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Calcium: Physiological Function, Deficiency and Absorption

¹EI Habbasha S.F. and ²Faten M. Ibrahim

¹Field Crops Research, National Research Center, 33 El Bohouth Street,
P.O. Box 12622, Dokki, Giza, Egypt

²Medicinal and Aromatic Plants Department, Pharmaceutical and Drug Industries
Division National Research Centre, 33 El Bohouth Street, P.O. Box 12622,
Dokki, Giza, Egypt

Abstract: Nutrition is a key factor for growth and development of plants. Among the main nutrients is calcium (Ca). Calcium, uptaken as Ca^{2+} , is essential element for the growth of the plants and fruit development, and it is important in the resistance of the plants to diseases due to with base in the protection of the cell wall. Ca plays important biochemical functions and supports many metabolic processes, in addition to activating several enzymatic systems, thus contributing to the proper development of plants. Ca fundamental role in the stability of the membrane and cell integrity. Among all organs, the leaves contain the highest concentration, Ca abundant in the leaves may be due to the formation of calcium pectate in the middle lamella of cells. As calcium is not mobile in the phloem, it cannot be retranslocated from old shoot tissues to young tissues, and its xylem transport into organs that do not have a high transpiration rate is low, Calcium is an element associated with the transport of N and interaction with potassium (K) and phosphorus (P). Abiotic stress often leads to an increase of free calcium in the cytoplasm of cells, which leads to gene expression which activates biochemical responses that allow the plant to adapt to adverse conditions of various kinds. Thus, the Ca is involved in the regulatory mechanisms that will enable the plant to make adjustments under adverse conditions such as high temperature, chilling, water stress and salinity.

Key words: Calcium ions, absorption, concentration.

Introduction

The nutrition of the plants depends on the availability and uptake of macro and micro nutrients contained in the soil. Calcium is an essential plant nutrient. As the divalent cation (Ca^{2+}), it is required for cell structural. Roles in the cell wall and membranes, as a counter-cation for inorganic and organic anion in the vacuole, and as an intracellular messenger in the cytosol¹. Calcium (Ca) has major functions in the plant, essential for the cell walls and the structure of the plant, maintains the structure of the plant tissue and acts as a factor that maintains cohesion cells together. Without calcium, the development of new root and shoot tissue stops (cell division and extension). Calcium is an element associated with the transport of N and interaction with potassium (K) and phosphorus (P)^{2,3}. In most plant nutrition experiments studying the effect of a single nutrient in plant growth, however, research examining the effect of more than one nutrient in the same experiment is limited, under this situation, interaction between the nutrients can be identified considering the effects of increasing the concentration of a nutrient in the absorption of other nutrients and the corresponding response of the crop⁴.

Ca plays an important role in plant resistance to disease based on the protection of the cell wall⁵. Calcium also has a positive effect on soil properties. This nutrient improves soil structure thereby increasing water penetration, and providing a more favorable soil environment for growth of plant roots and soil microorganisms. The concentration in a form usable by plants may be as low as 300 to 500 ppm in acid soils to more than 7,000 ppm in highly calcareous soils. Calcium in plants. Calcium is part of every plant cell. Much of the Ca in plants is part of the cell walls in a compound called calcium pectate. Without adequate Ca, cell walls would collapse and plants would not remain upright.

Calcium is not mobile in plants, it does not easily to move from old to young leaves. Ca is an essential element for plant growth and fruit development^{6,7}. Ca plays an important role in plant resistance to disease based on the protection of cell wall disintegrating enzyme secreted by pathogens⁵. In a study which evaluated Ca function in protecting tissues pumpkin Fruit *Botrytis cinerea* infection, it was determined that the Ca applied to fruit, increased the concentration of this element in the cell walls and thus decreased digestion of pectin by the fungus pectinolytic enzymes⁸. Ca involved in the formation of lecithin, a phospholipid which is important in the cell membrane and in the permeability of these membranes. Also acts in the mitotic cell division in the growth of meristems and the absorption of nitrate⁹.

