proficient in, plant physiology are the only prerequisites for the training that is here offered.

The work of this department has thus far been exclusively *graduate* work, so that all of our students are intellectually rather mature. The scarcity of opportunities for carrying on advanced work in plant physiology, together with the fact that numerous educational institutions offer opportunity for elementary academic courses in this and the related subjects, have made it appear undesirable to institute undergraduate courses here. Experience seems to show, furthermore, that the intellectual power of graduate students is greater among those who have migrated from one institution to another, than it is among those who have performed their undergraduate work in the same institution as that in which graduate work is undertaken. Whether a causal relation is mainly involved here is questionable, for the very fact of student migration generally bespeaks a serious purpose and a definite aim; but it is also undoubtedly true that student migration tends strongly to prevent and to obliterate provincial traits of mental character, and to give to the student who has thus migrated one or more times a more extensive series of interests and a deeper appreciation of relative values.

The general purpose in the training of our students may be expressed as the inculcation of scholarly habits and of personal judgment in the carrying out of research. To this end, the work of the department is carried on as though research itself—productive scientific study—were the main aim. The student thus becomes, as it were, an apprentice in what is planned to be creative physiological endeavor, and he develops through striving to solve physiological problems and to interpret and present the results obtained. He is thus led to read the literature because he seeks the knowledge that it contains, rather than because such reading has been assigned or prescribed. He also learns that the planning and the interpretation of experimental work require far more serious attention than does the work itself, for a poorly planned or poorly interpreted piece of work can result in but mediocre results. The actual operations of experimentation may be best learned by carrying out a well made plan, and the interpretation and presentation of the results obtained determine for the most part how valuable they shall be in the development of the science. Thus as much emphasis is placed upon clear imagination, clear thinking, and clear presentation, as upon the many details of the manipulation of apparatus, so frequently considered as constituting scientific knowledge. This department does not aim to *teach* the subject, but it carries out investigations and tries to help the workers to become independent in the planning, prosecution, and interpretation of research.

A single course of semi-formal lectures, lasting through the year, with prescribed laboratory experiments, suffices to bring the students into contact with the various phases of the subject, and instruction is thereafter mainly personal, in the form of conferences upon the numerous matters that arise in the prosecution of research. No attempt is made to standardize the students beyond the elementary phases of the subject, but each one is encouraged to develop along lines determined by its own natural bent. Consequently, problems for research are not generally "assigned," as the phrase goes in many university laboratories, but the prospective investigator is led and assisted to choose a problem according to his own earlier training and present interest and enthusiasm. An attempt is made, however, to discourage the taking up of any problem that does not promise results of a definite nature which, when they are obtained and interpreted, will surely fit into the general structure of plant physiology.

It appears probable that the majority of our students will eventually enter the field of practically applied physiology, as investigators in agricultural or forestry experiment stations, or in commercial establishments; but our point of view is always that of the pursuit of the science for its own sake, so that as many as may be needed may find places as teachers of the subject. For all these lines of endeavor the same general kind of training appears to be requisite, as has been pointed out. Such training must aim to make the student familiar with the great principles of the science, with some of the methods employed, and with enough of the literature so that he may make efficient use of the libraries in his future work. Above all, he must be led to a facile and versatile attitude of mind, which regards his science as a continuously changing thing, with new needs arising at every turn of its progress; also, he must be not over-timid in following his problem wherever it may lead, even into the fields of other sciences.

The Work so far Accomplished or in Progress

The accomplishment of a scientific research laboratory should be calculated as the sum of two different terms. The first of these is, obviously, the progress actually made in investigation, in the solving of problems, and in contributions toward what we name the general fund of human knowledge. The component parts of this term are usually easy of descriptive statement, but difficult of comparative evaluation. The second term includes what is commonly thought of in universities as the training of students, but it should also include the intellectual progress of the laboratory staff itself (which ought to accumulate to form an asset of some value) and likewise the aid and encouragement furnished by the laboratory to persons not directly connected with it at all. This term, as is readily seen, is the educational one, and its components are very difficult both of precise description and of comparative evaluation. Looked at in one way, it may be said that the first term measures the actual product of the laboratory as an institution for the *making* of knowledge, while the second measures the preparations made for the accomplishment of future work of many kinds, whether in research or other lines of human activity. Both these kinds of effort progress side by side in the life of every individual and of every institution; each day is partly devoted to actual accomplishment and partly to preparing for future accomplishments, and the two sorts of activity cannot be clearly separated. Especially is this true when it is appreciated that the accomplishment of one worker becomes preparation for the future activities of others, as well as of the same worker. These two aspects of our work may nevertheless be considered separately.

Educational and Preparatory.—Considering the period from October, 1909, to June, 1917, 38 persons, including the two members of the staff of the department, have made use of the laboratory of plant physiology. The periods of use were: One year for 24 persons, two years for 7 persons, three years for 5 persons, four years for 1 person, and eight years for 1 person. Thus, the laboratory has furnished facilities for mental development, roughly equivalent to those for 65 persons for a single year, or for an average of 8 persons per year. Ten of the 65 academic years considered are those of the professor (8) and instructor (2).

Of the 38 individuals who have used the laboratory, four have worked here after the attainment of the doctor's degree elsewhere (two of these are on the staff), four have attained the Ph. D. degree from this university, with Plant Physiology as principal subject, and five others plan to come up for the degree in June, 1917, with this as their principal subject. Plant Physiology has been selected as a subordinate subject (in the requirement for the Ph. D. degree) by 15 persons.

Of the four persons who have received the doctor's degree from this university, with their main work in this laboratory, one is now employed in the U. S. Department of Agriculture, two in state agricultural experiment stations, and one is on the staff of the University of the Philippines. Thus, three of these have entered applied research and one is devoting a portion of his time to teaching.

The investigation carried on here has itself been largely preparatory for future work; the problems that we have desired to attack could not be undertaken until the field (which is a new one) had been specially prepared, so that our contributions to the science are to be regarded largely as beginnings and preparations. It appears likely that many of these lines of work will be carried out elsewhere, either by students of this university or by others who become interested as the field is opened. The general nature of our problems will be touched upon in the following section.

One other feature of the educational and preparatory work carried on by this department deserves mention, a feature that may be fully as important as is the direct training of students. This laboratory has furnished information and advice to many persons not directly connected with it regarding problems bearing on the water relations of plants, and has thus been able to render more or less valuable aid to students in other institutions and investigators in experiment stations, etc. To a lesser degree we have been called upon to aid outside investigators in other fields of plant physiology. It has been the practice of the department to furnish ideas and suggestions quite freely to all inquirers, a practice involving the writing of explicit and detailed letters, but one which seems to be fully as legitimate and valuable as are the consultations with our own students in residence. It is intended that no such inquiries from outside the department shall be subject to neglect or perfunctory reply; such information and suggestions as we have are furnished promptly and freely to all who ask. This makes the handling of the correspondence of the department a somewhat serious undertaking, but one that is fully worthy of the time and energy so expended. The number of persons, in many regions of the world, who are thus more or less indirectly connected with this laboratory, is much larger than the number of workers who have actually been in residence here. Also, the director of this laboratory devotes considerable time to the editing of plant physiological papers prepared by workers in other institutions, especially for *Physiological Researches,* a series of publications with which the University has no official connection and for which it furnishes no financial assistance. An English translation of Palladin's *Plant Physiology,* with editorial additions, is about to be published from this department. It has been prepared from the German translation of the Sixth Russian edition, with incorporation of the main alterations occurring in the Seventh Russian edition.

Contributions to the Science, and Researches Now in Progress.—To give a clear idea of the nature of the investigations attempted in this department, it is desirable to present a brief discussion of the general field in which these investigations lie. The science of plant physiology deals with the processes or changes that go on in living plants. Now, to understand a change as fully as possible it is required to know the change first in a roughly descriptive sort of way, after which our knowledge is to be advanced by consideration of the dynamic and causal aspects of the process considered. Descriptive physiology involves statements of the various sorts of processes going on in the organism, and it should show in what regions of the body these changes occur, and when they occur. Thus, that ordinary green leaves take up the element carbon out of the air during periods of sunlight is a statement of descriptive physiology, in this sense. To inquire more deeply concerning this process of carbon-intake clearly leads to quantitive studies of the various rates at which this intake may go on, which may be correlated with the various concomitant conditions of the plant and of its surroundings. Such studies soon reveal the fact that the rate of carbon-absorption is determined by a host of conditions, each one of which requires to be measured with regard to its intensity, and it is found that the rate in question may assume different magnitudes as the conditional intensities vary. It is true that the process of carbon-entrance from the air usually ceases, and is replaced by one of carbon-exit, when light is absent, but the same alteration may be induced by many other changes in the surroundings; for example, by sufficiently high or low temperature, by sufficiently low water-content of the leaves, by a sufficiently high concentration of a poisonous gas in the air, etc. It soon becomes clear that no physiological process is to be regarded as at all well understood without a considerable knowledge of its quantitative control, and dynamic physiology deals with the more elaborate and quantitative statement of the physiological changes thus suggested. It relates them to their determining conditions within and without the organism.

From the work of earlier students many plant processes are now fairly well known in the simple, descriptive way, but none of these is yet at all well understood in the dynamic or etiological sense. This latter is the phase of physiology which is now beginning to attract the most serious attention, and to it will be devoted the energies of investigators for many generations to come. It is to this field of dynamic physiology that the researches of this laboratory are planned to apply.

While descriptive physiology, as above defined, is a comparatively old science, dynamic physiology is a young one, and the problems of the latter are complicated in the extreme—there are so many different kinds of conditions that may take part in the control of plant processes, and each of these conditions may be effective with so many different intensities. The complexity and newness of these dynamic problems explain the fact that the very methods needed for the sort of study here suggested are, for the most part, still to be devised. It is obvious that dynamic physiological investigations must rest upon comparative measurements of the intensities of effective conditions and of the concomitant or resulting rates of the processes that are to be investigated, so that studies of the possible ways by which such measurements and comparisons may be made must constitute the beginnings in this field. All of our work has aimed at this causal sort of explanation of process rates, but much of it, as so far carried out, has resulted in little more than giving us certain methods of study and certain incomplete results. The problems are so complex that broad generalizations cannot be looked for for a long time.

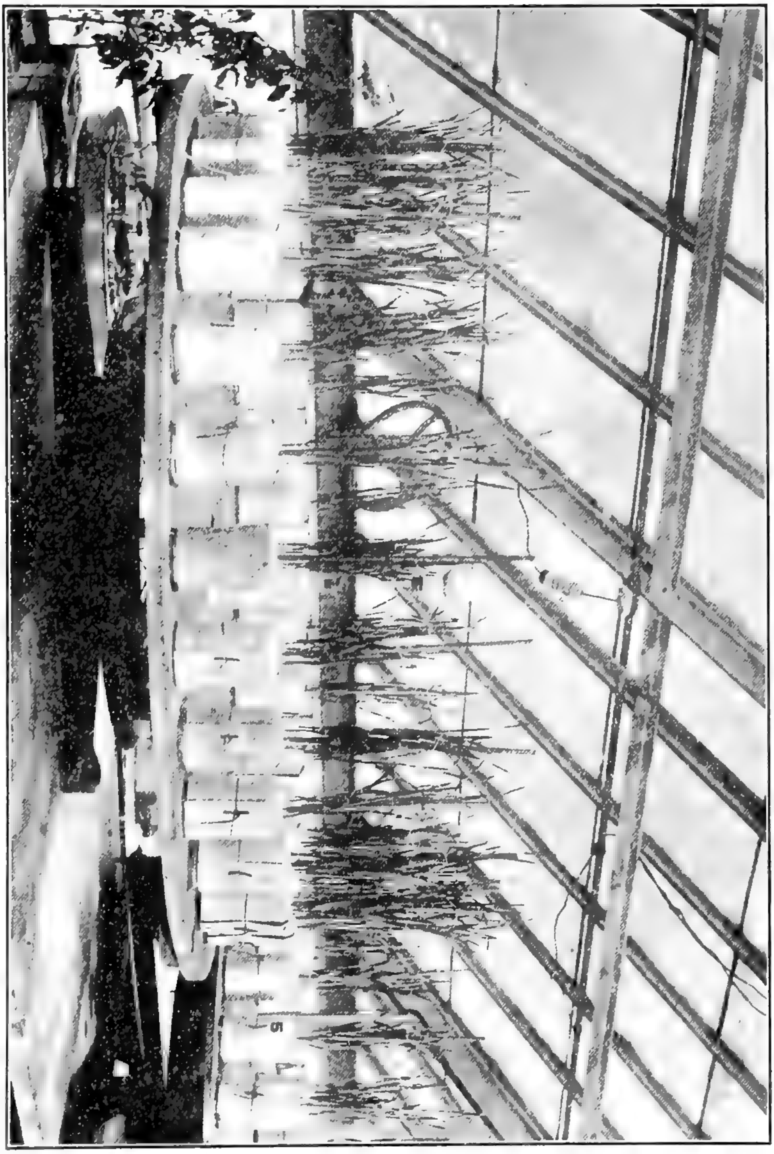
It has so happened that two phases of dynamic physiology have thus far occupied much of our attention, as far as research is concerned. At the same time, these two phases are among the most fundamental of all, as regards plant growth in general, and the agricultural and forestal production of plant material in particular, and they also appear to represent the very simplest problems in plant control. The first of these phases, or groups of dynamic problems, deals with the *water relations* of plants; the second deals with their *inorganic-salt relations.* The connotation of these two groups of problems may be roughly suggested to the reader by the statement that the agricultural operations of drainage and irrigation are related to plant water relations, while fertilizer practice is related to inorganic-salt relations. A large number of the contributions from this laboratory have dealt with one or the other of these general phases. The measurement and experimental control of the environmental conditions of moisture and of inorganic salts, and the relation of these conditions to plant growth, have thus received a large portion of our attention.

Along with the study of external conditions, the internal conditions of our experimental plants must, of course, receive consideration. While these conditions are generally much more difficult of adequate measurement than are those of the environment, some progress has nevertheless been made in this direction. For example, the work of this laboratory has aided the advance of our knowledge of the manner in which internal conditions control the rate of water-loss from plant leaves, a very important subject, both to the science of plant physiology and to the arts of agriculture and forestry.

The relations of temperature and of oxygen supply have recently begun to receive attention here, as well as the light relation (besides its consideration as a term in the water-relation). The complex relation holding between plant growth and what is generally understood by the vague word *climate,* also enters into some of our more recent undertakings.

This is not the place to attempt a presentation of the detailed results so far obtained in the research work of the Laboratory of Plant Physiology, although it may be remarked that some apparently valuable results have already rewarded our efforts. What most requires emphasis here is, however, that a large amount of necessary preparation has been accomplished, getting ready for rational experimentation in the future. Many new methods of operation and of interpretation have been evolved, and it appears as though the time may not be remote when some of the broader aspects of the conditional control of plant activities may be undertaken with some promise of a satisfactory outcome. Such broader problems will probably have to be left to other institutions, with more facilities and larger appropriations than are now generally available for university laboratories.

To summarize the last few paragraphs, our operations have been and are directed toward a dynamic analysis of plant activity. The point of view here employed may perhaps be envisaged if the reader will regard the living plant in somewhat the same general way as he might any complex machine, such as a gasoline motor, for example. To understand its working one must understand how and how much various conditions may affect such a machine; in short, he must become an *engineer* with respect to that particular mechanism. Dynamic plant physiology may be said, then, to be engineering science as applied to the operations of the living plant. It can progress only through quantitative studies,—through experimental tests under controlled or measured conditions, through the comparison of efficiency graphs and curve-tracings made by recording instruments, through the mathematical interpretation of relations between conditions and process rates, etc.,—and it is with just this sort of studies that our investigations have to do.



INTERIOR VIEW IN ONE OF THE EXPERIMENT ROOMS OF THE LABORATORY OF PLANT PHYSIOLOGY, SHOWING A ROTATING TABLE WITH WHEAT IN WATER-CULTURE AND A WHITE SPHERICAL POROUS-CUP ATMOMETER.

The following paragraphs present the main contributions thus far made by this laboratory.

