NATIONAL ACADEMY OF SCIENCES

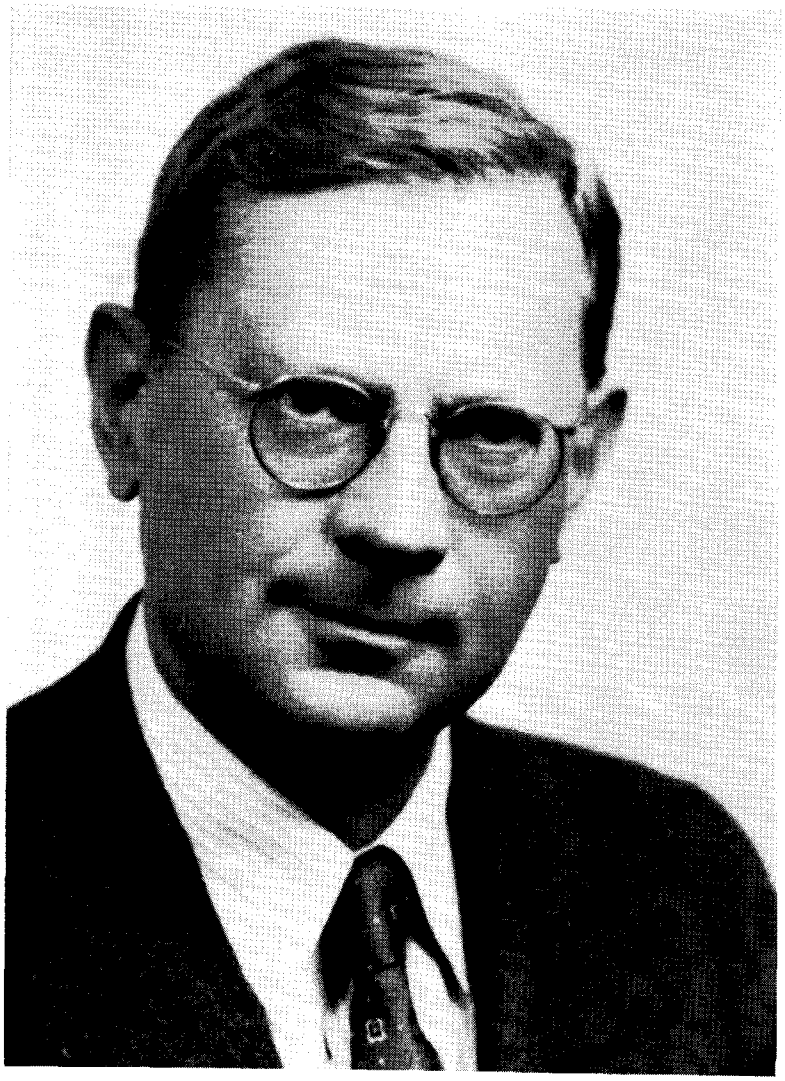
DENNIS ROBERT HOAGLAND

1884—1949

A Biographical Memoir by

WALTER P. KELLEY

Biographical Memoir



D R Hoagland

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THE DEATH of Dennis Robert Hoagland terminated the work of an exceptionally productive plant nutrition specialist. Coming on the scene at a time when but relatively little was known about the specific aspects of the mineral nutrition of plants, his researches made a lasting impression on scientific workers in this field. Hoagland was born in Golden, Colorado, April 2, 1884 and died in Oakland, California, September 5, 1949 after a lingering illness extending over several years. His scholastic education was obtained in the schools of Denver, Colorado, and his university and professional training was at Stanford University, where he specialized in chemistry, graduating with the A.B. degree in 1907. In 1913 the University of Wisconsin conferred on him the A.M. degree.

