Calcium nutrition of higher plants

H. Marschner[1]

Institut für Nutzpflanzenforschung – Pflanzenernährung –
der Technischen Universität Berlin, Berlin, Federal Republic of Germany

Summary

The increased occurrence of calcium deficiency in agricultural and horticultural plants has attracted considerable attention to calcium nutrition in recent years.

The functional requirement for calcium within the cell of higher plants seems low for a major nutrient. However, lack of both selective and active uptake as well as inability for retranslocation makes a high concentration at the root surface and an uninterrupted uptake of calcium necessary. The requirement for calcium also increases with the increase in supply of other mineral elements, particularly of cations.

Existing regulatory mechanisms seem to be more developed in the direction of restriction rather than promotion of the uptake and long-distance transport of calcium.

A better knowledge of the physiological aspects of calcium nutrition is necessary. In future more attention must be given to the use of inorganic fertilizers containing sufficient calcium. Other agricultural and horticultural practices must also be considered in relation to their effect on the calcium nutrition of plants.

The requirement of calcium as a nutrient for higher plants was already known at the time of Justus von Liebig. With the introduction of inorganic fertilizers calcium was supplied to the soils mainly indirectly with phosphate fertilizers such as basic slag and superphosphate. Large amounts of calcium were also supplied by liming acid soils and with the periodic liming necessary in humid climates to avoid decrease in soil pH. Typical symptomes of calcium deficiency such as hooking of stems and browning of veins (Bussler, 1963), however, appear relatively seldom on acid soils. The restricted growth of plants on acid mineral soils is caused mainly by decrease in availability of certain mineral elements, such as phosphate or molybdenum, and an excess of others, for example manganese or aluminium.

With the exception of certain soil types, in general for soils with pH values above 5, the calcium concentration in the soil solution is high compared to other cations (Mengel et al., 1969). This is also reflected in the high losses of calcium by leaching in humid climates. Comparing this high calcium concentration in the soil solution and therefore at the root surface with the requirement of the plants, one would think that calcium deficiency in higher plants should seldom occur.

During the last 20 years, however, an increasing number of physiological disorders caused by insufficient calcium nutrition have been reported. These include tip burn in lettuce, black-heart in celery, blossom end rot in tomato and water melon or bitter pit in apple. This calcium deficiency occurs mainly in association with intensive agriculture and horticulture. One reason for the increase of the problem is without doubt the reduction in the proportion of inorganic fertilizer calcium used in practice in relation to other

[1] Prof. Dr. H. Marschner, 1 Berlin-33, Lentzeallee 55-57, Bundesrepublik Deutschland.

Table 1. Average contents of K and Ca in leaves, fruits and storage organs.

Species	Leaves (mg/100 g)		mg/g dry matter fruits and storage organs		Reference
	K	Ca	K	Ca	
Paprica	55	45	75	1.0	Mix (1973)
Apple	15	10	7.5	0.6	Lüdders & Bünemann (1971)
Potato	32	28	33	0.8	Krauss & Marchner (unpublished)

major nutrients. This is especially the case when highly concentrated compound fertilizers are applied. However calcium deficiency can be prevented only in part by increasing the supply of calcium to the soil (Foroughi & Kloke, 1974), and foliar application might be desirable. In apple orchards, for instance, several additional sprays with calcium are necessary to prevent calcium deficiency (van Goor, 1971).

It can be frequently observed that calcium deficiency is restricted to certain plant parts, in particular to the shoot apex and fruits and storage organs with high water content. Even when the plant is adaquately supplied with calcium these organs are low in calcium content in comparison to the leaves (Table 1).

The appearance of calcium deficiency in certain parts of the plant, even when in other parts of the same plant the calcium content is high, indicates that higher plants are not adequately able to regulate their calcium distribution. This can be demonstrated by transferring plants from a substrate well supplied with calcium to one without calcium; calcium deficiency is then observed in the newly developing tissues (Loneragan & Snowball, 1969). Deposition in the tissue of annual plants appears to be largely permanent but in woody plants some remobilization may occur (Wieneke & Führ, 1973).