The water relation of plants.—This relation involves the plant responses that result from alterations in the supply and in the consumption or loss of water. For temperate regions it is the main conditional relation for plant growth in the open, whether the plants be wild or cultivated. Most of the water necessary for plant growth is given off into the air, by evaporation from the plant surfaces, almost as soon as the water is taken up from the soil; the amount of this liquid actually consumed in forming the plant body is very small. Active plants must be continuously impregnated with water, and the loss by evaporation may be likened to a very considerable but unavoidable *leak* in a steam engine. The rate of water supply to the plant must be great enough to counterbalance this loss by evaporation, or the growth process will be retarded. To understand the plant as a machine it is thus primarily necessary to study the conditions that control the rates of water-loss and of water-intake.

One of the principal conditions that affect the rate of water-loss by evaporation from plants is the *evaporating power of the air,* and this condition needs to be studied quantitatively. To accomplish this the porous-cup atmometer has been devised and perfected during the last decade, most of the work having been done in connection with this laboratory. The instrument, in various forms, is now widely employed by students of plant growth. The readings obtained by its means may be regarded as measures of the evaporating power of the air and they may be obtained for any desirable time intervals.

Another condition that takes part in the control of the rate of water loss from plants is the *intensity of absorbed radiant energy,* received directly or indirectly from the sun. It is therefore requisite to measure and integrate this intensity as it affects the evaporation of water from moist surfaces such as plant leaves. This is now possible by the use of the radio-atmometer, which has also been devised and perfected here, and this apparatus is likewise coming into general use.

The two conditions just mentioned are both effective *from without the plant;* they are external conditions. There is also an internal condition (effective *from within the plant*) that exerts great influence upon the rate of evaporational water-loss from plant surfaces, and this has been called, in our discussions, the *transpiring power* of the plant. Studies largely carried out in this laboratory have resulted in the perfection of methods by which the intensity of this internal condition may be evaluated, and integrated over convenient time periods. Reference is here made to the method of relative transpiration and to that of cobalt-chloride paper. Both are now frequently employed in studies of plant growth.

As has been mentioned, the rate of water-supply to the plant also requires attention in studies of the water relations. This is primarily the *water-supplying power of the soil,* another external condition. The need for quantitative study of this has led to investigations in the realm of soil physics, and our efforts have already resulted in some useful methods of approach, but more work will be necessary before we can deal with this subterranean condition as satisfactorily as is now possible with the conditions that are effective above the soil. Out of our work has come the auto-irrigator, an instrument which maintains the moisture conditions of the soil nearly constant throughout long periods of time. Its readings indicate the rates at which an experimental plant removes water from a soil mass thus automatically supplied with water. The auto-irrigator is now employed by many experimenters, in cases where it is desired to maintain a constant soil-moisture content. Soil osmometers have also been employed in the study of the water-supplying power of the soil as related to absorption by plant roots.

By the employment of these various methods, all perfected here within the last few years, we have been able to begin to understand some of the more fundamental features of the plant water relation, and the near future promises much greater advances.

The inorganic salt relation of plants.—This relation involves the plant responses that result from alterations in the supply and in the consumption or loss of inorganic salts. So far as studies of this relation have progressed, these have dealt mainly with the power of the surroundings to deliver inorganic salts (or the ions into which they dissociate) to plant roots, as this power is related to growth. This aspect of this relation has formed the subject of very many experimental investigations during the past century, but the work of this laboratory has approached the problem from a somewhat new point of view.

The soil presents such a very complicated physical and chemical system that it is quite hopeless, for the present, to attempt to understand the behavior of soil salts in any way adequate to the needs of plant physiology, and our attention has been turned exclusively to the study of plant growth in nutrient solutions and in sand cultures. For the growth of ordinary plants it requires only seven ions of inorganic salts to produce satisfactory growth, these being: potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), nitrate (No_3), sulphate (SO_4), and phosphate (PO_4). Iron is needed in relatively but very small amount, it being only necessary that the solution bathing the plant roots shall contain a trace of this ion. Variations in the partial concentrations, or in the supply, of the other six ions may produce marked alterations in growth, however, and it is with reference to these that our work was begun. By means of elaborate series of different culture solutions the effects upon the plant, of altering the salt proportions in the nutrient medium, have been experimentally studied. It has been possible to devise a 3-salt nutrient solution for use as a standard, in which the three salts ($CaNO_3$, $MgSO_4$ and KH_2PO_4) are present in proper proportions to produce a physiologically balanced solution, producing excellent growth. The proper salt proportions for any plant form, and for any given complex of external conditions may readily be determined. All the various standard nutrient solutions heretofore employed have contained at least four salts (besides the trace of iron), and have been correspondingly more complex and difficult to handle and interpret. This work applies to many phases of the art of fertilizer practice, as employed in agriculture, and it furnishes a method by which we may now begin to study the salt relation as influenced by the conditions of the water relation, the temperature relation, etc.

The effects of some other inorganic ions upon plants have begun to receive attention here, also the effects of variations in the oxygen content of the soil.

The relation of plants to climatic conditions.—The main climatic conditions that affect plants are air temperature, atmospheric evaporating power, and the effective intensity of solar radiation. Other climatic conditions generally affect plants only indirectly; for example, rainfall influences the water-supplying power of the soil.

The studies thus far undertaken in this laboratory have dealt with an attempt to find out in what manner and to what degree the annual march of the complex of climatic conditions may be related to the corresponding annual or seasonal march of plant growth-rates. From these studies has been developed a method by which it appears possible to compare climates (of different places at the same time or of the same place at different times) in terms of the growth-rates of a standard plant. The plant is thus employed as an automatically weighting and integrating instrument.

This general relation is of great importance to agriculture and forestry and the point of view here taken (that of the conditional control of plant processes) is attracting the attention of investigators in these subjects. The problems are exceedingly complex, but progross is being slowly made.

The reader will be able to form a somewhat more concrete conception of what has thus far been accomplished, by reference to the list of publications from this department, which follows the present paper.

LIST OF PUBLICATIONS FROM THE LABORATORY OF PLANT PHYSIOLOGY

October, 1909, to February, 1917.
(Arranged by years, the year beginning October 1.)

1909-1910

BROWN, W. H., and L. W. SHARP, The closing response in Dionaea. Bot. Gaz. **49**: 290-302. 1910.

HAWKINS, LON A., The porous clay cup for the automatic watering of plants. Plant World **13**: 220-227. 1910.

LIVINGSTON, B. E., The heath of Lüneburg. Plant World **12**: 231-237. 1909.

—— A rain-correcting atmometer for ecological instrumentation. Plant World **13**: 79-82. 1910.

—— Operation of the porous cup atmometer. Plant World **13**: 111-118. 1910.

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ATMOMETRIC UNITS

By Burton E. Livingston

The increasing interest in atmometry [1] and the fact that this subject is becoming recognized as of general and fundamental importance in many branches of scientific and practical endeavor, make it desirable that there be some uniformity in our conceptions as to the units employed in atmometric measurements. To approach the subject it is first necessary that the purpose of atmometric observations be clearly in mind; much vagueness still prevails in this connection. The rate of evaporation of water from any surface is dependent on two sets of conditions. One set (internal ones) are effective in or behind the surface and the other (external ones) are effective in front of the surface, that is, in the gas phase of the system. The internal conditions are the characteristics of the evaporating surface and include such features as the concentration of solutes in the liquid water, the influence exerted by the presence of a solid in which the water is imbibed, the shape and extent of the surface, its direction of exposure, its ability to absorb or emit radiant energy, the heat-conducting capacity of the material back of the surface, etc. The external conditions include primarily four characteristics of the space in front of the evaporating surface: the temperature of the gas phase, its moisture condition, the influence of movement or circulation of the gas over the surface, and the effective intensity of impinging radiation. I have used the term

[1] I employ the word as synonymous with and shorter than *atmidometry*, just as I have adopted atmometer in place of its rival, *atmidometer*. Both are etymologically correct, but the one formed from the root *atmo*, besides being shorter, has received the sanction of an international meteorological congress. Atmometer seems to have been coined by Sir John Leslie, 1813. (See Livingston, B. E., "Atmometry and the porous cup atmometer." Plant World 18: 21-30, 51-74, 95-111, 143-149. 1915. Other papers are there cited.)

evaporating power of the air to include the first three of these, since the gas phase is air in most studies and since these three features are properties of this gas. The fourth feature depends only indirectly, and to a comparatively slight degree, upon the characteristics of the gas phase next to the evaporating surface. In climatological atmometry this is the effective intensity of solar radiation, direct or indirect, which depends upon the season, the time of day and the state of the sky, as well as upon the nature of reflecting surfaces in the vicinity.

Since evaporation is a *process* and not a state of matter, its magnitude has to be expressed in terms of time rates. While temperature, for instance (being a state of matter), may be expressed in degrees on a thermometer scale, evaporation intensities must be stated as the amount of water evaporated in a unit of time. Atmospheric evaporating power refers to the external surroundings of the evaporating surface (usually to the air space above it, about it, etc.) and it need not specifically refer to the air itself, for if there were no air present this space would still possess an evaporating power. The evaporating power of the air over a surface is considered as proportional to the *reciprocal of the tendency of all the conditions effective in the space over that surface to resist the vaporization of water therefrom.*

There have been some who have objected to this expression, but they have not put forward another term. From a long-continued attempt to acquire modes of expression by which we may hope to deal with the dynamic aspect of plant and animal environments an alternative expression has developed, which may be brought forward here.

In all considerations of the dynamic relations between organisms and their surroundings we find it valuable to consider the internal and the external complexes of influential conditions separately, and each group of conditions may be expressed, for any process we may have to deal with, as a single value or *index.* We may thus speak of the index of transpiring power, the index of environmental radiation, and the index of the evaporating power of the air. From this last expression comes the new term, the *atmometric index* of the locality and time period considered.

The *atmometric index* is the relative measure of the evaporating power of the air, and it is to be expressed as a possible time rate of doing work; it is an index of a power. The unit of measurement must therefore be a unit of work, but it may just as well be a unit of process rate, if the same process be always employed. Thus it may be stated as the amount of water evaporated per unit of time. If the liquid water were always at the same temperature this would actually be a measure of work. That the water of evaporating surfaces varies in temperature has been thus far neglected in this whole line of enquiry, the errors thus arising being relatively small in the present early stages of our studies.

To determine the numerical value of the atmometric index, we must also consider a factor representing some standard unit of surface. It has been seen above that the power of any surface to give off water vapor is determined by the characteristics of that surface, and that the *extent* of the surface is not by any means the only characteristic that needs to be considered. The shape and the direction of exposure of the surface must be taken into account, and also the influence of the non-aqueous materials that are in or behind the surface, etc. It is therefore impossible to employ a surface unit defined by area alone. As soon as this is realized all attempts to express the atmometric index as a time rate of evaporation from a square centimeter (etc.) of free water surface are seen to be quite useless. A free water surface is more or less nearly plane and more or less nearly horizontal (depending upon the wind velocity, among other things), but it may be of any shape or size, and all these characteristics are important. With a given set of aerial conditions two different atmometer pans, for instance, can give off the same amount of water per hour, per square centimeter of surface, only when they are of the same size and shape. Also, the depth of the water and the nature of the pans themselves must be exactly alike. It is thus both theoretically and practically impossible to express the surface factor in the atmometric index by a unit that represents merely extent of surface.

Since the complex of internal conditions that make up the capacity of any surface to produce evaporation is very difficult of analysis, we may avoid the necessity of this analysis by simply using atmometer surfaces that *act alike.* Then the surface factor of our unit of measurement becomes the surface of our instrument (with whatever characteristics it may have), and we do not need to enquire what may be its area, etc. In all the studies so far carried out with porous clay and paper surfaces for measuring the evaporating power of the air, I have never been led to determine the area of the surface employed; it would have been useless to do so, although such a surface is easily measured. We are thus led to the proposition that the atmometric index is to be expressed in terms of (1) a weight unit of water, (2) a time unit, and (3) a given standard instrument. All these desiderata are supplied in such a statement as this: that the evaporating power of the air in a given locality and for a given period is such as to produce the evaporation of so and so many grams of water per hour from a standard spherical porous-cup atmometer. No unit of area is considered, although all the internal characteristics of the instrument are implied by its name.

It is clear that it makes no difference what sort of surface we may use as standard, but we must use the same standard throughout any series of comparative measurements, and when several instruments are needed we must be sure that their internal characteristics are as nearly alike as possible, as far as these characteristics may influence the rate of evaporation. The only feasible way to compare a number of instruments in this last regard is to place them all in the same environment (as far as environmental characteristics may influence the rate of evaporation) and then compare their evaporation rates. If these rates differ this must be because of internal differences in the instruments. That two porous cups or pans of water are of the same size, shape, color, etc., does not necessarily indicate that they may be expected to give like readings if placed in the same environment, for other, less easily recognized characteristics of the instruments may not be without influence, and the surfaces may differ with respect to some of these. This consideration leads to standardization and the use of a rotating table.

By this procedure an index is obtained that represents relative capacity of each of the instruments tested, to give off water vapor, and the index of each one is expressed as a coefficient of correction, a number by which the readings of that instrument are to be multiplied in order to give the reading that would have been obtained from the master standard instrument if it had been operated for the same time and at the same place. If an instrument is effectively just like the master standard its coefficient is unity. It is not possible, however, to obtain useful coefficients for instruments that differ appreciably from the standard in form, size, etc.

Since it is necessary that several instruments be practically alike if their readings are to be comparable, it is highly desirable that different workers use as few different forms of instrument as possible. For studies on the details of the evaporation process itself various kinds of surfaces are desirable, but for general climatic atmometry the number of kinds should be kept as small as may be. This seems to be not at all well understood, and workers who have not taken the trouble to appreciate just what is the purpose of atmometric measurements continue to construct new types of instruments and to employ them. For example, the idea is abroad that if the right sort of instrument might be devised its readings would indicate relative rates of plant transpiration. Obviously such an instrument would have to alter its internal conditions from minute to minute, just as would occur in the standard plant individual, and all other plants would usually differ from it. The idea is bootless. We do not wish to measure plant transpiration but to measure the atmometric index of the air in terms of its effect upon a standard instrument whose internal conditions do not change. The internal conditions of each plant or group of plants must be studied in relation to the unchanging ones of the instrument. A given temperature change does not affect all objects or processes alike, yet we do not construct a new thermometer scale for each object or process with which we deal. It may be well to mention in this connection that atmometry should furnish climatological data applicable to many fields of endeavor; the animal ecologist requires these data as much as does the plant ecologist, and irrigation engineers and students of atmospheric hygiene and ventilation all have use for atmometric measurements.

In choosing the instrument to be used the first condition to be met is that its internal conditions or characteristics should not alter; they should be uninfluenced by changes in the surroundings, for it is changes in the latter that we wish to measure. This requirement immediately excludes all forms of free water surfaces, since they alter with wind, etc. Nevertheless, since an open pan of water is the from of atmometer employed by the U. S. Weather Bureau, since this is the simplest form of instrument that is useful in any way, and since data obtained with this pan will surely prove of much greater value than no atmometric data at all, the pan of water must be accepted as the crudest and most imperfect form of atmometer. It should be added that if pans of water are used they should generally be of the same form, size, etc., as the standard recently adopted by the U. S. Weather Bureau. If this be adhered to, all pan measurements will be comparable among themselves and with the Weather Bureau data, as far as this is possible with that general class of instruments.

The second requirement for an evaporating surface is that it should be as sensitive to all the effective conditions of the surroundings as is possible, without any alteration in its internal characteristics. It should therefore be a surface that is freely exposed to wind action. A nearly ideal surface would be that of a small, spherical droplet of water suspended freely in the air. This is not practicable, but the Livingston standard spherical porous cup seems to approach this desideratum as nearly as is possible when general ease of manipulation is considered. Since we have been able to obtain these porcelain spheres I have regarded the quest for a practically perfect surface as at an end. Some form of imbibed porous surface is undoubtedly best for general purposes, and students of ecology, ventilation engineers, agriculturists, etc., should avoid the free water surface if possible, unless it is desired that the results obtained be roughly comparable with those obtained by the Weather Bureau.

A third requirement is not as important now as it will be later, after more atmometric data have been collected. This is, that the instrument should be like some form previously used, so as to give data that may be comparable with at least some of those already on record.

Of the different forms of imbibed porous surface there are four that should be more or less generally useful: the Piche paper disk, the Bellani porous clay disk, the Babinet cylinder and the Leslie sphere, the last three having been recently improved in our own work. Probably more measurements have been made with the Piche paper disk and with the Livingston standard cylinder than with any other types of instrument, but the Piche instrument has serious practical shortcomings and the sphere is more nearly perfect than the cylinder. The cylinder will remain an important instrument for a long time but the sphere will almost surely replace it eventually. A fourth feature of the porous sphere may be emphasized as desirable, namely, the ready applicability of this type of instrument to the measurement of effective radiation intensity, which is the other aerial condition of evaporation besides the evaporating power of the air. Since we have been able to obtain black porous spheres of the same size as the white ones, the spherical form has become almost essential in all work in atmometry involving radiation. The two spheres, one white and one black, when operated together, make up the radio-atmometer, for use in studies of radiation as an atmometric condition.

