

## MINERAL NUTRITION OF PLANTS

by A. G. Norman

Interest in the problem of the mineral nutrition of plants depends on the point of view of individual workers. Agronomists may be concerned with plant nutrients as they affect mineral composition and plant products in relation to utilization as food or feed, or they may be concerned with the capability of the soil to supply needed nutrients and the correction of deficiencies and inadequacies by fertilizer application. Those working with forest crops presumably care not at all about the mineral composition of the product, but may be concerned with site differences explicable in terms of available nutrients or nutrient inadequacies limiting growth rate.

There are certain genetic characters in crop plants that affect the composition of the plant, but the immediate ionic environment of the root may becloud the genetic-controlled composition differences. In forest genetics there has presumably yet been little opportunity to study characteristics that might affect nutrient utilization and composition, except insofar as these might be correlated in some way with growth rate.

It is important to say at the outset that most basic studies on the mineral nutrition of plants are carried out on young, quick-growing annuals. Mature woody species are less frequently studied.

It is now generally conceded that the search for plant nutrients is no longer a rewarding field of study, and there is general agreement on a list of twelve elements, six of which are usually regarded as major nutrient elements on the basis of the amount required, and six minor elements, no less essential but needed in small amounts. The proof of essentiality of major elements is easy but becomes more difficult with minor elements. Here the criteria of essentiality becomes important. It is necessary to show that the plant fails to complete its normal vegetative and reproductive sequence in the absence of an element believed essential, that the element in question cannot be completely replaced by another, and that the test plant species is fully representative. These criteria cannot be said to be fully met with many forest trees.

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Soil-grown plants contain many elements not shown to be essential in solution culture studies. Soil-grown plants always contain appreciable amounts of aluminum and silicon. Is the aluminum- or silicon-free plant a normal plant?

Complete explanations as to why certain elements are essential cannot be given. Paradoxically, more progress has been made in recent years in accounting for the minor elements. Enzyme systems known to be present in plant cells specifically require certain metals for activation. Deficiencies or inadequacies in supply are, therefore, accompanied by bio-chemical inadequacies in some or all of the cells of the plant; these bio-chemical inadequacies result in repression of growth and morphological abnormalities that are regarded as symptoms, and are recognized and described but not explained. Perhaps, of all elements, potassium presents the biggest enigma. In the ash of many trees potassium may be the largest single component. Potassium is an element of great mobility, and it may be that its role is to maintain an optimum ionic environment within the active cells for such components as the mitochondria and microsomes.

It has long been the goal of plant physiologists to be able to express the quantitative requirements of plants for mineral nutrients in order to be in a position to define an adequate diet. This is most difficult because the amount of a nutrient taken up is the function of supply rather than demand, and may also be affected by the water regime. Luxury consumption, that is uptake beyond the level accompanied by increased growth, is a familiar phenomenon. The requirements of plants for nutrients are not constant through their whole period of growth. Making available at one time all the nutrients in kind and amount that would be required for maximum growth would not necessarily ensure the optimum development of the plant. Initially it would be solidly in the luxury consumption zone, but some of the elements accumulated are not readily mobile within the plant and cannot later be transferred from older tissues to new tissues.

Although higher plants can be grown to maturity in culture solutions, the soil constitutes the normal root environment. In soil the quantity of nutrient and other elements actually in solution at any one time is very small. The crux of the situation is that the rate of renewal or replenishment may determine the quality of a soil. Exchange reactions between the clay colloids, the soil solution, and internal and external root surfaces are of great significance in cation uptake.

The actual mechanism of nutrient uptake has turned out to be a more troublesome problem than was earlier supposed, but the availability of radioisotopes has been particularly helpful. There has been revision of the classical concept of the root and acceptance of the view that an external solution can freely penetrate some parts of the root tissue spoken of as "apparent free space." The energy-requiring process of accumulation from the free space is partially selective and can be halted

by respiratory inhibitors. The essential features in uptake may be the binding of the nutrient ion to a carrier, the carrier being a compound, perhaps analogous to an enzyme. Carriers are presumed to possess specificity for particular ions, but this specificity is not absolute. Other ions chemically related may also be bound. The carrier-ion complex is presumed to be able to pass through some form of barrier or membrane not permeable to the ion alone. The evidence for the existence of ion carriers is indirect but is supported by kinetic studies.

Not all workers are in agreement with this picture of uptake mechanisms, but this new concept does permit explanations to be given for some of the puzzling features of plant nutrition, such as the presence in plants of substantial amounts of nonessential elements, certain aspects of luxury consumption, the inability to determine the quantitative requirements, the ready entry of large organic molecules into roots, and the leakage of inorganic and organic solutes from roots. There is a strong probability that, within the next few years as this concept matures and is subject to rigorous testing, there will be developed a more satisfactory account of the complicated steps involved in the nutrition of plants, both annual and perennial.