The reasons for lack of remobilization are only in some cases related to the insolubility of the calcium deposition (calcium oxalate in Chenopodiaceae, for example). In general, however, it is the result of the phloem immobility of calcium. The reasons for this immobility are unknown. Of the possibilities such as precipitation of calcium within the phloem, existence of a calcium specific efflux pump in the membranes of the phloem vessels or preferential accumulation of calcium in the cells surrounding the phloem, only the first possibility seems to be unlikely. Both the high pH and the high phosphate concentration in the phloem would obligatorily cause a precipitation of calcium and accumulation of calcium phosphate, and exert a detrimental effect on phosphate translocation. Indications for the importance of the third possibility are the abundance of calcium oxalate crystals very often found in cells near the phloem.

The possibility that traces of calcium are translocated in the phloem can certainly not be excluded. The occurrence of extensive calcium translocation in the phloem, however, is exceptional and appears to be restricted to certain plant species such as *Yucca* (Wiersum et al., 1971) or particular experimental conditions (Ringoet et al., 1968). Newly developing parts of plants have to be supplied continuously with calcium taken up directly from the soil solution. This holds true not only for the shoot, but also for the root. Translocation of calcium from basal parts of the root to the growing root tip does

not take place (Marschner & Richter, 1974a). Root growth through soil layers low in calcium is therefore severely restricted or prevented (Pearson et al., 1973).

Not only roots but also fruits like peanuts (Hallock & Garren, 1968) and storage organs as potato tubers (Krauss & Marschner, 1974a) growing in the soil have to meet their requirement for calcium by direct uptake from the soil solution because of the total absence of calcium translocation from the shoot.

In the first step in calcium uptake from the soil solution adsorption on to cation exchange sites (CEC) in the cell walls is important (Asher & Ozanne, 1961). At least part of the aluminium toxicity in acid soils is caused by blocking of these binding sites and is consequently decreasing the calcium uptake (Foy et al., 1972). The relationship between these binding sites in the cell walls and the calcium uptake is also reflected in the broad correlation between calcium concentration in the plant tops and the CEC of the roots (Loneragan et al., 1968).

Already thirty years ago Lundegårdh (1941) and Schuffelen & Loosjes (1946) stressed the importance of these binding sites and of the electrical charge of the root surface for ion uptake in general. Later these physico-chemical aspects of the ion uptake were certainly overestimated (Vervelde, 1953). With the advent of the carrier-theory and the emphasis on the importance of ion-specific structures in cell membranes the association between metabolism and uptake and transport of ions in cells was stressed and the exchange properties of the cell walls were considered of minor importance in ion uptake. This view certainly need to be critically reexamined at least for polyvalent cations.

It is still an open question wether calcium is taken up actively, i.e. with the consumption of metabolic energy, into the 'inner space' of the cell. It is well known that at least in comparison to potassium the correlation between metabolic activity and uptake (Schuffelen, 1948; Mengel, 1962) or translocation (Walker, 1969) of calcium is low. Based on the electro-chemical approach of ion transport through membranes the comparison between the calcium concentrations and electrical potential inside and outside of the cells an efflux pump for calcium would even be necessary for the maintenance of the relatively low calcium ion concentrations inside of the cells (Higinbotham et al., 1967). Presumably the well known action of calcium in decreasing membrane permeability restricts its own permeation into the cell.

In plant roots a more or less unrestricted permeation of calcium in the AFS of the cortex is possible. The existence of the endodermis, however, makes it necessary that for calcium to enter the stele it must also enter the cytoplasm. This entry into the cytoplasm appears to be a limiting factor of considerable importance. Although the endodermis does not entirely restrict calcium movement (Marschner & Richter, 1974b) uptake and translocation of calcium from the root tip region where the endodermis is either absent or not fully developed, is several-fold greater (Robarts et al., 1973; Marschner & Richter, 1974a) than in the other regions of the root.