Whatever type of evaporating surface is employed, this surface must be clearly defined, so that the data obtained will not, by any chance, be regarded as comparable with other data derived from another type of surface. This means that the essentials of the instrument must be described, but this can be accomplished by merely naming the instrument and referring to some previous description. Thus, it may be stated that a given set of data were obtained by means of the U. S. Weather Bureau pan, the Briggs and Shantz shallow pan, the Livingston standard sphere, etc. If a new type of instrument has to be used it requires a complete description.

In stating the amount of water lost from the given instruments during a unit of time, it is of course unimportant what water unit is employed, so long as it is definite enough for the work in hand. Since the whole aim of atmometry is to measure a power to do work, and since the amount of liquid water vaporized per unit of time is considered as a measure of this power, weight units rather than volume units should be used. Nevertheless, if the temperature does not vary too much, from reading to reading, and generally if there is no need for extreme precision, volume units may be used, and we may consider that a cubic centimeter of water weighs a gram.

Obviously, the volume or weight of water lost from a certain type of instrument for a unit of time may always be multiplied by any value that the worker may like, so long as this value is stated, and so long as it is always applied to all readings from this same type of instrument. This treatment does not alter the relative values of a series of comparable readings and the results remain comparable. This principle makes it logical to use depth units instead of volume units, for free water surfaces, for the depth of water lost from a given cylindrical pan is the volume lost, multiplied by the reciprocal of the surface area, this coefficient being a constant for the instrument.

With open pans it is easier to measure depth than volume, for rough approximations. It is true that volume or weight readings from other types of instrument than those employing an open pan, may also be multiplied by a constant throughout the series, and this constant might be the area of the surface employed, or any other number that may be chosen. But it cannot be too strongly emphasized that such treatment is to be applied only to series of readings that are already comparable, and that no constants can be found by which readings from different types of instruments may be rendered comparable.

The use of depth units in comparing water losses from open pans has introduced and supported a fallacy that is extremely hard to combat in the minds of those who have not given the subject of atmometry serious attention. This fallacy is based upon the mistaken idea that the area of the evaporating surface is the only surface characteristic that can influence the rate of evaporation. If different sizes of pans are employed the readings are incomparable, and they remain incomparable even after each one has been divided by the area of its own water surface. Readings must be stated as from a *certain instrument,* in any event, and the application of an areal coefficient only complicates matters. To avoid the continuation of this fallacy, as much as may be, it is highly desirable that all atmometric readings be stated in terms of weight or volume, even though they were originally obtained by measurements of depth.

The worst feature of the use of depth units in pan atmometry is that it has led to another fallacy, by which these depth units are taken to be equivalent to the other depth units that are employed in the measurement of rainfall. The two classes of units look alike but they are widely different in their meanings. An example may illustrate this very important point. Suppose that the rainfall for a certain place is found to be 75 cm. (of depth) for a certain year, and suppose that the observer states that the evaporation from a Weather Bureau pan for the same period was 90 cm. (also of depth). In such a case students of climatology have been led to say that evaporation exceeds precipitation by a certain depth, 15 cm. in this example. But this means nothing at all; if the pan used had been larger or smaller, of different shape or material, or if a wet soil surface had been employed, etc., the result would have been quite different, and the climatic conditions would surely not have been altered by merely changing the atmometer. On the other hand, if any other form or size of raingage had been employed the results would be sensibly the same. The amount of evaporation depends largely upon the atmometer but the amount of rainfall recorded is practically independent of the raingage, so long as the latter is a raingage at all. It is legitimate to state the index of rainfall in depth units, for this is not seriously influenced by the internal characteristics of the gage, a statement that cannot be made of the index of evaporation, nor even of the index of atmospheric evaporating power. The only logical way by which atmometric and precipitation measurements may be compared is by means of their *ratio,* in which case one set of measurements may be in depth units and the other in volume or weight units. They are not commensurable in any case, so it is best not to have them even appear as though they were commensurable. Other considerations, into which I cannot go in this place, lead unequivocally to the same conclusion.

Fortunately, there is no serious difficulty encountered in the statement of the time feature of atmometric measurements. For short periods the hour is most convenient, for longer periods the day, week and year are all suitable. Since months vary in length, monthly atmometric indices are unsatisfactory. After the three features of the unit to be used have been decided upon, it is necessary to remember that atmometric measurements, like other power measurements, always apply to a certain set of circumstances and to a certain time period. The set of circumstances here emphasized is the surroundings of the atmometer, they comprise the various features of its *exposure.* The readings refer to the evaporating power of the air only for the particular location in which the instrument was operated. The evaporating power of the air may be very different in two locations only a few centimeters apart. The differences here encountered are much greater than the similar ones met with in thermometry and the general exposure of the instrument needs to be stated in all climatological studies of atmometry. The readings obtained are taken as averages for the time period of operation and are stated with reference to a shorter time unit.

To summarize the points brought out above, every atmometric measurement should be formulated so as to include all the five features indicated by letters in the following statement, which is given as an illustration. The atmometric index for location *A*, for the period of operation *B*, is found to be *C* units of water lost per time unit *D* from an atmometer of type *E*. Filling in the features represented by these letters, to render the illustration more concrete, we may say: The atmometric index for a place 1 meter above the ground in the center of a large field of clover in northern Ohio, for the period of operation from May 1 to May 10, 1916, was found to be 12 grams of water lost per day from a standard white spherical atmometer. If any of these five features is omitted from the statement, the meaning is rendered vague and uncertain.

THE VAPOR TENSION DEFICIT AS AN INDEX OF THE MOISTURE CONDITION OF THE AIR

By Burton E. Livingston

Studies on the manner in which external conditions control the activities of animals and plants must deal with the moisture conditions of the air in all cases where the organisms considered are aerially exposed. While atmospheric evaporating power (measured with reference to some standard evaporating surface) furnishes an index of the air conditions that influence the rate of water loss from aerially exposed organisms, it is frequently desirable to analyze this complex condition into its two components, the moisture condition of the air and the velocity of air movement or circulation. For such an analysis atmometric observations are of course inadequate. Furthermore, it is often requisite to compare different evaporating powers of the air when the air movement is known to be constant, in which case the moisture condition is the only variable to be taken into account. Finally, in the artificial control of the air conditions of culture chambers, the rooms of dwellings, etc., it is frequently possible to maintain air circulation without much fluctuation and then to control the evaporating power by controlling the moisture condition. In such cases it becomes important that serious attention be given to the moisture condition of the air and its adequate measurement.

By *moisture condition* is here meant *that factor in atmospheric evaporating power that is independent of the rate of air movement.* It is thus an index of a condition determined by the state of saturation of the air (with aqueous vapor) and by the air temperature. Humidity, as commonly measured, does not involve temperature. To make these relations clearer, it may be added that the index of atmospheric evaporating power should be equal to the product of the index of the moisture condition and the index of circulation: $I_e = I_m \times I_c$, Of course it is here assumed that all measurements of conditions have been properly weighted and brought into correspondence, in deriving the indices. Otherwise a coefficient of proportionality needs to be applied to each of the quantities. In this equation, the value I_m is the one with which this discussion deals.

The tendency of water to evaporate into air lying next to the water surface is measured by the maximum vapor pressure possible with the prevailing conditions of the surface. If pure water is considered the maximum value may be obtained for any given temperature, from published physical tables. It will be lower than these published values if the water is impure, or if it is held by imbibing solids, etc. It is a gas pressure, and is expressed in pressure units, as the height of a mercury column, fractions of an atmosphere, etc. It may be considered as equal to the pressure that drives the water vapor out of the liquid surface, which may be termed the *vaporization pressure.* The temperature of the liquid lying close to the surface exerts a marked influence upon the magnitude of this pressure.

This tendency for water to evaporate is opposed by another tendency, that of the air to deposit liquid water on the evaporating surface; it is the tendency of water vapor to condense. This is measured by the partial pressure of water vapor in the air lying next to the evaporating surface, and it may have any value between zero and the maximum vapor pressure of water vapor for the given air temperature. It also is a gas pressure and is measured in pressure units. The most satisfactory method of measuring it is by means of the Regnault dew-point apparatus, through determining the temperature of the dew-point, the partial pressure of water vapor in the air being equivalent to the maximum vapor pressure of liquid water at the temperature of the dew-point of the air. Another less satisfactory method of determining this partial pressure is by means of the sling psychrometer, the readings being interpreted by physical tables published for this purpose. This actual partial pressure of water vapor in the air may be termed the *condensation pressure.*

From this it follows that the difference between the vaporization pressure and the condensation pressure must determine the value of that factor of atmospheric evaporating power that is not determined by air circulation. This difference is the vapor pressure deficit, measured as a pressure; it is the excess of vaporization pressure over condensation pressure. For most purposes of approximation it may be supposed that the temperature of the liquid surface and that of the general air are the same, but this is not strictly true, and the temperature value employed in deriving the vaporization pressure ought really to be measured just within the liquid, if the evaporating power of the air for any particular surface is to be studied. The condensation pressure should be determined for the general atmosphere of the space under consideration. If air circulation were infinitely rapid, which means, practically, if there is a high wind, this deficit value should be a measure of the evaporating power for the particular location considered. Also, if two sets of conditions are to be compared, in which the air circulation is the same, then the two atmospheric evaporating powers should be proportional to the corresponding vapor pressure deficits; for the other factor is then common to both sets.

To illustrate the use of the vapor pressure deficit, let it be supposed that there are two rooms in which the air circulation is alike, and let it be required to estimate the relative values of the evaporating powers corresponding to the two rooms. The data involved and the results obtained are shown below, together with the two relative humidity values, as usually given in such comparisons.

	Air temperature	Vapor Pressure Maximum	Vapor Pressure Actual	Vapor pressure deficit	Relative humidity
	deg. c.	*mm. of Hg.*	*mm. of Hg.*	*mm. of Hg.*	*per cent.*
Room 1.	20°	17.41	14.50	2.91	83
Room 2.	25°	23.55	6.14	17.41	26

The values used in this example have been so chosen that the deficit for Room 2 is 17.41 mm., just what it would be for Room 1 if the actual vapor pressure were taken as zero. This is the maximum deficit for a temperature of 20°. Nevertheless, it is seen that the actual vapor pressure for Room 2 is far from zero. This emphasizes the point that the maximum evaporating power of the air increases with the temperature, air pressure, and circulation remaining the same.

Such comparisons have usually been made in terms of *relative humidity,* the values for which are presented in the last column of the tabular arrangement just given. This mathematical abstraction is the *ratio* of the actual to the maximum vapor pressure of water vapor in the air, while the vapor pressure deficit is the *difference* between these two vapor pressures. Relative humidity percentages are without value unless the air temperature is also given, whereas the deficit values need no reference to air temperature for their interpretation.[1] The fallacy in the employment of relative humidity clearly lies in the fact that its values are ratios and that the denominator of the ratio varies with air temperature; different percentage values cannot be comparable unless they are calculated to the same base.

In the illustration given above, the relative humidity index for room 1 is 3.25 times as great as that for room 2, and the popular conception of relative humidity might lead to the erroneous supposition that the evaporating power of the air for room 2 should be 3.25 times as great as that for room 1, whereas this last number should be the value of the fraction $\frac{17.41}{2.91}$ or 5.98.

The real uselessness of the concept of relative humidity and the manner in which this concept is frequently misleading are brought out by the fact that the index of relative humidity may be identical for two rooms or for two climatic stations, and (owing to a difference in air temperature) the moisture factor of the evaporating power of the air may be very different in the two cases. Thus, a relative humidity of 60 per cent. corresponds to an air moisture factor of 10.44 mm. at 20°, and to one of 14.13 mm. at 25°. The moisture condition of the air in the second case is much higher, but the relative humidity values fail to suggest any difference.

One of the most serious reasons for discontinuing the use of relative humidity lies in the fact that the moisture condition of the air generally varies from hour to hour and from

[1] For some very true remarks in this connection, see: Stevens, Neil E., "A method for studying the humidity relations of fungi in culture." Phytopathology 6: 428-432. 1916. Other references are there given.

day to day, for the same place, which makes it necessary in climatic discussions to resort to averages and means. While the index of relative humidity for any instant may be readily interpreted by use of the corresponding air temperature, there is no possible way by which an average of several such indices may be so interpreted; the average temperature for the period is of no use for this purpose, since the march of temperature for the period is not necessarily at all related to that of the moisture condition. The only way to give definite meaning to a relative humidity mean is to obtain the original humidity values from which the mean was derived (together with the corresponding air temperatures), to substitute for each individual value the corresponding vapor pressure deficit, and to derive the mean of the deficits, thus discarding relative humidity altogether.

For biological experimentation, for hygienic studies of the air moisture condition in dwellings, and for general climatological purposes, it is very obvious that the whole concept of relative humidity is hopelessly misleading; the sooner this concept can be forgotten the more rapidly will knowledge advance. When it is not desirable or expedient to employ the index of atmospheric evaporating power itself (as determined directly by some form of atmometer), the moisture condition of the air should be stated in terms of the vapor pressure deficit, which demands no correction for air temperature and may represent evaporating power in all comparisons where the index of effective air circulation may be considered as constant.

INCIPIENT DRYING AND TEMPORARY AND PERMANENT WILTING OF PLANTS, AS RELATED TO EXTERNAL AND INTERNAL CONDITIONS

By Burton E. Livingston

It has been shown by Renner,[1] by Livingston and Brown,[2] by Lloyd[3] and by Edith B. Shreve,[4] that the water content of plant leaves, twigs, etc., is markedly lower after a period of relatively great transpiration (as in the middle of the day) than it is after a period of very small transpiration (as in the latter part of the night). The moisture content of leaves, for instance, was found (Livingston and Brown) to exhibit a diurnal march, the rate of water loss from these organs during the forenoon hours (or even during the whole period of sunshine) being greater than their rate of water intake, while the rate of foliar intake of water during the night hours was greater than the rate of water loss. The phenomenon indicated by diminished water content in the daytime was called *incipient drying* by Livingston and Brown. Renner employed the term *sätigungsdefizit* to denote the similar phenomenon encountered in his experiments. The experimentation of all but Renner, of the authors mentioned

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[1] Renner, O., "Experimentelle Beiträge zur Kenntnis der Wasserbewegung." *Flora* **103**: 171-247. 1911. *Idem.*, "Versuche zur Mechanik der Wasserversorgung. I. Der Druck in den Leitungsbahnen von Freilandpflanzen. *Ber. Deutsch. Bot. Ges.* **30**: 576-580. 1912.

[2] Livingston, B. E., and Brown, W. H., "Relation of the daily march of transpiration to variations in the water content of foliage leaves." *Bot. Gaz.* 53: 309-330. 1912.

[3] Lloyd, F. E., "The relation of transpiration and stomatal movements to the water content of the leaves of Fonquieria splendens." *Plant World* **15**: 1-14. 1912. *Idem.*, "Leaf water and stomatal movement in Gossypium, and a method of direct visual observation of stomata *in situ*. *Bull. Torrey Bot. Club* 40: 1-26. 1913.

[4] Shreve, Edith B., "The daily march of transpiration in a desert perennial." *Carnegie Inst. Wash. Pub.* **194**: Washington, 1914.

above, was carried out in an arid region, with high transpiration rates, but the results of Renner were obtained in a very moist summer in Munich, so that it appears to be fairly well established that this phenomenon is general in plants. Of course, incipient drying is more pronounced with high atmospheric evaporating power and intense sunshine than with aerial surroundings of less aridity, and it is less pronounced in plants with low transpiring power than it is in less xerophilous forms.

From Renner's experiments, and also from those of Livingston and Hawkins,[5] it appears that the rate of absorption of water by plant roots is determined by two conditions, which may be called, respectively, the absorbing power of the roots (internal) and the supplying power of the soil, or other medium in which the roots lie (external). It also appears that the internal one of these conditions (absorbing power of the roots) is at least partly controlled by the degree of incipient drying occurring in the plant, which, in turn is partly dependent upon the rate of transpiration. Other conditions being unchanged, the plant takes up more water from the soil when the transpiration rate is high than when it is lower. If incipient drying becomes sufficiently pronounced its presence is made evident, first by loss of turgor in the plant, then by temporary wilting[6] (from which the wilted tissues may recover when transpiration is subsequently decreased), then by permanent wilting[7] (from which the plants

[5] Livingston, B. E., and Hawkins, Lon A., "The water relation between plant and soil." *Carnegie Inst. Wash. Pub.* **204**: 5-48. Washington, 1915.

