INTRODUCTION TO VOLUME III

Trends in the Inorganic Nutrition of Plants

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Autotrophic plants can survive in an inorganic world. Indeed, the ability of plants to subsist on inorganic sources of nitrogen (nitrate or ammonia) is at least one of their distinguishing characteristics. The ability to utilize even elementary nitrogen, by biological nitrogen fixation (which is somewhat more widely dispersed through the plant kingdom than used to be thought) represents the highest degree of autotrophy for nitrogen. From this point of view certain blue-green algae that can both fix nitrogen and carry on photosynthesis are perhaps the most autotrophic organisms which are known. This may be part of their survival value and their role as early colonists of naked surfaces, which are otherwise free of organic matter, surfaces which range from volcanic laval slopes to the raised muds of salt marshes.

Essential and Dispensable Elements

When one considers the surprisingly small number of elements of the periodic table with which nature has elaborated the form and substance of plants, the elements of water and of carbon dioxide may be, and usually are, treated separately. The remaining elements are distinctively of mineral origin. Water is not usually considered to be a nutrient. However, water is by far the most abundant molecular species in cells and organisms. It may be calculated, for example, that a carrot root cell may contain about 10^{17} water molecules and about 10^{8} protein molecules of an assumed, but probable, average molecular weight. A nutrient is that which nourishes and out of which the substance of plants is built; in this sense water certainly performs an essentially nutritional role. In fact, so high is the percentage of water that one may say that the minute amount of mineral matter and the larger, but still small, amount of organic matter which constitute the organization of plants is what imparts to the mass of water they contain the distinctive properties by which the organisms are recognized. A medusa in the sea may be almost entirely composed of water, but its relatively minute amount of salts and organic matter impart to this mass of water the organization which makes it the distinctive creature that it is.

Thus, although not commonly regarded as an inorganic nutrient, water nevertheless enters into all aspects of the physiology of plants as the essential medium in which biological reactions occur, the essential and most abundant stuff of which plants are made and, through hydrogen bonding, water is also an essential part of the architecture of the complex substances and large molecules so important in the microscopic and submicroscopic morphology of living things. Water is also the molecule from which hydrogen is transferred to cause reduction, and to which it is restored in the essential step of transfer to oxygen, as in the terminal oxidative step of respiration. Thus water is the essential basis of so many of the energy exchanges in cells. Being composed of very small atoms, and by reason also of its molecular asymmetry, water packs a large amount of matter in the minimum of space and its physical properties (specific heat, latent heats of fusion and of vaporization, dielectric constant, surface tension) are unique among liquids at the prevailing temperatures of this earth. Therefore, one can as little conceive of life, as we know it, without the properties of water as one can conceive of it without the distinctive properties of carbon and of that element's ability to combine with itself to form the rings, chains, films, fibrils, and lamellae and the large molecules out of which the form of cells and organisms is so largely built. Thus, although commonly they are considered separately, the elements C, H, and O have their premier place in the list of essential elements.

The rich variety of the plant kingdom, from the thallophytes to the angiosperms, and the range and complexity of the physiological functions and biochemical reactions of plants are achieved by utilizing the chemical properties of only a very few of the total chemical elements of the periodic table. Though it is a long way from the "Earth, Air, Fire, and Water" of Aristotelian doctrine to modern knowledge of the ten essential macronutrient elements (C, H, O, N, P, S, K, Ca, Mg, Fe), to the five well-established micronutrient elements for angiosperms (B, Mn, Cu, Zn, and Mo) and to the more recently established elements which are either generally essential or beneficial in certain situations (Cl, Na, Si, and V), it is still surprising how dispensable are so many of the chemical elements, even those that are most abundant in the earth's surface.

The elements most utilized by plants are certainly not those which are the most common. Despite the abundance of sodium, it is so dispensable and so unable to replace the essential role of potassium that only recently has it been added to the list of elements that are essential for certain land plants (cf. Chapter 2). However, one cannot conceive of sea water and of marine plants apart from the properties of sodium.