Generally there is a high correlation between the transpiration rate and uptake rate of calcium. This, however, cannnot be used as evidence for a passive movement of calcium through the root especially for plants growing in soil. It can be shown that as the transpiration rate influences the mass flow of soil solution a higher calcium concentration may occur at the root/soil interphase (rhizosphere) than in the surrounding soil (Barber & Ozanne, 1970; Riley & Barber, 1970). There is no doubt that the uptake rate is more directly related to this concentration – or more precisely activity – at the root surface or in the AFS, than to the concentration in the bulk of the soil solution (Schuffelen, 1972).

In contrast to the varied views on the importance of exchange adsorption in the AFS, there is complete agreement on the decisive role of exchange adsorption for transport of

calcium within the plant (Bell & Biddulph, 1963; Wienecke, 1969). Due to the restriction of the long-distance transport of calcium to the xylem the transpiration is of special importance for the distribution of calcium within the shoot. The relatively low calcium content of fruits or storage organs compared to the leaves (Table 1) relates to the differrences in transpiration rates of both these organs. Consequently a further decrease in the transpiration rate of fruits decreases their calcium content and increase the occurence of calcium deficiency symptoms (Wiersum, 1966). The conclusion, however, that a high transpiration intensity of a plant therefore improves the calcium nutrition of all parts of the plant is only valid to a certain extent. Various parts of the shoot compete for transpiration water, and due to their large surface the leaves compete very effectively, presumably withdrawing water from the fruit via the xylem. This competition for water must exert a detrimental effect on the calcium nutrition of the fruit. A similar competition for water has been observed between leaves and storage organs, such as potato tubers (Krauss & Marschner, 1974b).

The complicated interaction between water balance and calcium translocation in a plant was demonstrated with cauliflower (Krug et al., 1972), where obviously periodical changes in the volume of the curds caused by changes in the transpiration intensity are necessary for the calcium translocation into the curds.

Another important factor in the calcium nutrition is the growth rate. There is a tendency that with the increasing growth rate of a fruit and therefore the increasing intensity of solute influx via the phloem, the calcium content in the fruit decreases (Wiersum, 1966). This relates directly to the reduction of influx of water (and calcium) via the xylem. Factors which influence the growth rate of fruits or storage organs such as temperature, the presence of other nutrients, leaf/fruit ratio, etc. therefore have indirect effects on the calcium nutrition, especially of fruits (Bangerth & Mostafawi, 1969; Bünemann & Lüdders, 1969).

The importance of the water movement in the xylem for the calcium distribution within the shoot, however, can be superimposed by other regulatory mechanisms. The influx rate for calcium decreases, for example during the ontogenesis of a bean leaf despite a constant transpiration rate (Koontz & Foote, 1966). Similar results were obtained in bean and paprica fruits (Mix, 1973). In fruits this decrease in influx of calcium might be indirectly associated to the increased flux rates of solutes in the phloem. In leaves, however, this interpretation is insufficient and presumably another factor is of greater importance: if the exchange adsorption in the xylem is of general importance for the long distance transport of calcium into a plant part, the removal of calcium from the exchange sites at the end of the transport chain is necessary and hence from the cell walls of the leaf cells. This removal can be induced either by formation of new binding sites associated with division and growth of cells or simultaneous accumulation of anions within the vacuoles of fully differentiated cells.

Certainly the nitrate reduction is another factor which influences the calcium influx into leaves. With decrease in nitrate reductase activity with increasing leaf age (Martin, 1971, van Egmond & Breteler, 1972) concomitant accumulation of nitrate decrease the further influx of nitrate, or anions in general. In plant species of the family Chenopodiaceae where oxalate is the most important organic anion which is produced for charge compensation from nitrate reduction, calcium ions are removed continuously from the exchange sites by information of calcium oxalate. Decreases in nitrate reduction will therefore result in increased concentration of calcium ions and this certainly depresses the further influx of calcium.