[6] Brown, W. H., "The relation of evaporation to the water content of the soil at the time of wilting." *Plant World* **15**: 121-134. 1912.

[7] Briggs, L. J., and Shantz, H. L., "The wilting coefficient for different plants and its indirect determination. *U. S. Dept. Agric. Bur. Plant Ind. Bull.* **230**: 1912. Caldwell, J. S., "The relation of environmental conditions to the phenomenon of permanent wilting in plants. *Physiol. Res.* **1**: 1-56. 1913. Shive, J. W., and Livingston, B. E., "The relation of atmospheric evaporating power to soil moisture content at permanent wilting in plants. *Plant World* **17**: 81-121. 1914.

cannot recover without special treatment), and finally by death and actual desiccation.

Incipient drying of leaves, whether they show any signs of wilting or not, may be said to be due to inadequate water supply to these organs; no matter how great might be the rate of foliar water loss, the transpiring cells should not suffer any diminution in their water content if the rate of entrance of water into these cells were only sufficiently great. The question therefore arises, as was mentioned by Livingston and Hawkins, to what extent is this inadequacy in the rate of foliar water supply to be considered as due to inadequate water supplying power of the soil, and to what extent may it be due to inadequate absorbing power of the roots and inadequate conducting power of the stems, petioles, etc.? In wilting leaves, for example, is the insufficient rate of water supply due to an external condition in the soil or to an internal condition, within the plant body?

This is a very important question, both with regard to the general problem of plant water relations and with respect to the practical problem of drought resistance in plants. A quantitative answer for plants growing in the open is of course impossible at present, but some light has been thrown upon the consideration of this question by some experiments recently carried out in the Laboratory of Plant Physiology.[8] The matter in hand was approached by making the water-supplying power of the root surroundings very great; the test plants were grown in water-culture instead of in soil, so that the external resistance offered to water absorption by the root surfaces may be considered as practically nil and therefore constant. Under such conditions the actual rate of water absorption must be very nearly proportional to the absorbing power of the root system.

Two methods were employed, for both of which the transpirational rates were determined by weighing, in the ordi-

[8] Mr. E. S. Johnston carried out the manipulations in these experiments.

nary way. By one method the absorption rates were determined as volumes, the plant being sealed into a bottle completely filled with the nutrient solution and furnished with a burette for measuring the volume of water absorbed. Temperature changes were corrected for by means of readings taken from a similar arrangement of bottle and burette without any plant. By the other method arrangement was made by which the plant could be suspended from the balance arm, its roots in the culture solution, with the surface of the latter always at the same mark on the basal part of the stem when the balance was in equilibrium. Thus, the buoyancy tending to lift the plant was very nearly the same at all weighings. During this weighing the split cork otherwise closing the culture jar was removed. Observations were obtained usually at hour intervals, from before daylight in the morning to late in the evening. The plants used were: *Coleus blumei, Fagopyrum esculentum* (buckwheat) and *Mimosa pudica* (sensitive plant). The experiments were carried out in an experiment greenhouse, in the autumn and early winter. The nutrient solution employed was of the Shive 3-salt type, apparently physiologically balanced as to salt proportions, and its total osmotic concentration was about 1.75 atmospheres. The results of eight tests, at different times of the year, may be briefly stated as follows.

(1) Sept. 20, clear sky. Buckwheat plant. Transpiration was greater than absorption for the period 8:50 a. m. to 1:50 p. m., incipient drying amounting to 0.63 g. Absorption was greater than transpiration for the period 1:50 to 5:50 p. m., the plant gaining in weight 0.15 g. Wilting began during hour ending 10:50 a. m., when incipient drying amounted to 0.27 g. Transpiration for this hour was 0.81 g. and absorption was 0.59 g. Transpiration for last hour of incipient drying was 0.98 g. and absorption was 0.96 g. Five out of six leaves were permanently wilted and never recovered.

(2) Sept. 21, clear sky. Buckwheat plant. Transpiration was greater than absorption for the period 9:20 a. m. to 1:20 p. m., incipient drying amounting to 0.24 g. Absorption was greater than transpiration for the period 1:20 to 9:20 p. m., the plant gaining in weight 0.38 g. Wilting began during hour ending 10:20 a. m., when incipient drying amounted to 0.08 g. For this hour transpira-

tion was 1.36 g. and absorption was 1.28 g. Transpiration for the last hour of incipient drying was 1.26 g. and absorption was 1.18 g. No permanent wilting occurred.

(3) Sept. 23, cloudy or partly cloudy. Buckwheat plant. Absorption was greater than transpiration for the period 6:50 to 7:20 a. m., the plant gaining 0.03 g. Transpiration and absorption were equal (0.08 g.) for the period 7:20 to 7:50 a. m. Transpiration was greater than absorption for the period 7:50 a. m. to 2:20 p. m., incipient drying amounting to 0.59 g. Wilting began during hour ending 10.20, when incipient drying amounted to 0.33 g. Transpiration for this hour was 0.56 g. and absorption was 0.44 g. Transpiration and absorption for the period of incipient drying (7.50 to 9.20 a. m.) were 0.67 and 0.46 g.; for the last period of incipient drying (12.30 to 2.20 p. m.) they were 1.49 and 1.43 g., respectively. Three out of five leaves were permanently wilted and never recovered.

(4) Nov. 3, clear sky. Dark red Coleus plant. Transpiration and absorption were equal (0.29 g.) for the hour 7:30 to 8:30 a. m. Transpiration was greater for the period 8:30 to 11:30 a. m., incipient drying amounting to 0.35 g. Absorption was greater for the period 11:30 a. m. to 7:30 p. m., the plant gaining in weight 0.68 g. Transpiration and absorption were equal (0.16 g.) for the period 7:30 to 9:30 p. m. No wilting was noted. The evaporating power of the air was 1.02 cc. (per hour, from the Livingston standard white spherical atmometer) for the first hour of incipient drying. Transpiration for this hour was 0.76 g. and absorption was 0.70 g.

(5) Nov. 4, cloudy. Dark red Coleus plant. Transpiration and absorption were equal (0.11 g.) for the period 5:30 to 7:30 a. m. Transpiration was greater for the period 7:30 a. m. to 2:30 p. m., incipient drying amounting to 0.47 g. Absorption was greater for the period 2:30 to 5:30 p. m., the plant gaining in weight 0.10 g. No wilting was noted. The atmometric index for first hour of incipient drying was 0.33 cc. Transpiration for this hour was 0.10 g. and absorption was 0.01 g.

(6) Nov. 16, clear sky. Two buckwheat plants bound together at base. Transpiration was greater than absorption for the period 9:30 to 11:30 a. m., incipient drying amounting to 0.17 g. Absorption was greater for the period 11:30 a. m. to 10:30 p. m., the plants gaining in weight 0.33 g. No wilting was noted. Atmometric index for last hour of incipient drying was 0.9 cc. Transpiration for this hour was 1.83 g. and absorption was 1.79 g.

(7) Nov. 16, clear sky. Dark red Coleus plant. Transpiration was greater than absorption for the period 9:45 a. m. to 3:45 p. m., incipient drying amounting to 0.89 g. Absorption was greater than transpiration for the period 3:45 to 7:45 p. m., the plant gaining in weight 0.78 g. No wilting was noted. The atmometric index

for last hour of incipient drying was 1.3 cc. Transpiration for this hour was 0.38 g., and absorption was 0.11 cc.

(8) Dec. 1, cloudy. Mimosa plant. Transpiration was greater than absorption for the period 7:55 a. m. to 3:55 p. m., incipient drying amounting to 2.97 g. Absorption was greater than transpiration for the period 3:55 to 5:55 p. m., the plant gaining in weight 0.27 g. No wilting was noted; the leaves were in night position at end of last hour. Atmometric index for last hour of incipient drying was 0.7 cc. Transpiration for this hour was 1.03 g. and absorption was 0.87 cc.

These data show very clearly that incipient drying, temporary wilting, and even permanent wilting of most of the leaves, may occur without any resistance at all to water-absorption by roots. These phenomena are here quite independent of such resistance to water intake as may be offered by unsaturated soils. Furthermore, in the complete absence of environmental resistance to water absorption by the root system, incipient drying may begin with an evaporating power of the air as low as 0.33 cc. per hour from the Livingston standard white sphere (Coleus, Nov. 4). Consequently, it does not require a high atmometric index to render the transpiration rate larger than the rate of absorption, in the case of some plants at least. The truth of this statement must be much more pronounced when the plant roots are surrounded by ordinary, fairly dry soils, which interpose an external resistance to water intake.

Unfortunately, atmometric observations were omitted in the first three tests, so that it is not possible to state what order of atmometric index values produced the wilting phenomena recorded for Sept. 20, 21 and 23. It is, of course, certain that these index values were not exceptionally high, however; the index for Baltimore is never high, and there was no artificial heat applied to the greenhouse on these days, so that the index value was not artificially raised. It is worth something to note that permanent wilting of most of the leaves of healthy buckwheat plants occurred in an unheated greenhouse in Baltimore on Sept. 20, with clear sky, and on Sept. 23, with partly cloudy sky.

Obviously, the absorbing powers of these plants were inadequate to supply water as rapidly as it was lost by transpiration during the hours when this loss was most rapid; the inadequacy was within the plant, an *internal* condition. It is suggested that the power of stem and petioles to *conduct* water from roots to leaves is here also inadequate, but on this point further experimentation will be required.

One definite advance in our knowledge of the water relations of plants is made by the data here considered; it may now be clearly stated that none of these three stages or degrees of incipient drying need *necessarily* be related to *soil-moisture conditions* at all. That they may *sometimes* be so related, when the soil about the root system fails to supply moisture to the root surfaces as rapidly as these are able to absorb it, is sufficiently clear on *a priori* grounds.

THE EFFECT OF DEFICIENT SOIL OXYGEN ON THE ROOTS OF HIGHER PLANTS

By B. E. Livingston and E. E. Free

During the last three years experiments have been in progress in the Laboratory of Plant Physiology on the oxygen requirement of the root systems of higher plants. A technique has been devised by which the root system, contained in normal soil, can be sealed off from the air and the soil atmosphere controlled in composition as may be desired. The aerial portions of the plants project into the atmosphere of the greenhouse. Water is supplied to the roots by means of the Livingston auto-irrigator.[1] It has been found that

[1] Livingston, B. E., "A method for controlling plant moisture." Plant World 11: 39-40. 1908. Hawkins, Lon A., "The porous clay cup for the automatic watering of plants." Plant World 13: 220-227. 1910. Livingston, B. E., and Hawkins, Lon A., "The water-relation between plant and soil." Carnegie Inst. Wash. Pub. 204: 5-48. 1915.

the response of the root-system to deficiency of oxygen in the soil atmosphere varies widely in different kinds of plants. Some species are injured by a very slight deficiency below the oxygen content of the general atmosphere. A swamp willow, probably *Salix nigra,* endures successfully the complete, or almost complete, exclusion of oxygen from its roots.

In the case of those plants which are injured by deficient soil oxygen it is interesting physiologically that the first effect of oxygen deprivation is an interference with the absorption of water by the roots. In the experiments the apparatus for the supply of water is so arranged that the amount of water taken up by the soil from the porous cups of the auto-irrigator can be measured for periods as short as one hour. The amount of water thus taken up depends in part on the temperature. The surface tension of the water films in the soil varies with temperature and this controls the amount of water held in the water-film system. However, this error disappears for periods the initial and final temperatures of which are nearly the same (for instance, the usual 24-hour period) and a correction can be made for the error in the case of shorter periods or other periods which do not satisfy this condition. When the temperature error is thus eliminated, the absorption of water from the auto-irrigator is closely parallel to the intake of water by the plant roots. With the plants that are sensitive to deficiency of oxygen in the soil air, it is found that the replacement of the normal soil atmosphere by nitrogen is followed within a few hours by nearly complete cessation of water-intake by the roots. With the most sensitive species tested, namely, *Coleus blumei* and *Heliotropium peruvianum,* this cessation of water-intake occurs always within 24 hours, usually within 12 hours, after the soil oxygen is removed. This time period varies with the individual plant, perhaps because of differences in the root-system but probably also because of differences in the completeness with which the soil oxygen originally present is replaced by the nitrogen. Since the oxygen must be displaced by washing out with the nitrogen it is impossible to be sure that the replacement is ever absolutely complete at the beginning of the experiment.

The cessation of water intake, as shown by the stoppage of absorption from the auto-irrigator, is always the first sign of injury. With Coleus and Heliotropium it is followed in from one to six days by progressively lessened turgor of the shoot and leaves and finally by wilting and death. With Coleus, the admission of oxygen to the soil before death has actually occurred is followed by the slow recovery of the plant. Heliotropium does not so recover, even if oxygen is re-supplied before the wilting has become extensive or severe. With *Nerium oleander,* which does not wilt, the symptom of injury which follows next after the cessation of water intake by the roots is the yellowing and loss of leaves.

On removal and examination of the injured plants the root systems are found to be dead and the roots partly disintegrated. When the injury has been slight or recent, individual roots are determinately dead only in parts of their length, regions of brown discoloration alternating with regions of apparently healthy root. When Coleus is first injured and then revived by re-admission of oxygen it forms a new root system, the new healthy roots being clearly distinguishable from the older dead ones. These new roots start always from the base of the stem, as in a rooted cutting. They have never been observed to start from any portion of the older root system. If one begins with a Coleus plant which has a small root system, or with an unrooted cutting, or with a previously injured plant which will form new roots, it is possible to grow such a plant with a soil atmosphere somewhat below normal in oxygen content. In this case the shoot does not attain so large a size as the shoot of a normal control plant and is more susceptible to injury by drouth, as, for instance, by increase in the evaporating power of the air. The root system of such a plant, grown with deficient oxygen, is less developed than that of a normal plant and the roots are long, thin and little branched, and range widely through the soil.

When Coleus plants of different sizes are deprived of soil oxygen, the cessation of water intake and the subsequent symptoms of injury appear first and are most severe on the plants which have the larger root systems. Again, a plant with a small root system will tolerate a lesser oxygen content in the soil than will a plant with a large root system. This implies that the crucial matter is the supply of oxygen per unit of root surface (or volume) and this is confirmed by the fact that a low oxygen content in a frequently changed atmosphere is less injurious than a higher oxygen content with less frequent changes.

The evidence suggests that the cause of injury by exclusion of oxygen from the roots is an interference with the respiration of the protoplasm of the root cells, resulting in the death of this protoplasm and the consequent failure of the roots to function as water absorbers for the plant. There is no reason, however, to assume any "vital" function of the root protoplasm in promoting water absorption. The protoplasmic coagulation which is, or accompanies, what is called death would constitute in itself a sufficient change to explain, on a purely physical basis, this effect on water absorption. The fact that the roots of at least one plant (Salix) appear to function normally in the absence of free oxygen raises the interesting question whether the respiration of these roots may not be anaerobic. It is impossible to answer this question finally. There is a theoretical possibility, in our experiments, of some small access of free oxygen from some source not now suspected. However, the sharp difference in the behavior of Salix and of Coleus under identical treatments suggests some important difference in the respiratory habits of the roots of the two species.

THE EXPERIMENTAL DETERMINATION OF A DYNAMIC SOIL-MOISTURE MINIMUM

By Howard E. Pulling

The conditions determining the rates of water movement in soils have long been recognized as of great importance in plant physiology, since they not only limit the amount of water a given root system may receive but also modify the effects of all soil processes upon rooted plants. In aerated soils water is moved by surface forces of the soil-moisture films. The magnitude of these forces is dependent upon the curvature of the film-air surfaces and not upon the amount of water in the soil, so that a soil volume might augment its water content at the expense of another contiguous soil volume that contained actually less water than the first. The *amount* of water that may be moved in unit time depends, however, also upon the amount of water in the films and a certain minimum should exist below which the quantity of water subject to capillary movement is too small to admit of any but negligible rates, regardless of the magnitude of the surface forces.