Aluminum and silicon are also among the most abundant chemical elements in the earth's crust, but again, apart from certain special situations in which they may contribute to the skeletal substances of plants (as for example silicon in diatoms and in certain plant cell walls), these elements also are essentially dispensable. But aluminum and silicon, like carbon, enter into chemical configurations which permit almost indefinitely repeating patterns in space. However, carbon, by its small size and its ability to combine directly with itself, can form such repeating patterns alone, whereas other elements (oxygen, aluminum, boron, etc.) must be interposed in the case of silicon. Thus, while carbon forms the essential skeleton of many large molecules important in nature and together with nitrogen and phosphorus forms the essential structure of proteins and nucleoproteins, without which terrestrial biology could not exist, the large molecules which are built from silicon, with aluminum and oxygen, etc., provide the repeating patterns in space, which are the basis of much inorganic form in minerals and in soils. But for all practical purposes the elements silicon and aluminum are dispensable by plants.

It is almost essential to believe that primeval life utilized the minimum number of elements and, as morphological specialization developed, its requirements became more exacting, and life adapted to and utilized the special properties of an increasing range of substances. In this way the properties of a given chemical element could be used in a given molecular situation. The highly specialized molecular situations in which micronutrient or trace elements form part of specific enzymes are obvious examples here. The more advanced and specialized cells and organisms become, the more prescribed are their nutritional requirements. (Calcium is not commonly required by bacteria and fungi, and there is little or no evidence of boron requirement for these organisms.) In fact, it is still a puzzle why such elaborate molecules had to be developed to permit an inorganic element to perform what often seems to be a simple function. For example, the oxygen-carrying properties of iron in hemoglobin or myoglobin is but one of many similar examples in both plants and animals. Despite the complexity of some of these relationships (as for example iron to cytochromes), it is surprising how generally distributed they now are and how little evidence one can see of what may be called a progressive biochemical evolution parallel to the morphological evidence.

Some Historical Landmarks

From their early origins in Aristotelian doctrine, the primitive concepts of mineral nutrition of plants advanced but slowly, or not at all, through the Middle Ages. Van Helmont, and later others who resorted to experiment, ushered in the modern period in which the mineral nutrition of plants was to be based on a rational system of chemistry. With Théodore de Saussure's well-known book of 1804, entitled "Recherches chimiques sur la végétation," this trend was firmly established; and by the end of the nineteenth century the ideas of mineral nutrition had reached such a level that, although details were still to be added, the essential structure did not need to be changed.

The nineteenth century saw very rapid advances to knowledge of plant nutrition; this is ably summarized in many available sources, such as E. J. Russell's "Soil Conditions and Plant Growth," Sach's "History of Botany to 1860" and its companion volume by Reynolds Green for the period to 1900. (A work which is quite different in style and scope by Th. Weavers also treats the first half of the twentieth century.) However, scientific discovery is not made only at the volition of the investigator and the research worker, for it is also a product of the intellectual climate of the day, and it requires a setting which is necessary for successful advances to be made and to be applied. The course of mineral nutrition since the seventeenth century is interesting in this connection.

The great wave of progress, virtually nonexistent through the Middle Ages, acquired a slow start with Van Helmont. Van Helmont's classical experiment, in the early seventeenth century, with the growth of a willow twig may have been anticipated by Nicholas of Cusa in the fifteenth century, even as it was repeated by Robert Boyle later in the seventeenth century. Through the observations of John Woodward (1699) and others, progress gathered pace especially in the early nineteenth century, and it has continued ever since. (A short but useful account of early 18th century plant nutrition and agriculture by G. E. Fussell is to be found in the *Proceedings of the Chemical Society* for June 1960, pages 193–198.)

