Dennis Robert Hoagland: 1884–1949

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DENNIS ROBERT HOAGLAND, professor of plant nutrition in the University of California, distinguished plant physiologist, and the world's leading authority in the field of plant and soil interrelations, died in Oakland, California, on September 5, 1949. For more than thirty years, Professor Hoagland's life and work exerted a profound influence on the evolution of plant and soil science in America and abroad. But, as with most great men, the totality of his achievement is greater than the sum of his impressive individual contributions. He personified the qualities of mind and character that led some to observe that the scientist with a broad outlook on his work and the world around him is among the finest products of Western civilization.

D. R. Hoagland spent his first eight years in the town of his birth, Golden, Colorado; his later childhood was passed in Denver, where he received his primary and secondary education. During his high-school days he first acquired a definite interest in science, in his own words "as a result of discussions of the theory of evolution which was condemned at that time by many ministers of the city: my thinking was greatly stimulated by the ideas and points of view of biology with regard to man's place in nature."

Hoagland left Denver to enter Stanford University, where he elected chemistry as his field of study. Upon his graduation in 1907 he was elected to Phi Beta Kappa and to the Chemistry Honor Society (now Phi Lambda Upsilon). After graduation he undertook graduate work in chemistry at Stanford, but in January 1908, he took a fateful turn in his career by accepting a position as an instructor and assistant in the laboratory of Animal Nutrition at the University of California. The new position brought him for the first time into professional contact with biology and took him to Berkeley, where, except for a few short gaps, he was to spend the rest of his life.

Hoagland remained in the field of animal nutrition and biochemistry from 1908 to 1913. In 1910 he joined the Consulting Referee Board of Scientific Experts of the USDA, an assignment that took him to Philadelphia. After the completion of the work of the Referee Board in 1912, he accepted a graduate scholarship to work in animal biochemistry with E. V. McCollum in the Department of Agricultural Chemistry at the University of Wisconsin. In later years Hoagland looked back on the year of graduate study under Professor McCollum as his real inspiration for a life devoted to scientific research. In 1913 he received his Master's Degree, and in the same year published with E. V. McCollum a series of three papers on the *Endogenous Metabolism of the Pig as Modified by Various Factors.*

In 1913 Hoagland had thus completed a period of five years of continuous work in animal nutrition, and there would normally have been every expectation that he would continue in this field, which was then on the eve of revolutionary advances. Circumstances intervened, however, and he abandoned the subject in which he had already amassed considerable experience. For this, plant science will always remain indebted to John S. Burd, then head of the Division of Agricultural Chemistry, College of Agriculture, University of California. In 1913 Professor Burd invited Hoagland to come to Berkeley as an assistant professor of agricultural chemistry. His acceptance initiated his scientific activity in a field in which he worked with distinction till the end of his days.

The appointment in the Division of Agricultural Chemistry of the University of California was a real opportunity to one who had already acquired an attachment for fundamental research. The department was chiefly interested in problems of fertilizers and soil chemistry. Practical and immediate as these questions appeared, Burd had the vision to encourage the search for principles rather than *ad hoc* solutions.

The interruption of commerce in World War I focused attention on American dependence on German sources of potash fertilizers. There was considerable interest in exploring domestic sources of potassium, and the giant kelps of the Pacific Coast were suggested as a possible source of supply. Hoagland undertook a systematic study of the inorganic and organic composition of kelps. His conclusions as to the possibility of commercial exploitation of these organisms were not very encouraging, but this research led him into an investigation of the accumulation of ions by plants. He was impressed with the remarkable ability of kelps to accumulate potassium and iodine many times in excess of the concentrations found in sea water.

The second of his early research activities concerned itself with the effect of hydrogen ion concentration on plant growth. This was the era of "hydrogen ion concentration" in biology, when great expectations were centered around the introduction of the hydrogen electrode for the measurement of pH of biological systems. One of the accepted tenets of agricultural teaching in those days was that plants could only grow well at neutral or slightly alkaline reactions. It was with great surprise, therefore, that Hoagland discovered that barley plants made excellent growth in nutrient solutions at pH 5. It seemed that the chief importance of the hydrogen ion was in relation to other ions rather than in its direct effect on the plant. It was also apparent that the inherent complexity of soils rendered untrustworthy many sweeping generalizations based on local conditions. It became clear that the complex problems of soil and plant interrelations must be studied by techniques that would permit rigid experimental control and the isolation of individual variables.