Most of the Ca is accumulated in the plant cell walls and membranes. In the cell wall, accumulation is facilitated by binding to pectin polymers, particularly of the middle lamella to form a network of cell wall increases mechanical strength^{10,11}. Among all organs, the leaves contain the highest concentration, Ca abundant in the leaves may be due to the formation of calcium pectate in the middle lamella of cells¹². There is evidence of the effect of Ca on the delayed senescence and controlling physiological disorders as spongy tissue¹³ and some benefits as winter hardiness in grafted seedlings of eggplant¹⁴, overcome the negative impact of high salinity¹⁵.¹⁶ Reported that balanced supply of Ca compared to other nutrients increases plant height and dry matter. In soybean (*Glycine max L.*), the Ca in the nutrient solution produces a positive effect on the chlorophyll content, chlorophyll a/b and carotenoids in photosynthesis¹⁷.

Calcium is a critical part of the cell wall that produces strong structural rigidity by forming cross-links within the pectin polysaccharide matrix. In the primary cell wall, cellulose microfibrils are linked together by cross-linking glycans, usually xyloglucan (XG) polymers but also glucoarabinoxylans in Poaceae (Gramineae) and other monocots¹⁸. Calcium ions (Ca^{2+}) bridge phosphate and carboxylate groups of phospholipids and proteins at membrane surfaces⁶, helping to maintain membrane structure. Also, some effect occurs in the middle of the membrane, possibly through interaction of the calcium and proteins that are an integral part of membranes^{19,20}. Possibly, calcium may link adjacent phosphatidyl-serine head groups, binding the phospholipids together in certain areas that are then more rigid than the surrounding areas²¹. An involvement of calcium in the actions of phytohormones seems likely as root growth ceases within only a few hours of the removal of calcium from a nutrient solution²².

The element appears to be involved in cell division and in cell elongation²³ and is linked to the action of auxins. It has been known for a long time that calcium is essential for the growth of pollen tubes. A gradient of cytoplasmic calcium concentration occurs along the pollen tube, with the highest concentrations being found in the tip. The fastest rate of influx of calcium occurs at the tip, but there are oscillations in the rate of pollen tube growth and calcium influx that are approximately in step²⁴. It seems probable that the calcium exerts an influence on the growth of the pollen tube mediated by calmodulin and calmodulin-like domain protein kinases²⁵. Uptake can be enhanced by applying calcium in the soluble form (i.e., calcium nitrate or calcium chloride, either of which is immediately available for uptake). With many rapidly growing crops, insoluble sources will not provide adequate calcium fertility. Surface application of urea with soluble calcium fertilizer solutions reduces ammonia volatilization. The soluble calcium fertilizer source, either calcium nitrate or calcium chloride, for example, precipitates the carbonate component from the solutions as calcium carbonate. As a result, the concentrated fertilizer solution pH is decreased. Subsequently, less ammonia is lost. Water soluble calcium fertilizer sources are key in this reaction. Calcium sources such as lime, gypsum and soil exchangeable calcium cannot reduce ammonia volatilization loss.

Physiological Function of Calcium

Ca plays important biochemical functions and supports many metabolic processes, in addition to activating several enzymatic systems, thus contributing to the proper development of plants^{26,27}. Ca fundamental

role in the stability of the membrane and cell integrity is reflected in several ways. This can be demonstrated by increased leakage of low molecular weight solutes from tissue cells deficient in calcium and, in plants with severe deficiency of the latter, with a breakdown of the membrane structures and a loss of compartmentalization cell¹. Ca preserves the integrity of the membrane in two ways: by delaying changes in lipids that form due to senescence and increasing the restructuring¹¹. Most Ca functions as a structural component of macromolecules are related to their ability to coordinate, through which it provides stable intermolecular connection mechanisms, but reversible, predominantly in the cell walls and in the plasma membrane. Ca stabilizes cell membranes to bind the phosphate group and the carboxylic acid in phospholipids and proteins, preferably at the membrane surface¹. Calcium moves toward roots by diffusion and mass flow^{28, 29} in the soil.

A number of calcium specific ion channels occur in the membranes of root cells, through which influx occurs, but these channels appear to be more involved in enabling rapid fluxes of calcium into the cytoplasm and organelles as part of signalling mechanisms³⁰, then Ca moved into vacuoles, endoplasmic reticulum, or other organelles, with movement occurring by means of calcium-specific transporters³¹. The mass entry of calcium into roots occurs initially into the cell walls and in the intercellular spaces of the roots, giving a continuum between calcium in the soil and calcium in the root³². For calcium to move from the roots to the rest of the plant, it has to enter the xylem, but the Casparian band of the endodermis is an effective barrier to its movement into the xylem apoplastically. However, when endodermis is first formed, the Casparian band is a cellulosic strip that passes round the radial cell wall (state I endodermis), so calcium is able to pass into the xylem if it passes into the endodermal cells from the cortex and then out again into the pericycle, through the plasmalemma abutting the wall³³. The transport seems to occur, with the calcium moving into the endodermal cells (and hence into the symplasm) through ion channels and from the endodermis into the pericycle (and ultimately into the much higher concentration of calcium already present in the xylem) by transporters^{34,35}.

