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*PLANT PHYSIOLOGY—PRESENT PROBLEMS.**

To the very year one century has elapsed since Theodore de Saussure published his remarkable investigations relating to the nutrition of plants and to the influences upon plants of certain well-known physical forces. Although preceded by the publications of Duhamel, Hales, Ingenhouss and Senebier, as well as by those in a somewhat different line, by Konrad Sprengel and others, we may look upon the work of de Saussure as a wonderful production for his time and as strikingly indicative of the status of plant physiological problems a century ago. His paper may be regarded in a sense as the original charter or constitution of plant physiology. Fortunately, it is assigned to an eminent and experienced botanical historian to recite the amendments which mark the wonderful growth of this historic instrument. There remains, therefore, the task of suggesting some directions of future growth.

No distinction need here be made between those problems which are readily seen to involve the closest work in such other sciences as physics and chemistry and those which do not show a relationship so close. There is certainly much in physiology which must be based upon physics and chemistry, but when dealing with the causes of the activities of living organisms, it is in relatively few cases that explanations may ever be offered in terms of

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physics and chemistry alone. Nor is it possible to offer such explanations without the assistance of these sciences. The progress of the work in physiology is indissolubly bound up in the development of other sciences. The benefits are, however, mutual, and as physiology acknowledges the fundamental importance of these related sciences, they in turn must acknowledge the important contributions, often of fundamental nature, which have resulted through physiological investigation.

In such a paper it would be impossible to do more than outline briefly some of the relationships of special problems which, for one reason or another, merit emphasis. In general, the problems in plant physiology have been well brought out and systematized through the monumental work recently completed by Professor Pfeffer. To him the science owes a debt of gratitude which may be acknowledged as well by one who attempts to suggest future work as by the historian. Again, due recognition should be made of those who have in recent years based upon this or any similar topic valedictory addresses before various botanical organizations—notably, those of Professors Vines, Ward, Barnes, Reynolds Green and others.

The fact that every cell or organ requires its food materials, or at least its nutrients, in liquid form, readily emphasizes the fundamental importance of those problems suggested by the relation of the plant to solutions. The mechanisms for absorption and the general and special diosmotic properties of the living cell, all of which have been studied with the most consummate skill, have yielded matchless results; yet the rewards for future research show at present no distinct limitations. It has not been possible to determine the nature of the plasmatic membrane which directly or indirectly possesses such marked powers of selection and accumulation. The conditions under which the activities of this membrane may be modified are but poorly understood; and it is, perhaps, quite beyond the present possibilities to determine the mechanism of this modification, for in that must be involved one of the most important vital activities of protoplasm. Perhaps, when much more data have been accumulated by a study of plants of diverse habitat, the conditions of this modification may be more clearly distinguished. It is known that continued endosmosis of a particular solute depends largely upon the use or transformation of this solute within, yet it is not always possible to demonstrate any change in the substance absorbed. In any event, it is necessary to ask further light upon the exosmotic resistance of the plasmatic membrane to the accumulation of turgor-producing substances, or, in other words, to a further explanation of what may be termed one way penetration. To these phenomena the processes of excretion and secretion are closely allied, whether they are ultimately, periodically, or continuously the function of certain protoplasts.

Further chemical knowledge is needed dealing with the meaning of high pressures and of the accommodation of very high pressures in the fungi. As a rule, those protoplasts seem to be resistant to such high pressures which are also resistant to cold, desiccation and other stimulation. Mayerburg, working under the instruction of Professor Pfeffer, has recently applied himself to a study of the method by means of which the organism may regulate its turgor. It is evident that one of two propositions must be assumed, and that increased turgor may be produced either (1) by the penetration of substances from without, or (2) by substances of strong osmotic action produced within the cell through the stimulative action of external agents. It was determined in this case that in general no absorption of the substances bathing the plant occurs; therefore, osmotic substances are produced within the cell and largely by increased concentration of the normal organic cell products. The extent and method of this capability for turgor regulation are highly important, as is also the general question of the relation of turgor to growth. In recent times some of the important problems in this connection have been well suggested by the work of Rysselberghe, Puriewitsch, Overton, Copeland and Livingston.

The absorptive systems of plants seem to be admirably adapted for their needs from a diosmotic point of view. Diffusion may, therefore, be sufficiently rapid to supply all demands of the absorbing cells or organs. Nevertheless, the assumption that ordinarily diffusion through the cell and plasmatic membrane is sufficiently rapid properly to provide for the translocation of metabolic products from cell to cell is certainly open to further inquiry. Present knowledge of the translocatory processes is insufficient. Plasmatic connections between cells are now known to be of common occurrence, and this fact has given further interest to the above inquiry. Brown and Escombe are of the opinion that the plasmatic connections are eminently adapted for all of those phenomena which they have found to belong, as subsequently mentioned, to multiperforate septa. They claim, further, that with slight differences of osmotic pressure the necessary concentration of gradient for increased translocation would be very simply effected.

Thus far it has been difficult to throw any light upon cell-absorption and selection in many complex natural relationships by calling in the assistance of the dissociation theory and the ionic relationships of the salts in the soil. The external relationships of nutrient salts, or the relative abundance of these in substrata supporting vegetation, constitutes a problem with which the physiologist must be concerned. It is only necessary to glance at the results of work done by various experiment stations in this country to be convinced of the great physiological importance which may be attached to such studies.