He gave expression to his convictions about the value of artificial culture methods in plant research by developing the water-culture technique for growing plants. Under the influence of the soil solution studies conducted by Burd, Hoagland devised a culture solution to imitate a soil solution obtained from a soil of proven fertility. "Hoagland's solution" became, and remains to this day, a "household" term in laboratories of plant physiology throughout the world. The formulation of his culture solution was accompanied by a study of certain basic concepts, such as concentration versus total supply of ions, specific proportions of nutrients and the like, which underlie the use of nutrient solutions. He critically examined and rejected the idea of an "optimum nutrient solution," a point of view fully corroborated by later work.

His early researches into plant and soil chemistry convinced him that the study of soil and plant interrelations could be pursued most auspiciously by a closer union between workers in soil chemistry and plant physiology. This opinion was given administrative sanction in 1922 by the organization of a Division of Plant Nutrition within the University of California College of Agriculture. Hoagland was designated its head. In the new division his major research interest became the absorption and accumulation of ions by plants. The quality of the immense contribution which he, with his collaborators and associates, made to this fundamental process of plant physiology can only be judged against a background of the ideas and concepts that prevailed when his work got under way. There was no clear view as to how inorganic elements are absorbed by plants. Discussions of this subject usually invoked such concepts as osmosis, permeability, antagonism, none of which, as he later demonstrated, could explain the absorption, accumulation, and retention against a concentration gradient of anions and cations by plant cells.

Hoagland opened the study of ion absorption by using intact barley plants. Promising as the early results were, he readily perceived the advantages of working with a unicellular organism from which relatively pure vacuolar sap could be obtained. At the suggestion of the late Nathaniel Gardner, he selected the fresh-water alga *Nitella*. This work clearly demonstrated that absorption of ions by plants is a metabolic process and not a question of simple permeability. For example, absorption and accumulation of bromide could take place in Nitella only under the right metabolic conditions—proper temperature and illumination. The accumulated ions were not precipitated in the sap but remained as free ions, the concentration of electrolytes in the Nitella sap being twenty-five times greater than that in the surrounding medium. Although the concept of "ion antagonism" had no strict applicability to the normal process of nutrient absorption, there was clear evidence of reciprocal effects of one ion on the absorption of another, as, for example, potassium on calcium and nitrate on phosphate. Here was painted in bold outline a theory which at once correlated a host of observations in the field and laboratory and made it possible to approach an infinitely complex subject with principles instead of mere empirical observations.

The next important phase of his researches on ion accumulation brought him closer to the problem that was uppermost in his mind—the absorption of nutrients by the roots of higher plants. In its solution, Hoagland displayed his remarkable gift for resolving a complex question into its essential components and arranging them unerringly in an order of relative importance. Though a chemist by training, he early acquired the outlook of a biologist and was mindful of the inherent complexity of biological systems and their adaptivity to varying conditions; hence he distrusted the spectacular short-cut or facile generalization unless it was supported by solid experimental evidence. As far as salt absorption by roots was concerned, he decided in the late 1920s that the most important prerequisite for future work was the development of a technique that would make available biological material of a definable and reproducible physiological status. Only in this manner could the various conflicting observations be resolved and a systematic effort directed toward the elucidation of unknown factors.

He concluded that the fundamental questions of ion absorption by root cells can be studied most effectively by eliminating the complications of shoot and root relationships. He concentrated, therefore, on excised roots obtained from plants grown under experimental conditions designed to yield, subsequent to the removal of shoots, root systems with a high capacity for salt absorption. Among the essential conditions for a high capacity for ion absorption by roots were a low salt and a high carbohydrate status. Under these conditions the excised roots were found to be "the most active salt-accumulating system so far [1936] investigated."

Once the tedious but indispensable job of evolving a suitable physiological technique was completed, progress was rapid and gratifying. An impressive array of data was amassed over the years on the influence of temperature, light, hydrogen ion concentration, ion selectivity, concentration of anions and cations, differences in rates of absorption, and the effect of one ion on the absorption of another ion of the same or opposite charge. A striking correlation was obtained between the supply of oxygen and the absorption of salts by roots against a concentration gradient. A solid scientific foundation was thus laid for the understanding of the importance of aeration in soils and for the interpretation and prediction of a multiplicity of plant responses to fertilization treatments, and other chemical changes in the soil.