Hoagland's first position after graduation from Stanford was assistant chemist in the laboratory of M. E. Jaffa of the University of California beginning in 1908. In this position his work was largely routine analysis of feed stuffs for livestock and poultry. In 1910 he was appointed assistant chemist in the Food and Drug Administration of the United States Department of Agriculture where he was assigned to work under the late Alonzo Taylor, who was then engaged in investigating the toxicity of Al, Cu, and S compounds as contaminants of canned foods and dried fruits. In 1912 Hoagland was awarded a graduate scholarship in the University of Wisconsin, where he spent a year studying under E. V. Mc-

Collum. In 1913 he returned to Berkeley as Assistant Professor of Agricultural Chemistry in the University of California. In 1922 he was promoted to Associate Professor of Plant Nutrition and to the Professorship in 1927.

From 1913, when he returned to California, until his death in 1949 Hoagland's scientific work was centered in the University of California at Berkeley. It was here that he made major contributions in the field of plant nutrition. His work dealt with a wide range of plant nutritional problems, and also included several studies on the soil.

During American participation in World War I, when access to the then chief source of K in Germany was no longer available to the United States, Hoagland, under the general guidance of Professor John S. Burd, investigated the beds of giant kelp off the coast of California as a possible source of K for use in commercial fertilizers and also from the standpoint of its organic constituents. In connection with this work, Hoagland's attention was drawn to the remarkable ability of the kelp plant to absorb from ocean water and to retain in its tissues large amounts of K as well as of Br and I. This raised a question in his mind as to what is responsible for the absorption by growing plants of inorganic elements in general.

Reflection over this and related questions gave rise to a long series of investigations by Hoagland, culminating in many scientific papers. This work brought him wide recognition as a leading authority on the inorganic nutrition of plants.

When Hoagland's work was first begun, there was no acceptable explanation as to why plants are able to absorb elements from dilute solutions and especially at different rates. As a matter of fact, a full explanation still remains to be given. Nor has the exact function of most of the essential elements been determined as yet. But Hoagland made important advances towards an understanding of plant nutrition. His contributions will be discussed under appropriate heads.

SOIL SOLUTION

Some years before Hoagland became active in plant nutrition investigations, the publications of certain members of the United States Department of Agriculture had focused attention on the so-called soil solution, that is the constituents of the soil dissolved in the thin films of water surrounding the soil particles when the moisture content corresponds to that of good tilth. These investigators held that, since all mineral soils contain more or less the same kinds of minerals, the soil solution must be saturated with these minerals and therefore are essentially alike in all cases. Hoagland's work soon showed the essential falsity of this idea. He was able to show that, as the growth of plants takes place, the total concentration of the liquid phase of the soil may decrease substantially, also that the relative proportions of the several dissolved elements become markedly altered. In the case of those elements which are absorbed most rapidly by plants, their concentration in the soil solution declines significantly in response to absorption by the growing plant. Thus, the untenability of the previously held view was definitely established.

The investigations of Hoagland caused him to place special emphasis on the soil solution in its relations to plant growth. Perhaps it was but to be expected that he would tend to minimize the influence of other aspects of the soil. In retrospect it now seems probable that he unduly emphasized the role of the solution phase and underemphasized the solid phase of the soil. In principle this need not be surprising, for in dealing with other complex systems and complicated processes there have been many oversimplifications at one time or another in the history of science.

SOLUTION CULTURES

Hoagland's work on the soil solution together with his experiences in connection with studies on the giant kelp stimulated a long series of investigations designed to shed light on the process of absorption of nutrients by plants. Many phases of this complex subject were investigated by Hoagland and his assistants and students. When this work was begun, the prevailing views of plant physiologists about absorption were characterized by pronounced vagueness. His investigations definitely established that absorption of mineral nutrients by plants is a metabolic process and not a simple physical process depending on permeability, osmosis, etc., as had previously been assumed. The presence of free oxygen around the absorbing roots, the quality and intensity of the illumination, the temperature, and the carbohydrate status of the tissues all have marked effect on absorption. Nothing, perhaps, could better show that absorption by plants is not a simple osmotic process than the fact that the concentration of a given ion in the vacuolar solution of certain plants may attain a value manyfold that of the nutrient medium. In this work Hoagland was able to utilize most effectively the exceptionally large celled fresh water alga, Nitella, from which adequate quantities for analysis could be obtained of the vacuolar solution largely uncontaminated.