Recent results tend to emphasize the importance of considering to a greater degree the physical conditions of the soil. Some have even gone so far as to claim that practically all soils contain a sufficient quantity of plant food; and that the all-important question is the regulation of the water supply in accordance with the quality of the particular soil. This latter, however, is an error into which few physiologists have fallen. Nevertheless, precise studies upon the relation of plants to the physical characters of soils afford problems which should receive the best attention. Many of the problems are not new, and in a qualitative way, at least, the problem of the relationship of the conservation of moisture and the tilth of the soil to productiveness has been duly appreciated by the best agronomists. We must notice with regret, therefore, that botanists have not always appreciated the importance of such work. Either directly or indirectly the water factor is a chief one in regulating the activities of the living plant and must be considered from every possible point of view.

It may, perhaps, be less a problem than a routine matter to determine the relation of the rate of absorption of salts in the soil solutions to water under the varying conditions of growth and transpiration. Nevertheless, information of this nature is important.

In spite of all the recent work, the physical explanation of the ascent of water in trees is a problem which must be mentioned. The renewed investigations which have been made along this line from an objective point of view will undoubtedly contribute to its eventual solution.

It is a matter of interest that in their studies of the physics of transpiration, Brown and Escombe have found evidence to regard this process also as a matter of diffusion through multiperforate septa, rather than a matter of mass action. It is calculated that by diffusion water may pass out of the stomates to an extent as much as six times the actual amount of transpiration which has been observed in special cases.

The great number of cytological investigations which have been completed within the past ten years indicate notable advancements in a most important field; and this is particularly true with relation to the study of nuclear phenomena. Through this work light has been thrown upon many problems of cell physiology and of development: and as a result of the latter new theories of heredity have been advanced. Nevertheless, the field for investigation has been constantly broadened and many new lines of research made possible. In spite of the excellent results accomplished, there is yet great uncertainty as to the interpretations which have frequently been made. In no field of work, perhaps, is it possible for the personal factor to enter into the results more largely than in this. Again, it is unfortunately true that fixed material has been studied almost to the exclusion of all other and that even general observations relating to the conditions of growth have been omitted in many instances. Much attention has been bestowed upon the minutest details which seem to be of morphological significance in the nucleus; but often the purely physiological side has been insufficiently emphasized. It is quite possible that in different plants, the exact method of chromosome division, or the manner of nucleolar disappearance, may not be similar; and it is certainly well known that external conditions may considerably modify the details of spindle formation, and perhaps other details in nuclear and cell division. The important point in every case is to determine if the same physiological purpose may be accomplished.

It is extremely important, however, to the subject of physiology that the methods which have made possible these cytological advances shall be extended and utilized in developing a knowledge of all of the various activities of the cell. In this way, a clearer insight may be given of many abstruse metabolic processes; and certainly further light may be thrown upon the matter of protoplasmic decompositions and secretions, the production of enzymes and alkaloids, tannins and other products. Going hand in hand with observations upon fresh material, the limitations of microchemistry alone should determine the possibilities in this direction of the work.

In such cytological investigations, Fischer's work on the artificial production of effects resembling those seen in fixed protoplasm should be borne well in mind. This work is timely, and may assist in checking irrational developments by forcing a proper regard for a comparison of the effects observed in fixed tissues with those shown by the living material.

There are, moreover, but few directions in which the study of metabolism and metabolic products may not profit from cytological research. A notable instance of what there is to be done is well indicated by the work of the late Dr. Timberlake on the division of plastids and the development of the starch grain.

Photosynthesis is a topic which has received a full share of physiological investigation throughout the past century; yet the problems demanding attention are too numerous for complete enumeration. The mechanism of gaseous exchange in leaves has repeatedly been experimentally proved to be the function of the stomates. After critical physical experimentation, Brown and Escombe have recently reported that the results of their studies of diffusivity through multiperforate septa are closely applicable to the herbaceous leaf with its stomates and substomatic chambers. Assuming their calculations to be correct, and granting that all of the incoming carbon dioxide is removed, it is estimated that with the stomates open the maximum observed rate of fixation of CO_2 in *Helianthus* (which is .134 c.c. per square centimeter per hour) would be only 5.2 to 6.3 per cent. of the theoretical capacity of the diffusion apparatus of the plant. In other words, with a gradient between the outer and inner air of only 5 to 6.5 per cent. pressure, the maximum observed fixation is well accounted for.

Important problems in the general study of photosynthesis may well begin with that of a better knowledge of the structure of the chloroplasts and the constitution of chlorophyll. Neither of these, however, is absolutely essential to further physiological observations of a fruitful kind. One of the questions long ago raised is still pertinent: what is the connection between chlorophyll and the plastid in which it is embedded? An answer to this question may perhaps afford in time an answer to the general inquiry as to the location of the true photosynthetic property. If chlorophyll is always the same chemically, it is perhaps probable that the first product of photosynthesis may always be the same, although this is not necessarily true. In any case, the chief problems hinge upon the method of decomposition of carbon dioxide and water and the synthesis of the first organic product. Neither the hypothesis of Bayer, Erlenmeyer, Crato, Bach, Putz, nor any other, has, to any considerable degree, been made capable of experimental proof, although that of Bayer has been most generally accepted. Each of these assumptions offers some suggestions for future work. Perhaps it may as well be said that they, to a certain extent, bias future research. Nevertheless, even when the chemical reactions in this synthesis become known it may yet remain problematical how the energy of sunlight, that is, of those rays most absorbed, with wave lengths of 660 to 680 μ is made available, or whether it is this energy directly or indirectly which is concerned in the decomposition. It has been well assumed that the light waves may not be immediately serviceable, but only after transformation into other forms of energy. Further, it is not known to what extent this energy is operative in subsequent transformations. The conditions under which photosynthesis occurs have been worked out with a fair degree of accuracy, the status of these problems having been well set forth by Ewart and others. It is known that when deleterious agents act at a given concentration merely to inhibit the assimilatory function (the cell not being permanently injured) there is no evident change in the chlorophyll, from which it has been inferred that the assimilatory arrest has its origin in the plasmatic stroma. In all cases photosynthesis can not long proceed except under conditions of health of the protoplasts. Nevertheless, the effects of deleterious agents have not always been studied by very delicate tests, and further attention might be bestowed upon this matter by the use of the photobacterial method, or other delicate methods, recently suggested, for it is of considerable interest to determine the relation of the photosynthetic activity to such agents as compared with other activities.