The final phase of Hoagland's investigations on absorption of ions occurred just before and during World War II. With excised barley roots he studied the effect of reversing the external concentration gradient on ion entry and the influence of inhibitors on ion accumulation. He returned to Nitella, this time employing radioactive isotopes—a sensitive technique that permitted the separation of the two stages of ion absorption by cells: from the external medium into the cytoplasm, and from the cytoplasm into the vacuole. The fundamental conclusion, which he and his colleagues reached almost two decades earlier, that ion accumulation is a metabolically linked process, was confirmed. With the use of radioisotopes it was possible to show that ions first accumulate in the cytoplasm, but that subsequently they migrate to the vacuole by a process akin to secretion, until the vacuolar concentration becomes higher than that in the cytoplasm and decidedly higher than that of the external dilute solution.

Dominant as his lifelong interest in the process of ion absorption was, it by no means prevented him from pursuing with vigor other phases of plant nutrition, to which he, with his associates, made outstanding contributions. He studied the upward movement and distribution of inorganic solutes in the plant. In the late 1930s, when radioactive isotopes from the cyclotron became available, he used them in resolving some of the hitherto perplexing uncertainties as to the path of ion movement in higher plants. In a series of experiments on the relation between the movement of solutes and absorption of water by plants, he again demonstrated the extent to which the two are related to, as well as independent of, each other.

Hoagland was keenly aware of the immense importance for physiological studies of the control of light, temperature, and humidity, as well as of the culture medium. He was instrumental in securing an installation for the control of environmental factors in Berkeley, one of the first in America. He envisaged "the development of a quantitative plant physiology in relation to mineral nutrition when it will be possible to do exactly the same thing twice."

Preoccupation with precise laboratory experiments and insistence on an exact though "artificial" culture condition in no way diminished his appreciation of the importance of direct studies on soils and on crops grown in soil. In his own words,

> Viewing the field as a whole, the attack on problems of plant nutrition assumes wide dissimilarity of method. At one time, the appropriate tool may be a spade or a soil auger; at another time a highly specialized and refined tool of physics or chemistry may be required. For some purposes, crude measurements in terms of pounds or ounces may suffice; for other purposes, a thousandth of a milligram or even much less than that is of consequence.

His own work on problems of soil chemistry insofar as it affects the nutrition of crops grown in the field was especially concerned with zinc, potassium, and phosphate deficiencies of fruit trees in California. He contributed to the identification of one of the most important physiological diseases of fruit trees in California—"little leaf"—with zinc deficiency, and reproduced it under controlled greenhouse conditions. His investigations of potassium nutrition had a bearing on "prune dieback," another nutritional disease of fruit trees in California, and led to extended studies of the chemical aspects of potassium availability in soils. His interest in the nutrition of fruit trees continued, and in 1940 he produced, under controlled conditions, the first molybdenum-deficiency symptoms in a fruit tree species.

In summarizing Hoagland's contribution to plant nutrition, it is pertinent to record that he did not regard the field as a unified discipline. In his own words, "An essential condition in the field of study of Plant Nutrition . . . is the uniting, although not according to any rigid pattern, of persons of varied technical interests, in a research program that has a common objective." Although he himself was mainly engaged in studies of the mineral nutrition of plants, he was keenly aware of the importance of the biochemical aspects of plant nutrition. Under his leadership the Division of Plant Nutrition became an outstanding center of research, encompassing a diversity of investigations seldom encountered within the confines of a rather small administrative unit. His scientific influence was not confined to the numerous graduate students who sought the privilege of associating with him; it included many mature scholars and colleagues from all parts of the world who came to work in his laboratory at Berkeley.

Hoagland's entire life as a productive scientist was spent in association with agricultural research. He had a profound faith in the importance to agriculture of fundamental research, without thought and expectation of immediate practical returns. He was fully aware of the often wide gap between the laboratory result obtained under controlled conditions and field application. In dealing with living plants and animals he was mindful that "it still takes the wheat plant six or nine months to develop and cows bring forth their calves neither more quickly nor more numerously for us than they did for Abraham." He believed that the contribution of science to agriculture must be judged not only by its material achievements but also by the enlightenment it proffers to the farmer and city dweller alike.

As an administrator, Hoagland was anxious not to fritter away his time and energy on the minutiae of scientific housekeeping and administrative procedure but sought to discharge his responsibility to the university by concentrating on the encouragement and development of the broad aspects of his field of science. In relations with his colleagues, young and old, he always comported himself with the courtesy and understanding of the true scholar for the scientific interests and activities of others. He was singularly free from any notion that notable advances in fundamental knowledge can be attained by administrative direction.