In the course of Hoagland's nutrient solution studies he prepared and used successfully in a wide range of experiments a particular solution which has come to be known all over the world as Hoagland's culture solution. The composition of this solution was originally patterned after the displaced soil solution obtained from certain soils of high productivity. However, the fact that Hoagland made extensive use of the nutrient solution which bears his name should not be interpreted to mean that he magnified its importance. He repeatedly emphasized that there is no such thing as the best nutrient solution. In other words, the optimum concentration and ratios of constitutent elements in the nutrient solution are not rigidly fixed. Rather, they may be varied over a considerable range without noticeable effects on the growth rate. Adequacy of the amount present of a given nutrient ion is vastly more important than concentration. Indeed, Hoagland showed quite definitely that certain plants are able to satisfy their requirements for nutrient elements and at the same time to grow at a normal rate in quite dilute nutrient solutions, provided the volume of the solution available to the absorbing roots is sufficiently large.

Another point of special interest that came to light in the course of Hoagland's researches is that certain species of plants are able to grow equally well in solutions of widely different pH, which was quite contrary to the prevailing view among plant physiologists at that time. Over a rather wide range of H-ion concentrations the important matter is not the pH of the nutrient solution but the adequacy of supply of all essential nutrient elements. However, Hoagland clearly recognized that pH may have great effect on the availability of certain elements in the soil, probably through its effect on solubility.

Hoagland investigated, mainly by solution culture technique, many aspects of absorption. As indicated above, he showed that free oxygen around the roots of plants plays an extremely important role. Indeed without free oxygen absorption is at first retarded, and later ceases altogether. At the same time, growth is inhibited. Respiration, as indicated by CO_2 given off by the roots, is likewise related to the oxygen supply as well as to the carbohydrate status of the tissues and the absorption of inorganic nutrients. Thus it follows that respiration affords the necessary energy for absorption. Likewise, temperature also plays an important role. Hoagland showed that absorption is closely correlated with temperature and that permeability and osmosis as understood by early biologists are entirely inadequate to account for absorption.

Hoagland and his associates made many experiments on the several aspects of the movement of solutes in plants. He determined the actual paths taken by nutrient elements in passing from the absorbing roots to the several parts of the plant. In this work, radioactive isotopes were found to be especially useful. He followed the course of the movement in the zylem, phloem, woody and bark tissues of the plant. In general, it was found that the absorbed elements pass chiefly along the path of living tissues, and that transpiration, although related to the movement of solutes, by no means accounts for all translocation of solutes. In collaboration with his associates Hoagland was able to show that electrolytes pass around incisions in the plant and that P in particular normally follows well defined channels in the plant, finally becoming largely concentrated in the reproductive organs.

Hoagland laid special emphasis on the importance of the activity of living cells in the whole sequence of events connected with the absorption and movement of solutes within the plant. The expression, metabolic process, repeatedly used by him, was meant to include the whole range of the activity of living cells.

The biochemical aspects of absorption were considered by Hoagland in relation to respiration, organic acids, the utilization of nitrogen in different forms, protein synthesis, etc. He was impressed with the needs for detailed knowledge concerning the specific chemical reactions that are involved in the absorption of nutrients by plants and in their growth. He showed that there is a fairly definite relation between anion and cation absorption and also in the movement of each within the plant. In certain cases, cations are absorbed more rapidly than their associated anions; in others the reverse was found.

Although Hoagland did not determine the specific chemical reactions in which any of the essential elements take part in absorption and growth processes, nevertheless, he was convinced that the indispensability of these elements must rest on chemical reactions and that these reactions are of vital significance in the growth processes. Throughout his extensive researches his purpose was, evidently, to shed light on the role of the elements in terms of known chemical and physical principles. It is safe to say that he rejected the idea that something mysterious is involved in the processes of living plants. To be sure, he referred again and again to absorption and translocation of the elements as metabolic processes, but this does not mean that he conceived these processes as being controlled by anything but straightforward chemical and physical forces.

