SOME MODERN ADVANCES IN THE STUDY OF PLANT NUTRITION

By D. R. Hoagland

(Presented January, 1940, American Association Sugar Beet Technologists, Denver, Colorado)

Two types of discussion might be envisaged in preparation for this occasion. One type would be concerned with the intensive development of some specialized phase of research in plant nutrition; the other with a general survey of a broader field. After consultation with a representative of your program committee I decided to attempt the latter. It is my understanding that many technical interests are represented in this association and that perhaps only a relatively small group will have spent much time in the study of the literature of the aspects of plant nutrition with which I shall deal. From those who are specialists in this field of study I must ask forbearance while I discuss questions already familiar to them. I should also like to explain, in this introductory remark, that a considerable part of my illustrative material will be taken from research conducted at the University of California Agricultural Experiment Station, not because I have any wish to magnify this particular work, but because it seems to me that a more effective presentation of a subject can be made, if the speaker draws heavily on the experience with which he has had a more or less immediate contact.*

My general theme is that of certain basic research underlying the management of the soil as a medium for supplying essential mineral elements for plant growth. It might be anticipated that I should therefore at once embark on a discussion of the subject of "plant foods." But it seems to me that this conventional approach may be misleading. The term "plant foods" itself as used to designate a few of the elements derived by the plant from the soil, although too well established to be displaced, may give us a very incomplete and inaccurate impression of our general problem. We are in the danger of relegating too far in the background of our thinking the physiology of the plant. We grow crops because the green plant has the power of synthesizing from simple substances, principally carbon dioxide and water, organic compounds which not only serve as its own food and structural material, but also as the food of animals, and as industrial products.

The basis of this synthetic power resides in that unique process, photosynthesis, by virtue of which the radiant energy of sunlight is fixed and thus the energy imported from outside our planet made available. Time worn as the idea may be, it is worth repeating that animal life, and civilization, in both its beneficient and malevolent manifestations, is in the present stage of scientific development, utterly dependent on photosynthesis, as it occurs from year to year or as it has occurred in past geological ages. There is not yet any foundation for the picture sometimes imagined by popular writers, of great factories gathering sunlight on the roof and producing a stream of sugar. Indeed the sucrose of the plant has not yet been synthesized by even the most intricate processes of the laboratory. You may be confident that you are engaged in one of the most fundamental occupations of mankind.

It is true that the process of photosynthesis has a low over-all efficiency. Usually less than 1% of the total radiant energy of the sun falling on any given area will be stored in the plant. But it is necessary to recall that the true biological efficiency of this process must be measured in terms of energy absorbed by the surface of the choroplastid where the photosynthetic

*A series of lantern slides was presented but the illustrations are omitted from this publication. No attempt is made in this general discussion to give literature citations. A large bibliography would be required.

process occurs. Considered in this way the efficiency of utilization of energy may be remarkably high, for example, 60% or 70%, according to the results of some early investigations. But recent scientific reports reveal divergent evidence as to just what degree of efficiency the photosynthetic process can attain. Some conclude that the efficiency is much lower than that mentioned above. Many difficult questions of technique and of the interpretation of results arise. There are, however, indications, of special interest to our present discussion, that the efficiency of the photosynthetic process may vary with the status of the plant in respect to mineral elements and may be dependent in part on the adequacy of the amounts available to the photosynthetic system of elements like iron, manganese, copper and zinc which function on a microscale. I shall later say something further of elements in this category.

Understanding as we do the role of sunlight energy in the synthesis of plant products, it is worthy of remark that so little effort is made by agronomists or horticulturists to measure and record the intensity and quality of the sunlight energy available to crops in their diverse locations, together with other interrelated climatic data. The importance of this general question was impressed on my mind last summer during a visit to the Hawaiian Islands. As some of you know, in these islands, extraordinary differences in rainfall and in sunlight conditions may occur within short distances. The Sugar Planters Experiment Station has conducted some experiments on the growth of sugar cane at two localities, one of high rainfall and low sunlight values, the other of relatively low rainfall and high light values. Temperature differences are not very great. Soil was transported from each locality to the other, so that plants could be grown in the two types of soil under the two climatic conditions. At the high-light station the cane plants produced several times as much sugar as at the low-light station as a result of both higher yields and higher percentages of sugar, when plants were grown in amply fertilizer soil from either station. In other words, the potentialities of fertilizer applications to increase plant growth and sugar synthesis could not be understood without reference to climatic conditions.

