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EFFECTS OF ENVIRONMENT AND CULTURAL PRACTICES ON CALCIUM NUTRITION

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ABSTRACT

An attempt will be made to elucidate how the basic phenomena governing Ca uptake and distribution in the plant respond to manipulation.

Effects on Ca uptake through manipulation of the root medium seem to be mainly caused by shifts in competition or relative availability of Ca and ions such as K, NH_4, and some others. Cultural practices, which affect the above ground environment of the plant can have effect in two ways. Primary distribution of Ca in its xylem pathway may be affected or an influence on the redistribution can be assumed. Exchange, fixation, and sometimes even mobilization are affected by light, temperature and transpiration.

Direct manipulation of the plant itself - such as grafting, pruning, application of growth regulators, disease control, etc. - can in many cases also be related to certain processes involved in Ca-distribution over the plant.

The multitude of processes involved makes the forecasting of effects still rather difficult, but effective ameliorative measures are available.

INTRODUCTION

Although the actual amount of available calcium in most cropped soils can be considered adequate, disorders linked to insufficient levels of calcium still occur frequently. In most cases these disorders are only evident in parts of the plant, which is caused by the transport characteristics of this element, which have already been discussed in this symposium.

Both uptake and transport processes are subject to environmental influences. However, these variable factors may act at many different links - and sometimes on different links simultaneously - of the chain of processes providing the affected plant with calcium. In this presentation an attempt will be made to piece together certain facts of the existing knowledge by trying to elucidate how environmental variations or cultural practices could act on the basic phenomena of uptake and translocation of calcium. It will then probably become more clear how difficult it often is to achieve compatibility between a large yield and a healthy product.

THE BASIC PHENOMENA

Calcium provision of any part of the plant is the ultimate result of quite a series of processes (Fig. 1). The first step to be considered is the uptake through the roots and secretion into the xylem, taking an adequate availability in the soil for granted. This adequate availability can be met by concentrations ranging from 5 - 40 ppm Ca (100 - 1000 µM) at the root surface (24, 29, 33), unless ionic antagonism caused by an unbalanced composition of the soil solution interferes. The absorption process is subject to variations in active root surface, permeability changes, and metabolism.

The second step is the longitudinal translocation in the xylem to those plant parts where water is consumed. It has now been adequately demonstrated that along this long pathway calcium may be fixed through absorption, exchanged against other ions (6, 8, 11, 60, 88) or lost by fixation into surrounding tissue (10, 35). These processes may be enhanced or retarded, depending on whether calcium occurs in ionic or in chelated form in the xylem sap (3, 9). These possibilities may all be controlled by environmental factors or crop manipulation. This ultimately results in the fact that the primary provision of calcium to the transpiring plant parts is not necessarily correlated with their supply of water. What happens along the way may be decisive.

An external and continuous good supply of calcium to the xylem seems necessary as remobilization of stored calcium in wood and bark seems difficult, although it can occur (21).

The ultimate calcium content of any plant part will be the result of both influx and efflux of this element. The influx is

