

CALCIUM AND MAGNESIUM IN THE PLANT*

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Introduction

Some 60 of the total of 92 natural elements have been found in plants. Various plants differ to some extent in their mineral nutrient requirements. For example, certain species such as *Atriplex vesicaria* and *Halogeton glomeratus*, in addition to the so-called essential elements, require sodium and celery, beets and turnips grow better in the presence of this element. Silicon is particularly abundant in the monocotyledons, especially in the grasses, and in *Equisetum*; small quantities stimulate the growth of several plants and may be an essential element for some. Aluminium is found in most plants, often in large amounts in the lycopods or club mosses and cobalt is necessary for the growth of blue-green algae. Vanadium is required by the green alga *Scenedesmus obliquus*, and can apparently substitute for molybdenum in certain bacteria. Selenium is readily absorbed by certain species in the genera *Astragalus*, *Oenopsis* and *Xylorrhiza*. Gold can be accumulated by *Equisetum*. Present but apparently not required are elements such as radium, silver, lithium, cesium, nickel, lead, titanium and barium, and probably others as well. It seems possible that to some degree a plant will absorb from its soil environment any element existing in a soluble form. It has, of course, the partial ability to select the rate at which it absorbs various ions so that absorption is not necessarily in direct proportion to nutrient availability.

The criteria of essentiality of an element are well established. These are: (1) that normal plant growth and reproduction cannot occur in the complete absence of the element; (2) that the requirement is specific and cannot be replaced by substituting another element; and (3) that the element should act directly *in vivo* and not simply cause another element to be more readily available or simply antagonize a toxic effect of another.

However, it is difficult to demonstrate positively that an element is not essential because some elements are needed in trace amounts. Also, there is evidence of some elements substituting for others, such as sodium or rubidium for potassium, strontium for calcium, vanadium for molybdenum and bromine for chlorine.

The list of essential elements now stands at 16 and it has been known for about 100 years now that calcium and magnesium are mineral elements essential for plant growth and development. Elements are utilised by plants in four basic ways. They may: (1) form part of certain structural

units, such as carbon in cellulose or nitrogen in protein, or (2) be incorporated into organic molecules important in metabolism, like phosphorus in ATP; or (3) function as enzyme activators in certain enzymatic reactions; or (4) help to maintain the osmotic balance, as for example potassium in ionic form in guard cells. Magnesium fits particularly well into categories (2) and (3) and partially into (4) above, and calcium into categories (2) and (4) and partially into (1) and (3).

The elements calcium and magnesium are the dissociation products of mineral salts which derive from rocks of the lithosphere. They are positively charged divalent cations which are washed by rain and rivers into soils, lakes and oceans where they may become absorbed and incorporated in the biosphere. They can be recycled by the breakdown of waste products and the organic remains of plants and have to be replenished mostly by use of artificial fertilizers.

Elemental composition and requirements of plants

The main constituent of plant ash is potassium. After potassium, calcium is the most abundant element and its concentration ranges widely, from 50 to 50 000 ppm. Up to 77 per cent of the dry weight of mature sunflower leaves may be calcium although normally it forms from 0,1 to 3,5 per cent of the whole plant. A wheat crop will remove about 12 kg ha⁻¹ calcium and 8 kg ha⁻¹ magnesium from the soil in one growing season as compared with 76, 42, 14 and 0,03 kg ha⁻¹ of nitrogen, potassium, phosphorus and copper, respectively.

All green plants require calcium. It is a constituent of the cell wall where it occurs in the form of calcium pectate. As an essential constituent it affects the permeability of membranes and membranous organelles as well as the hydration of colloids. Calcium is often found in combination with organic acids in the plant. Oxalic acid, for example, is soluble and toxic to the plant if it reaches a high concentration. Calcium precipitates this acid in the form of crystals of calcium oxalate, acting in the process as a detoxification agent. Calcium favours the translocation of carbohydrates and amino acids and stimulates root development. It is necessary for normal mitosis, probably as a component of the chromosomes of mitotic spindles. In pollinia and more precisely in the reproductive nuclei in the process of division, calcium attaches itself preferentially to the hereditary material (Steffensen and Bergeron, 1959). It is a constituent of the ribosome, binding together the subunits making up this organelle. It is a co-factor or activator of enzymes involved in the hydrolysis of ATP and phospholipids. Calcium is quite immobile in the plant, except when in the zylem. Therefore deficiency symp-

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toms appear first in the buds and younger leaves in the form of a necrosis. It is usually preceded by a pale green chlorosis and a downward bending of leaf tips. An unusually short, stubby and highly branched plant results. Cell enlargement and progressive vacuolation occurs in sub-apical areas resulting in ultimate death of the terminal meristems.