Recently the effects of temperature on photosynthesis have been carefully worked out by Miss Matthaei. She states that the curve of synthetic activity rises with increased temperature, that it is in general convex to the temperature abscissæ and somewhat similar to the curve of relation between temperature and respiration. There is a certain maximum for each temperature. It has also been ascertained that there is a certain economic light intensity beyond which there is no increased photosynthetic activity, and doubtless only injury. This is of special interest in connection with some recent work by Weis. Recognizing the fact that plants are of very different types with relation to their light requirements, he has sought to get an expression of their assimilatory energy. He finds that *Œnothera biennis*, a well-marked sun plant, fixes under favorable conditions of temperature, and in direct sunlight, about three times as much CO_2 as in diffuse light (light of one sixtieth to one ninetieth this intensity). On the other hand, *Polypodium vulgare* assimilates in diffuse light somewhat more energetically than in direct, while *Marchantia polymorpha* occupies a position intermediate. This will be welcomed by physiologists as a field for wholesome ecological study, for an extension of such investigations to an analysis of plant associations with relation to the light factor may yield profitable results.

In 1901, Freidel made the surprising report of success in securing outside of the living plant a gas exchange similar to the photosynthetic action of chlorophyll. He was later unable to confirm his previous conclusions, nor were the subsequent results of Macchiata and Herzog concordant. Recently, Molisch has employed upon this problem the photobacterial method of Beijernick. He finds that the expressed sap of certain plants may for a time maintain photosynthetic activity, but since usually the sap loses this power when filtered through a Chamberlain filter, it is believed to be due to the presence of living plasmatic particles. Nevertheless, it is claimed that an exchange of gases characteristic of photosynthesis may proceed in a solution of the leaves of *Lamium album* dried crisp at 35° C. and then 'rubbed up' in water and filtered. The observation demands much further study, for it must be remembered that the test is by means of the liberation of oxygen, and Ewart has shown that some bacterial pigments may have the power of evolving oxygen. In the last-named case the gas evolved appears to be, as he states, 'occluded oxygen absorbed from the air by the pigment substance excreted by the bacteria.'

It can not be stated at the present time, however, as was assumed from Freidel's first work, that there is any enzyme concerned in the photosynthetic activity.

To a large extent the problems involved in a study of the assimilation of nitrogen are limited by the very imperfect chemical knowledge of nitrogenous products, and may not, therefore, be very clearly defined. Practically, the whole question of the formation of amides, proteids or other nitrogenous compounds in plants remains in obscurity. It is known that these are formed in both non-chlorophyllous and chlorophyllous plants and that while in the former it may proceed in darkness, in the latter, light is apparently required for the most vigorous synthesis. In the latter case it may seem to suggest that there is need of the active cooperation of the chlorophyll apparatus; but here again the influence may be only indirect, since the roots, as well as the aerial parts of chlorophyll-bearing plants, are said to possess, to a certain extent, this synthetic power. Interesting suggestions have been recently made by Godlewski. The part played in photosynthesis by nucleus and cytoplasm, respectively, is unknown and may be important.

Some careful studies have been made dealing with the sources of organic nitrogen in certain of the molds, but owing to the very great variety of fungous habitats, further studies may indicate unusual specialization—perhaps even to such extent as is now known to be true with the bacteria.

Saida has confirmed and extended the early work of Puriewitsch and others, clearly demonstrating that under certain conditions some of the fungi are able to utilize to a variable degree the atmospheric nitrogen. It would be interesting in this connection to give further attention to various groups of saprophytic fungi. In a public lecture Moore has recently made known the results of remarkably definite experiments showing that the organism (or organisms) of leguminous tubercles assimilates free nitrogen apart from its hosts, and that, therefore, the symbiotic association gives the parasite no nitrogen-assimilating advantages. Moreover, this nitrogen assimilating capacity increases under conditions of artificial culture, and this increased power is heritable to a considerable extent at least. This is an important fact and deserves further attention.

Recently Reinke, Benecke and others have focused our attention upon the nitrogen supply in sea water. They find that the organisms *Clostridium Pasteurianum* and *Azotobakter chroococcum* are found in the ooze of sea bottoms; and the suggestion is made that the external but, nevertheless, close association of these micro-organisms with certain marine algæ may explain the power of these algæ to grow so vigorously in situations in which they are found. The nitrogen supply is probably one of the most important problems relating to the marine algæ. It is to be borne in mind, however, that the question of fundamental interest is always that of how these micro-organisms are able to utilize the nitrogen which is absorbed in gaseous state. No such power is known among phanerogams. It has not yet been demonstrated to be possible with the lower algæ, and certainly none of the interesting results so far obtained indicates that it is a very fundamental character of fungi and bacteria. In this connection, perhaps, it may also be stated that nothing whatever is known concerning the method by which carbon dioxide is chemo-synthetically utilized by the nitrite and nitrate bacteria.