However, the time was especially ripe for developments in plant nutrition to occur in western Europe after the Napoleonic wars. During the Napoleonic wars the prices of grain soared so that borderline lands were brought into cultivation. In the depression that followed, the impoverished economy and unbalanced agriculture of western Europe was revived by the birth of the fertilizer industry and by the marriage of the science of chemistry with agriculture. The population increase, which was to be stimulated by the Industrial Revolution, placed even greater demands on agriculture. Boussingault in France, Liebig in Germany, Lawes and Gilbert in Britain, all were influenced by the nineteenth century trend toward, and the search for, a more efficient agriculture through a knowledge of the manurial and crop rotation practices that would give the best response in terms of plant growth. The role of nitrogen in manurial practice, the importance of legumes in a plan of crop rotation, the paramount importance of N, P, K in artificial fertilizers and the foundations of soil microbiology were all to be well appreciated by the end of that century. Boussingault's quantitative field experiments, Liebig's ill-fated artificial fertilizer, were as much in tune with the needs of the times as Lawes' more successful venture into the solubilization of rock phosphate as superphosphate of lime. The celebrated partnership of Lawes and Gilbert was to study the application of the new chemistry to agriculture. But it was Sir John Lawes, using his family estate and the income from the new fertilizer industry, who far-sightedly installed, in perpetuity, the Lawes plots at Rothamsted to demonstrate the responses of the growth of plants to specified manurial practices.

It has been said, however, that part of the pressure that prompted this development by Lawes and Gilbert was a new imbalance in a long established economy between London and its agricultural environs. This economy stressed sheep as the source of meat and root crops to feed the sheep over the winter. Farm produce reached the city in horse-drawn carts, and the predominantly horse-drawn transport of the city furnished return loads of stable manure to fertilize the fields. With the rise of population in the vicinity of London, this precarious balance became disturbed, and alternative means to stimulate the growth of crops needed to be sought. It was in this atmosphere that the contributions of Lawes and Gilbert were to be made. With the later use of sand and nutrient solution techniques, the elaboration of the ten essential elements, well known by the turn of the century, and with the furnishing of these elements in the simplest mixtures of salts (calcium nitrate, potassium dihydrogen phosphate, magnesium sulfate, with a little iron) science seemed to have largely closed the book of plant nutrition by the end of the nineteenth century and the first decade of the twentieth.

However, during and after the First World War, plant nutrition profited from the great stimulus to chemistry which that scientific period fostered. When Germany was cut off by sea power from Chilean sources of nitrate, her agriculture was maintained by chemical fixation of atmospheric nitrogen by the Haber process, which received its first great impetus at this time. Indeed, it was in this postwar period that the knowledge of trace elements [that is nutrient elements needed in such small amount that, as foreshadowed by Mazé (1914), they had been overlooked in the erstwhile list of ten essential elements] became known. In the period after the Second World War plant physiology responded to the stimulus from physics and physical chemistry, which was to be a distinctive feature of that time. The search for sources of power and of energy was now paramount. Wars and the needs of industry had plundered the fossil fuels or stored products of the photosynthesis of bygone days, and the so-called population explosion called in question the ability of conventional agriculture to feed the world population. In plant physiology at this time there was a heavy preoccupation with the need to understand photosynthesis as the means by which plants utilize the energy of the sun and also to understand the way that energy, once stored, is applied to biological work of all kinds. The recognized importance of the expanse of the oceans in the total fixation of solar energy led to such ideas as those of "farming of the seas" as sources of food to meet man's needs. Also, in this productive period the now available radioactive isotopes soon penetrated into all branches of nutritional and metabolic study.

Thus, plant physiology and the study of plant nutrition has repeatedly responded to the trend of the time. Its progress has likewise interacted with the fluctuating balance between agriculture and industry, between urban and rural societies and with the onset of population pressures. These more general implications merit some further comment below.

Inorganic Plant Nutrition: Its Place in the Economy of Nature and of Man

Plants are still the ultimate source of organic nitrogen for both man and beast. Agriculture—i.e., plant and animal husbandry—turns inorganic nitrogen into usable protein. Thus the inorganic nutrition of crop plants has been dominated by nitrogen, though even today—despite the efficiency of agriculture and of artificial nitrogen fertilizers—much of the world's population is protein poor. Despite all man-made means to refurnish nitrogen in forms chemically fixed from the air, the biological means of returning plant and animal waste through the nitrogen cycle and the biological means of nitrogen fixation are by far the most important. In this respect the standards of Western urban civilization, which returns so much nutritional wastes eventually to the sea, presents a constant drain upon the nitrogenous reserves of the soil. Since an acre of shallow sea may furnish annually amounts of organic matter which are the rough equivalent of that produced by an acre of arable land and, since the seas occupy so much of the earth's surface, thought is now being given to the seas as the solution of man's food problems. Phosphate and nitrate, replenished by the rising currents from great depths, are often in limitingly low concentrations in the shallow seas, and ideas of "farming the sea" in landlocked shallow bays are perhaps no more visionary than those of hydroponics and of large scale algal culture. None of these ideas, which contemplate the large-scale growth of food plants in water and which have been prominently suggested in the twentieth century, would have seemed either feasible or necessary in an earlier day. But there was then less awareness than now that man's reproduction may soon tax the earth's resources and that also man may shortly venture into space. Thus plant physiology and the inorganic nutrition of plants is fraught with intensely practical applications which are closely bound up with the destiny of man.