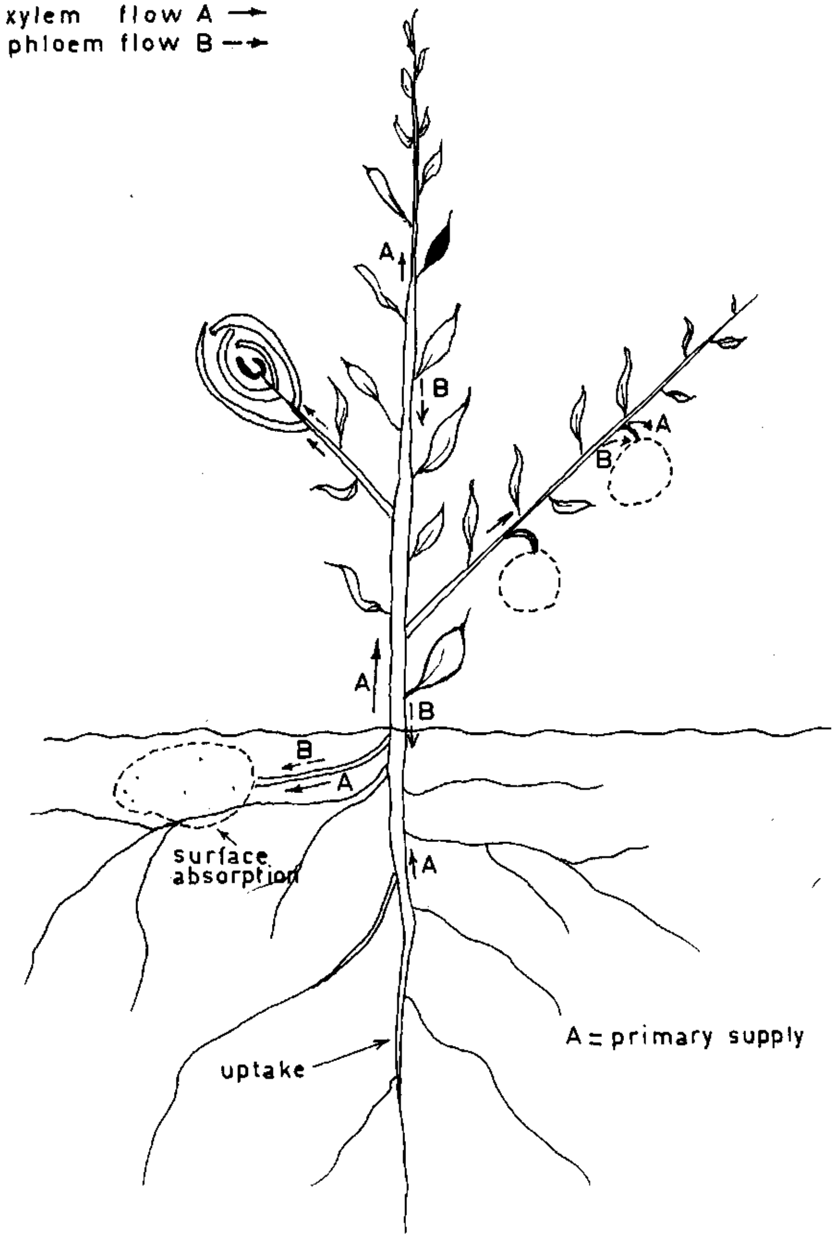

FIG. 1.

Schematic diagram of calcium transport in the plant.

the sum of the primary supply via the xylem and the secondary supply through the phloem. Their relative contributions are subject to large variations, depending on many conditions (71, 46, 80, 81). In plant parts requiring large amounts of assimilates for their growth the phloem supply may dominate; the more so as the surface: volume ratio decreases and thus transpiration proportionally diminishes in importance(13). The efflux is usually small and can be neglected for our purpose(43).

As redistribution of calcium mainly depends on phloem transport - mobilization of stored calcium into the xylem being rather exceptional and probably restricted to spring sap-flow - the third step to consider is the provision of the phloem with this element. As the phloem sap may be considered to be a continuum with the cytoplasm (symplasm), it demonstrates the same very low calcium content. The concentration of this element in the sieve-tubes is thus mainly regulated by the processes also governing the cytoplasmic contents (22, 84), such as its potential low solubility(22, 70, 72).

The fourth step by which redistribution is brought about is the translocation of calcium along the phloem. On account of its very low content (49, 69, 86) only small amounts are carried along by the sap stream. Sinks fed mainly by the phloem are thus always low in calcium content (42, 43, 44, 79), although not always to an extreme extent (31). It seems that phloem transport, as such, often carries inadequate amounts of calcium to provide carbohydrate sinks with the required amount, and that some additional influx via the xylem is necessary. In its movement along the sieve tubes, calcium is subject to the same type of phenomena as in xylem transport, depending on the conditions.

The consequence of the above-mentioned facts is that source-sink relations are quite often by no means simple (66, 68), especially if additional supply mechanisms seem possible (44). For our discussion, an attempt will be made to elucidate how environmental factors may affect calcium content through their actions on these various processes. Figure 1 gives a schematic and concise synopsis of the basic phenomena that will be taken into account.

ENVIRONMENTAL EFFECTS

A. Soil conditions

Many soils are not in the most favourable condition for sustaining large plants. But, luckily, it is feasible to ameliorate most soils to obtain the conditions required to allow adequate root development and provide water and nutrients.

Manipulation of the soil volume accomodating the root system through tillage, subsoiling, or drainage is not likely to affect calcium supply much, unless acid or otherwise toxic subsoils are involved. Prevention of excessive moisture or a high water table may, however, contribute to a better calcium supply (46,59). The increased volume of soil available for rooting will result in increased root surface active in uptake, thus facilitating absorption of less easily available nutrients. As calcium is usually carried along to the root surface by the water withdrawn from the soil in amounts exceeding plant requirement, the size of the root system is of little value in this case (2, 83). But in modern techniques of growing plants in small containers or in soilless culture, available space for root development may be extremely reduced. Although nutrients usually are in continuous supply, the relatively low maximum influx rate of calcium makes this one of the first nutrients to suffer from extreme reduction in root surface (74).

Tillage of the soil surface, mainly for the purpose of eradication of weeds, can be more important. In many soils the fertilized topsoil may contain a higher calcium content than the subsoil. Tillage can in this case eradicate roots in the top layers, thus restricting utilization of part of the available stock. But as it mostly has a comparable effect on some other main nutrients, a special influence on the calcium content of the crop is seldom evident. In some cases the absence of roots in the warmer topsoil may even encrease calcium absorption relatively, as this is less affected by lower temperatures in deeper layers than the highly active uptake of potassium.