There are many interesting problems afforded by the general phenomena of metabolism, with relation both to those products which may be immediately utilized and to those which may be stored up for future use. It is well known that during active growth special foods may be taken out of circulation and stored up. The stimulus to such storage is not easily determined. In many instances it is apparently the protoplasm which is decomposed in order that these storage products may be formed; therefore, so far as possible a study of all protoplasmic decomposition phenomena is especially necessary. The deposition of the cell plate and the storage of reserve cellulose are especially interesting. It will be extremely difficult to follow the succession of changes involved, yet some information will undoubtedly be gained.

The migration of compounds, particularly of those containing nitrogen, magnesium and potash, to growing vegetative parts and to the developing seed is most remarkable. The production, whether regulatory or otherwise, of the numerous by-products in the cell, such as tannin, pigments, organic acids, etc., is also of peculiar interest. The functions of some of these compounds must be most important, and should receive further attention. Tannin, particularly, is doubtless of much economic importance in the regulation of turgor and in augmenting the resistance to injurious external agents. Astruc has recently shown that acids are found in the younger parts of non-succulents and mostly in the region of maximum turgescence; and that there is a progressive decrease of such compounds in the older organs. In succulents, moreover, very slight changes in the external conditions materially affect the acid content.

It can not be expected that all of the information desirable with relation to the composition and action of hydrolyzing and oxidizing enzymes will be obtainable until more is known of the proteids, to which group the ferments seem to belong, or with which they are at least closely related. Whether these enzymes are concerned with the metamorphoses involved in rendering soluble or transforming pectin, proteids, glucosides, starches, cellulose, fats, or sugars, their physiological activities are in the highest degree remarkable, and worthy of the closest study. The problems which relate to their occurrence, composition, production and action require, however, the combined attention of physiologists and organic and physical chemists. In recent times, through the work of Brown and Morris, Fischer, Green, Prescott, Vines, Loew, Beijerinck, Newcombe, Woods, and many others, these compounds have received renewed attention. It may be that at present too many obscure phenomena are passed over with the superficial explanation that they are the result of enzyme action, and, therefore, require no further consideration. It is known that the ferments are largely concerned with the regulatory production of modification of numerous metabolic products. The activity of each enzyme is circumscribed, yet the power to do work borders upon the miraculous. It is asserted that invertin may invert 100,000 times its volume of cane sugar, and pepsin may transform 800,000 times its volume of proteids. The chemist is especially concerned with the composition and occurrence of these, but the physiologist is interested not alone in the occurrence and specific action of the enzymes, but also with the effects upon the general metabolism of the individual plant, with the methods and conditions regulating the secretion of these products, and with their vitalities or limiting external conditions. Ferments may be concerned with external cellular digestion, that is, with the solution and absorption of foodstuffs from without, thus necessitating exosmosis, or with intracellular modifications, preparatory to the direct use of the substances modified in metabolism or in translocation. Again, the ferments may be present only at a certain definite period in the life of a cell, produced, undoubtedly, by special requirements and special stimulation.

When isolated, or at least when outside of the cell, many enzymes are most active at temperatures far above those which may be maintained within the living cell. An explanation of this fact is difficult. Comparative studies of their reactions to light, heat, toxic agents and other stimuli should be made. In the penetration of parasites, cellulose-dissolving ferments are important, but further information is needed before it can be said that the presence or absence of such enzymes to any great extent affects the resistance of certain varieties and species to fungous attacks. It has been stated that the resistance of plants to fungus attacks is due largely to the presence of certain enzymes or toxalbumens present in the cells of the host; and by others it has been suggested that susceptibility is frequently a special property due to the presence of certain oxidases, which are regulated by external conditions.

It has been shown that the mosaic disease of tobacco and other similar diseases are accompanied by certain oxidase ferments which appear to prevent the digestion of reserve food. The ferment is developed in the growing parts of the plant, it may be transferred from plant to plant, and on the decay of the diseased organism, it is supposed to be set free in the soil. It is believed that it is then capable of diosmosis and infection of the young seedling. While it can not be shown at present that the enzyme is beyond all question the direct cause of the disease, this field of work is certainly one which might yield most interesting results. In this connection it may be stated that peach yellows and several other important contagious diseases are believed to be of somewhat similar nature. It is also claimed that the keeping qualities of fruits may bear a certain relation to the amount of enzymes present at the time of storage; and, therefore, a knowledge of the time and conditions of the production of such enzymes would have great economic value.

In general, Czapek found no enzymes to occur in the excretions from the roots of higher plants, and it is now generally believed that the roots of one plant may develop no excretions injurious to neighboring plants, and, therefore, there may be no biological relation between the roots of non-parasitic plants associated in the given plant society. It must be said, however, that the information at hand may not be taken as final. There are yet some peculiar facts with relation to the rotation of crops which may not be readily explained on the grounds of the exhaustion of plant nutrients or of the physical condition of the soil.

The fermentation of tobacco and tea, or hay and manure, involves enzyme actions which in recent times have received some attention, although the problems which are of most physiological importance require solution. The general belief is that in all cases of enzyme action these compounds do not form a part of the substance upon which their action is exerted, but they act as a key in each particular case, unlocking, or rendering labile, a certain organic compound, which is then subject to rearrangement and transformation. This is all, however, too speculative for profitable consideration, although such speculation may have no evil influence if it is not permitted to encourage the reference of all unusual phenomena to an unusually obscure and difficult process.

The early perfection of water culture methods permitted a careful study of the mineral nutrient requirements in the higher plants. Pure culture methods have afforded a more accurate means of studying the needs of fungi and certain algæ. As usually installed, water cultures of the higher plants contain bacteria, so that they afford only a practical test of the requirements. The problem demands some confirmatory tests, at least, under pure culture conditions, particularly when organic compounds are employed. It is possible to grow, in a limited way, higher plants under pure culture conditions.