I have spoken of the process of photosynthesis, a special function of green plants, but there is another physiological process that occurs in all living organisms, namely — respiration, which must always receive consideration along with photosynthesis. Respiration, in contrast to photosynthesis, leads to a loss of carbon and the growth of the plant with increase of its dry weight is a net result of the two opposing processes.

The mineral nutrition of the plant can be understood only on the basis of the interrelations between mineral elements absorbed by the plant and the synthesis of organic constituents or their destruction -- photosynthesis and respiration. A conspicuous illustration of the general idea is found in the utilization of nitrogen, usually absorbed by the plant as nitrate. Long ago the concept of nitrogen-carbohydrate relations in the plant was formulated, but at an earlier period there often existed lack of appreciation of the complexity of these relations and attempts were sometimes made to interpret them in a too narrow way. An important modern advance in our knowledge of plant nutrition is provided by research workers in the fields of plant bio-chemistry and plant physiology, who have made a good beginning in the study of the chemical processes involved in the reactions of carbohydrates, organic acids and absorbed nitrogen. In simple terms we may say that by altering the balance of these reactions, the plant may be profoundly influenced in its type of growth with respect to processes of reproduction or of storage of sugar or other carbohydrate reserves. Therefore the intake of nitrogen and the climatic factors affecting photosynthesis and respiration, in relation to vegetative growth, reproduction and storage of sugar or other carbohydrates, require evaluation. It should be recalled that while photosynthesis is accelerated by increasing temperature, within certain temperature limits, under conditions of darkness or deficient light, only the process of respiration, resulting in loss of carbon, is increased with increase of temperature. As another factor, recent evidence shows that excess nitrogen may greatly increase the rate of respiration in plant tissues.

An illustration of nitrogen-sugar relations of a type familiar to you may be cited from an experiment on the sugar beet in California. In certain districts in which beets are grown in peat soils, it has been found that the high nitrate level maintained in the soil over a long period results in a great lowering of sugar content. On the other hand, in other experiments with different soils and under other climatic conditions, applications of nitrogen have given increased yields as well as high percentages of sugar. In the latter case the initially high supply of nitrogen was not maintained too long during the season of growth. Another example may be found in certain work being carried on in Hawaii with the pineapple, in which it is sought to control nitrogen fertilization with regard to the stage of growth of the plant and the climatic factors, especially the sunlight factor, as influencing sugar synthesis. It is believed that a large measure of economy has been effected in the use of nitrogen fertilizers.

I raise these questions, which are of course not new ones, because it seems to me worthwhile to suggest that far more investigation is needed of the nitrogen metabolism of plants with the aid of the methods of the biochemist and plant physiologist now under active development. The biochemical experiments of the laboratory would require too much time to describe, but I should like to mention the work at Cornell in which the photosynthesis of apple trees growing under natural field conditions is being successfully studied. Of great interest are the researches of Thomas and Hill in Utah. These investigators have devised ingenious, automatic apparatus for measuring the rate of photosynthesis or respiration in the alfalfa or other plants, as influenced by climatic and other physiological conditions. It can scarcely be doubted that a better understanding of photosnythesis and respiration in relation to nitrogen metabolism has a definite practical interest for problems of soil fertilization. An excellent example is that of the sugar beet.

The mineral elements absorbed from the soil are essential to the processes of photosynthesis, respiration and all other metabolic processes in the plant, but it is likewise true that the absorption of these mineral elements is dependent on the organic metabolism of the plant. It is therefore appropriate to present some principles regarding the absorption of mineral elements by roots. In this presentation it is convenient to eliminate the complexities of the soil from consideration for the moment, and to assume that we are studying plants growing with their roots immersed in a dilute nutrient solution -- the method known as water-culture. At an earlier period agricultural chemists and plant physiologists commonly conceived that in such a system the roots absorbed the mineral nutrients by a process of simple diffusion. Sometimes the root was even likened to a collodian bag as far as the absorption of the mineral nutrients was concerned, We know now that any such view is untenable. Actually the root cells normally absorb mineral solutes against concentration gradients and this demands expenditure of energy. The absorption is a function of living, respiring cells. A supply of oxygen and of organic compounds capable of yielding energy is essential. Further, the temperature of the root must be suitable for the maintenance of the chemical reactions of the living cell at a sufficiently rapid pace and yet not too high to produce excessive respiration.