He was an ideal collaborator in scientific research, never seeking dominance for his own point of view but always inviting a free flow of ideas. He was meticulously careful in giving credit where credit was due and was generous in acknowledging the contributions of his associates. He was a master of clear exposition and had a real feeling for style, but he always preferred to defer publication of results until the evidence was carefully assembled and checked.

Hoagland's chief characteristic, whether in scientific matters or in personal relationships, was integrity and objectivity of outlook. In evaluating scientific evidence he had the "four things" which Socrates said "belong to a judge: to hear courteously, to answer wisely, to consider soberly, and to decide impartially." He applied the same critical standards to his own work as to that of others. He accepted no blanket authority in science and expected every single piece of research to stand on its own merits regardless of its source. In personal relationships he possessed the engaging quality of always seeking the good in men and their work. In approaching students he had a rare gift of making them sense the good will and confidence in their ability with which he always credited them at the start. His students were spurred to special efforts by a desire to prove themselves worthy of his trust. Hoagland's confidence and friendship once given were not easily withdrawn. Never demonstrative in manner, he had a deep loyality and an unfailing concern for the welfare of his friends and associates.

Hoagland carried the scientific mode of thinking outside his own specialty into diverse areas of human thought and achievement. He maintained an active interest not only in many departments of science but also in fundamental questions of education and in the social and political problems of the contemporary scene. It was a stimulating experience to witness his well-stocked mind analyze a complex issue with clarity and insight that unerringly penetrated to the root of the matter. In the seventeen years during which I was associated with him as student, colleague, and friend, I never once heard him discuss a person or an issue, scientific or otherwise, except in a fair and objective manner.

It is only natural that his accomplishments, his qualities of mind and character, should gain him wide recognition and many honors. His counsel was sought and valued within his own university, to which he gave unstintingly of time and effort in many arduous administrative assignments, usually at the expense of his own leisure and in later years at the expense of his health. In 1934 he was elected a member of the National Academy of Sciences. The American Society of Plant Physiologists, which was his closest scientific affiliation, bestowed upon him its highest honor by granting him, in 1929, the first Stephen Hales Award in recognition of his outstanding research contributions. He was also elected president of the society and occupied other important offices in it. The high esteem in which he was held by plant physiologists throughout the world is attested by his appointment as president of the Section of Plant Physiology at the VIIth International Botanical Congress in Sweden this year. Unfortunately, poor health forced him to decline this international honor.

Many other societies in which he held membership honored him by election to their presidency: Western Society of Soil Science (1924); Western Society of Naturalists (1931); Botanical Society of America, Pacific Division (1929); American Association for the Advancement of Science, Pacific Division (1941). He served as consulting editor for *Soil Science* and took a prominent part in the organization of the *Annual Review of Biochemistry*, serving from its very inception on the Advisory Board and, later, on the Board of Directors of *Annual Reviews*. He was a member of the Board of Collaborators for the U. S. Department of Agriculture Salinity Laboratory at Riverside, California, and the Soil, Plant and Animal Nutrition Laboratory at Cornell University.

In 1940 the American Association for the Advancement of Science awarded him its $1,000 prize for the outstanding paper presented at the Philadelphia meetings. In 1942 he was invited by Harvard University to give the John M. Prather lectures. The lectures were later published in book form and constitute the only book that he found the leisure to prepare. His own colleagues in the various faculties bestowed upon him the highest honor within the university by appointing him faculty research lecturer in 1942.

Hoagland was never in robust health, but a strong sense of duty compelled him to work without a thought for his own personal well-being. The last four years of his life were marred by serious illness, but he carried on with courage and determination to within the last few months of his life, when his eyesight failed him almost completely. This latter blow was the severest of all, for throughout his life he enjoyed reading on a wide variety of subjects. It was characteristic of the man that once he gave up hope of regaining his health, he requested retirement from the university, ignoring the serious financial adjustment that such a step would involve. He was officially retired on July 1, 1949, and died two months later.

In 1920, he married Jessie A. Smiley, who died in 1933, leaving him the responsibility of bringing up three young boys. His three sons, his mother, and a brother survive him.

The scientific influence of Professor Hoagland's life has not come to an end with his death, but will continue through the deep impression it has made on the minds and hearts of his students and friends.