In aerated soils the water that responds to surface tension urge is accumulated around the points of contact of soil grains, so that the water adsorbed upon the surface of the grains, imbibed by the soil colloids and held as water of hydration by the grain constituents need not be considered in the present discussion. It is apparent that the greater the number of such points of contact between the soil grains in a given gross volume of soil, the greater should be the number of similar capillary masses of water and, consequently, the greater should be the amount of water in the soil when the rate of capillary movement becomes negligible. Accordingly a complete statement of this minimum for any soil may be represented not by a point but by a curve, in which the conditions of the soil-air-water system are represented in terms of any two of the three components.

For convenience the components soil grains and water may be selected. The number of points of contact in any gross volume are determined by the number, size, shape and arrangement of the soil grains. In a sufficiently large volume (a few cubic centimeters, for arable soils) the soil grains may be considered as possessing an average density, size and shape, and this average will not change when other samples of the same soil are considered. Likewise if two samples of the same volume have the same number of soil grains, possessing the same average characteristics, it may be assumed that the average arrangement of grains is the same in each. This will be the more strictly true the longer the grains have existed in those volumes, since the forces of surface tension and gravity will tend to place them in the most stable positions. A relative measure of the properties of a mass of soil grains may thus be obtained for any one soil in terms of its dry weight per unit of gross volume, termed the packing.

The properties of the water masses in the soil may also be considered as being of average character and since these properties depend upon the shape and size of the water masses, which in turn depend upon the shape and size of the spaces about the points of contact of the soil grains, the number of these points and the amount of water in the soil, they will be sufficiently defined by the amount of water and the amount of soil contained in each unit of gross volume. When these amounts are determined for samples of any given soil, each uniformly packed and permitting only a negligible rate of water movement, the data are at hand for plotting the experimental approximation to the minimum moisture curve between the limits of packing encountered in the samples.

A method has been devised by the use of which samples of any given soil, each of approximately uniform packing, may be obtained with water contents so small that the rate of water movement is about 0.001 gram in 24 hours through an area of 30 square millimeters. If the water contents per unit of gross volume of a number of such samples of the same soil are plotted as ordinates, and the corresponding dry weights are plotted as abscissas, the graph obtained by connecting the points is the positive portion of an approximately paraboliform curve that is symmetrical about the horizontal axis. This graph ascends steeply in the region of light packings, indicating the relatively large effect of adding more soil to a volume of low soil content. Its tendency to become horizontal indicates that, with dense packings, the addition of more soil but slightly increases the water content at the dynamic minimum.

The amount of water that exists in a given soil at a given packing above the minimum point for that packing is subject to capillary movement, so that the determination of the minimum is of great value in calculating the maximum rate at which water may move through the given soil under those conditions. Because the graphs vary in height and slope, at corresponding points, from one soil to another they should also serve as soil characteristics by which various soils might be recognized.

SOME UNUSUAL FEATURES OF A SUB-ARCTIC SOIL

By Howard E. Pulling

A preliminary survey of the ecological features of some sub-arctic forests during the past summer yielded information concerning the soils that emphasizes the need of including the physical root environment in an ecological study of such regions. The chief soil over the major portion of the area visited[1] was a gray to buff colored lacustrine clay

[1] The valleys of the Nelson river and its tributaries near Split Lake, which is situated in northern Manitoba, Canada, at about 56° north latitude and 96° west longitude.

formed from rock flour in the bed of ancient lake Aggasiz. The upper limit of frozen soil encountered during the summer varied from a depth of a few inches, near the water's edge on a shore with a north exposure, to about six feet on a slope well above the water line and with a southeast exposure. It is highly probable that one of the most effective agencies conditioning local distribution of plant species is the depth at which frozen soil is encountered. Large trees and other deeply rooted plants could not exist in soils made too shallow by the presence of perpetually frozen soil near the surface.

The soil of the spruce forest, which is the characteristic type of this region, is covered chiefly by sphagnum, often to a depth of several feet. Large amounts of water are held by the moss so that these forests resemble those of temperate regions at the borders of swamps and marshes. If the forest is situated on a hillside, however, the soil underneath the moss is usually dry and if exposed in windy weather will blow as dust. This may perhaps be explained in the light of knowledge of the conditions above and below the dry layer. This dry stratum rests upon frozen soil, which because of its lower vapor pressure and of other probably less effective properties, should continually absorb water from the adjacent, unfrozen soil. Thus, making the easily justified assumption that the soil was originally wet, the conditions exist for almost completely drying it, provided it should not regain the water lost. The light snowfall in this region would be unlikely to produce large amounts of water in the spring, especially on these slopes where drainage in the spring is rapid over the frozen surface of the soil, the relatively small amount remaining being conceivably retained by the highly absorbent sphagnum covering. The summer rains, which, although frequent, bring comparatively little water, are apparently no more than sufficient to supply the transpiration loss of the plants exposed to almost continuous winds and often to bright sunshine for many hours a day.

Roots penetrate this dry layer only to a slight extent, although organic deposits occur down to the frost line. These deposits are lamelliform, and each appears to be continuous from its lowest point to the surface of the soil. Whether they originated from the decay of roots that had penetrated this layer while it contained more water than it does now, or whether they were formed by slow seepage from the surface, cannot be decided from the information at hand. The occurrence of small landslides in which dry soil was found above and below the layer in which the slipping occurred, indicates, however, that water may move in a thin sheet of soil and either form these deposits by carrying organic matter from the surface, or, finding them ready formed, traverse them to the deeper portions. Since these layers are rich in organic matter it is probable that their constituents would cohere when frozen, which is not true of the dryer soil about them. This may perhaps account for the statements often made that in the winter or spring, frozen soil may be encountered at the surface and also below it, in sheets, at intervals.

Whether due to this drying and being frozen in the dry condition, or to other more obscure causes, the soil of this dry layer is often flocculated to such a degree that it resembles a mass of small clay pellets. Even after wetting this flocculated soil retains its spherulate character.

THE GEOGRAPHICAL DISTRIBUTION OF THE CITRUS DISEASES, MELANOSE AND STEM-END ROT

By H. S. Fawcett

A general survey of the citrus districts of the United States and Cuba has shown that the distribution-areas of some of the important fungus diseases are not coextensive with the areas where the host is cultivated. This fact is strikingly brought out by an examination of the distribution of some of the diseases that have been present in these regions for a long time.

An interesting example of an old, well-known disease with a rather limited distribution is melanose, which is due to *Phomopsis citri.* The fungus produces small, brown pustules on the surface of rapidly growing leaves, twigs and fruit. It was discovered in 1892 and was first definitely described, by Webber, in 1897. At that time melanose was already a rather serious disease in the middle portion of the peninsula of Florida. During the past 20 years, citrus nursery stock has been freely interchanged between different parts of Florida, and thousands of acres in Cuba have been brought into citrus culture for the first time, the stock for planting being derived from Florida, and yet the area over which the disease is now of serious commercial importance is confined roughly between the parallels of 27½° and 29½° N. latitude in Florida.

Southward from this area melanose gradually becomes less and less severe and it finally disappears entirely, so that the southernmost citrus districts of the state are free from it. In Cuba, if the disease occurs at all, it is of no commercial importance; I was unable to find any evidence of it in the island in January, 1914. North of the Florida area of most serious injury, melanose occurs in a less severe form, and a mild form of the same disease has been reported for southern Alabama and Louisiana, but it is apparently not serious in these regions. No trace of this disease has ever been found in California.

The same Phomopsis that produces melanose also plays a part in the so-called stem-end rot of mature or nearly mature citrus fruits, and it is an interesting fact that this fruit rot has never been known to be serious outside of the areas where melanose is also of commercial importance. Like melanose, stem-end rot has not been reported as occurring either in Cuba or in California.

The reasons for the peculiar distribution of *Phomopsis citri,* as above described, are not at all understood, and we cannot regard our knowledge of melanose and stem-end rot as at all nearly complete until a properly substantiated explanation of these geographical limitations may be found. Such problems as this are worthy of serious attention. Some of the logical possibilities of this particular case may be mentioned, by way of preparing for further observations and for constructive experimentation.

One possibility that always presents itself in connection with a limited geographical distribution of any parasite is that sufficient opportunity or time may not yet have been afforded for the parasite to become distributed throughout the area occupied by the host. But this possibility seems not to apply in the present case. As has been mentioned, after melanose had become common in central peninsular Florida there took place a free interchange of many kinds of citrus nursery stock between Florida, on the one hand, and California and Cuba, on the other. Many carloads of young citrus trees were shipped from nurseries located in the Florida area where this Phomopsis was most virulent, no effective quarantine regulations were in operation at that time, and it is impossible that the fungus has not long since been thoroughly distributed. All or nearly all of the citrus varieties grown in Florida have been planted, at one time or another, in California, and the recent and extensive Cuban plantings have been made with nursery stock from Florida.

Of course, climatic conditions may furnish an explanation of the facts here dealt with, but the climatic relations of a fungus like *Phomopsis citri* are probably even more complex than are those of higher plants. For the growth of such a parasite it is not only necessary that the climatic conditions be suitable for this organism, but it is also essential that the complex of these conditions be naturally so arranged or balanced that the host-plant may be in just the proper state to favor the virulent development of the parasite. The time factor is especially important in the process of infection; it must happen that the host is in a condition to be readily infected just at the time when the fungus spores reach it.

One of the necessary conditions for the occurrence of melanose, when Phomopsis is present, appears to be a considerable degree of air humidity, at the season of most rapid growth of new shoots and of the fruit, and the absence of the disease in California may possibly be accounted for by the dryness of the air at the time when the trees are most susceptible to infection. This, however, does not seem to be a sufficient reason for the absence of melanose in the southernmost parts of Florida and Cuba.

Edgerton has recently emphasized the apparent bearing of temperature conditions on the occurrence of certain plant diseases in sub-tropical climates. He is convinced that the absence of anthracnose in beans grown at certain seasons in Louisiana is due to the fact that the average temperatures for those seasons are above the optimum for the growth of the pathogenic fungus. If this is true in the case of anthracnose it may also be true in the case of melanose. The first requirement for a test of this suggestion is, of course, some definite knowledge concerning the temperature relations of Phomopsis itself, and experimentation is now in progress in this direction.

PRELIMINARY NOTE ON THE RELATION OF TEMPERATURE TO THE GROWTH OF CERTAIN PARASITIC FUNGI IN CULTURES

By H. S. Fawcett

Interest in the temperature relations of plant growth is rapidly increasing, and, as improved methods become available, increasingly precise studies are being made of the influence of temperature upon growth as variously measured. The study upon which the writer is at present engaged aims to compare the temperature-growth curves for cultures of a number of fungi that produce diseases of citrus trees and that are confined to limited geographical areas. It is hoped that the results obtained may be of value, not only in interpreting the geographical distribution and seasonal occurrence of these diseases, but in suggesting further means for their control.

A suitable solid medium in petri dishes is employed, a transfer (of spores or a small piece of mycelium) being made to the center of each culture dish, and the resulting growth is measured in terms of the 24-hourly increase in the mean diameter or radius of the nearly circular area occupied by the fungus. Various precautions are taken to have all conditions, excepting that of temperature, as nearly alike as possible throughout the entire investigation.

The preliminary work so far carried out has been confined largely to *Pythiacystis citrophthora,* which attacks both the trunk and fruit of the lemon tree. To illustrate the kind of results obtained, at the temperatures 10°, 20°, 28° and 33°C. the radial, 24-hourly growth-rates of this fungus were 2.5, 6, 7.5 and 2.6mm., respectively. For a rise of temperature from 10° to 20° the growth rate was thus somewhat more than doubled, from 20° to 28° it increased 25 per cent., and at 33° the rate was nearly the same as at 10°. This kind of a relation between the growth-rate and temperature was of course to be expected, and interest in this research will lie largely in the differences between the temperature-growth curves of the different fungi, especially in the differences between their optimum temperatures for growth.

Although bacteria and fungi, as studied by other workers, appear to exhibit gradually diminished growth-rates when temperature and the other environmental conditions are maintained unchanged for a long time, yet no such slowing down of growth has been encountered with this Pythiacystis; for example, the same growth-rate has been observed to continue unchanged for a period of eight days or more.

SYMPTOMS OF POISONING BY CERTAIN ELEMENTS, IN PELARGONIUM AND OTHER PLANTS

By E. E. Free

In connection with other experiments on the effects of poisonous elements on plants, qualitative tests have been made of the symptoms of poisoning exhibited by the common cultivated geranium (*Pelargonium zonale*) and by several other plants, under the action of certain poisonous elements. The plants were grown in soil under ordinary greenhouse conditions. The poisons were applied by pouring the proper solutions on the soil when the latter was sufficiently dry to absorb and retain all of the added solution. Seven elements were applied to Pelargonium in five concentrations each. These were the following. Concentrations are in parts of the poisonous element per million parts of soil by weight.

	Concentrations p. p. m.
Arsenic, as trioxide (As_2O_3)	2 to 500
Boron, as borax ($Na_2B_4O_7$)	2 to 500
Copper, as sulphate ($CuSO_4$)	4 to 1000
Iron, as ferrous sulphate ($FeSO_4$)	20 to 5000
Lead, as nitrate ($Pb(NO_3)_2$)	4 to 1000
Manganese, as sulphate ($MnSO_4$)	8 to 2000
Zinc, as sulphate ($ZnSO_4$)	8 to 2000

In addition to these seven elements the following were applied in one concentration only, namely 500 parts per million:—barium, as chloride ($BaCl_2$); bromine, as potassium bromide (KBr); cobalt, as sulphate ($CoSO_4$); chromium, as potassium chromate (K_2CrO_4); iodine, as potassium iodide (KI); lithium, as sulphate (Li_2SO_4); mercury, as mercuric chloride ($HgCl_2$); nickel, as sulphate ($NiSO_4$); silver, as nitrate ($AgNO_3$); uranium, as uranyl nitrate ($UO_2(NO_3)_2$); and vanadium, as chloride (VCl_2). All of these elements except iron were applied to *Impatiens sultani, Coleus blumei* and *Vicia faba* as well as to Pelargonium. The first ten elements (arsenic, boron, copper, manganese, zinc, lead, mercury, iodine, chromium, and barium) were applied also to *Chrysanthemum frutecens, Bryophyllum calycinum* and castor bean (*Ricinis communis*). Except as noted, all applications were in the concentration of 500 parts of the poisonous element per million parts of soil. In order to avoid local injuries to the stem large applications were frequently divided and added in several portions at intervals of a few days.

The following elements gave no determinable poisonous effects on any plant, in the concentrations used: arsenic, barium, bromine, cobalt, copper, lead, manganese, nickel, silver, uranium, vanadium and zinc. A slight improvement of color and general condition was noticed in Pelargonium with manganese and zinc. There was also a slight, but unmistakable, stimulation of the growth of this plant by arsenic in the higher concentrations but this conceivably may have been due to some chemical action in making more available the phosphorus or other nutrients in the soil.

Pronounced toxic effects were observed with boron, chromium, iodine, lithium and mercury, and it is interesting that these effects were largely so specific as to permit immediate recognition of the particular poison by mere inspection of the plant. Thus on Pelargonium the effect of boron is the development of dark-green areas, 1 to 5 mm. wide, inward from the edges of the leaves. This altered strip gradually dries and hardens, without becoming brown, and the leaf falls after from one to four weeks. The dark-green coloration does not extend to the whole leaf. Lithium shows a somewhat similar behavior, but the altered area on the edge of the leaf is wider and is a light gray-green instead of dark green. It shows a very characteristic banding of the color in narrow light and dark lines parallel to the leaf edge. With iodine the leaves turn yellow on the edges and this yellowing gradually extends inward over the whole leaf. Not until the leaf has turned entirely yellow does it fall or wilt appreciably. Mercury produces a somewhat similar yellowing of the leaves, but wilting begins immediately and the leaf usually falls long before it is entirely yellow. The first effect of chromium is a brown discoloration in the vascular bundles of the petioles and veins. This is followed by a change of the leaf color to a dark green, and the early fall of the leaves. The regularity and specificity of these changes is attested by many repeated observations on different leaves and different plant individuals. Similar specificities were observed with the plants other than Pelargonium. It seems probable, therefore, that the recognition of a poisonous agent by the specific symptoms of its action is as possible with these plants as with animal organisms.

