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SOME NEW ASPECTS OF PLANT NUTRITION

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FOR many years I have been keenly interested in the biochemistry of plant life. My interest in this field was first aroused when I first learned of the antithetical but complementary relationships of plant and animal life as shown by the so-called "cycles" of life, such as the "carbon cycle," the "nitrogen cycle," etc., in which plants take from and restore to the atmosphere or soil the elements which are given to and withdrawn from these same ultimate sources of supply by the processes of animal life. This led to a further interest in the biochemical processes and exchanges of energy in syntheses by plants and in metabolism by animals. Soon it became apparent to me that while these processes are generally antithetical in direction and final results, the route along which they travel and the conditions which determine their velocities are strikingly similar.

For example, the pigments which are associated with the rate, and in a sense the regulators of, energy changes in plant and animal growth, namely, haemoglobin and chlorophyl, respectively, were shown to be strikingly similar in chemical constitution, being made up of the same pyrrol units linked together in the same general relationships, the only essential difference being in the metallic element through which the linkage occurs, namely, iron in haemoglobin and magnesium in chlorophyl. Moreover, within the past two or three years, it has been shown, as will be discussed later in this paper, that the element copper has apparently the same relation to the production of chlorophyl in chlorotic plants that it has to the regeneration of haemoglobin in anemic animals.

Again, enzymes, or organic catalysts, once they were discovered and the nature and method of their action studied, showed remarkable similarities in the plant and the animal biochemical processes which they initiate or regulate. In fact, the reversibility of the reaction which is accelerated by a particular enzyme is often illustrated in antithetical processes of plant and animal life.

As I became interested in these matters and began to study possibilities of research in the field of the chemistry of plant life, I found that the term "biochemistry," although etymologically embracing the chemistry of all life processes, was generally used only in connection with animal investigations, and its branch, known as "physiological chemistry," was used almost exclusively as referring to the chemistry of animal life processes, especially those of human physiology. In fact, nearly if not all of the departments and laboratories of biochemistry in this country were at that time (some twenty years ago) organized in the medical schools. A few laboratories in Europe, such as those of Willstätter, Euler, Czapek and Emil Fischer, were beginning to study the chemistry of the organic compounds found in plant tissues and the newly discovered group of enzymes, or "organic ferments," as they were called, were being found to exist largely in plant organisms, so that active interest in the biochemistry of plant life was beginning to appear.

Early in 1913, I went to the University of Minnesota to become head of the department of agricultural biochemistry, with the intention on my part and the understanding of the administration there that I would attempt to develop a corps of workers and a program of research in the field of the biochemistry of resistance to disease in plants. Work on this program went far enough to demonstrate conclusively that there is a series of biochemical phenomena and processes in plants, by means of which they are either sensitive or resistant to infection by parasites, which are quite comparable, if not actually parallel, to the biochemical processes by which the animal body reacts to infectious and parasitic diseases. My own connection with this problem ceased because of my transfer to administrative work, and much of the subsequent program of the department of agricultural biochemistry at the University of Minnesota has since been done in the field of animal and human biochemistry. But enough of the progress that has been made upon the original program has come to my knowledge to keep alive my keen interest in the general problem of the parallelism of the biochemistry of plant and of animal life.

Quite recently, I have become interested in the possible parallelism between certain aspects of the nutrition of plants and of animals which has thus far escaped notice and which I believe to be worthy of careful investigation. In fact, I am already laying out a tentative program for a series of studies in this field when I transfer to the research professorship in the Massachusetts Agricultural Experiment Station, which the board of trustees has made available to me after my retirement from my present position.

My fundamental thesis is that there already is enough experimental evidence to justify the formulation of a hypothesis that there exists in the field of plant nutrition a series of phenomena which are quite comparable in their operation and effects to those which are now recognized and accepted in the field of animal nutrition as being due to the existence of and necessity for certain accessory food substances commonly known as "vitamins."