Highly developed endodermis has suberin lamellae laid down inside the cell wall around the entire cell and in the oldest parts of the root; there is a further layer of cellulose inside this. This restriction in effect limits the movement of calcium into the stele to the youngest part of the root. Some movement occurs into the xylem in older parts of the root, and this transport can occur by two means. It is suggested that movement of calcium through endodermis might occur where it is penetrated by developing lateral roots, but the Casparian band rapidly develops here to form a complete network around the endodermal cells of the main and lateral roots. The second site of movement of calcium into the stele is through passage cells. They tend to be adjacent to the poles of protoxylem in the stele, and they are the site of calcium movement from cortex to pericycle.

In some plants (e.g., wheat, barley, oats), the epidermis and cortex are lost from the roots, especially in drought, so the passage cells are the only position where the symplast is in contact with the rhizosphere. Most angiosperms form an exodermis immediately inside the epidermis, and the cells of this tissue also develop Casparian bands and suberin lamellae, with passage cells in some places³³. Absorption of calcium into the roots may be passive and dependent on root cation-exchange capacity (CEC)³⁶. Transfer of calcium into roots is hardly affected by respiratory uncouplers, although its transfer into the xylem is affected^{32,37}. Once in the xylem the calcium moves in the transpiration stream, and movement around the plant is restricted almost entirely to the xylem^{38,39} as it is present in the phloem only at similarly low concentrations to those that occur in the cytoplasm.

As calcium is not mobile in the phloem, it cannot be retranslocated from old shoot tissues to young tissues, and its xylem transport into organs that do not have a high transpiration rate is low²². Its flux into leaves also declines after maturity, even though the rate of transpiration by the leaf remains constant⁴⁰, and this response could be related to a decline in nitrate reductase activity as new leaves in the plant take over a more significant assimilatory role^{22,41}. The plant acts as a giant cation exchanger, taking up calcium in proportion to its rate of growth. Supplying calcium to decapitated plants at increased ion activity (concentration) leads to increased uptake of the ion, a process that appears to contradict this concept. However, in intact plants, the rate of uptake is independent of external ion activity, as long as the ratios of activities of other cations are constant relative to the activity of (Ca²⁺)^{42,43}. The theory that calcium travels across the root in the apoplastic pathway, until it reaches the Casparian band of the endodermis and at which its passage to the xylem becomes symplastic, is not entirely without problems.

The walls of xylem vessels have cation-exchange sites on them; in addition to the whole plant having a CEC, the xylem represents a long cation-exchange column with the Ca²⁺ ions moving along in a series of

jumps. The distance between each site where cation exchange occurs depends on the velocity of the xylem sap and the concentration of Ca^{2+} ions in it. Thus, for transpiring organs such as mature leaves, the calcium moves into them quickly, but for growing tissues such as the areas close to meristems, the supply of calcium is dependent on the deposition of cell walls and the formation of new cation-exchange sites. It has been suggested that transpiring organs receive their calcium in the transpiration stream during the day, and growing tissues receive their calcium as a result of root pressure during the night³². Xylem fluid goes preferentially to actively transpiring leaves, giving a lower input of calcium into developing fruits⁴⁴. A period of hot, sunny weather not only gives rise to so much transpiration that calcium is actively pulled into leaves, but gives rates of photosynthesis that are enhanced to the extent that fruits expand very rapidly.