However, Hoagland clearly recognized that the processes involved directly or indirectly in absorption and translocation of the nutrient elements are extremely complex. He, therefore, distrusted simple explanations. Upon many occasions and in various ways, he evinced disapproval of attempted theoretical explanations. He was convinced that the compelling need was for facts rather than for theory. This does not mean that he believed in the absence of scientific principles as the controlling force in absorption and growth processes; in fact, quite the contrary. He held that when enough facts are available they may be integrated into a sound theory, but that, unsupported by facts, theory serves little or no useful purpose. Hoagland was, therefore, primarily an experimentalist rather than a theorist.

SOLUTION VERSUS SOIL CULTURES

Numerous experiments by Hoagland and his associates demonstrated that many plant species, normally grown in soil, thrive well in properly aerated solution cultures; in fact, their whole life cycle can be completed, apparently normally, when grown in nutrient solution. This, of course, was already known from the work of previous plant physiologists. However, one of Hoagland's colleagues came to emphasize solution-culture technique, under the name of hydroponics, as a substitute for soil culture. The claim was made, either directly or by obvious implication, that hydroponics affords a practical means of crop production, and that yields much greater than are normally obtained from soil can be obtained by this means. The propaganda literature on hydroponics became widespread and voluminous.

As a means of testing some of the wild claims then being made, Hoagland in collaboration with Arnon set up an experiment in which a solution culture, arranged in the maner recommended for hydroponics, could be fairly compared with a fertile soil as media for the growth of tomatoes. The experiment was made in the greenhouse with all conditions other than the nutrient medium essentially alike. The soil used was naturally quite productive but was further enriched by thorough mixing with a heavy application of barnyard manure. Soon it became apparent that there was no essential difference between the nutrient solution and this soil as culture media for tomato plants. Exceptionally large and approximately equal yields of fruits were obtained from both cultures. The alleged superiority of hydroponics thus seemed to be largely fictional.

The advantage of hydroponics, if indeed there be any, must rest then, not on the intrinsic superiority of a free solution as a medium for plant growth, but rather on the ease of maintaining near optimum concentration of the necessary nutrient elements. As already pointed out Hoagland showed that under ordinary soil conditions, the concentration and relative ratios of essential elements in the soil solution may change rapidly as absorption by growing plants takes place. Further evidence that plants do not necessarily grow best in a free solution is found in the fact that sand cultures irrigated at suitable intervals with a nutrient solution are not inferior to the nutrient solution as culture media.

Hoagland, therefore, was inclined to look upon the soil as performing its chief function in plant growth by serving as the immediate source of plant nutrients, and that the essential elements become absorbable by plant roots by first passing into solution in the soil moisture. Something closely similar to this view has been uppermost in the minds of agronomists and soil scientists ever since the time of Liebig. Undoubtedly solubility is a most important consideration. Unfortunately recognition of this fact has tended to cause soil scientists to neglect the investigation of the processes and principles by which the nutrient elements become available to growing plants.

MINOR ELEMENTS

Previous to about 1920 practically all plant physiologists held that only ten elements are essential to the growth of plants. More recently a number of other elements have been found to be necessary. Hoagland had an important part in these new advances. In association with W. H. Chandler he discovered that the abnormality of peach trees, known as "little leaf" and previously referred to as a "physiological disease," was caused by zinc deficiency. This soon led to the finding that the widely occurring condition in the growth and functioning of citrus trees known as "mottle leaf" is likewise caused by zinc deficiency.

A noteworthy feature of these researches is the discovery that, at least with certain species of fruit trees, zinc deficiency can be overcome readily by a dilute solution of zinc applied as a spray to the foliage rather than to the soil. In fact zinc dust applied to citrus trees is quite effective. This, of course, denotes that absorption is not limited to the roots of plants.

By the use of carefully purified salts dissolved in especially prepared distilled water and held in special kinds of containers, Hoagland was able to establish the essentiality of molybdenum for the growth of tomato plants. Through his work and that of several other students of the subject, it is now generally recognized that some half-dozen elements in addition to the original ten are absolutely necessary for the normal growth of many species of plants. The list of essential elements is augmented more or less continuously and the end is by no means certain. It is quite possible that minute amounts of many other elements are required for the normal functioning of plants in general.