Prior to about twenty years ago animal nutrition was studied and feeding standards or human dietaries were recommended wholly on the basis of a so-called "balanced ration" of the essential groups of nutrition known as the proteins, fats, carbohydrates and salts or mineral nutrients. These types of animal nutrients were all well-known chemical compounds, whose presence in foods or in animal tissues could be readily detected, both qualitatively and quantitatively, by chemical analysis. In 1906, however, Eijkman, a Dutch chemist working in Java, and Hopkins, in England, both postulated the existence of certain accessory food substances of an entirely different type, the absence of which from the diet produces certain specific nutrition-deficiency diseases. In 1911, Casimir Funk gave the name "vitamin" to the one of these accessory food materials which is preventative of beri-beri or polyneuritis, because of a conception, which was later proved to be erroneous, that its specific beneficial effects were a function of the chemical constitution indicated by this particular name. Funk also believed that other similar acessory food substances would be found to have similar chemical constitution and that the name "vitamins" might properly be used as a general group name. This is, of course, now known not to be true. However, this name has survived competition with other suggested names for popular use as a group designation.

Following the announcement of the vitamin hypothesis, a tremendous amount of study has been directed toward the solution of questions of how many such vitamins actually exist, of the chemical constitution of each vitamin itself, of the specificity of its requirement for a particular physiological function in the animal body, and of the natural sources for each particular vitamin. Naturally, a first step in all this work has been the devising and perfection of methods of technique for determining both qualitatively and quantitatively the presence or absence of any one of these substances in any product which is under investigation. Since their chemical constitution is as yet unknown, this technique must, at present, be based upon measurements of their biological effects instead of upon specific chemical tests for their presence in the material which is studied.

My point is that the discovery of these essential elements of animal nutrition, which are necessary in much smaller quantities than is true of the other nutritional substances and whose chemical nature is not yet known, has developed, during the last twenty years, an entirely new type of investigation, which already has produced results of tremendous theoretical and practical importance to human welfare. Further, it is a field to which a large group of highly trained specialists are devoting a major part or all of their research activities. It is to the possibilities of a similar development in the field of plant nutrition that this paper is intended to direct attention.

Turning now to the possible parallelism in the field of plant nutrition to the developments in the field of animal nutrition that I have just mentioned, I may point out that prior to about twenty years ago problems of "soil fertility" (which was the term used to describe the supply of anergic plant food from the soil to crops) were considered solely from the standpoint of a few so-called "essential elements," whose presence in the soil or plant in question can readily be determined by standard methods of chemical analysis. Field and plot tests to ascertain whether profitable economic returns are possible from the use of "fertilizers" dealt almost exclusively with the three of these elements which are called the "critical elements of fertility," namely, phosphorus, potassium and nitrogen. Sulfur and calcium also began to be generally recognized as possible limiting factors in soil productivity and later magnesium was added to the list as necessary to be considered in some special cases. Iron, silicon and possibly sodium and aluminium were known to be taken from the soil by plants, but were generally so abundant in all agricultural soils that, while often mentioned as "essential elements," they were not much studied in connection with practical problems of plant nutrition.

In all such considerations the problem was that of the supply of these elements as plant food in proper amounts and proportions, entirely similar to the basis of total nutrients and balanced ration in animal feeding, and the general methods of chemical analysis of materials and of feeding trials were similar in purpose and character in the two fields of nutrition. Fertilizer formulas, comparable to feeding standards for farm animals and human dietaries, were based upon supplies from appropriate commercial materials of these critical elements in properly balanced proportions.

To be sure, the literature of the subject for the past fifty years has contained occasional references to the finding of other elements more or less widely present in small amounts in plant tissues, and an occasional speculative consideration of their possible physiological function or necessity to plant life. In fact, Palladin, in his "Plant Physiology," published in 1923, lists 31 chemical elements as having been reported to have been found by chemical analysis to be present in plant tissues. However, even at that late date, he includes only the commonly accepted ten in his list of the "essential elements of fertility."