Certain features of the localization of injury in the plants is suggestive of relations to transpiration. For instance, with boron and lithium on Pelargonium the limitation of injury to the edges of the leaves implies its occurrence only where the final evaporation of the water of the transpiration stream localizes the poison in a concentration sufficient to be toxic. A similar conclusion follows from the fact that injury occurs first, and sometimes only, on leaves of moderate age, that is on those which are in their period of most vigorous transpiration. Younger leaves and older leaves on the same plant are usually uninjured. Similarly, when a Pelargonium plant is poisoned but not killed, by either boron, lithium, mercury or iodine, new leaves produced thereafter do not show injury while they are young, but develop it after from two to six weeks of growth. The same observation was made with boron and iodine on Chrysanthemum. Further confirmation is the failure of Bryophyllum, which has a very low transpiring power, to show injury with any poison except boron. Even in this case the injury developed eleven weeks later than it did on Pelargonium and all the other plants. All of this evidence suggests that, in the concentrations used, the poisons were carried into the plant incidentally by the transpiration stream and produced injury only when and where the evaporation of the transpired water increased the concentration of the poison in a local tissue area. The symptoms observed with chromium imply that it may form an exception to this behavior, but even with this element it was observed that Pelargonium leaves were injured only when of middle age; young and old leaves being unaffected.

THE EFFECT OF AERATION ON THE GROWTH OF BUCKWHEAT IN WATER-CULTURES

By E. E. Free

In connection with other work on the oxygen requirements of plant roots experiments have been made on the relations between the degree of aeration of the culture solution and the growth of buckwheat in water-cultures. The plants were grown in quart jars in the usual manner, three plants to a jar. The solution was that found by Shive [1] to be the best for the growth of buckwheat. The experiment included 18 jars divided into six sets of three jars each. One set, used as control, was handled according to the usual technique, with free access of air to the solution. Another set was sealed, the seal about the young plants being made with a parafine-vaseline mixture according to the method of Briggs and Shantz.[2] With the third set, a slow stream of air was bubbled through the culture solution, a bubble about 5 mm. in diameter passing about once a second. The three remaining sets were treated in the same way with oxygen, nitrogen and carbon dioxide, respectively. Precautions were taken to remove deleterious impurities from the gases. Water evaporated from the culture solutions was replaced when necessary.

The cultures with oxygen, nitrogen and air showed no departure from the open controls or from the sealed cultures.

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[1] Shive, John W., "A three-salt nutrient solution for plants." *Amer. Jour. Bot.* 2: 157-160, 1915.

[2] Briggs, L. J., and Shantz, H. L., "A wax seal method for determining the lower limit of available soil moisture." *Bot. Gaz.* 51: 210-219. 1911.

Rate of growth and weight of dry matter produced was essentially the same in all. All plants grew to maturity and nearly all set seed. It appears that the degree of aeration of the culture solution is without important influence on the growth of buckwheat under the conditions described; a conclusion that may have value in general water-culture practice.

It may be added that in the cultures treated with carbon dioxide the plants sickened and wilted within a few hours and died within a few days. In one case the stream of carbon dioxide was replaced after the first day by a stream of air. In this case the plants recovered partially but remained permanently smaller than the other plants of the experiment.

THE EFFECTS OF CERTAIN MINERAL POISONS ON YOUNG WHEAT PLANTS IN THREE-SALT NUTRIENT SOLUTIONS

By E. E. Free and S. F. Trelease

A large part of the experimentation which has been done in the past on the effects of mineral poisons on plants is unsatisfactory and contradictory, for the reason that the nutrient materials available to the plants, in the soil or nutrient solution employed, were different in the different experiments. The reactions of plants to the various poisons appear to vary with such differences in the available nutrients. In connection with other work on nutrient solutions, tests have been made on the effects of certain poisonous elements on the growth of young wheat plants in water-cultures. The salt combination used in the nutrient solution was that found by Shive[1] to be best for the production of dry weight of

[1] Shive, J. W., "A three-salt nutrient solution for plants." *Amer. Jour. Bot.* 2: 157-160. 1915. *Idem,* "A study of physiological balance in nutrient media." *Physiol. Res.* 1: 327-397. 1915. (Especially p. 352-364.)

tops for wheat. The total concentration of the solution corresponded to an osmotic pressure of 1.75 atmospheres at 25° C. The technique was essentially the same as that employed by Shive.

The minimum concentrations at which the various poisons began to produce clearly marked injury, as indicated by smaller dry weights of tops, are given in the following table. Concentrations are given in parts of the poisonous element per million parts of the nutrient solution. In most cases the concentration at which injury begins is not sharply marked, and, therefore, the figures given have only approximate quantitative value.

Element	*Compound used*	Toxic Concentration of element. *p. p. m.*
Arsenic	trioxide (As_2O_3)	1
Boron	borax ($Na_2B_4O_7$)	10
Cobalt	sulphate ($CoSO_4$)	7
Copper	sulphate ($CuSO_4$)	1
Manganese	sulphate ($MnSO_4$)	1000
Mercury	bichloride ($HgCl_2$)	40
Nickel	sulphate ($NiSO_4$)	5
Vanadium	chloride (VCl_2)	20
Zinc	sulphate ($ZnSO_4$)	100

Experiments were made also with lead, as lead nitrate ($Pb(NO_3)_2$), and with uranium as uranyl nitrate ($UO_2(NO_3)_2$), but both of these elements were precipitated by the constituents of the nutrient solution. The maximum concentrations obtainable in the solution were approximately 100 parts per million in case of lead and 20 parts per million in the case of uranium. Neither of these was toxic.

A slight stimulating effect, indicated by greater production of tops, was observed with manganese, between the concentrations of 4 and 20 parts per million, and with vanadium, between 2 and 7 parts per million. There was a clear stimulation in the uranium cultures above a concentration of 50 parts per million of uranium, but it is possible that this was due to the nitrate in the uranium salt. No stimulation was observed with any other of the elements tested.

This failure to secure determinable stimulating effects with most of the elements is surprising and is contrary to the results of many previous investigations. It seems possible that it may be due to the fact that the Shive solution, in the concentration and salt proportions employed, is itself slightly toxic because of its high content of magnesium. This solution, although it gives the best production of dry weight of tops, produces plants many of which show the morphological modifications characteristic of magnesium poisoning.[2] These observations form one of several bits of evidence which suggest that the best growth of a plant, as measured by production of dry matter, occurs only when the plant is slightly poisoned. It may be a general rule that increased growth is the first response to agents or circumstances which would prove injuriously toxic in greater concentration or on longer exposure.

We have found some confirmation of this suggestion in our experiments on the effect of boron on Canada field pea. Using the Shive solutions containing salt proportions other than the ones above referred to, and adding borax to these solutions, considerable stimulations were obtained. The experiments need to be extended and confirmed, but the present indication is that borax is stimulating in those nutrient solutions which contain less magnesium than the one giving greatest dry weight of tops. In other words, slight poisoning, such as that caused by magnesium or boron, is essential for the production of the greatest dry weight of tops. Either magnesium or boron will serve. Probably other poisons would be equally efficacious.

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[2] Shive, *loc. cit.* (2), p. 370-374. Tottingham, William E., "A quantitative chemical and physiological study of nutrient solutions for plant cultures." *Physiol. Res.* 1: 133-245. 1914.

LEAF-PRODUCT AS AN INDEX OF GROWTH IN SOY-BEAN

By F. Merrill Hildebrandt

It has been pointed out by McLean [1] that the sum of the products of the length and breadth of all the leaflets on a soy-bean plant 4 weeks old is approximately proportional to the total leaf area of that plant, and he adds that the leaf area is itself nearly proportional to the total dry weight of stem and leaves. The sum just mentioned has been called the leaf-product by the same writer, his observations being based on measurements obtained at two stations in Maryland, Easton and Oakland, in the project carried out during the summer of 1914 by the Maryland State Weather Service in co-operation with the Laboratory of Plant Physiology of the Johns Hopkins University. That project included similar studies of the relation of plant growth to climatic conditions at seven other stations in Maryland, besides Easton and Oakland, and the present paper aims to bring out the fact that this interesting relation between leaf-product, leaf area and dry yield of tops applies generally to the soy-bean data for all nine stations.

If the method proposed by Livingston [2] and McLean, of employing the growth rates of standard plants as indices for the comparison of different climates as these influence plant growth in general, is to be of value, it is of course necessary that suitable plant characteristics be chosen for measurement in determining the growth rates, and it is desirable that the measurements be such as may be made from time to time without injury to the plants. The most generally accepted

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[1] McLean, F. T., "A preliminary study of climatic conditions in Maryland, as related to plant growth." *Physiol. Res.* **2**: 129-208. 1917.

[2] Livingston, B. E., and McLean, F. T., "A living climatological instrument." *Science*, n. s. 43: 362-363. 1916.

criterion of plant growth, dry weight of tops, can be obtained but once for any individual plant, since the plant is destroyed during the determination. Also, the accurate determination of leaf area is very difficult unless the plants are destroyed. On the other hand, as McLean has emphasized, leaf dimensions may be obtained repeatedly during the development of the plant without serious danger of inflicting injury. It may therefore be of considerable importance if leaf area, and even dry weight, can be satisfactorily estimated for soy-bean by the employment of the leaf-product as an index.

The general procedure followed in obtaining the observational data upon which are based the results here considered has been described by McLean, who conducted all the cultures personally (see his paper cited above). For the present purpose it is sufficient to state that cultures, each of 6 soy-bean plants, were started from the seed every two weeks throughout the summer season, at each of the nine stations employed, and that plant measurements were taken after about two and after about four weeks of growth. Dry weight and actual leaf area were determined only for the four-week periods, the plants being then destroyed, but the lengths and breadths of all leaflets were obtained for both the two-week and the four-week periods. Consequently, to study the correlation between total leaf area and total leaf-product per plant, only the four-week data are available, and these are the ones here considered. Thus, each of the nine stations is represented by a series of consecutive four-week culture periods, each period overlapping on to the next preceding and next following one. A large number of different sets of climatic conditions is thus represented by the whole series for the nine stations, which includes 97 4-week culture periods in all.

The leaf measurements here dealt with have all been obtained by the writer from photographic contact prints made by Dr. McLean from the fresh leaves immediately after these were removed from the plants. Areas were obtained from the same prints with a planimeter. The leaflet length was taken from tip to junction of blade and petiole for each leaflet, and the corresponding leaflet breadth was measured at the point of greatest width, at right angles to the long axis of the leaflet. Since soy-bean leaflets are approximately elliptical in form and since the area of an ellipse is proportional to the product of its axes, the leaflet-product (length times breadth) of any leaflet should be nearly proportional to the area of that leaflet. Whether this relation may hold during the growth of the leaflet under different sets of climatic conditions depends upon how nearly the elliptical form is retained. The sum of the individual leaflet-products of any plant, which is the total leaf-product for that plant, should be approximately proportional to the total leaf area of the plant, if the relation given above holds. In the discussion that follows it will be shown that such an approximate proportionality does exist in the case of the four-week soy-bean plants.

In order to find out whether the actual area of the leaves in these cultures was proportional to the leaf-products, the ratio of the two quantities was worked out for a number of the stations. It was found that the leaf-product divided by the leaf area gives a number that varies only slightly from the value 1.28. In other words, if we measure the two diameters of the leaflets of a four-week soy-bean plant, multiply these two numbers, and add the products, a number is obtained which, when divided by 1.28, closely approximates the actual leaf area of that plant. Instead of using the sum of the products of length and breadth as an index of the area per plant we may use the sum of the squares of the lengths of the leaflets or the sum of the squares of the breadths of the leaflets of the plant. The numbers thus secured do not, however, bear as nearly constant a ratio to the actual leaf area as does the total leaf-product, and hence neither is as satisfactory an index of the area as is the leaf-product itself.

One of the most interesting properties of the four-week soy-bean plant is that the dry weight of stem and leaves is proportional, approximately, to the total leaf area. Having, therefore, a means by which the leaf area may be conveniently measured, it is possible to calculate the dry weight of the plant approximately, by multiplying the leaf-area by the proper constant. The proportionality between the weight of the plant and its leaf area is not quite so constant as that between leaf area and leaf product, but in the great majority of cases the variation in the ratio of dry weight to leaf area, from a constant value, is less than 10 per cent. The relations given hold over a very wide range of climatic conditions and for plants varying in height from 2 or 3 centimeters to 18 or 20 centimeters. Since none of the plants in these experiments were grown to maturity, it is impossible to say whether this relation holds up to that time.

From the foregoing facts it may be concluded that the dry weight and leaf area of soy-beans 4 weeks old from the seed can be determined approximately from their leaflet dimensions. Soy-bean should therefore be very suitable for use as a standard plant for the measurement of climate in the manner suggested by Livingston and McLean, since the rate of its growth can be approximately determined from easily obtained leaf measurements. Also, the properties of soy-bean given above should make it a useful plant for any piece of physiological research in which it is desired to know approximately the dry weight of the plant used, at various stages of its development.

A METHOD FOR APPROXIMATING SUNSHINE INTENSITY FROM OCULAR OBSERVATIONS OF CLOUDINESS

By F. Merrill Hildebrandt

Air temperature, the evaporating power of the air, and sunshine intensity may be considered the main climatic conditions affecting plant growth and one of the first essentials in ecological, agricultural, and forestal studies is some means by which these may be measured in the field. We are already provided with instruments for measuring the first two, but the means thus far available for measuring sunshine intensity are difficult to apply in field studies. A method is here presented by which a roughly approximate index of sunshine intensity during any period for any station may be made from records such as are kept by the observers of the U. S. Weather Bureau.

The total heat equivalent of the actual sunshine for any given period at a station is primarily a function of three terms: (1) the maximum possible number of hours of sunshine (determined by latitude and season); (2) the mean intensity of full sunshine for the period and station, expressed in terms of heat; (3) the condition of the sky, whether overcast, partly overcast or clear. The daily values for the first two of these terms vary in a regular manner throughout the year at any given place, and the ones for the third term are roughly stated in the observer's records, as just mentioned. It was desired to combine these three terms so as to get approximations of sunshine intensity for a number of different stations in Maryland for the summer of 1914, in order to make comparisons of the summer march of sunshine intensity with that of corresponding measurements of plant growth. This has been accomplished in the manner described below.

The first two terms are combined in the ordinates of the graph given by Kimball[1] for the maximum possible total radiation received per day at Mount Weather, Virginia. Since this station is at about the same latitude as the stations in Maryland, the ordinate values may be taken as approximate measures of the total radiation intensity for the corresponding dates at any place in the state. These values represent the total amount of heat, expressed in gram-calories per square centimeter of horizontal surface exposed, received from the sun and sky on clear days at Mount Weather. The method

[1] Kimball, Herbert H., "The total radiation received on a horizontal surface from the sun and sky at Mount Weather. *Monthly Weather Rev.* **42**: 474-487. 1914. (See especially fig. 8, p. 484).

of using the graph and a weather observer's report for estimating sunshine will be best shown by an example.

Suppose it is desired to estimate the average daily sunshine intensity for some station in the general region of Mount Weather, for the first week of August. The average ordinate value for this week is first obtained from Kimball's graph. For periods as short as a week or two this may be done by averaging the values for the first and last days of the period, since the curve may be taken as a straight line for such short intervals. From the report of the weather observer at the place in question, the number of clear, partly cloudy, and cloudy days is next determined for the days August 1 to August 7, inclusive, and some arbitrary weighting is given to each kind of day. We may, for instance, call clear days whole days of sunshine, partly cloudy days half days of sunshine, and assume that cloudy days are days without any sunshine. The scheme of weighting adopted must, of course, be adhered to in all the estimates made for different periods and stations. The system of weighting given above was used in the studies for which this method of approximating sunshine was developed. By summing these weighted daily values a number is obtained which represents the equivalent number of clear days for the period considered. Suppose, in the example selected, that this equivalent number of clear days is 3.5, which is 0.5 of the total number of days in the period. The latter value may be termed "the coefficient of clear weather." By multiplying the average daily intensity value for clear days, as obtained from the curve, by this coefficient of clear weather a number is secured that is a rough approximation of the average daily sunshine intensity for the week.

While it is certain that solar radiation affects plants in other ways than through its heating effect, it is no less certain that by far the greater part of the energy of sunshine absorbed by plants is converted into heat (largely as latent heat of the vaporization of water), and it seems probable that the other effects produced upon the plant may be more or less proportional to the total energy equivalent of sunshine. The method of measurement of light here given, although it is only a rough approximation and depends on the heating effect of the sunshine, has been shown, as a matter of fact, to give numbers rather definitely correlated with plant growth. It has been found, for instance, that the amount of dry substance produced per unit of leaf area in young soy-bean plants decreases from the beginning to the end of the growing season, in a manner which generally parallels a corresponding fall in the light intensity values as determined in the manner described above.