Under these conditions, it is likely that localized deficiencies of calcium will occur in the distal end of the fruits, furthest from where the xylem enters them. It has been thought in the past that salinity, which increases water potential in the root medium, would likewise restrict calcium import into the fruit, accounting for increased incidence of blossom end rot (BER) that is known to occur under saline conditions. This effect of salinity could be important in some natural soils, but is also important in glasshouse production of tomatoes as high-electroconductivity (EC) nutrient solutions are sometimes used because they increase dry matter production in fruits and improve flavor. Cultivars differ in susceptibility to blossom end rot (BER), with beefsteak and plum types of tomato being particularly susceptible. Susceptibility is related partly to fruit yield, and two susceptible cultivars of tomato (Calypso and Spectra) were shown to have a higher rate of fruit set than a nonsusceptible cultivar (Counter). Cultivars with relatively small fruits, such as Counter⁴⁵, and with xylem development in the fruit that is still strong under saline conditions⁴⁶, are able to accumulate comparatively high proportions of their calcium in the distal end of the fruits under such conditions and are less susceptible to blossom end rot (BER). However, cultivars with low yields of fruits per plant may show even lower incidence of blossom end rot (BER) than those with high yields⁴⁷. Losses of tomatoes to BER in commercial horticulture can reach 5% in some crops, representing a substantial loss of potential income. The main approaches to prevent BER are to use less-susceptible cultivars and to cover the south-facing side of the glasshouse with white plastic to limit the amount of solar radiation of the nearest plants and prevent their fruits from developing too quickly in relation to their abilities to accumulate calcium.

Deficiency of Calcium

Ca deficiencies are rare in nature but can occur in soils with low base saturation and high levels of acid deposition. Because the transport is preferably performed by the dead cells of the xylem, visual symptoms are generally deficiency observed in young tissues. Ca deficiencies are manifested⁹, with lower protein synthesis capacity in the plants, lesser root development, leaf chlorosis marked mainly young, little growth of stems and leaves, producing also a death of meristems, the plant is grown and exhibits less developed. A deficiency of Ca in pink is associated with a blighting the apex of floral petals⁴⁸. And also the "rollover Tulip" is described as a symptom of Ca deficiency, characterized by the bending of stems at the neck of the plant, the flower form^{49,50}.

Meristematic zones of roots, stems and leaves, which are permanent cell division, are most susceptible, perhaps because it is essential for the formation of a new middle lamella⁵¹. Its deficiency may be due to improper transport by vascular conduits of the plant caused by low absorption or availability in soil⁵². According to^{53,54}, Ca deficiency in fruit can also be due to various physical and/or physiological: firstly, the high temperature and solar radiation, which increase leaf photosynthesis and this increases the supply of photo-assimilates to the fruit, an increase in cell expansion of the fruit on the other hand, the deficiency of oxygen in the substrate, extreme temperatures, low supply of Ca, high contribution of NH_4^+ , high concentration of soluble salts (EC), high N supply, low humidity, high breathability in the foliage, low Ca uptake by roots under the fruit Ca transport, restriction xylem development, little deposition of calcium in the distal the fruit.

Abiotic stress often leads to an increase of free calcium in the cytoplasm of cells, which leads to gene expression which activates biochemical responses that allow the plant to adapt to adverse conditions of various kinds. Thus, the Ca is involved in the regulatory mechanisms that will enable the plant to make adjustments under adverse conditions such as high temperature, chilling, water stress and salinity⁵⁵. This has led to failures related element of the plant tissue with the appearance of physiological disorders presented in different crops, especially in tissues and organs that have low transpiration rate as flowers, fruits and bulbs⁵⁶. Usually by water deficiency promotes a high temperature environment, followed by a rapid change in the moisture supplied to the plants, however, this phenomenon may increase due to reduced rigidity of the cell walls by the low

concentration of Ca^{57,58}. When the Ca content in the fruit is low, the respiratory metabolism increases and accelerates ripening and senescence⁵⁹.

Absorption of Calcium

Ca is absorbed as the divalent ion Ca⁶⁰, through the root system by the flow generated by the transpiration stream, being responsible for the bulk absorption. This process occurs primarily in the root hairs and the young root tips⁶¹, so that the amount of Ca which is accumulated in the root depends, among other things, its concentration in the solution and crop transpiration coefficient^{62,63}. It has been shown that Ca is mobilized to the roots of the plants mainly by the mass flow⁶² and in solutions with low osmotic potential (diluted) greater availability of water, by having a higher water potential⁶⁴. It is well known that Ca moves unidirectional long distance xylem, and is virtually immobile in phloem, so the route used for transportation may be through plasmodesmata (symplast) or the intercellular space (apoplast). At the plant, a large amount of Ca complexes with organic anions and inorganic malate such as NO³⁻ and chloride, are stored in the vacuoles, chloroplast and rough endoplasmic reticulum, while its concentration in the cytoplasm is extremely low. Low concentration of Ca in the cytoplasm is essential to prevent the precipitation of inorganic phosphate¹.

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