But beginning about twenty years ago, experimental evidence was accumulated to show that certain elements which had been found in plant tissues in such small amounts as to be considered more or less accidental constituents, taken from the soil by purely mechanical processes and hence not essential plant nutrients, are actually just as necessary to plant growth as are the other mineral elements of fertility.

For example, Miss Brenchley[1] at Cambridge, in England, published in 1914 a monograph entitled "Inorganic Plant Poisons and Stimulants," reporting the results of her studies of the use in plant nutrient solutions of salts of copper, arsenic, manganese, zinc, and boron, which were assumed to be toxic to plants, in proportions less than injurious dosages, in which she found that in such proportions salts of manganese, zinc and boron gave positively stimulating effects upon plant growth, varying, however, with the different crops and producing varying anatomical changes in the growing plants. She found copper and arsenic salts not to be "stimulating," even in minute dosages.

In this country, McHargue and his associates at the Kentucky Experiment Station,[2] demostrated that copper, manganese and zinc, in "very small amounts," are essential to growth of many, if not all, farm crops. Lipman and his associates at the University of California[3] showed that while boron, in the form of salts of boric acid, is positively toxic to farm crops if present in the soil to the extent of three parts per million or more, lesser amounts than this are so necessary as to be an actual limiting factor in crop production if absent from the nutrient medium. Numerous other experimental results of similar purport are current in the literature of soil science in this country and abroad for the past ten years, some of which will be referred to a little later in this paper in connection with the nutrient functions of particular elements.

I think that it is not stretching the truth in favor

[1] Winifred E. Brenchley, "Inorganic Plant Poisons and Stimulants." Cambridge University Press, London, 1914.

[2] J. S. McHargue, "The Occurrences of Copper, Manganese, Zinc, Nickel and Cobalt in Soils, Plants and Animals, and their Possible Function as Vital Factors," *Jour. Agr. Research*, 30 (No. 2): 193–196. 1925.

[3] A. L. Sommer and C. B. Lipman, "Evidence on the Indispensable Nature of Zinc and Boron for Higher Green Plants," *Plant Physiology*, 1 (No. 3): 231–249. 1926.

of my hypothesis of parallelism of these facts and phenomena of plant nutrition to those of the vitamin relationships in animal nutrition to point out the following points of similarity.

First, the essential nature of these elements to proper plant nutrition was first discovered, in many cases, by plant pathologists in connection with experimental studies of the causes of and possible remedies for so-called "physiological" or "nutritional" diseases of farm crops, or as a result of observations of beneficial results upon crop yields of applications of these materials to crops as fungicidal sprays which could not be accurately attributed to control of parasitic diseases.

Second, only very minute amounts of these elements are necessary to accomplish their essential function in nutrition.

Third, these accessory elements of plant nutrition are generally so widely distributed in soils (the natural source for anergic plant food), in adequate amounts for general crop needs, that definitely recognized deficiency diseases due to an inadequate supply of them are relatively rare and limited to special soil or crop conditions; while, on the other hand, there is already some evidence that the addition of small amounts of these accessory elements to soils previously considered to be adequate sources of necessary plant nutrients gives beneficial results in increased vigor of growth and final yields of crops.

Fourth, in many cases, some of which will be detailed in later paragraphs of this paper, absence or inadequacy of these elements in the nutrient medium has been shown to result in definite and specific anatomical abnormalities or abnormal physiological functioning in the plant or crop in question, quite similar to, if not actually parallel with, the symptoms of vitamin-deficiency abnormalities in animals.