What is the significance of these conclusions in terms of availability of mineral nutrients? It is this: that availability in its physiological, and therefore practical application, is not merely a question of the presence of the nutrients in the culture medium in proper form and amount, but is just as definitely a question of the physiological status of the root determining its ability to grow, and increase in surface, not excluding that some passive movement of nutrients may take place through injured or physiologically inactive roots, as a result of transpiration.

We are faced then with the general problem of the essential requirements for root growth and activity. In the external environment there must be provided an adequate assortment and supply of oxygen; and in the internal environment, a store of sugar or other labile carbohydrates initially synthesized in the leaf and then transported to the root. Are there other internal or external requirements? This question is now receiving careful study in a number of laboratories. One method of attack is to grow roots from excised root tips in a sterile culture solution of known composition. Sugar is presented to the roots in the solution since the top of the plant cannot supply sugar to the root. Some years ago it was proved by several investigators that tomato roots could be kept growing in this way indefinitely, in certain types of culture solutions. One of the essential components of the solutions was an extract of yeast. Subsequently several investigators independently obtained evidence that one principal reason why yeast extract was necessary was that it contained a vitamin -- known to the animal physiologist as vitamin B_1. This vitamin was found to be indispensable for growth of roots of the species of plants investigated. Later work suggests that still other vitamins or growth substances may be necessary; for example, nicotinic acid, the antipellagra vitamin of the animal physiologist. Such substances exert their effects in amazingly small quantities. A definitive result has been attained from even one millionth of a milligram of vitamin B_1. It is becoming clear that plants do not synthesize vitamins as a philanthropic act for the benefit of the animal. Some, possibly all of these substances, have a role in the plant's own growth.

Let us attempt to summarize these researches on roots in terms of crop growth under natural conditions. The root is the organ by which the plant makes its contact with the soil and the absorption of mineral nutrients depends on the physiological activity of the roots and on their growth and extension of surface, which determines the number of contacts made with soil particles. Since oxygen is necessary for root growth and normal absorption of mineral nutrients the importance of soil aeration at once becomes obvious, with all that this implies in terms of irrigation practice, soil cultivation, and cover crop practices. Sugar and growth substances are required by the roots and these are synthesized in the top of the plant, with the aid of solar energy. Therefore climatic conditions affecting photosynthesis have an influence in determining the relation of the soil to the plant through its root system.

Thus far I have been assuming that roots absorb the mineral nutrients from a simple nutrient solution. As applied to the soil this is the soil solution theory which has for many years usefully served as an interpretation of the mechanism by which mineral nutrients become accessible to the plant. The concept is that these nutrients are absorbed by roots only after they have first dissolved in the soil solution. Undoubtedly the absorption of nutrients from the soil solution does have a major significance, as is indeed evident from the fact that some important nutrients, especially nitrate, are not adsorbed to any important degree by the colloids of the soil, and the negatively charged nitrate ion is necessarily accompanied in the soil solution by equivalent quantities of positively charged ions such as calcium, magnesium and potassium. Nevertheless, evidence has been obtained by Jenny and Overstreet in our laboratory, and by several other investigators, in favor of the view that an additional mechanism exists for the intake by the plant of certain nutrients which can be held in adsorbed condition by the colloids of the soil. This mechanism has been called "contact" intake of ions. Briefly, the idea is that the roots and soil colloid can make such an intimate contact that ions can migrate through the combined colloidal system of the root surface and soil colloid without having to enter a soil solution phase at all or, in non-scientific language, potassium, for example, can jump from the soil to the plant root. There is a physical-chemical basis for this theory, but its discussion would not fall within the scope of this paper. I may add that some of the experimental evidence has been gained by the use of a new method of research made available by that remarkable development in physics by which many chemical elements can artificially be made radioactive. The radioactive elements become tagged and their movement in the plant or animal can be followed by detection of the radioactivity, for which exceedingly sensitive methods exist. The application of this new tool constitutes one of the important recent advances in the study of plant and animal nutrition.