Additional to the large area of the earth's surface (approximately four-fifths) which is occupied by sea and to that which is limited for conventional agriculture either because it is desert, or too cold or too mountainous, there are still vast areas which are occupied by forest. Indeed, forest trees may compose about 80% of the living matter on land. Prior to man's intervention, a large part of the North Temperate Zone was in fact occupied by a climax forest vegetation. From the early exploitation of the oak forests in Britain for shipbuilding (to furnish Britain's traditional "wooden-walls") and for the later smelting of iron ore, to the wholesale cutting of the North American forests in this century, the balanced nutrition of the climax forest has been disturbed, and one may note that the timber industry removes at one harvest even more of the accumulated fertility of the forest than a conventional annual agricultural crop would do. Whereas planned rotational and fertilizer practices in food crop production are ancient, the knowledge and the economical practice of the nutrition of forest trees are still relatively immature. Thus, in the full use of the energy of the sun to meet man's needs, the nutrition of forest trees has a role which is still to be perfected. Indeed, the same is also true of the full use of vast areas of tropical land. In both these great areas—the nutrition of forest trees and of tropical plants and vegetation—knowledge is still meager.

The balance between agriculture, as the source of food, and industry as the means of satisfying man's technological needs has loomed large in human affairs ever since the Middle Ages. This and the prevailing standards of urban and rural civilization have had their implications in relation to plant nutrition. In the fifteenth and sixteenth centuries the open fields gave place to inclosures and, because of the wealth in wool, the landlords of Britain gave over their land largely to sheep, so that measures were enforced to curb the conversion of arable land to grazing for sheep. "By the 39th year of the reign of Elizabeth (1597) arable land made pasture since 1st Elizabeth (1558) shall be again turned into tillage, and what is arable shall not be converted into pasture." This quotation shows an early attempt to stem the inroads of technology upon the food of man and to balance agriculture and industry in the economy. The first references to the fattening of sheep on turnips in winter and to the beneficial effects of animal dung to improve the efficiency of food production occurred toward the end of the seventeenth century. Clover and probably also turnips were introduced to Britain from Holland about 1652 by a Sir Richard Weston to increase the efficiency of agricultural operations, and he is said to have described, with startling accuracy in the light of modern knowledge, how to grow a stand of clover on a light heath soil after it was cleared, burnt, and lime was added to the ashes. After several years of cropping the clover, the land would then yield well in wheat for several years more! The balance between industrial and agricultural technology has now swung far in the other direction since, particularly in the United States, efficient control of nutrient supply—particularly of nitrogen—and an efficient mechanized agriculture permit a very small fraction of the population to produce food in sufficient, even excessive, quantities for the whole population.