Besides the more or less indirect and unspecific regulatory mechanisms for uptake and

translocation of calcium one cannot exclude the existence of specific ones. Various observations as the stimulation of the calcium influx into leaves after application of kinetin (Shear & Faust, 1970) or the depressing effect of TIBA on the calcium influx into fruits like apple (Bangerth & Fizurek, 1971) provide an indication of possible direct relationship between growth substances and calcium translocation. More evidence is necessary also to prove that the preferential influx of calcium into the shoot apex, for example, is not directly regulated by growth substances but only indirectly mediated by formation of new binding sites, and therefore more rapid removal of calcium ions from the exchange sites in the xylem.

In comparison to other mineral elements, potassium in particular, the calcium nutrition of higher plants seem to have developed regulatory mechanisms more in the direction of restriction for both uptake and translocation. Examples for this are not only in the restrictive function of the endodermis for the radial transport of calcium through the cortex of the root or the phloem immobility of calcium but also the formation of oxalates in leaf petioles (Hanger, 1974) fruit stems (Liegel, 1970) and the testa of bean and pea seeds (Garz, 1965).

Without doubt these restrictions in calcium translocation must be of physiological importance for the plant. This is directly related to the question of the requirement of the cell and the plant for calcium. The calcium content of plant tissue is relatively high, 1-2 % of the dry matter in average. This, of course, is no evidence that calcium is necessary in the same order of magnitude. There also exist typical differences between plant species in both content of calcium and requirement for calcium. A classification into calcicole and calcifuge species with a high and a low requirement resp. for calcium, however is a crude simplification and cannot be used as an indicator for true differences between both these groups in the calcium requirement on a physiological basis (Burström, 1967).

Certainly the view is too extreme that the requirement of higher plants for calcium actually is in the range of trace elements and that the usually much higher requirement is due to the function of calcium to compensate for the excess of other cations within the cell (Jones & Lunt, 1967). It is a fact, however, that under controlled conditions and maintenance of a constant supply of calcium combined with low levels of other cations the requirement for calcium indicated by the content in the tissue for optimal growth performance also for herbaceous plant species is considerably lower than expected (Loneragan & Snowball, 1969). A further indication of the low functional requirement of calcium in cells of higher plants is the low calcium content of most fruits and storage organs (Table 1, e.g.). The comparable much higher calcium content in the leaves of the same plant is no evidence that these organs actually have a higher requirement.

The calcium content in a tissue is an inadaquate criterion both for requirement and physiological availability. In older leaves of sugar-beet, for example, more than 80 % of the calcium is present as calcium oxalate (van Egmond & Houba, 1970). The level of functional available calcium is therefore low. It is not surprising then that in the chloroplast of sugar-beet leaves the calcium content is only 2 mg/g dry matter compared to approximately 20 mg/g dry matter in chloroplasts from bean leaves (Mix & Marschner, 1974).

Similar high proportions of calcium bound as oxalate as in sugar-beet leaves are found in the testas of bean seeds (Garz, 1965). This calcium cannot be mobilized during seed germination (Helms & David, 1973). Also in other plant species like Zea mays the calcium from the seed can be mobilized during germination only to a very limited amount (Klein & Urban, 1967). In contrast to the other essential mineral element calcium has therefore

to be present in the external medium right from the beginning of germination.

Among the essential plant nutrients calcium has a special position insofar as the functional requirement within the cell is obviously low for a major nutrient. The supply of calcium in the soil solution and at the root surface, however, has to be permanently high. This is important because of either the absence or only very low ability of the plants for active and selective uptake of calcium even under conditions of calcium deficiency (Mostafa & Ulrich, 1974) and the inability of plants to retranslocate calcium. The competition which always exists more or less in uptake as well as within the cell between ions of the same charge, i.e. cations or anions, seems to be especially pronounced in the case of calcium. The requirements of plants for calcium in both supply in the substrate and concentration in the tissue, therefore increases with the increase in supply of other mineral elements. To prevent growth depressions of high NaCl concentrations, for example, the supply of calcium has to be increased simultaneously (Lahaye & Epstein, 1971).

To overcome inadequate calcium nutrition in certain plant parts, mainly fruits and storage organs, additional supply of calcium as sprays to the aerial parts may be applied as a short-term method to prevent calcium deficiency. In the long term, however, this is not satisfactory. A better knowledge of the endogenous regulatory mechanisms affecting uptake and long distance transport of calcium is urgently required, including the effect of growth substances and the form of nitrogen (nitrate versus ammonium) on the calcium distribution within the shoot (Shear & Faust, 1970).