Much more research will have to be conducted before the full implications of the contact theory of intake of nutrients by plants becomes apparent. It may be said, however, that another reason has been presented for emphasizing the limitations of existing knowledge and the difficulties that arise in devising methods for appraising the availability of nutrients in the soil.

Now that I have outlined some problems of the movement of nutrients into the plant, it is in order to consider the present status of knowledge as to the chemical elements that are indispensable for plant growth. Not very many years ago the prevailing view of students of botany and of plant nutrition was that the plant required, in terms of absolute essentiality, only 10 chemical elements. These were carbon, hydrogen and oxygen and of soil origin, nitrogen, potassium, calcium, magnesium, iron, phosphorus and sulphur. Mazé in France, about 1914, presented certain experimental evidence on the corn plant which indicated that other chemical elements were also essential, but his views received no general acceptance at the time. Then came a period of reinvestigation of this question with the use of highly refined technique. Generally the water culture method for growing plants was found to be best suited for the purpose. Nutrient salts, even of C. P. grade, were repurified, and water for the cultures was distilled and redistilled. With these and other precautions experiments were performed which gave perfectly clear results. The plants studied would not grow normally, or indeed might make scarcely any growth at all, unless supplied with small amounts of boron, copper, manganese, and zinc, in addition to the usually supplied nutrient elements. Still further improvement of technique has enabled two of my colleagues, within the past several years, to obtain evidence strongly supporting the view that molybdenum is also one of the essential elements. We cannot say, however, that the list is closed. It can only be safely asserted, for any particular set of experimental conditions, that chemical elements not deliberately added to the culture medium are needed in quantities not greater than those unavoidably present as impurities. New refinements of technique in the future may disclose still other indispensable chemical elements. In fact, even now there are indications that other elements may be required in minute quantities, such as sodium, aluminum and silicon.

Perhaps some of you would like to raise the query as to whether the same elements are indispensable for all species of higher plants. With regard to boron, zinc, copper, and manganese, this seems highly probable on the basis of existing knowledge. The effects of deficiencies of these elements are so profound as to indicate that they play some universally vital role in the plant's metabolism. For two of the elements, boron and manganese, so many different botanical groups are represented in the investigations already made, that no valid objection can be entered to the extension of the conclusions to species of plants which have not been subject to actual experimental test. For that matter, it has not been shown by actual experiment on every species of plant that potassium is an essential element, but we do not doubt it. It may be true, nevertheless, that some specific mineral requirements do exist. To cite one case, experiments have been made on certain leguminous plants that have an exceptional power to absorb the element selenium, and the suggestion has been proposed that these plants may require selenium for their normal growth, or at least that this element may have a highly beneficial effect. Incidentally, the selenium absorbed by the plant may be highly toxic to the animal which feeds on it.

In the earlier phase of the investigation of elements required by plants in minute quantity one might well have doubted the practical value of the knowledge gained by growing plants in highly purified nutrient solutions. Was it reasonable that deficiencies of elements needed in such minute amounts would occur under ordinary crop conditions?

Today we can answer this question with certainty. In recent years reports have come from many parts of the world to the effect that in some localities nutritional crop diseases have been overcome by the use of boron, manganese, copper, or zinc, as the case may be. Most numerous are the reports of boron deficiencies. As you know, the sugar beet has responded to boron applications in a considerable number of instances, and certain diseases of the beet are caused directly or indirectly by boron deficiencies. Excessive liming of soils may apparently induce boron deficiency in some soils. On the other hand, in California, boron toxicity to crops may occur not infrequently because of too high content of boron in the irrigation water. It is one of the characteristics of elements of this type that, while they are indispensable in minute quantity, they also readily produce injury to the plant at low concentrations.