With the fungi, exact studies may be made upon the influence of the different nutrients on the general form and upon the production of conidia, etc. It has been found, for instance, that, in the absence of potassium, *Sterigmatocytis niger* may produce no conidia or very curious modifications of the conidiophores. By far the most interesting problems with relation to the mineral nutrients are those which have to do with the rôles of these elements in metabolism. The effect of the lack of one or another element is made manifest by some general macroscopic change, and sooner or later, by disturbing pathological changes and subsequent death. It is reported, for example, that the absence of iron prevents the development of a healthy green color, and a scarcity of potassium is made evident, especially, in reduced photosynthesis.

We are yet merely at the threshold of these problems. A cytological and microchemical study of numerous plants in various conditions of culture is needed. Loew has instituted some good work in this direction. He attempted a careful microscopic study of *Spirogyra* under the conditions indicated. Although well rewarded, he has not followed up the result. The problem is, nevertheless, again under serious investigation, and when much time and thought shall have been devoted to it, with the utilization of the best cytological methods available, important results may be anticipated. The possibilities of the future are particularly dependent upon this, that investigation must be made of all macroscopic changes as well as of all demonstrable microscopic changes.

The interrelations of parasites and hosts, or of symbionts, are of such great physiological interest that some of the most significant problems may not justly be omitted in this connection. It has long been assumed that the conditions of nutrition of a host plant determine to a considerable extent its immunity to parasitic attack. Ward was unable to detect in the bromes any modification of resistance due to either high cultivation or to lack of sufficient mineral nutrients.

The results which have been attained with the Uredinaceæ have established the fact of the existence of 'biologic forms.' This opened a new problem in the study of the Uredinaceæ and it was later ascertained that similar host-restricted forms are present in other groups of the fungi, especially in the powdery mildew *Erysiphe graminis*. Salmon has found bridging host species by means of which the parasite may pass from one species or host to another; for example, the form of *E. graminis* on *Bromus racemosus* is incapable of affecting *B. commutatus*, but does not fail to affect *B. hordeaceus;* and the spores produced on the latter will then affect the previously immune *B. commutatus*. From infection studies it is further found that there are biologic forms among the grass hosts as well. Salmon reports that this restriction of the parasite to certain hosts may be broken down if the vitality of the leaf has been lowered by traumatic means. In this case penetration would result either in the injured area or certainly within the sphere of the traumatic influence. Spores produced by such infections proved capable of infecting uninjured leaves. The application of these results is certainly far-reaching; yet they must be extended and confirmed before a conservative explanation may be advanced. It is undoubtedly more or less in line with the well-known capacity of such fungi as *Botrytis, Nectria* and certain Basidiomycetes to become parasitic under special conditions. Two leading inquiries may be suggested: (1) What constitutes immunity or resistance in the host? (2) What constitutes virulence or attenuation in the parasite?

As the result of practical experiments in cross inoculation, on the one hand, and of close morphological study, on the other, some investigators have long claimed that there are racial or specific differences between the organisms producing the tubercles on the roots of certain leguminous plants. From the results obtained by Moore (in the U. S. Department of Agriculture) which have been reported, but not yet published, I am permitted to recite a further interesting fact of accommodation. When an organism isolated from one host species is grown for a time artificially, under special conditions of nutrition, its host limitations are in great measure broken down, and it may produce tubercles on a variety of leguminous plants. It is likewise conceivable that in the case of certain yeasts the temperatures at which spores are formed, and the specific fermentative activities, may be changed by special conditions of cultivation.

In view, therefore, of the work already accomplished it is certainly evident that the propriety of basing what are termed species upon certain physiological characters has distinct limitations. I do not intend to bring into this paper a discussion of the inadequacy of the present nomenclature system from a physiological point of view. It may be said, however, that it is scarcely possible for the systematist to consider all physiological characteristics, or to appreciate the confused ideals of the physiologist.

Stimulated by the marked advancement which has been made in physical chemistry, especially in the knowledge of electrolytic dissociation, the past few years have added much to our fund of information with relation to the toxic action upon plants of solutions of both acids and salts, as well also as of certain non-electrolytes. The work of Kahlenberg and True, Heald, Krönig and Paul, Clark and others has contributed enough data for an appreciation of the limitations of toxic action. Nevertheless, no broad generalizations are as yet possible. Indeed, it is not generalizations which are wanted, but further experimental data bearing upon the relation to the toxicity of the ions and molecules and their respective interactions.

Studies may well be made dealing with the relation of nutrition to toxic agents, the effects of temperature and other conditions upon such action, and the accommodation of organisms to increasing strengths of deleterious agents. Naegeli's work on the oligo-dynamic action of copper is beginning to be appreciated and in one way or another the results have in recent times been repeatedly confirmed. In most cases, however, no allowance has been made for the action of the nutrient salts which may be present in the culture fluid and which may affect in a very dissimilar way two different electrolytes. In this connection it is only necessary to call attention to the toxic action of certain compounds of mercury, in which increased toxicity, due to the presence of small amounts of some other salt of the same acid as the mercury salt used, is indeed quite remarkable. Within the past few months an unusually interesting paper has appeared in which Kanda reports the action of certain toxic agents upon plants grown in pots as compared with those plants grown in water cultures. His important conclusions are as follows: (1) A strongly dilute copper sulphate solution, even 0.000,000,249 per cent., is injurious to seedlings of the common garden pea in water cultures; and neither a solution ten times nor one a hundred times more dilute produced any stimulative effect. (2) In pot experiments with soil, the same seedlings are uninjured when watered twice a week during a period of from five to eight weeks with a solution of .249 per cent.; in other words, even after from five to seven grams of copper sulphate were present in each pot. No explanation is offered of this remarkable diversity of action, but within the past few months another paper has appeared which may throw light upon the results given. True has ascertained that finely divided paraffin, quartz sand, filter paper or other insoluble substances are all found to reduce the toxic action of the deleterious salt. It is explained on the assumption of an absorption of the toxic molecules by the surface of the insoluble particles. Increasing the number of grains of sand, for instance, in any toxic solution produced the same effect as increasing the dilution. From the results of these two papers it would seem, therefore, that we have two entirely different sets of conditions to deal with when any test of such action is made in water cultures, on the one hand, and in soils, on the other. If Kanda's results are confirmed, an extensive series of tests with both fungi and higher plants should be made in order to determine some relation which may give a working basis for further comparisons. In fact, much of the work thus far done will have to be reexamined in the light of these results, for if any precipitate or other solid particles have been present in the solutions, an error will enter into the calculations. The question will also arise if the surface extent of the vessel used in the culture is of any consequence. The practical bearing of these results in the treatment of soils is a matter which may prove of unusual economic interest.