In future the application of calcium has to be increased to return to an adequate level in relation to the other nutrients supplied as inorganic fertilizers. The effects of the other agricultural and horticultural practices which influence ion uptake, growth rate, etc. have also to be considered more in relation to their influence on the calcium nutrition. One example of such an interaction is the effect of soil aeration on the potassium/calcium ratio in the shoot (Visser et al., 1972).

Finally, the genetic variability which exists within one species with respect to calcium nutrition (Greenleaf & Adams, 1969) has to be used more systematically in breeding and selection programmes in the future.

Acknowledgement

References

Asher, C. J. & P. G. Ozanne, 1961. The cation exchange capacity of plant roots, and its relationship to the uptake of insoluble nutrients. *Aust. J. agric. Res.* 12: 755–766.

Bangerth, F. & M. Mostafawi, 1969. Einfluss der Wasserversorgung und des Fruchtgewichtes auf den Mineralstoffgehalt und die Stippigkeit von Apfelfrüchten. *Erwerbsobstbau* 11: 101–104.

Barber, S. A. & P. G. Ozanne, 1970. Autoradiographic evidence for the differential effect of four plant species in alterning the calcium content of the rhizosphere soil. *Proc. Soil Sci. Soc. Am.* 34: 635–637.

Bell, C. W. & O. Biddulph, 1963. Translocation of calcium. Exchange various mass flow. *Pl. Physiol.* 38: 610–614.

Breteler, H., 1973. A comparison between ammonium and nitrate nutrition of young sugar beet plants grown in nutrient solutions at constant acidity. 1. Production of dry mattern, ionic balance and chemical composition. *Neth. J. agric. Sci.* 21: 227–244.

Bünemann, G. & P. Lüdders, 1969. Die Wirkung des Zeitpunktes von Harnstoffspritzungen auf Apfel-bäumen. II. Stippigkeit. *Z. PflErnähr. Bodenk.* 124: 193–201.

Burström, H., 1968. Calcium and plant growth. *Biol. Rev.* 43: 287–316.

Bussler, W., 1963. Die Entwicklung von Calcium-Mangelsymptomen. *Z. PflErnähr. Düng. Bodenk.* 100: 53–58.

Egmond, F. van & H. Breteler, 1972. Nitrate reductase activity and oxalate content of sugar beet leaves. *Neth. J. agric. Sci.* 20: 193–198.

Egmond, F. van & V. J. G. Houba, 1970. Production of carboxylates (C-A) by young sugar beet plants grown in nutrient solution. *Neth. J. agric Sci.* 18: 182–187.

Foroughi, M. & A. Kloke, 1974. Blütenendfäule an *Citrullus vulgaris* (Schrad.)-Wassermelone. *Pl. Soil* 40: 57–64.

Foy, C. D., A. L. Fleming & G. C. Gerloff, 1972. Differential aluminium tolerance in two snapbean varieties. *Agron. J.* 64: 815–818.

Garz, J., 1966. Menge, Verteilung und Bindungsform der Mineralstoffe (P, K, Mg und Ca) in den Leguminosensamen in Abhängigkeit von der Mineralstoffumlagerung innerhalb der Pflanze und den Ernährungsbedingungen. *Kühn-Arch.* 80: 137–194.

Goor, B. J. van, 1971. The effect of frequent spraying with calcium nitrate solutions on the mineral composition and the occurrence of bitter pit of the apple Cox's orange pippin. *J. hort. Sci.* 46: 341–364.

Greensleaf, W. H. & F. Adams, 1969. Genetic control on blossom end rot disease in tomatoes through calcium metabolism. *J. Am. Soc. hort. Sci.* 94: 248–250.

Gubbels, G. H. & R. L. Carolus, 1971. Influence of atmospheric moisture, ion balance, and ion concentration on growth, transpiration and black heart of celery (Apium graveolens L.). *J. Am. Soc. hort. Sci.* 96 (2): 201–204.