It is, I think, entirely justifiable to conclude that the researches, in the laboratory and in the field, on chemical elements effective in minute amounts for plant growth, constitute one of the most important of modern advances in plant nutrition. We should be always alert to the possibility that deficiencies of elements of this category may already exist or may develop with continued cropping. Yet a note of caution should be introduced. Not all soils, by any means, require the addition of boron, manganese, copper or zinc. And when a need does exist it may not necessarily follow that the impurities present in some particular form of fertilizer will be effective. The fixing power of the soil, or power to render such elements inaccessible to the plant, may be such that far larger amounts may be required than would be furnished by impurities present in any standard fertilizer. This point is well illustrated in the treatment in California of the zinc deficiency disease of fruit trees known as "little leaf" or "mottle leaf." Generally the treatment has to be made directly to the plant, as for example, by spraying with zinc containing spray mixtures, because of the great expense and difficulty of soil treatment.

I have made the effort in the foregoing discussion to sketch -- necessarily inadequately -- some general principles and points of view applying to plant and soil interrelations with the emphasis on the physiological approach. In the remainder of the paper, I shall outline certain problems in the same general field of study, but with the emphasis on the soil.

In the fertilization of a soil, we are often inclined to think that we are adding certain nutrients, or "plant foods," and thereby increasing the supply ready for absorption by the plant in proportion to the amounts added. This would only be true if we added the fertilizer to a totally inert medium. But the soil is far from an inert medium. As soon as a fertilizer is added to it the system is disturbed and many chemical reactions take place, and more slowly, microbiological effects manifest themselves. In the laboratory with which I am associated, and in many others, during recent years the old problems of fixation of potassium and phosphate by soils have been re-examined. On some of the theoretical aspects of these problems an entire reorientation has occurred because of new discoveries on the nature of soil colloids. Until comparatively few years ago soil colloids and colloids in general, were regarded simply as matter in a very fine state of division with great development of surface. They were thought of as essentially amorphous. Then came the application of a new tool of research, at least new to the field of soil science -- the X-ray diffraction analysis. The X-rays employed are of such short wave length that they can be reflected from planes of atoms and give evidence of the arrangement of these atoms by effects produced on photographic films. Examined in this way, many preparations of soil colloids were shown to be crystalline in the sense that the atoms are arranged according to definite patterns, determined by the laws of valence. Fundamental building units in these crystalline colloids are oxygen, silicon and aluminum. They are present in electrically charged form or crystal lattice ions. I can do more than bring this development to your attention. Its adequate discussion would require a long period and the authority of a specialist in this field of work. I may add that the study of the crystal structure of soil colloids is now becoming one of the active fields of research in soil science and a number of investigators in Europe and America have published reports during the past few years.

The whole field of soil and plant interrelations has been illumined by the steady growth of our understanding of the phenomena of base exchange in soil colloids. We can now perceive a certain unity in the reactions of diverse types of soil, which before seemed to have no relation to each other. Many features of acid soils of humid regions and alkali soils of arid regions are both explicable in terms of theories of base replacement. In the one case calcium ions have been displaced to a greater or lesser degree by hydrogen ions; in the other by sodium ions, with all the important consequences, theoretical and practical, of such ionic interchanges. Researches on base exchange have had a profound influence on liming practices and on methods of reclaiming alkali soils, or of preventing their formation. Guided by the principles of base exchange, my colleague, Dr. Kelley, has successfully reclaimed black alkali soil, which twenty years ago seemed hopeless of change to a crop bearing soil.

In the realm of fertilizer practice we are concerned with the fate of potassium and we know that this element when added to the soil may become fixed and displace equivalent quantities of other bases, calcium, magnesium and sodium, from the colloid system. The potassium so fixed will be available to roots when displaced by hydrogen ions excreted by the roots as carbonic acid, within certain limitations imposed by the degree of saturation of the colloid with potassium and the nature of the other ions held by the colloid. But the researches of recent years have made it evident that the problem is more complex than these statements would imply. In many soils of neutral or alkaline reaction potassium added to the soil may be fixed in what is called for convenience "non-exchangeable form." This means that after fixation the potassium is displaced only with greatest difficulty by chemical reagents and it may become only slightly available to the plant. Consequently all the potash fertilizer added to a soil and unused by the crop is not necessarily stored away in available form for future crops. Also fixation in either replaceable or non-replaceable form will mean that roots developing below the zone of fixation will not benefit by the fertilizer application of potassium except to the degree, perhaps very slight, that potassium is released and moved downward. A practical problem arises then with deep rooted plants, like fruit trees, if potassium fertilization of the soil is needed.