MOISTURE EQUILIBRIUM IN POTS OF SOIL EQUIPPED WITH AUTO-IRRIGATORS

By F. S. Holmes

While the auto-irrigator devised by Livingston [1] has been employed by several writers,[2] for maintaining uniform moisture conditions in potted soils, the details of adjustment required by this device, for different soils and for maintaining different moisture contents, remain still to be worked out. In order to throw some light upon this general question, a study of three different soils was undertaken to determine the relation between the equilibrium point of the soil-moisture content and the number of irrigator cups employed.

One soil was a medium-fine white sand, one was a light

[1] Livingston, B. E., "A method of controlling plant moisture." *Plant World* **11**: 39-40. 1908.

[2] Hawkins, Lon A., "The porous clay cup for the automatic watering of plants." *Plant World* **13**: 220-227. 1910. Transeau, E. N., "Apparatus for the study of comparative transpiration." *Bot. Gaz.* **52**: 54-60. 1911. Livingston, B. E., and Lon A. Hawkins, "The water relation between plant and soil." Carnegie Inst. Wash. Pub. **204**: 5-48. 1915. Hibbard, R. P., and O. E. Harrington, "Depression of the freezing-point in triturated plant tissues, and the magnitude of this depression as related to soil moisture." *Physiol. Res.* **1**: 441-454. 1916.

clay loam, and the third was a mixture, of equal parts, by volume, of the other two. Pots of each kind of soil were equipped with auto-irrigators having respectively one, three and five porous cups, thus giving nine combinations. The containers were tinned sheet-metal cylinders approximately 15 cm. in diameter and 17 cm. in height. The porous cups were evenly distributed within the soil mass, when but one was used it occupied the center. A mercury tube was so arranged that all water entered the soil against a pressure of from 5 to 6 cm. of a mercury column. Evaporation was prevented by sealing covers on the containers with plastiline. The cylinders were filled to a uniform depth of 16 cm., an attempt being made to secure as uniform packing as possible throughout the entire series.

Weighings of the containers were made at intervals of two or three days, for the first twenty days, and thereafter at weekly intervals, to determine the rates at which water was being absorbed and to approximate the moisture content of the soil. Approximately three-fourths of the water taken up by the loam and by the sand-loam mixture occurred during the first ten days, but the sand took up only about one-half of its total amount in the same period. Approximate equilibrium of the soil moisture content was reached in about seventy-five days, in the case of the loam; in about eighty days in the case of the mixture; and in about ninety days in the case of the sand. The number of porous clay cups employed seemed to have no influence upon the length of time required for the attainment of equilibrium by either the loam or the loam-sand mixture. With the sand, however, the number of cups appeared to influence the length of this time period. With three cups equilibrium was reached sooner than with one, and with five sooner than with three.

When the weighings of the cylinders and observations on the water reservoirs showed that the soil had ceased to absorb water, the cylinders were opened and samples were taken for soil-moisture determinations. Two 1-cm., full-depth cores were taken from each container, one core from as near a cup as possible, the other as far removed as possible. The average of the two was taken to be representative of the entire soil mass. Each sample was removed and dried in eight 2-cm. sections, so that it was possible to study both the vertical and horizontal distribution of the soil moisture in the cylinder. There was a horizontal as well as a vertical variation of small magnitude in the soil-moisture content of all the cylinders, the water content being almost always somewhat higher near the cups and at the bottom of the soil mass. The distribution of the moisture, both horizontal and vertical, was more uniform in the sand-loam mixture than in the sand, and also more uniform in the loam than in the mixture. The number of porous cups used had very little influence, if any, upon the soil moisture content of the loam; it varied as 100 : 106 : 103, for the containers having one, three and five porous cups, respectively. This influence of the number of cups was more pronounced in the case of the sand-loam mixture, the variation, with one, three and five cups, being 100 : 147 : 168. With the sand there was a still more marked effect, the moisture contents for the three cup numbers being 100 : 191 : 277 in this case. These variations are all smaller than the corresponding variations in the value of the ratio of cup number to soil mass, these values varying as 100 : 321 : 576, for all three soils. For the containers with three cups the actual average soil moisture content (on the basis of dry weight) was 11.0 per cent. for the loam, 5.2 per cent. for the mixture, and 1.1 per cent. for the sand.

With the pressure here used (averaging 5.5 cm. of a mercury column) the soil moisture content at equilibrium was too low for plant cultures in the sand and perhaps also in the sand-loam mixture. In the loam, however, it was surely high enough to supply plants with the water necessary for their growth under ordinary greenhouse conditions.

SEASONAL VARIATIONS IN THE GROWTH-RATES OF BUCKWHEAT PLANTS UNDER GREENHOUSE CONDITIONS

By Earl S. Johnston

Seasonal variations in greenhouse plants are of considerable importance to plant growers as well as to experimenters in plant physiology, but it is especially with reference to physiological experimentation that this study was undertaken. When it is necessary to repeat an experiment on plant growth it often occurs that the results of the second experiment are in more or less pronounced disagreement with those of the first. Since the controlled external conditions must be regarded as the same for both experiments, such disagreement appears to be related either to initial differences in the plants used (internal conditions) or to uncontrolled external conditions as these vary with the season. The first of these possibilities is probably not as important as the second in most cases, for care is usually taken to select plants for the second experiment that are apparently similar to those used for the first. While this problem of similarity of internal conditions of different lots of plants is a very difficult one and is hardly susceptible of quantitative study at the present time, it is quite possible to carry out studies on the relation of growth to the usually uncontrolled (or only partially controlled) external conditions of a greenhouse, as these conditions change throughout the year. A portion of the results obtained from such study are here presented.

A set of similar water cultures was started every two weeks and each was continued for a period of four weeks, so that the periods of successive sets overlapped. A single set consisted of ten plants, each suitably supported in a glass jar containing about 425 cc. of nutrient solution. These jars were covered, to exclude most of the light from the plant roots. The solution was renewed at the middle of each four-week period. At the end of each week several different kinds of measurements of the plants were made, and the data thus obtained were studied to bring out the seasonal variations in growth-rates. Since the solutions were alike for all sets and the seedlings used were selected for likeness, it is fair to suppose that observed differences in growth-rates, between the different sets of cultures, must have been mainly due to fluctuations in the uncontrolled conditions of the surroundings, such as temperature, light and the evaporating power of the air.

The experiments were carried out in one of the experiment greenhouses of the Laboratory of Plant Physiology. No artificial shade was applied to the greenhouse. Two sets of cultures were always carried out simultaneously, one under unmodified greenhouse conditions and the other in a cheesecloth chamber in the greenhouse, but the data obtained from the chamber cultures will not be dealt with in the present paper. A continuously rotating table 76 cm. in diameter was used in each case, the jars standing near the margin of the table.

Japanese buckwheat, *Fagopyrum esculentum* Moench., was employed, and Shive's[1] three-salt nutrient solution, no. R 4C2 (total osmotic value 1.75 atmospheres), was used throughout the entire series. Aside from renewing the solution at the middle of the four-week period, water was always added at the end of the third week of growth, to bring the solution back to its original volume. When the transpiration rates were excessive a still further addition of water was made during the fourth week of growth, in order to prevent the root systems from becoming unduly exposed. The first experiment began Feb. 14, 1916.

Of the plant characteristics measured at the end of each four-week period of growth, only stem height, total dry weight and total area of the leaves (one surface only) are here con-

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[1] Shive, John W., "A study of physiological balance in nutrient media." *Physiol. Res.* 1: 327-397. 1915.

sidered, the values obtained being expressed as averages per plant, for each of the four-week periods. The temperature conditions, the evaporating power of the air and the intensity of radiation were recorded for each of the two exposures, but these are left out of the present consideration.

The results obtained from these three plant measurements are shown in the accompanying table, wherein all the values are expressed in terms of the corresponding value for the period ending May 22. In this table the dates of beginning and ending of the several culture periods are shown in the first two columns. Each value given in the table represents an average growth-rate representing a single plant, for a time period of 28 days.

EXPERIMENTAL DATA

Period		Stem	Total	Total	Av'ge of
Beginning	Ending	Height.	Dry Wt.	Leaf Area	Wt. & Area
Feb. 14	Mar. 13	.73	.50	.63	.57
Feb. 28	Mar. 27	.83	.62	.81	.72
Mar. 13	Apr. 10	.85	.72	.77	.75
Mar. 27	Apr. 24	.94	.80	.76	.78
Apr. 10	May 8	.98	.89	.76	.83
Apr. 24	May 22	1.00 (67.5 cm.)	1.00 (1.338 g.)	1.00 (213.5 sq. cm.)	1.00
May 8	June 5	.93	.91	.93	.92
May 22	June 19	.83	.93	.98	.96
June 5	July 3	.73	.93	1.00 (214.1 sq. cm.)	.97
June 19	July 17	.77	.88	.88	.88
July 3	July 31	.97	.91	.92	.92
July 17	Aug. 14	1.04	.82	.83	.83
July 31	Aug. 28	.91	.67	.77	.72
Aug. 14	Sept. 11*	——	——	——	——
Aug. 28	Sept. 25	1.07	.76	.70	.73
Sept. 11	Oct. 9	.97	.55	.58	.57
Sept. 25	Oct. 23	.78	.34	.43	.39
Oct. 9	Nov. 6	.79	.36	.51	.44

The different kinds of growth-rates are seen to vary independently, from period to period, but two of the growth

* Data not obtained because of insect injury to plants.

criteria, weight and area, show variations that correspond rather closely. Both of these show high rates for the summer and low ones for the spring and autumn. Judged by dry weight of plant produced the growth-rate reached its maximum (1.34 g. per plant, in 28 days) with the period ending May 22, but this value remains high until after the period ending July 31. Judged by the total leaf area, the rate does not attain its maximum (214 sq. cm. per plant, in 28 days) until later, this occurring with the period ending July 3, but this value is high for the three preceding periods and for the two following. Roughly speaking, it may be said that these two criteria give rates that are proportional, and that they agree in indicating a period of very rapid growth, extending from about May 8 to about July 17. Before the period with its middle at May 8 the rates are lower, forming a generally ascending series, from the very low values of the early spring, and after the period with its middle at July 17 they decrease rapidly (with a low secondary maximum indicated for the period ending Sept. 25) to very low values in the autumn.

The rates of growth in height fail to show this sort of seasonal march; the maximum rate (49 cm. per plant, in 28 days) being shown for the period ending July 3, but this rate also has very low values for the periods ending March 13, Oct. 23 and Nov. 6. By this criterion, the maximum for the period considered (72.5 cm. per plant, in 28 days) occurs with the period ending Sept. 25, but pronounced secondary maxima are shown for the periods ending May 22 and Aug. 14. This rate of growth in height appears to vary considerably from period to period, but in a manner entirely independent of the general advance of the season and quite independent of the variations in rates of increase in dry weight and in leaf area. As far as these data go, it therefore appears that there is nothing in the usually uncontrolled external conditions of a greenhouse in this climate, that may be expected to produce a regular march of growth-rates in height, for healthy buckwheat plants, during the spring, summer and autumn.

McLean [2] has pointed out the approximate proportionality of the rates of production of dry weight and leaf surface, for the first four weeks of growth of soy-bean plants, and he also found that the rate of stem elongation varied quite differently from the rates of production of dry weight and surface. It may be of fundamental significance that two plants as widely different, in many other respects, as are buckwheat and soy-bean, exhibit these remarkable agreements in the manner of variation in these three growth-rates with differences in the climatic conditions of the environment.

The general agreement between the seasonal variations shown by the rates of increase in dry weight and in leaf area is so marked that it appears quite permissible to combine these two criteria by averaging their relative values, to give a single value representing both together, and the averages so derived are given in the last column of the table. Of course, these two measurements of growth-rate are not directly commensurable, and the average values here introduced are to be regarded merely as numerical indices of the rates of growth. This value has its maximum (1.00) for the period ending May 22, and it of course shows high value for the five following periods. Its minimum value (0.39) occurs for the period ending Oct. 23.

Of course there are many other considerations to receive attention in a study of this sort, but it already seems clear that a regular and pronounced seasonal variation in the rates of production of dry weight and leaf area may be expected in healthy buckwheat plants growing in a greenhouse in this kind of climate, although the same nutrient medium is always employed. If the weight-area indices be represented

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[2] McLean, Forman T., "A preliminary study of climatic conditions in Maryland, as related to plant growth." *Physiol. Res.* **2**: 129-208. 1917.

graphically they give only comparatively slight variations from a smooth curve and the actual graph may readily be smoothed to give such a curve. After this has been done the ordinates of the smoothed curve, corresponding to the various culture periods, may be measured, and the series of graphically derived values thus obtained may be taken as a tentative scale to indicate approximately the relative growth-rates to be expected for this plant in these general surroundings. Of course, the seasonal march of the climatic conditions in this particular greenhouse must be expected to vary from year to year, and it surely varies from greenhouse to greenhouse; nevertheless, the tentative scale derived as just described may be of value in several ways.

For the first sixteen four-week periods of the present study, beginning with Feb. 14, as given in the table presented above, these relative seasonal indices of growth-rate (by either dry weight or leaf area, which appear to be proportional, or by their average) are respectively as follows: 61, 71, 79, 86, 91, 96, 99, 100, 99, 96, 92, 87, 81, 75, 68, 61. In this scale of growth-rate values the maximum (100) occurs for the period ending June 19, and it represents actual average growth-rates, as obtained in this study, of 1.24 g. of dry weight and 209 sq. cm. of leaf area (one surface only), per plant, per period of 28 days. While these derived results are extremely tentative and probably only very roughly approximate, it is clear that we have here a new kind of description of the climatic conditions of this greenhouse for the spring, summer and autumn of 1916, these conditions and their seasonal march being described in terms of their ability to produce dry material and leaf surface in the standard plant here employed.

By such a method as this the climatic plant-producing power for any four-week period may be directly compared with that of any other similar period, no matter when or where these periods occur, the standard plant being used as an automatically integrating instrument for the measurement of the effective climatic conditions. This general method for the comparative study of climatic conditions has been suggested by Livingston and McLean [3] and a first attempt at its employment was carried out by McLean in the paper already mentioned.

ON THE RELATION OF CHLORINE TO PLANT GROWTH

By W. E. Tottingham

As a result of experiments conducted early in the development of the water-culture method, chlorine has been considered as one of the unessential elements for the growth of plants in general. Nevertheless, all seeds contain more or less of this element and in no instance has a plant been limited to this original source of chlorine through successive generations, so that it may still be said that the question here raised has never been really tested. Practically all soils contain considerable amounts of chlorine in the form of chlorides and its occurrence in plants appears to be confined to this form. That this element may have important effects under some conditions, when applied as an agricultural fertilizer, is indicated by a common practice in some parts of Europe, of adding common salt to stimulate the growth of mangel-wurzel and of mixed meadow grasses, but the manner in which this effect is produced has not been made clear. It has been observed that unrestricted application of chlorides may lead to poisoning of the soil, and agriculturists have been advised specially against the use of potassium chloride as a source of potassium for tobacco, the potato and the sugar beet. European investigators have reported a decreased content of starch in the potato tuber as a result of the substitution of this salt for potassium sulphate.

[3] Livingston, B. E., and McLean, F. T., "A living climatological instrument." *Science*, n. s. 43: 362-363. 1916.

The investigations here considered in a preliminary way were planned to supplement our knowledge of this subject. They are as yet in early stages of progress, having been begun under the auspices of the Wisconsin Agricultural Experiment Station. It was purposed to measure the responses of various plants, in form and in the weight of plant material produced, to the application of certain chlorides, and to determine any specific results brought about by this application of chlorine, upon the chemical composition of the plants. Greenhouse cultures were grown in nutrient solutions, in pure sand and in Miami silt loam, and field cultures were grown in loam. It may be said of these greehouse cultures, which were partly carried out in the winter, that, while growth is retarded by the decreased light intensities of the winter months, the partial control of climatic and soil conditions in such greenhouse cultures assures more reliable comparative results than are usually derived from field plots, with their natural fluctuation of climatic conditions from season to season and of fertility from plot to plot.