Loew observed that marked injury results when such a plant as *Spirogyra* is placed in a solution of a magnesium salt, or in a solution in which magnesium is in excess. From all of the results obtained Loew has inferred that there is present in all plants requiring calcium an essential calcium protein compound. When magnesium must, owing to the predominance of this element, be substituted for calcium in this proteid compound there results a lessening of the capacity for imbibition, attended by unfavorable consequences. It has been further ascertained by the work of May, Kearney and Cameron, Kusano, Aso and others, that there is for each plant a certain more or less definite relation between calcium and magnesium. Nevertheless, further experimental proof is needed before this brilliant hypothesis may be acceptable in its entirety. It may here be noted that in a paper read by the writer before the Society for Plant Morphology and Physiology it is indicated that magnesium compounds exert upon the marine algæ the least injurious action of all nutrient bases. On the other hand, it has not been demonstrated that the marine algæ require calcium.

The general phenomenon of chemotaxy, or chemotropism, demands searching investigation in view of the recent work of Jennings on flagellates, that of Newcombe on root responses, and other studies on the fungi. There is much to be done in determining the effects of heat and cold upon special processes, in a study of the relations of temperatures to other conditions of the environment, and in showing the limitations of accommodation phenomena. In the latter study, moreover, the effects of accommodation upon the general constitution of the organism should be followed. Stimulation at high or low temperatures merely expresses an intensified or modified irritability. It may be observed in this place that death at the supramaximal or subminimal may be due to changes of a very definite nature; but as Vines has indicated, this means very little. To say that death at the supramaximal is due to the coagulation of an albuminoid as suggested by Kuehne is insufficient. For the immediate effect upon the protoplasm of this high temperature must also be of consequence. The external conditions of temperature of the effects of a modification of conditions are more or less readily determinable; but it has not been possible to follow the internal changes which result. It may be noted that the freezing point of a plant is lower than that of the expressed sap; yet of course the freezing point is not necessarily a valuable indicator of injury. The effects of temperature upon reproduction will be treated of later.

The symbiotic relationship of fungus and root to *Mycorhiza* offers a fine opportunity for careful investigation. The studies which have already been made serve only to put the reader in a state of hopeless confusion.

The universal phenomenon of irritability as manifested by trophic phenomena has been a fruitful field of investigation. The general methods of irritable response have been determined; and the best work of such investigators as Haberlandt, Noll, Czapek, Newcombe, MacDougal and others has more recently been directed to the deeper problems relating to the internal mechanism of response and to the exact methods of transmission of the stimulus, as well as to the immediate changes in the cells affected.

A word may be said concerning the regeneration phenomena which are strikingly characteristic of the lower groups of plants, but which in the higher plants do not seem to be well emphasized, and are certainly less understood. The regeneration of the root tip has been best studied. In none of the higher plants has it been possible from a single isolated active non-sexual cell, or a small group of cells, to regenerate the plant.

Although a study of the physiology of reproduction may be said to have had its origin in the early observations of Camerarius, all early studies represented largely only the ecological aspect of the subject. It is only in very recent years that rapid strides have been made in the general physiology of reproduction. The effect of conditions upon the production of antheridial or archegonial thalli or of pistillate or staminate flowers among diœcious and polygamous plants has received very slight attention. During the present year Laurent has published the results of experimentation during a period of seven years with the effects of fertilizers, or plant nutrients, upon spinach, hemp and *Mercurialias annua*. It will be seen that according to his results an excess of nitrogen or calcium has a tendency to produce staminate flowers in the spinach, while potassium or phosphorus tends to increase the production of pistillate flowers. The seed produced on the pistillate flowers of these plants gave a preponderance of female plants; but from these plants, in turn, the seed yielded a larger number of staminate plants. So far as I have been able to learn, it has never been determined if in a case of diœcious perennial plants it is possible by a change of conditions to induce a temporary or permanent change from pistillate to staminate flowers, or *vice versa*. In the same way, the influence of grafting or budding a scion of one upon the other has not been made out, although it is assumed that the flower will be characteristic of the scion.