There is also the now well confirmed and interesting observation that in some soils fixation of potassium in non-replaceable form is greatly accelerated by alternate wetting and drying the soil.

If we deal with the potassium naturally present in the soil in an effort to determine its availability by chemical procedures, we are faced by another complexity. As I have just indicated, potassium held by the soil in the so-called non-replaceable form may sometimes be largely unavailable to the plant, but this is not necessarily true. There exist soils from which plant roots can extract potassium in reasonably adequate quantities and yet the chemist in the laboratory finds that to extract by chemical means similar quantities of potassium requires such drastic reagents, or so long a period of leaching, that the methods employed cannot be interpreted as biologically significant. The contact phenomena of root with soil particles, together with the remarkable biological activity of the root in absorbing potassium, are involved in a system which has not so far been successfully imitated in the test tube. We need then feel no surprise if a short-cut method of determining potassium availability often fails to give us the information we should like to have. A great many soils have been examined in California by the Neubauer method, which determines the amount of potassium removed from a given weight of soil by rye seedlings. In many instances much more potassium is removed by the plants than by chemical reagents usually employed in the laboratory to determine potassium availability.

Modern researches on phosphate-fixation also aid greatly in the clarification of the nature of the problem of availability of phosphate to the plant. The fixation of phosphate in the soil may be classified in a general way into two types of processes; fixation by chemical precipitation, with special reference to calcium phosphate, and adsorption fixation by colloids. The latter may imply a high degree of unavailability to most crops, though the degree of saturation of the colloid with phosphate is an important modifying factor. In the category of colloid fixation of phosphate, new evidence has been obtained in the study of kaolinitic colloids. Very finely divided kaolin possesses a remarkably high capacity to fix phosphate and the phosphate thus fixed is not dissolved by acids of ordinary strength, from the point of view of plant nutrition. Instead it is displaced by hydroxyl ions of an alkaline solution. A type of anion exchange takes place. The phosphate held by the colloid may also be displaced by certain organic acid anions, for example, by citric acid, not because of hydrogen-ion effects, but because of the character of the anion. Some colloidal iron compounds may exhibit similar reactions. Generally of greater importance, in soil systems governed by calcium and phosphate equilibria, are complex buffer effects influencing the solution of phosphate.

The researches on the fixation of phosphate by soils have in themselves great interest for the soil chemist, but in interpreting their meaning for crop production, again we must consider the whole system, which includes the plant. From the same soil one species of plant may secure an adequate supply of phosphate and another may make only feeble growth because of phosphate deficiency. The reason for the differences is far from clear, but several factors readily suggest themselves. One is the length of the season for adsorption of phosphate -- for example -- the period would be much longer for a fruit tree than for a barley plant. Then there are to be considered those internal physiological factors which determine the growth of roots and the number of contacts which can be made with colloidal particles of the soil. Since organic acids have a special property of displacing phosphate from certain colloidal complexes, the question follows if some types of plants secrete -- or leave as a residue from root decay -- organic acids in such kinds and amounts as to result in important increases in the supply of phosphate to the root system. Finally, some recent researches have dealt with organic forms of phosphate which may escape fixation in the soil. Whether or not it is feasible to use organic phosphates as fertilizers, the relation of organic matter added to the soil to phosphate availability is important. All these questions of fixation of phosphate and potash have a practical bearing on the methods of fertilizer application. A recent agricultural writer suggests that one of the greatest practical advances in plant nutrition is found in the studies on the proper placement of fertilizers.

I am not sure the plan of this discussion has been a wise one, but I have at least made the attempt in this rapid survey to bring before you for further consideration aspects of investigations of soil and plant interrelations, which seem to me to represent some significant approaches to the general problems of plant nutrition. Perhaps much of what I have said may appear to have little direct bearing on the subject of sugar beet production. My own view would be that the sugar beet industry does have a vital concern with researches on basic principles of plant nutrition. It is true that the growing of crops is not now, and presumably never will be, subject to the precise control of a chemical factory. But we still may entertain high hopes, on the basis of past experiences, that increasing scientific knowledge in the field of this discussion will not fail in due time to yield economic rewards. I like to think also that those engaged in the growing and utilization of crops have an interest in the relation of the plant to its environment apart from considerations of economic gain.