In the water-culture experiments, in the greenhouse, the plants were grown to maturity, in either Tottingham's or Knop's nutrient solution,[1] containing $Ca(NO_3)_2$, KNO_3, $MgSO_4$ and KH_2PO_4, in proper proportions, with a trace of iron as $FePO_4$. The former had a total osmotic concentration value of about 1.75 atmospheres (0.4 per cent. of salts by weight) and the total osmotic value of the latter was about 0.9 atmospheres (0.2 per cent. of salts by weight). In some cases chlorine was introduced by replacing the $MgSO_4$ of the 4-salt solution with a molecularly equivalent quantity of $MgCl_2$, in other cases KNO_3 was replaced by KCl, and in still other cases NaCl was superimposed upon the salts usually present. Replacement of $MgSO_4$ by $MgCl_2$ resulted in an increased length of roots, for pea, wheat and clover, amount-

[1] Tottingham, W. E., "A quantitative chemical and physiological study of nutrient solutions for plant cultures." *Physiol. Res.* 1: 247-288. 1914.

ing to from 100 to 300 per cent. This gain in root length was correlated with somewhat smaller gains in dry weight. With wheat and clover the production of dry weight of tops was depressed by this treatment but the percentage of nitrogen contained in the dry tops was unaffected. It will be noted that the interpretation of these effects is complicated by the fact that sulphur was absent where chlorine was present in the solution.

Buckwheat was grown in Knop's solution modified by having KNO_3 partly or wholly replaced by KCl, thus avoiding the omission of sulphur. Such treatment led to a slightly increased production of stem and root when the replacement was only partial, but complete replacement depressed the root length and the dry weight of roots and leaves, the amount of water lost by transpiration being proportionately decreased. Total replacement of KNO_3 by NaCl depressed growth more than when KCl was used and transpirational water loss was more than proportionately decreased. Comparison with the necessary control solutions indicated that this effect is to be considered specific for the NaCl molecule, an observation which adds to the accumulating evidence that molecules must be taken into consideration, and not ions only, in dealing with the relations between the plant and the solutes of a nutrient solution. The conclusion of earlier investigators, that chlorine must be added to the nutrient solution for the complete development of buckwheat, finds no support in the present work.

The sand cultures of this study (also in the greenhouse) were conducted on 20-kilogram portions of sand, in open boxes with paraffined inner surfaces. The insoluble salts were incorporated with the dry sand and the others were added in successive portions of solution. The total application of salts was about 0.25 per cent. of the dry weight of the sand. With mangel-wurzel, an increase of from 40 to 120 per cent. in the dry weight of roots resulted from the application of KCl in a complete fertilizer ration, but greater increase followed where NaCl was superimposed upon the usual complete ration.

For the greenhouse cultures in Miami silt loam, fifteen or twenty kilograms of air-dry soil were employed, in cypress boxes, the salts being added as in the case of the sand cultures. The total application of salts approximated from 0.06 to 0.15 per cent. of the dry weight of the soil.

The sugar beet produced 50 per cent. more dry substance (root) when chlorine was included with the usual salt ration than when the ration without chlorine was used. The glucose content of the root was increased somewhat, percentagely on the basis of dry weight, but the sucrose content was uninfluenced by this treatment. Preliminary experiments with the radish indicate that it is little affected by the chlorine supply, while the growth of the carrot is stimulated and that of the parsnip is depressed as regards content of dry matter and percentage of sugars. Similar experiments with the potato ("Triumph" and "Rural New Yorker" varieties) gave the same dry weights of tubers, whether potassium was supplied as the chloride or as the sulphate.

In the field experiments, sugar beet roots showed an increase of from 10 to 30 per cent., by weight, where NaCl was applied to the soil at the rate of from 260 to 520 pounds per acre, as compared with those of the unfertilized plot. The glucose content was increased, but that of sucrose was unaffected by this treatment.

The potato ("Triumph" variety) produced the same yield, both of total and marketable tubers, whether supplied with potassium as KCl or as K_2SO_4, in the complete fertilizer ration. The addition of NaCl without other salts depressed the yield. Another experiment with potato ("Rural New Yorker" variety) showed that the starch content and cooking qualities of the tuber were the same whether potassium was supplied as KCl or as K_2SO_4, in the complete fertilizer. Fertilization with NaCl alone gave tubers of lower starch content and poor quality. It thus appears that the depressing effect of chlorine, as reported[2] for starch content and cooking quality of potato tubers, does not obtain under all conditions of culture, and fails to make itself manifest with the climatic and soil conditions of these experiments.

The results outlined above leave the question of the influence of the chlorine ion and chlorides upon plants still in a very complicated and unsatisfactory condition. Perhaps the most valuable general conclusion that can be drawn from a review of all the work so far reported upon this subject, is that the influence here considered appears to be impossible of any general statement. It appears that the effect of chlorine upon any given plant depends upon the nature of the plant, upon the soil conditions (aside from chloride content) and upon the conditions of the surroundings generally classed as climatic. It may be that each particular case of acceleration or retardation of growth processes by chlorine presents a special problem, and that broad generalizations are not to be expected until much progress has been made toward the interpretation of environmental complexes as a whole; for the present, we are constrained to study these conditions piecemeal. It seems that the promise of progress in these very complicated problems of agricultural science lies largely in more complete experimental control of the very numerous conditions that make up the environment of the plant. It is the summed or integrated effects of all of these that is registered by our plants in growth and crop production.

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[2] For example, see: Süchting, H., "Ueber die schädigende Wirkung der Kalirohsalze auf die Kartoffel." *Landw. Versuchsst.* 61: 397-449. 1905.

A STUDY OF SALT PROPORTIONS IN A NUTRIENT SOLUTION CONTAINING CHLORIDE, AS RELATED TO THE GROWTH OF YOUNG WHEAT PLANTS

By S. F. Trelease

Chlorine has been considered an unnecessary element in the nutrition of most plants, but it seems to have produced a beneficial influence in certain cases that have been recorded. There is some practical as well as scientific interest in the question thus raised, since potassium chloride is frequently used as an agricultural fertilizer, and the influence of the chlorine thus put into the soil may not be without importance. In the experiments of which this is a preliminary report the chlorine ion was introduced into nutrient solutions that already contained all the essential elements usually absorbed by plant roots. These essential elements (N, S, P, Ca, Mg, K, and Fe) may be supplied to the young wheat plants as a nutrient solution containing the three salts $Ca(NO_3)_2$, $MgSO_4$, and KH_2PO_4, with a trace of iron as $FePO_4$. To introduce chlorine, KCl was added to the list just given, thus making a 4-salt solution. A solution made from these four salts was used by Knop and Nobbe, and Grafe [1] recommends these same salts as most generally useful. Detmer [2] employed one set of proportions of these four salts, and this solution has been designated by Tottingham [3] as Detmer's solution. In the experiments considered in this paper the same general methods were used as were

[1] Grafe, V. "Ernährungsphysiologisches Praktikum der höheren Pflanzen." Berlin, 1914.

[2] Detmer, W., "Practical plant physiology." Translated by S. A. Moor. London, 1898.

[3] Tottingham, W. E., "A quantitative chemical and physiological study of nutrient solutions for plant cultures." *Physiol Res.* 1: 133-245. 1914.

employed by Tottingham and by Shive.[4] The total concentration of the nutrient solution corresponded to an osmotic pressure of approximately 1.6 atmospheres at 25° C., and the relative proportions of the four component salts were varied in all possible ways, by increments of one-tenth of this total concentration. Eighty-four different solutions were thus included in each complete set; all of these had approximately the same total osmotic concentration, but no two had the same relative proportions of the four component salts. Six plants were grown in each culture, and the solutions were renewed every four days.

The various salt proportions proved to be very different in their ability to produce growth of the young wheat plants. As has been found by other writers, the solution giving the greatest dry yield of tops is not the one giving the greatest yield of roots, and the solution producing the highest dry weight of tops and roots together has still another set of salt proportions. The highest dry yield of tops was obtained with the following partial volume-molecular concentrations of the four main constituent salts: 0.0067M KCl, 0.0138M KH_2PO_4, 0.0047M $Ca(NO_3)_2$, and 0.0081M $MgSO_4$. A trace of iron was, of course, added, as a suspension of ferric phosphate.

This highest yield of wheat tops with the 4-salt solution containing chlorine was not higher, however, than was obtained, in these experiments, with the best salt proportions, without chlorine, of the Birner and Lucanus (Shive) 3-salt solution and of the Knop (Tottingham) 4-salt solution. If the best salt proportions are used in all three cases these three very different types of solutions give practically the same result. It therefore appears to be impossible to improve the growth of young wheat plants, as this occurs in Shive's and Tottingham's best salt proportions, by the introduction of

[4] Shive, J. W., "A three-salt nutrient solution for plants." *Amer. Jour. Bot.* 2: 157-160. 1915. *Idem*, "A study of physiological balance in nutrient media." *Physiol. Res.* 1: 327-397. 1915.

chlorine into the solution. Furthermore, the best 4-salt solution with chlorine contains the three essential salts in nearly the same proportions as those in which they occur in Shive's best 3-salt solution, which has the following composition: 0.0180M KH_2PO_4, 0.0052M $Ca(NO_3)_2$, and 0.0150M $MgSO_4$. The main difference in this respect lies in the Mg/Ca quotient; in Shive's best solution this quotient has the value 2.88, and in the best 4-salt solution with chlorine it has the value 1.72. Both are characterized by relatively high proportions of KH_2PO_4, and low proportions of $Ca(NO_3)_2$, which is rather surprising, since many nutrient solutions heretofore proposed have a relatively high concentration of $Ca(NO_3)_2$. In general, the occurrence of the morphological leaf modifications tions recognized as magnesium injury in such series as these (Tottingham, Shive) was not altered by the presence of the chlorine ion in the solution.

A marked improvement over Detmer's salt proportions was obtained in the present study. The best solution gave an increase in dry weight of tops of 27 per cent. and 20 per cent., respectively, over the yields obtained in two solutions of the present series closely resembling Detmer's in salt proportions. An even more marked improvement over the growth obtained with Detmer's exact proportions is reported by Shive, for his best 3-salt solution, which, as has been mentioned, gave practically the same yield as did the best 4-salt solution used in this study.

While it seems impossible to obtain higher top yields of these plants in the 4-salt solution containing chlorine, than in the 3-salt solution without this element, it should nevertheless be remarked that the presence of chlorine may diminish to some extent the retarding effect produced by the three salts of the essential elements when these are not in the best proportions. Thus, if we start with an unbalanced 3-salt solution, a proper addition of chlorine may sometimes accelerate the growth of the plants. The addition of a non-essential element may improve the physiological properties of a solution containing the essential elements in improper proportions.

Perhaps the main result of this study is, in general, that no matter whether we employ (1) the three salts KH_2PO_4, $Ca(NO_3)_2$, and $MgSO_4$, (2) the four salts KH_2PO_4, $Ca(NO_3)_2$, $MgSO_4$, and KNO_3, or (3) the four-salts KH_2PO_4, $Ca(NO_3)_2$, $MgSO_4$, and KCl, if we use the *best proportions* of the salts in each case we may expect to obtain about the same growth. This generalization has an important bearing on the whole problem of physiological balance in nutrient solutions and furnishes what may be important suggestions bearing on our general conceptions of conditional control and conditional optima for plant activities.

THE RELATION OF THE CONCENTRATION OF THE NUTRIENT SOLUTION TO THE GROWTH OF YOUNG WHEAT PLANTS IN WATER-CULTURES

By S. F. Trelease

In these experiments the salt proportions were the same in all the different solutions of each series, but the solutions differed from each other in total concentration. Three series of cultures, all carried out at the same time, are considered, each series including a concentration range of from 0.5 to 7.0 atmospheres. A different set of salt proportions was used in each series. Six plants were grown in each culture and the cultures were in duplicate, upon a rotating table. The experiment lasted for 32 days, from January 23 to February 24, 1917, the solutions being renewed every 4 days.

In the first series the nutrient solutions contained the 4 salts KH_2PO_4, $MgSO_4$, KCl, and $Ca(NO_3)_2$ in the following relative molecular proportions: 1.000, 0.587, 0.485, 0.341. The average dry weight of tops and the average total water loss by transpiration, for six plants, are shown in the following table, whch also shows the total concentration employed in all three series.

Concentration, *atm.*	Dry Weight, Tops, *grams.*	Transpiration, *cc.*
0.5	0.926	651
1.0	0.947	618
1.6	1.152	646
2.5	1.117	554
3.5	1.030	468
4.5	0.904	386
5.5	0.821	311
7.0	0.769	246

For this particular set of salt proportions the maximum yield of tops was obtained when the nutrient solution had a total osmotic concentration of 1.6 atm. With lower concentrations growth was considerably less, as is also true, and to a greater degree, with concentrations above the optimum. Between the concentrations 1.6 and 7.0 atm. the dry weight of tops is approximately a linear function of the concentration, the dry weight decreasing as the concentration increases. The transpiration values show the same general relation to the concentration, except that below 1.6 atm. the decrease is less clearly shown; in fact, with a concentration of 0.5 atm. the transpiration is slightly higher than with 1.6 atm.

In the second series the culture solutions were the same as those just described, except that KCl was not included. In these cultures the relations of dry weight and transpiration, to total concentration, were essentially the same as in the cultures of the first series, with KCl.

In the third series the salts used were the same as in the first, but in different relative molecular proportions, as follows: 1.000, 1.155, 7.282, 0.699. The relation between transpiration and concentration was the same as in the first series, but in this case there was a perfectly definite maximum of transpiration at 1.6 atm. For production of dry weight of tops, however, while the general relation to concentration was the same as in the first two series, the optimum concentration was 4.5 instead of 1.6 atm.

The interesting features of these results may be summarized as follows: (1) Transpiration and dry weight showed an approximately linear relation to the concentration of the medium above the optimum, these decreasing with an increase in concentration. (2) The optimum concentration for dry weight of tops was altered from 1.6 atm. to 4.5 atm. by changing the proportions of the four salts used in the first and third series. (3) With the salt proportions of the three other salts used in the first series, the omission of KCl did not alter the relation between growth and concentration.

THE EFFECT OF RENEWAL OF CULTURE SOLUTIONS ON THE GROWTH OF YOUNG WHEAT PLANTS IN WATER-CULTURES

By S. F. Trelease and E. E. Free

One of the practical problems in work with water-cultures is that of the frequency with which the culture solution must be renewed in order to obtain the best results. This note reports experiments in this connection on the growth of young wheat plants in the nutrient solution found by Shive [1] to be best for the production of dry weight of tops in wheat. The culture jars had a capacity of 250 cc. Six plants were grown in each jar and each culture was in triplicate. The volume of the culture solution was made up to normal by the addition of distilled water every 4 days or oftener. The details of the technique were the same as employed by Shive. All cultures ran 41 days, from January 6, to February 16, 1916. The results are given in the following table, in the form of dry weights of tops produced, each weight being the average of the three parallel cultures.

	Dry Weight. *grams.*
Changed daily	1.243
Changed every 3 days	1.012
Changed every week	1.020
Changed after 1 week, then every 3 days	0.995
Changed every 2 weeks	0.780
Changed after 2 weeks, then every 3 days	1.131
Changed after 2 weeks, then every week	0.969
Changed after 1 month	0.654
Not changed at all	0.621

[1] Shive, J. W., "A study of the physiological balance in nutrient media." *Physiol. Res.* **1**: 327-397. 1915.

It is apparent that the yield is better the more frequently the solution is changed. If, after an initial period, the frequency of changing is increased the yield is improved. It is important, practically, that there is small difference between the cultures changed every 3 days and those changed every week. Daily change produces substantial improvement. Allowing the solution to remain unchanged for so long as 2 weeks is markedly injurious.

The above cultures were grown on a rotating table. An additional set was grown in the same greenhouse at the same time but not on the rotating table. The results follow:

	Dry Weight. *grams.*
Continuous flow of solution through culture jar at rate of about 1 liter daily	1.678
Changed every 3 days	1.222
Not changed at all	0.666

This experiment is not strictly comparable with the one done on the rotating table, but it seems probable that continuous flow of the solution must be regarded as more beneficial even than daily change.

Parallel with the experiments on the rotating table, one set of three cultures was treated by removing the solution weekly and shaking it with bone black. The solution was then filtered and restored to the culture jars. These cultures gave an average yield of 0.780 gram, as compared with 0.621 gram for the unchanged culture not treated with bone black. Evidently the bone black treatment improved the solution slightly but did not correct in important degree the harmful effects of infrequent changing. It was noticed incidentally that the magnesium injury that is characteristic of this solution, for wheat, appeared more frequently and severely when the changing was frequent than when it was not. The color of the plants was greener in the more frequently changed solutions.