Hallock, D. L. & K. H. Garren, 1968. Pod breakdown, yield, and grade of Virginia type peanuts as affected by Ca, Mg and K sulfates. *Agron. J.* 60: 253–257.

Hanger, B. C., 1973. The relationship of calcium oxalate crystal deposition to the stage of development of clover leaves. *Proc. int. Pl. Physiol. Symp.* (Palmerston-North, New Zealand, 1973).

Helms, K. & D. J. David, 1973. For red and white light-promoted utilization of calcium by seedlings of *Phaseolus vulgaris* L. *Pl. Physiol.* 51: 37–42.

Higinbotham, N., B. Etherton & R. J. Foster, 1967. Mineral ion contents and cell transmembrane electropotentials of pea and oat seedlings tissue. *Pl. Physiol.* 42: 37–46.

Houba, V. J. G., F. van Egmond & E. M. Wittich, 1971. Changes in production of organic nitrogen and carboxylates (C-A) in young sugar beet plants grown in nutrient solutions of different nitrogen composition. *Neth. J. agric. Sci.* 19: 39–47.

Jones, R. G. W. & O. R. Lunt, 1967. The function of calcium in plants. *Bot. Rev. (N.Y.)* 33: 407–426.

Klein, P. & K. Urban, 1967. Untersuchungen über den Mineralstoffhaushalt unter besonderer Berücksichtigung der Sorten 'Schindelmeiser' und 'Siloma'. *Thaer-Arch.* 11: 619–628.

Koontz, H. V. & R. E. Foote, 1966. Transpiration and calcium deposition by unifoliate leaves of *Phaseolus vulgaris* differing in maturity. *Physiologia Pl.* 14: 313–321.

Kraus, A. & H. Marschner, 1974a. Einfluss der Höhe des Ca-Angebotes auf Wachstumsrate und Mineralstoffgehalt von Kartoffelknollen. *Z. f. Pfl.Ernähr. Bodenk.* (im Druck).

Krauss, A. & H. Marschner, 1974b. Einfluss der Tag/Nacht-Periodik auf Knollengewicht und Ca-Verlagerung in Stolonen von Kartoffelpflanzen. *Z. PflErnähr. Bodenk.* 137: 116–123.

Krug, H., H.-J. Wiebe & A. Jungk, 1973. Calciummangel an Blumenkohl unter konstanten Klimabedingungen. *Z. PflErnähr. Bodenk.* 133: 213–226.

Lahaye, P. A. & E. Epstein, 1971. Calcium and salt tolerance by bean plants. *Physiologia Pl.* 25: 213–218.

Liegel, W., 1970. Calciumoxalat-Abscheidungen in Fruchtstielen einiger Apfelvarietäten. *Angew. Bot.* 44: 223–232.

Loneragan, J. F. & Snowball, 1969. Calcium requirements of plants. *Aust. J. agric. Res.* 20: 465–478.

Loneragan, J. F., J. S. Gladstone & W. J. Simmons, 1968. Mineral elements in temperate crop and pasture plants. II. Calcium. *Aust. J. agric. Res.* 19: 353–364.

Lüdders, P. & G. Bünemann, 1970. Der Einfluss jahreszeitlich unterschiedlicher Stickstoffversorgung auf das Wachtum von Apfelbäumen. V. Der Einfluss auf die Blatt- und die Fruchtinhaltsstoffe. *Gartenbauwissenschaft.* 35 (17): 185–216.

Lundegårdh, H., 1941. Untersuchungen über das chemisch-physikalische Verhalten der Oberflächen lebender Zellen. *Protoplasma* 35: 548.

Marschner, H. & Ch. Richter, 1947a. Calcium-Transport in Wurzeln von Mais- und Bohnenkeimpflanzen.

Marschner, H. & Ch. Richter, 1947a. Calcium-Transport in Wurzeln von Mais- und Bohnenkeimpflanzen. *Pl. Soil* 40: 193–210.