But as Britain became ever more intensely industrialized it became less and less self-sufficient until, prior to the First and Second World Wars, Britain depended more upon its permanently established grass lands than upon its arable lands. In such a situation the imported fertility from other lands, in the form of grain, supported both man and beast; the latter were fattened and fed to convert much imported plant protein, somewhat inefficiently (about 15%), into animal protein; and, after human consumption, much of this fertility was destined for the sea under Western systems of sanitation and hygiene. Such an expensive agricultural practice and imbalanced economy can be supported only by a rich community which is able to export the product of its industry. However, experiments made in Germany in the immediate postwar period showed that certain plant sources of protein were entirely adequate as a substitute for milk in the feeding of infants, especially if it is fortified by the addition of methionine and lysine. Moreover, the postwar trend even in Britain has been to replace much of the imported grain for livestock by high protein grass, harvested early and kept well nourished directly by the use of nitrate and phosphate and lime under a so-called "ley-farming" system. Thus the maximum use may now be made of well-nourished pasture which is grown especially for its high content of leaf protein. Work is also under way to make, from the harvested foliage, a nutritionally effective source of leaf protein even for humans which, if necessary, may be supplemented by the critically limiting amino acids such as methionine and lysine. Although this is a still somewhat visionary possibility of solving the food problems of large populations, nevertheless the inefficient conversion of leaf protein to animal protein for human nutrition might eventually be circumvented in this way. Thus we can see that the food chain links the fertility factors that determine the growth of plants, as regulated by supplies of inorganic nutrients, to the state of balance or imbalance between agricultural and industrial production and to the nutritional status of Western urban communities with their high protein requirements.

Certain regions of southwest England—for long thought to be unsuited to cattle—are now known to produce pasture which is toxically rich in molybdenum, a condition which is paradoxically aggravated by "improving" the pasture with clover but which may be alleviated by the use of ammonium sulfate to discourage the clover and to foster the growth of grasses. Also, large areas of Australian pasture, hitherto deficient in traces of molybdenum, have been brought into more efficient production by supplying this essential nutrient. Thus, the late discovery of the role of minute amounts of molybdenum in plant nutrition, which may seem academically remote from the considerations that determine the complex balance between an industrial population and its food supply, nevertheless plays a part in the over-all dependence of man and his society on the nutrition and growth of plants.

Thus science has come a long way from John Woodward's (1699) insistence that some sort of terrestrial matter determined the growth of mint sprigs! But as man embarks upon the space age, his nutritional problems are once again being posed in unfamiliar terms; these problems may be left to the future to solve. However, for any kind of continuously balanced system of men in missiles, or on space platforms, the inorganic nutrition of plants in all its ramifications will be needed to harness light energy to make carbohydrates and thence to convert inorganic nitrate into protein.

Some Modern Concepts and Future Trends

In the nineteenth century the cell doctrine and the study of cells and organisms—with the impending rise of genetics—produced unifying concepts that permeated the whole of biology. Some now familiar aphorisms gave expression to essential truths, as it was seen that all cells came from preceding cells, all nuclei from preceding nuclei, etc.; and that self-duplication is an inherent characteristic of the way cells grow and divide. While cell biology in general profited greatly from these broad generalizations, the students of plant nutrition, for a while, seemed to become bogged down in a search for a fastidiously prescribed "best" nutrient solution for this or that plant. Indeed, long before the full range of variables and parameters was properly realized, there was a somewhat sterile attempt to control the osmotic pressure of nutrient solutions and to vary only the relative proportions of those three known main constituents of culture solutions, namely the salts calcium nitrate, potassium dihydrogen phosphate, and magnesium sulfate, to which a small amount of an iron salt was added. In retrospect this approach monopolized far too much time and effort, until by the greater use of statistical methods it was shown about 1921 that many of the supposed differences between the growth in the different solutions were often not statistically significant.

For the next great wave of development the science of plant nutrition was to be enriched by the stimulus of enzymology and by concurrent developments in genetics. The gene-enzyme hypothesis of Beadle and Tatum; the accumulated knowledge of proteins as enzymes and of their regulatory role in metabolism; the purification and crystallization of enzyme proteins, all consolidated the view that certain metals, known to be essential in trace quantities for the growth of plants, could owe their essentiality to their role in metalloproteins which also function as enzymes concerned with some reaction which is essential for growth or metabolism—so much so that a new metal, found to be essential for growth, now leads almost inevitably to the first presumption that it may function by virtue of its relation to an enzyme. Nevertheless, despite the stimulus of this modern approach, there are still trace elements whose essential role is not yet adequately explained—for example, boron.