Magnesium is a constituent of the chlorophyll molecule and occupies a central position in it. Chlorophyll is the only major plant compound that contains magnesium as a stable component. Chromatin contains magnesium which seems to form bonds between a portion of the phosphate residues in the nucleic acids and the mononucleotides that are relatively abundant in the interior of the nucleus. The magnesium in the chromatin is in competition with histones for the possession of the acid bond of the phosphate residues. One function of magnesium is to safeguard the freedom of activity of some of the attachments on the nuclear molecules against the inhibitory action of the histones (Buvat, 1969). Many enzymes, such as those that involve a transfer of phosphate are activated by magnesium ions. Magnesium deficiency consequently rapidly affects many aspects of energy metabolism. Deficiency of magnesium results in the development of pale, sickly foliage, a condition called chlorosis. It is a common symptom in economic crop plants. Iron however, can also cause chlorosis. Chlorosis is initially interveinal but, because this ion is more mobile than calcium, chlorosis first appears in older leaves. In severe cases all leaves become yellow or white and premature abscission occurs.

One of the effects of calcium and magnesium deficiency is on the development of the grana lamellae in the chloroplasts. In calcium deficient chloroplasts the membranes are reduced and do not form characteristic grana. In magnesium-deficient chloroplasts the membranes are greatly reduced with thickened areas of pseudo-thylakoid nature. The photosynthetic process in such cases is adversely affected.

Absorption and movement of calcium and magnesium

Absorption of Ions

The question of transport of materials across membranes is basically a question of permeability. Different substances exhibit greatly different degrees of permeability and the membranes of the cell — plasmalemma, tonoplast and the numerous membranous organelles — are the least permeable of the barriers that must be traversed, as compared with the cell walls, cytoplasm and vacuoles for example. All membranes seem to have differential permeability. The penetration of ions is complex. A general rule states that the permeability of membranes to electrolytes is inversely related to the charge on the electrolyte, after the increase in size of the ion due to its water of hydration is accounted for. Walls do not constitute a barrier

to uptake; they are permeable to particles of all substances (exception: suberized walls). Membranes are highly permeable to water, gases, and most substances with molecular weights of about 60 or less. They are more permeable to undissociated molecules than to their ions.

Membranes are a pervasive structural component of a protoplast and in addition are the site of many essential functions. Since they are differentially permeable they control the movement of various substances, from ions to macromolecules, into and out of the cell. Some substances are carried across membranes by active transport systems in the membranes. Such active transport requires energy. Plasma membranes may have pinocytic invaginations. They are composed of phospholipids and proteins. Calcium, as the calcium salt of lecithin, is an essential constituent and, in calcium-deficient plants, the membranes disintegrate. Several hypothetical models of membrane structure have been proposed and there is increasing evidence in support of a concept of membrane structure combining aspects of the lipid-globular-protein-mosaic (Singer and Nicholson, 1972) and greater membrane (Lehninger, 1968) models.

The organization of lipids in membranes is affected by interactions between calcium and the polar group. Lowering the calcium concentration increases water permeability of the membranes. Calcium makes both natural and artificial membranes more hydrophobic. Removal of calcium allows polar groups to become more mobile and to move apart. The degree of packing density of phospholipid molecules depends on calcium concentration. Interactions between calcium and the membrane which alters the spacing of polar groups by only 0,1–0,2 nm, cause significant changes in the degree of order of the hydrocarbon phase.

Uptake of Ions

The concentration of free ions in a soil solution is generally low, with the greater portion of the cations absorbed on to the negatively-charged sites of clay micelles and organic materials in the soil. Free anions are absorbed by plants almost entirely from the soil solution, whereas cations may be exchanged directly between roots and soil particles by the process of contact exchange. According to this hypothesis cations may be transferred from clay colloids on to roots without appearing as free ions in the soil solution. This is a result of the oscillation of absorbed ions within a small volume of space. When the oscillating volume of an ion overlaps that of another ion then an exchange of ions may occur. This concept is not universally accepted.