In fact, it seems to me to be no very visionary idea to suppose that we may soon recognize in the field of plant nutrition certain definite factors which may be designated by some such terms as "the anti-chlorosis factor," "the meristem-stimulating factor," "the inflorescence stimulator" and the like, comparable to the "anti-scorbutic," "growth-promoting," "antisterility" vitamins. As examples of what I mean, may I cite the following:

Copper has been found by Allison[4] to be a specific limiting factor in the growth of at least sixty different crop plants on the raw peat lands of the Florida Everglades and by Felix[5] for onions and lettuce on the reclaimed muck lands of central New York. In the latter case, lack of copper produces a specific anatomical abnormality, known as "rabbit-ear," in that lettuce which should develop solid "heads" produces instead long slender leaves which are the basis for the common name of the trouble. Onions, too, are reported to produce better-colored and thicker "scales" when fertilized with copper sulfate. In Florida, the general evidence of absence of copper in the soil is a marked chlorosis of the foliage of the plants, which may be remedied by addition of as little as 10 pounds per acre of copper sulfate to the soil or by spraying of dilute solutions of copper salts upon this foliage. The descriptions of the results of experimental studies of the chlorophyl regeneration in these copper-starved plants are strikingly similar to those of the specificity of copper as a necessary adjunct to iron in the regeneration of haemoglobin in artificially produced anemia in animals by Hart and Peterson[6] and their associates at the University of Wisconsin.

Manganese has been found by several different investigators to be a specific remedy for chlorosis of plants due to excessive lime in the soil. But its action is not general, in that on the same soil, or in the same culture medium, its beneficial effects will be shown by some crops and not by others. Willis, of North Carolina,[7] reports that manganese sulfate overcomes this type of chlorosis on soybeans but not on corn. McHargue, in Kentucky,[8] finding similar results, suggests the association of manganese with chlorophyl-formation similar to that of copper already mentioned. Mann[9] has offered an explanation of the North Carolina results on the basis of a specific requirement of soybeans for this type of aid in chlorophyl formation.

Workers at the Rhode Island Agricultural Experiment Station[10] found beneficial results from the use of as little as 8 pounds per acre of manganese sulfate applied to the soil as a fertilizer, which could be duplicated by applying the chemical to the foliage in a spray. But recent experiments at the Connecticut

4 R. V. Allison, O. C. Bryan and J. H. Hunter, "The Stimulation of Plant Response on the Raw Peat Soils of the Florida Everglades through the Use of Copper Sulfate and Other Chemicals," *Fla. Agri. Exp. Stat. Bul.*, 190: 33–80. 1927.

5 E. L. Felix, "Correction of Unproductive Muck by the Addition of Copper," *Phytopathology*, 17 (No. 1): 49–50. 1927.

6 J. Waddell, H. Steenbock and E. B. Hart, "The Specificity of Copper as a Supplement to Iron in the Cure of Nutritional Anemia," *Jour. Biol. Chem.*, 84 (No. 1): 115–130. 1929.

7 L. G. Willis, "The Response of Oats and Soybeans to Manganese on Some Coastal Plains Soils," *No. Car. Agric. Exp. Sta. Bul.*, 257, pp. 13. 1928.

8 J. S. McHargue, "The Occurrence and Distribution of Manganese," *Ky. Agri. Exp. Sta. Rept.*, Pt. 1, 16–18. 1926.

9 H. B. Mann, "Availability of Manganese and of Iron as Affected by Applications of Calcium and Magnesium Carbonates to the Soil," *Soil Sci.*, 30 (No. 2): 117–141. 1930.

10 B. E. Gilbert and F. T. McLean, "The Lack of Available Manganese in a Lime-Induced Chlorosis," *Soil Sci.*, 26 (No. 1): 27–31. 1928.

Tobacco Station[11] resulted in abnormal physiological symptoms in tobacco if the amounts of manganese in the soil exceeded a certain optimum.