A notable feature of the minor-element question is the fact that the range in permissible concentration of some of these elements is quite narrow. If the concentration of Cu, for example, exceeds a very low value, marked toxicity develops, although a small amount is absolutely essential for the normal growth of many plant species. On the other hand, the concentration of Ca and other of the so-called major elements may be varied rather widely without injury to the growth of plants. The reason for this difference is not known. As a matter of fact the specific function of none of the required elements is fully known. This is one of the many unsolved problems that confront plant physiologists.

SOIL INVESTIGATIONS

The center of Hoagland's interest and the major part of his scientific work were on plant nutritional problems. It was in this field that he made his most notable contributions and for which he became known and his influence felt all over the scientific world. Nevertheless, he manifested considerable interest in certain aspects of more strictly soil science questions. Early in his career Hoagland, in collaboration with L. T. Sharp, showed that the so-called pH of the soil is amenable to measurement by the H electrode. Growing out of this pioneering work, the literature on soil pH has become voluminous until now pH determination is one of the most common measurements that is applied to soils by soil scientists, agronomists, horticulturists, and agricultural workers in general.

Another soil question received considerable attention from Hoagland, namely, the so-called fixation of K by soils. In this work, although essentially empirical, he and his associates showed that the power of certain soils to withdraw K from solution and hold the same rather tenaciously are especially marked. He found that this property of certain soil types is associated with what is known in California as die-back of prunes, and that the disturbance can be overcome, at least in part, by large applications of soluble K compounds. The specific cause of this fixation of K still remains to be determined.

Being a member of the faculty of the College of Agriculture, Hoagland, as would be expected, took special interest in soil-plant interrelationships. He sought a better understanding of what is commonly known as the availability of plant nutrients in soils. To this end, he investigated such questions as the K supplying power of the soil, the rate of solution of K, exchangeable and non-exchangeable K, the relation of Ca, P and N to the absorption of K, the role of K in the buffer system of the plant, and other related questions. None of these researches led to definite conclusions of immediate practical value.

In 1919 Sharp and Waynick called attention to the marked variability of the soils of California. This made a lasting impression on Hoagland and influenced his outlook for the remainder of his life. It led him to question the value of field experiments as they were currently being conducted. In addition he came to have strong misgivings about the value and interpretation of soil analyses both partial and complete. The rate of solution of certain nutrient elements of the soil appears to be highly important in the growth of plants and this is not ordinarily determined by soil analysts.

Hoagland seemed to think that a guide to practical fertilizer application can be most reliably obtained by trial and error. Unfortunately this is still the case to a large extent and is probably destined to remain so for some time. To be sure, it is well established that by empirical chemical methods a working guide can be obtained regarding the fertilizer requirements of many soils, but marked exceptions are frequently found. With better knowledge about the essential principles that govern soil processes, it seems reasonable to expect that soil science will become more exact. Hoagland's views on this subject were reflected in his papers on Fertilizer Problems and Soil Analysis published as Circulars of the California Agricultural Experiment Station. Perhaps, it was partly because of his doubt about the value of soil analysis that he directed major attention to the plant rather than the soil.

Thus, it is apparent that Hoagland's work dealt with a wide range of problems. Undoubtedly, his most important contributions were on the absorption of minerals nutrient elements by plants and their relations to physiological processes. Although he clearly established that absorption and related processes are essentially metabolic in nature, it was this general fact rather than the mechanism of the process or the chemical or physical forces involved in the process with which he dealt and on which his researches shed the greatest light.

Hoagland's work attracted the attention of and markedly stimulated many scientific workers in this field. In the course of his studies, he became well acquainted with the literature on the subject. A large element in his success was his personality. He had the happy faculty of stimulating his associates and was ever ready to confer with his associates and students and to lend friendly advice and help. It was this, rather than the originality or profundity of his ideas, that was largely responsible for his influence. Students of plant nutrition were attracted to him from many countries and his advice was sought by many scientists. He came to be recognized as an authority on plant nutrition. This is attested by the fact that he was requested to serve as consultant and collaborator in two different branches of the United States Department of Agriculture, namely, the Salinity Laboratory at Riverside, California and the Animal Nutrition Laboratory at Cornell. In this capacity he served each of these laboratories for many years.