Another possibility is that hydrogen ions exchange with the cations absorbed on to soil particles. The hydrogen ions are provided by carbonic acid formed from respiratory CO_2 in the soil. The cation thus released then diffuses through the soil to the root surface where absorption takes place.

Initial entry of ions is mainly through the first few centimetres behind the tip of the root.

Antagonism

A seedling placed in dilute solution of potassium chloride will show severe toxic symptoms after a short period of time because potassium ions are accumulated and chloride ions along with them. However, if a small quantity of calcium chloride is added to the solution, then neither potassium or calcium ions are taken up in toxic amounts. The small quantities of calcium ions are said to antagonize the toxic effects of the potassium ions. Calcium ions will also antagonize the toxic effects of sodium ions, or potassium or sodium ions will antagonize the toxic effect of calcium ions.

The less closely these ions are related in the periodic table, the more effective they seem to be as antagonists. Thus sodium and potassium do not antagonize each other as effectively as to sodium and calcium or potassium and barium. Furthermore, only traces of antagonizing ions are required to produce the effect. Suggestions put forward to explain antagonism remain unsatisfying.

Accumulation

Concentrations of many solutes often become higher inside plant cells than in the surrounding medium. Such solutes are said to be accumulated. Potassium ions are commonly present in higher concentrations inside than outside plant cells but this is not the case with calcium. However, different species accumulate various ions to different degrees.

Competition

Epstein (1965) has shown that potassium or cesium ions inhibit the uptake of rubidium, but that sodium or lithium had little effect upon the process. Likewise, strontium and barium ions but not magnesium, compete with calcium. Apparently calcium, strontium and barium compete for specific sites on the carrier.

Distribution of calcium and magnesium

Calcium and magnesium are relatively immobile ions and calcium, in particular, is one of the least circulated elements within the plant. Once in the transpiration stream it is carried to various parts of the plant. Calcium is present in sieve tube sap and its transport in the phloem is well established (Peel, 1974). However, once deposited it is prevented from circulation. Certain elements are withdrawn from a leaf and other organs during senescence and prior to abscission. Magnesium is one of these but sodium, boron, manganese, silicon and calcium remain.

Very little calcium in the sieve tube is available for redistribution. The absence of calcium may be the reason for the disintegration of the sieve cell content and especi-

ally of various membranous structures which may be a prerequisite for the longitudinal conduction of solution flow.

A high ratio of magnesium to calcium is characteristic of phloem saps and it is speculated that this feature may be important if the translocation mechanism involved a contractile protein. Streaming in *Nitella* cells is promoted by magnesium but depressed by calcium. The motive force for this streaming is generated by bundles of microfilaments each 5 nm in diameter. Much of the protein found in the sieve tube is in the form of microfilament termed P-protein and it has been suggested that these filaments may generate a force of sufficient magnitude to drive the phloem sap along the sieve tubes.

During development of storage organs such as bulbs, corms, fruits, rhizomes, seeds and tubers, materials, including inorganic ions, are diverted from various other parts of the plant. Because there is very little transpiration from storage organs, sap flow in their xylem is slow and the bulk of solute movement must occur in the phloem. Nitrogen, phosphorus and potassium levels in leaves and stems fall and the amounts of these elements carried in the phloem to the storage organs is vastly in excess of the quantity carried in the xylem. However, accumulation of calcium is proportional to the calcium content of the xylem sap. Some transport of calcium in the phloem does occur in pea pedicles but not in fruits of the groundnut. Groundnuts develop below the soil surface at the end of a gynophore a structure which is able to absorb calcium directly from soil.

Calcium is transported less readily from germinating seeds and cotyledons. In pea about 25 per cent of all calcium in the cotyledons moves into the axis. Magnesium is more mobile in this respect, as mobile as nitrogen and phosphorus, but less so than potassium.

Calcium and magnesium play key roles in the plant as regulatory ions and between them they control a wide range of membrane and intracellular functions. There is, however, still much speculation in regard to their precise functioning and much research awaits the plant physiologist.

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