It is with reference to the effects of external conditions upon the production of sexual and asexual fruiting organs that unusual progress has been made. In this direction a field of great magnitude has been opened by the work of Klebs, and it is evidently being pursued along all possible lines. As yet this work has been extended only to a few green algæ (as, for example, *Hydrodictyon* and *Vaucheria*); several fungi (*Sporodinia grandis* and *Saprolegnia mixta* especially); certain yeasts and bacteria, and finally, to several species of phanerogams. While with the algæ the light relation is of prevailing importance, with the fungi it is more particularly a matter of nutrition or transpiration. As a rule, with the latter Klebs finds the stimulus to reproduction in the failure of the food supply in the immediate vicinity of growth. That is, beginning with a well nourished mycelium a diminution of food supply, other conditions being constant, usually compels reproduction. A change in the specific chemical content may be effective, and in other cases there are other concurrent stimuli. In the study of phanerogams it would seem that the problem is one which is, as a rule, far more complex. It has, however, been found possible with a few species to produce at will continuous vegetative growth or continuous flowering, to induce fruiting in a well nourished vegetative shoot, and to incite vegetative growth in a flowering axis. It is probable that all shades of difference will be found in the capability of plants to have these processes distinguished by releasing stimuli; and it remains for the future to determine to what extent this is possible.

The general law which seems to be warranted is, that conditions most favorable for growth do not favor reproduction. The problem then is to determine for every organism what are these conditions under which, on the one side, growth, and on the other, reproduction, may occur. Whether, under any circumstances the complete cycle of development may be run without any change in conditions apparently awaits proof.

In grafting it would seem that seldom, if ever, do any characters of the stock pass into those of the scion except such characters as may be due to the presence of diffusible metabolic products, or products capable of self-propagation upon requisite stimulation. In this manner it has been shown that albinism may be transmitted from stock to scion. Again, Strasburger has indicated that atropin is accumulated in the potato when on a potato stock there is grafted a scion of *Datura stramonium*. It has been found that hardiness in the stock may affect the scion to a marked degree, but here the real problem is to determine what constitutes hardiness.

Fusion possibilities in vegetative cells are more or less common in all groups of plants. In basidiomycetes parallel filaments fuse under many conditions of development, and a pseudoparenchymatous tissue may result. In grafting, the layers which fuse may represent different species or even different genera. Little is known concerning the factors influencing such fusions. Allusion may also be made to the fact that plasmodia of the same species of myxomycetes (at least when produced in nearly similar conditions) fuse with one another. It should be accurately determined if this is an inherent property of the same race or species only, and if this fusion tendency may be weakened or dissipated by diversity of conditions under which the plants may be grown. The solution of such problems with simple and rapidly culturable organisms may even throw some light upon the more complex problems of self sterility and prepotence (in the sense in which these terms are used horticulturally) in higher plants—phenomena which may not be explained with present information. It has been found that tomato and tobacco fruits are sometimes formed without pollination; and the same is true of other plants. In certain cucurbits the act of pollination seems to afford a stimulus for the development of the fruit, even the dead pollen serving to call forth this response. Under such circumstances it may well be that other chemical stimuli may produce the same effect. On the whole, there are no more interesting problems in physiology than those relating to pollination, the penetration of the pollen tube, and conditions of fertilization. Many phases of these problems have thus far been studied by gardeners and horticulturists alone.

In this connection may be mentioned another fusion phenomenon of physiological interest—that of double fertilization in the angiosperms. This fusion of the second sperm nucleus with the endosperm nucleus (itself a compound of two nuclei of the gametic groups) or with one of the polar nuclei, may have a special significance, or it may be merely the expression of the fusion tendency which has not been lost, although the function of the endosperm nucleus may have undergone specialization. In the case of the pine, it will be remembered that the second sperm nucleus frequently undergoes division in the cytoplasm of the egg. What is meant by the fusion of the gametes? This is always a fundamental problem. It may be strictly a matter of the fusion of characters, or it may further be a stimulus to embryonic growth. It is a remarkable fact, however, that this stimulus to embryonic growth does not merely involve the embryo itself. The limitations of the correlations which seem to exist between the mere process of fertilization and incitation to growth in the extra-carpellary structures are extremely complex. On the other hand, the process of fusion is often immediately followed by the resting period.

It would be extremely well if further attention could be directed to the matter of parthenogenesis in the higher plants. Except in the case of Nathanson's studies upon Marsilia, little has been done to indicate the conditions which may induce or which may tend to induce this process. In recent years, artificial fertilization, or stimulus to a certain growth of the egg in the lower animals, has been effected by chemical agents, by changes in the density of the solution, and by other means. This work has demanded world-wide attention from animal physiologists. It has been too much neglected from a botanical point of view, although the difficulties involved in similar studies with plants would be, for the most part, immeasurably greater. Yet it is certainly possible to prosecute such studies along the lines indicated.

Except in the case of *Sporodinia grandis*, and perhaps one or two other species of Mucoraceæ, mycologists have experienced great difficulty in securing the zygosporic stage of these fungi. The recent paper by Blakeslee, announcing the conditions governing zygosporic formation in this family, seems to open a field for investigation wholly novel and suggestive. The substance of his results is that this family may be divided into two principal categories, designated, respectively, as homothallic and hetereothallic, these terms corresponding to monoecious and dioecious forms among higher plants. *Sporodinia grandis* belongs to the homothallic type, both gametes in every union developing from the same thallus. *Rhizopus nigricans* belongs to the second and larger class, the hetereothallic type, in which the two gametes are invariably the product of two mycelia, which mycelia are sometimes of diverse vigor. When in culture, the two strains, as they are termed, grow together, zygospores are abundantly produced along the lines of contact. These are the striking results of this important paper; but other related physiological facts have been observed, and only further investigation can tell whether this is a special case of gametic union in the fungi, or whether similar phenomena may be found to be characteristic of other groups where there is gametic union.