In 1929 the American Society of Plant Physiologists bestowed on Hoagland the Stephen Hales Award. In 1934 he was elected to membership in the National Academy of Sciences. The American Association for the Advancement of Science awarded him a $1,000 prize for the outstanding paper presented at the Philadelphia meeting in 1940. A specially notable mark of esteem for his scientific work is found in the invitation extended to him by Harvard University to give the Prather Lectures in 1942. These lectures were published in book form by the Chronica Botanica Company in 1944. In the same year he was selected by his colleagues in the University of California at Berkeley to give the annual Faculty Research lecture.

Hoagland was a member of many scientific organizations. He was president of Western Society of Soil Science (1924); Botanical

Society of America, Pacific Division (1929); Western Society of Naturalists (1931); American Association for the Advancement of Science, Pacific Division (1941). For many years he was Consulting Editor of *Soil Science, American Journal of Botany,* and *Plant Physiology*. He was a member of Phi Beta Kappa, Sigma Xi and Phi Lambda Epsilon honor societies.

Professor Hoagland was not narrowly interested in science; current world movements and problems were of special concern to him. These he often discussed with friends. He was blessed with a friendly and approachable disposition and had many close friends. Hoagland took an objective view whatever the subject, and was never too busy to confer with colleagues, students, and friends. He made a lasting impression on everyone with whom he came in contact. Politically Hoagland was a liberal in the best sense. He took active part in the work of the faculties of the University, serving on many committees including the chairmanship for one year of the arduous Budget Committee of the faculty. From 1922 until near the time of death he was chairman of the Division of Plant Nutrition and for one year he also served as chairman of the Department of Botany.

Hoagland was married to Jessie A. Smiley in 1920, who died prematurely in 1933 leaving him the care and upbringing of three sons. He took great interest in his family and was deeply concerned about the education and welfare of his sons.

KEY TO ABBREVIATIONS

Agr. Chem. = Agricultural Chemicals
Am. J. Bot. = American Journal of Botany
Am. J. Phys. = American Journal of Physiology
Ann. Rev. Biochem. = Annual Review of Biochemistry
Biol. Rev. = Biological Review
Bot. Gaz. = Botanical Gazette
Bot. Rev. = Botanical Review
Calif. Agr. Expt. Sta. Circ. = California Agricultural Experiment Station, Circular
Calif. Agr. Expt. Sta. Hilg. = California Agricultural Experiment Station, Hilgardia
Calif. Agr. Expt. Sta. Tech. P. = California Agricultural Experiment Station, Technical Paper
Contrib. Marine Biol. = Contributions to Marine Biology
Int. Conf. Soil Sci. = International Conference of Soil Science
Int. Cong. Soil Sci. = International Congress of Soil Science
J. Agr. Res. = Journal of Agricultural Research
J. Biol. Chem. = Journal of Biological Chemistry
J. Gen. Phys. = Journal of General Physiology
J. Ind. Eng. Chem. = Journal of Industrial and Engineering Chemistry
Mo. Bull. Calf. Dept. Agr. = Monthly Bulletin of California Department of Agriculture
Plant Phys. = Plant Physiology
Proc. Am. Soc. Hort. Sci. = Proceedings American Society of Horticultural Science
Proc. Am. Soc. Sugar Beet Tech. = Proceedings American Society of Sugar Beet Technology
Rev. Arch. Biochem. = Review Archive Biochemistry
Sci. Agr. = Scientific Agriculture
Sci. Mo. = Scientific Monthly
Soil Sci. = Soil Science
Soil Sci. Soc. Am. Proc. = Soil Science Society of America Proceedings
Sci. Univ. Calif. = Science in University of California
Trans. Far. Soc. = Transactions of Faraday Society
Trop. Agr. = Tropical Agriculture
Univ. Calif. Pub. Agr. Sci. = University of California Publications in Agriculture Science

Univ. Calif. Pub. Path. = University of California Publications in Pathology

Univ. Calif. Pub. Phys. = University of California Publications in Physiology

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