Marschner, H. & Ch. Richter, 1947b. Akkumulation und Translokation von K+, Na+ und Ca²+ bei Angebot zu einzelnen Wurzelzonen von Maispflanzen. *Z. PflErnähr. Bodenk.* 135: 1–15.

Martin, P., 1971. Reduktion von ¹⁵NO₃-Stickstoff und Einbau in das Eiweiss in verschieden alten Blättern von Buschbohnenpflanzen. *Z. PflErnähr. Bodenk.* 128: 143–153.

Mengel, K., 1962. Die K- und Ca-Aufnahme der Pflanze in Abhängigkeit vom Kohlenhydratgehalt ihrer Wurzel. *Z. PflErnähr. Düng. Bodenk.* 98: 44-54.

Mengel, K., H. Grimme & K. Németh, 1969. Potentielle und effektive Verfügbarkeit von Pflanzennähr-stoffen im Boden. *Landw. Forsch.* 33 (Sonderh. 16): 79–91.

Mix, G. P., 1973. Ca-Einlagerung in Früchten von Bohne und Paprika sowie Quitte und Hagebutte. Dissertation, Technische Universität Berlin, D 83 Nr. 30.

Mix, G. & H. Marschner, 1974. Mineralstoffverteilung zwischen Chloroplasten und übrigem Blatt-gewebe. *Z. PflPhysiol.* 73: 307–312.

Mostafa, M. A. E. & A. Ulrich, 1974. Calcium uptake by sugar beets relative to concentration and activity of calcium. *Soil Sci.* 116: 432–436.

Pearson, R. W., J. Childs & Z. F. Lund, 1973. Uniformity of limestone mixing in acid subsoil as a factor in cotton root penetration. *Proc. Soil Sci. Soc. Am.* 37: 727–732.

Riley, D. & S. A. Barber, 1970. Salt accumulation of the soybean *(Glycine max. L. merr.)* root soil interface. *Proc. Soil Sci. Soc. Am.* 34: 154–155.

Ringoet, A., G. Sauer & A. J. Gielink, 1968. Phloem transport of calcium in oat leaves. *Planta 80:* 15–20.

Robards, A. W., S. M. Jackson, D. T. Clarkson & J. Sanderson, 1973. The structure of barley roots in relation to the transport of ions into the stele. *Protoplasma* 77: 291–311.

Schuffelen, A. C., 1948. Growth substances and ion absorption. *Pl. Soil* 1: 121-126.

Schuffelen, A. C., 1972. Nährstoffvorrat und Nährstofflieferung im Boden. In: Chemie und Landwirt-schaftliche Produktion, p. 27–42.

Schuffelen, A. C. & R. Loosjes, 1946. The importance of the ion activity of the medium and the root potential for the cation-absorption by the plant. *Proc. Kon. ned. Akad. Wet.* 49: 80–86.

Shear, C. B. & M. Faust, 1970. Calcium transport in apples trees. *Pl. Physiol.* 45: 670–674.

Vervelde, G. J., 1953. The Donnan-principle in the ionic relations of plant roots. *Pl. Soil* 4: 309–322.

Visser, J., J. Th. Locher & R. Brouwer, 1971. Effect of aeration and mineral supply on growth and mineral content of shoots and roots of apple trees (var. 'Golden Delicious' on M. IX). *Neth. J. agric. Sci.* 19: 125–137.

Walker, J. M., 1969. One-degree increments in soil temperatures effect maize seedling behavior. *Proc. Soil Sci. Soc. Am.* 33: 729–736.

Wieneke, J. & F. Führ, 1973. Untersuchungen zur Translokation von ⁴⁵Ca im Apfelbaum. I. Transport und Verteilung in Abhängigkeit vom Aufnahmezeitpunkt. *Gartenbauwissenschaft* 38: 91–108.

Wiersum, L. K., 1966. Calcium content of fruits and storage tissue in relation to the mode of water supply. *Acta bot. neerl.* 15: 406–418.

Wiersum, L. K., C. A. Vonk & P. M. L. Tammes, 1971. Movement of ⁴⁵Ca in the phloem of Yucca. *Naturwissenschaften* 58: 99.