The discovery of Mendel's hybridization studies and the independent confirmatory evidence furnished by de Vries, Correns and others all indicate the necessity of differentiating unit characters and of following separately the inheritance of each unit character. The idea which it involves of the purity of the gametes with respect to unit characters, the segregation of unit characters in the formation of the gametes, is one of fundamental importance. Such work has given a marvelous impetus to studies in inheritance. Numerous investigators have followed up this work, but it will be many years, perhaps, before a test of the Mendelian laws can be carefully made with any great number of plants and animals. The exceptional instances already reported of the appearance of mosaic characters and the dissimilarity in the product of reciprocal crosses themselves indicate further fields for experimental research. Only a word need be said bearing upon the phylogenetic side of physiological work, since phylogeny, as well as pathology or ecology, constitutes a separate section of biological science. The admirable work accomplished by de Vries, serving beyond all question to demonstrate experimentally the origin of species by leaps or mutations, necessitates laying further stress upon discontinuous variation as a factor in the origination of existing species of plants. It is to be doubted, however, that most botanists will at present concur in such an opinion as that the evidence advanced is sufficient to disregard or disparage the part which is played by continuous variation in the origination of species. Continuous variation must be manifest by relatively slight variations; and it would be unfair to expect at this time the experimental proof of its efficiency. It may even be assumed that there is a complete series between continuous variations and discontinuous variations, as well, perhaps, as between the possibilities of inheriting immediately or ultimately such variations. Many of the problems in plant physiology are distinctly practical problems. The task of the physiologist is primarily to study the activities of plants irrespective of practical bearing. To have the greatest possible breadth and force, however, the cultivated plant may not be neglected in any of its artificial environmental conditions. It is unfortunate that as yet physiological botany has not been made fundamental to agronomy, horticulture, forestry and other sciences, arts or commercial pursuits. Physiology can not be limited by any practical problems, nor can any sacrifices be made, but a sympathy with commercial endeavor will invigorate the work, will afford equipment and will contribute towards the common good.

In conclusion, it may be said that present-day physiology, even more than any other section of biological science, is fundamental. Many phases of pathology, ecology, phylogeny and experimental morphology, especially, may not be clearly differentiated as sections. Broadly conceived, plant physiology concerns itself:

1. With the relationships of existing organisms, ontogenetically and phylogenetically. Phylogeny would necessarily claim much of this general field, as would also morphology, ecology and other subdivisions.

2. With the functions or activities of organs, tissues and cells, and the interactions and interrelations of these one with another and with external forces. It is here that morphology touches physiology

most closely and here experimental morphology must have its basis.

3. With the incorporation and excretion of matter, metabolism and growth, the sources and uses of energy, irritability, and the minute constitution of living matter. In this last are included many of the most fundamental problems, not necessarily problems involving the question 'What is life?' but problems concerned with the resolution of those factors and an intimate knowledge of those materials which make life possible.

BENJAMIN M. DUGGAR.

SCIENTIFIC BOOKS.

THE BAHAMA ISLANDS.*

This handsome volume on the Bahama Islands is of merit in two regards. It is an appropriate expression of the energetic initiative of its editor in developing an interest in geography in Baltimore, and it is a serious scientific study of a peculiar group of islands.

Professor Shattuck offered a course of lectures on physical geography to the teachers of Baltimore several years ago. The course proved attractive and was well attended; it was followed by an association of the teachers for more lectures and for field excursions under Shattuck's guidance. This association was soon succeeded by the organization of the Geographical Society of Baltimore under the presidency of D. C. Gilman and the direction of a distinguished board of trustees. The membership in the society rose to something like 1,500 in its first year of existence. Its objects were to place before the public of Baltimore an annual course of lectures dealing with geographical subjects, to foster geographical research, and from time to time to publish monographs of geographical investigations. All these objects have now been realized; hence although the activity of the society has been sadly interfered with during the past year by the disastrous conflagration of 1904, the secretary, as director and editor of the Bahama expedition, has had so notable a success in bringing out a monographic volume on the first investigation undertaken by the society that we confidently expect a revival to full activity in due time, and a vigorous continuation of the work thus begun.

Shattuck having made a preliminary visit to the Bahamas in 1902, the expedition of over twenty members left Baltimore June 1, 1903, in the *Van Name,* a hundred-ton schooner, provisioned for a two-months' cruise, and with an equipment to which the governmental bureaus at Washington and the Johns Hopkins University had contributed. The results of the expedition are now set forth in sixteen chapters by nearly as many authors. Shattuck and Miller describe the geology and physiography of the islands; Dall discusses the fossils and the non-marine mollusks; Fassig reports on magnetic and climatic observations, and Shidy on tides. The soils are elaborately classified by Mooney; Coker describes the vegetation, and Coffin tells of the mosquitoes. The fishes, birds, reptiles and mammals are reported on by Bean, Stejneger, Riley and Miller; the sanitary conditions by Penrose. The longest chapter is a history of the islands by Wright, and the volume closes with some general geographical considerations by Shattuck. The illustrations are numerous and good.

Earlier observers have shown that the Bahamas consist of 29 islands, some of which are mere skeletons or strips of land, with numerous small keys and rocks, in all some three thousand in number, rising from a shallow submarine platform or plateau, which in turn stands up rather abruptly from the deep ocean floor. The material of the platform as far as known and of all the islands is altogether calcareous, of shell and coral origin, worked over by waves and winds. On the islands the rock is weathered into a ragged and pitted surface; its texture is so weak that it is sawed or chopped into blocks for house building. The area of the islands is but a fraction of that of the platform, partly be-

* The Geographical Society of Baltimore. The Bahama Islands. Edited by George Burbank Shattuck, Ph.D., associate professor of physiographic geology in the Johns Hopkins University. New York, Macmillan. 1905. 630 pages, 93 plates, 7 figures.