Boron, in the form of salts of boric acids, especially borax, has been known for some time to be very toxic to farm crops if in concentrations of more than three parts per million in the nutrient medium. But in less concentrations (the optimum being about 1:1,500,000) it has been found by Lipman and his associates[3] at the University of California, by Brenchley[12] in England and by Warrington[13] in Sweden to be absolutely indispensable for satisfactory growth of many crop plants. Both Miss Brenchley and Miss Warrington report that insufficient supplies of boron in the nutrient medium result in definite anatomical abnormalities in the plants, particularly retardation of the development of meristem tissue, with certain specific discolorations in the stems of the plants which are recognizable as definite diagnostic symptoms for the boron-deficiency.

Zinc has been shown, by Sommer,[14] by Brenchley[1] and by McHargue and Shedd[15] to be a specific necessary nutrient for certain types of crops, but apparently not so, at least in the same degree, for others. The macroscopic evidence of zinc-deficiency is cited as an alteration of the normal proportion of straw and grain, but this is of course only a final result of some disturbance in the plant's metabolism or physiological processes the nature of which has not yet been studied.

These examples are probably adequate to indicate the basis for my assumption of a series of phenomena and principles of plant nutrition parallel to or at least comparable with the vitamin function in animal nutrition.

Fortunately for the proposed experimental study of this hypothesis, the elements to which these specific nutritional functions are apparently attached are presumably well-known chemical entities, for which qualitative and quantitative methods of testing are already available, thus making unnecessary one type of investigation which is essential in vitamin studies. But there does remain to be done a large amount of experimental study of the conditions and limitations of the requirements for these accessory factors of plant nutrition, and of the forms of compounds and conditions of protoplasm under which they exert their specific effects, together with a wide range of studies of the actual ill effects, physiologically and anatomically, of deficiencies in the diet of different types of farm crops of these plant "vitamins." For this latter type of studies, a new technique will probably have to be developed, as was the case with the animal vitamins. I believe, however, that this is a very promising field of research, and, as I said, I hope to have an opportunity soon to enter upon a definite program of investigations in it. It is to possible cooperation in this undertaking that I invite the attention of interested agronomists, chemists and plant physiologists.

THE RISE OF GENETICS. II

By Professor T. H. MORGAN

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INFLUENCE OF THE GENES ON THE CYTOPLASM

IF another branch of zoology that was actively cultivated at the end of the last century had realized its ambitions, it might have been possible to-day to bridge the gap between gene and character, but despite its high-sounding name of *Entwicklungsmechanik* nothing that was really quantitative or mechanistic was forthcoming. Instead, philosophical platitudes were invoked rather than experimentally determined factors. Then, too, experimental embryology ran for a while after false gods that landed it finally in a maze of metaphysical subtleties. It is unfortunate, therefore, that from this source we can not add, to the three contributory lines of research which led to the rise of genetics, a fourth and greatly needed contribution to bridge an unfortunate gap. I say this with much regret, for, during that time and even now, I have not lost interest in this fascinating field of embryological experimentation. It is true that a great deal of factual evidence came to light, and it is true that many misleading ideas were set aside, but the upshot was negative so far as the formulation of any of the factors of development, whether mecha-

11 H. G. M. Jacobsen and T. R. Swanback, "Manganese Toxicity in Tobacco," SCIENCE, 76 (No. 1812): 283–284. 1929.

12 Winifred E. Brenchley, "Investigations on the Effect of Boron on Plant Life," *Agr. Prog.* (*Agr. Ed. Assn., London*), 3: 104–105. 1926.

13 Katherine Warrington, "The Changes Induced in the Anatomical Structure of *Vicia faba* by the Absence of Boron from the Nutrient Solution," *Ann. Bot.* (*London*), 40 (No. 157): 27–42. 1926.

14 A. L. Sommer, "Further Evidence of the Essential Nature of Zinc for the Growth of the Higher Green Plants," *Plant Physiology*, 3 (No. 2): 217–221. 1928.

15 J. S. McHargue and O. M. Shedd, "The Effect of Manganese, Copper, Zinc, Boron, and Arsenic on the Growth of Oats," *Jour. Am. Soc. Agron.*, 22 (No. 8): 739–746. 1930.