But some developments that may well determine much of the future trend of research were slow, and still are slow, to come about. For a long time the inorganic nutrition of plants seemed to require rather fixed nutrients in fixed amounts, at least above some ill-defined minimum. The idea that there is no universally applicable nutrient requirement to cover all environmental conditions and all phases of plant development was seemingly slow to emerge. Also, the need to see the importance of the nutrient elements not merely in terms of their individual and separate actions, but also in terms of their interactions with each other and with climatic and environmental conditions, is a still emerging but potentially very important concept. Interactions among potassium, nitrogen, and light were prominently noted years ago (1935); and interactions among nitrogen, phosphorus, and respiration were also seen in the same general period. For one reason or another, such pairs of factors as calcium and boron; copper and molybdenum; iron and manganese; zinc and insolation; need to be considered together, because they have interacting effects which suggest that they impinge ultimately upon the same site of metabolic action.

But why was it ever supposed that the inorganic nutrient requirements of plants and of their constituent cells are fixed irrespective of the conditions that affect their growth and development? Nutrient requirements are commonly held to begin with the seed, but does not this neglect the all-important development of the zygote in the ovule and its consequential dependence on its parent sporophyte? Why should all cells of the plant body, despite their variety of form and function, be assumed to require the same essential nutrients as the whole plant? Do such morphologically distinct plants as a long- or a short-day plant, as a high- or a low-night temperature plant, require the same nutrients in the same concentrations? Why indeed should nutrition have ever been regarded as a requirement which is fixed throughout development? To the extent that these problems become obtrusive, questions of the mobilization of specific nutrients in the different regions and organs of the plant body also arise; this also involves those problems of uptake and accumulation of particular ions by cells, as well as the mechanism of their transport, which are dealt with in Volume II. Thus there is still much room for new work and new discovery, but work in this field poses some especially difficult logistic problems.

Even after the problem of interacting effects is recognized and it is also granted that the criteria of nutrient action should be extended to include the full range of developmental and metabolic processes that may be affected by nutrition (even when visible symptoms of abnormality are not apparent), there is still a real dilemma. How should one design the experiments, collect all the necessary data, and then interpret them in such a way that due weight is given to all the parameters of this complex system and to the factors which interact with each other? The use of statistics and the design of experiments which will permit subsequent statistical analysis of the data are now conspicuous features of the current scene. These were largely stimulated, initially, by R. A. Fisher and by those in plant nutrition, notably by F. G. Gregory and his school, who seized upon the significance of Fisher's monumental work. But, nevertheless, the full complexity of the task that faces those who would make even further contributions to plant nutritional knowledge may, even yet, not be widely or fully appreciated. As growth-controlling installations and climate-controlling devices come into general use in plant physiology, the problems of the complex design in experiments which require a team approach to the problems of nutrition will need to be faced and, no doubt, modern computing machines will also be needed to analyze and formulate what all the data mean. Indeed, if the science of plant nutrition were ever to be complete, would it not then be feasible, in advance, to prescribe all the requirements and the responses of a given fertilized egg, or of a spore, throughout its subsequent growth under all conditions?

An astonishing amount of current plant nutritional knowledge derives from but a few economically important plants. In fact, the essentiality of trace elements has been largely demonstrated for crop plants which are often grown in habitats which are very different from those to which the plants were first adapted. Thus, crop plants will often show field symptoms of nutritional disorders when the adjacent native plants, or even the trees, show no such signs. This observation leads to the following considerations.

The inorganic nutrition of plants is essentially a function of the environment during their growth, even as it is of the plant in question. It is also beginning to appear as a function of the genetic constitution of the plants involved. As recently as 1953 Pope and Munger found inorganic nutrition to be governed by a single gene which regulated the requirement of celery plants for boron, while another gene determined the requirement for magnesium. Such genetically determined mineral requirements and genetically determined nutritional levels mean that constant watch should now be kept upon inorganic nutrition from this point of view. By mutation, or by the work of plant breeders, new nutritional disorders that can be corrected only by the intervention of specific chemical elements may even be created. It would be interesting, for example, to re-examine the required trace element nutrition of a wild, still uncultivated species compared with the derived varieties and strains that have been bred from it to fit them for practical use.

Inorganic plant nutrition, therefore, now impinges upon all other branches of plant science, and the book of plant nutrition that seemed about to be closed at the turn of this century now presents as much challenge to the investigator, or rather to the team of investigators, as at any period in the history of plant science.