Both drainage and irrigation are widely used for regulating and optimizing the water supply in the soil. There is a number of ways in which variations in water content of the soil may have an effect on calcium supply. Both calcium concentration in the soil solution and its mobility are involved. Raising the water content of the soil usually will result in a lowering of the soil solution concentration. If it does, the calcium content will be more reduced than that of the monovalent ions as the result of exchange phenomena. The total amount of dissolved calcium and its mobility will however be raised. Another counteracting effect might be brought about by a higher water content of the soil if it is accompanied by gradually reduced aeration. If this results in a raised bicarbonate content, more calcium is to be expected in the soil solution (82). Lack of water would be expected to curtail the supply of this ion, thus reducing uptake (46). Taking all things together, it does not seem that variations in water content of the soil are apt to have a clear, specific effect on calcium provision by the soil (54).

Water stress on the root system can, however, reduce its permeability and transport capacity (53, 85). This will impede uptake. Increased moisture content of the soil will generally enhance active potassium absorption to a greater extent, thus raising the K:Ca ratio in the plant as a whole (21).

But all variations in availability of water in the soil have repercussions on the internal water balance of the crop and the competition for the absorbed amounts between the different plant parts. The resulting induced shifts in growth patterns, metabolism, and carbohydrate translocation will also affect the distribution of minerals (30). Upward translocation of calcium is apt to diminish under water stress, partly on account of reduced passive intake along with water and partly as a result of slower xylem transport. The primary provision would thus be reduced.

More severely affected will be the distribution of this element. Phloem transport seems to be much less sensitive to water stress than xylem transport(76), but it only carries very small amounts of calcium. In periods of water stress the only minimally transpiring but fast growing parts of the plant, i. e. buds, fruits, tubers, and seeds will temporarily be phloem-fed only. An adequate calcium supply may thus be lacking during these periods. Even competition for water by the leaves may withdraw water from these bodies and thus remove minute amounts of calcium. Optimalizing water supply of the plant thus promotes the provision of calcium to these mainly phloem-fed plant parts by allowing the necessary additional xylem influx of water with a high calcium content. But a sudden moisture supply after a period of drought can stimulate additional vegetative growth, especially in the later part of in the season. This can be somewhat detrimental on account of increased leaf competition for water. (20).

The effect of fertilizing has already been discussed in this symposium. The main point seems to be that administering lime to obtain the required pH, which is often considered as an indicator of the calcium supply level, does not always result in increased calcium uptake, partly as a result of competition by high amounts of K, NH_4, Na or Mg (1, 12, 19, 28, 36, 37, 52, 57, 61, 73). Even inhibitory effects by the micro-element Mn have been indicated (56). Taking recent research into account, the unfavourable effects of high potassium may also be due to its enhancing phloem transport, thus retarding calcium influx via the xylem into sink tissues(40). For ammonium it has been demonstrated that it can both lower the calcium concentration in the xylem exudate as well as reduce exudation (87).

We still lack a good method of ascertaining the calcium supply status of the soil in relation to its availability to the plant. The fear of high applications of lime to avoid an excessively high pH which reduces minor element availability has probably discouraged research on other methods of applying this element.

The intricacy of fertilizer effects can be illustrated by the way in which nitrate may act. In uptake by the root, nitrate has been found to enhance calcium uptake (4, 8). But its conversion into proteins results in a more or less equivalent production of organic anions, which are, for the greater part, deposited in the vacuoles. Their negative charge is usually largely counterbalanced by calcium ions, so, in these cases, the vacuoles act as strong sinks for calcium. This fixation capacity of the vacuoles, which detracts calcium from the xylem and possibly even from the phloem, is even stronger when oxalic acid formation occurs, thus lowering the supply at the end of the transport route(10).

The nutrient status of the soil is not only of importance in relation to the uptake of calcium, but it also affects calcium distribution through its effects on growth and metabolism. Nitrogen supply - in terms of its level as well as its form - can be of influence (7, 8). This element may affect the formation of slower buds, fruit bearing, and vegetative growth. Stimulation of vegetative growth can be deleterious to the calcium supply of fruits, seeds, tubers, and enclosed vegetation points mainly through the effects of reduced xylem influx as a result of competition for water and raised phloem influx as a result of increased production of assimulates. But if nitrogen application results in increased fruitfulness and bearing is enhanced, then it may have favourable results.

A corrective measure, which aims at a direct supply to the affected plant parts is the spraying of solutions containing calcium salts on the aboveground plant parts (16, 34, 39).

Nowadays, the possibilities of trickle irrigation are attracting much attention. In combining water and dissolved nutrients it offers a possibility of achieving a stable and equilibrated supply. However, the system has one drawback. Nutrient uptake by the root requires a certain equilibrium between all dissolved ions at the root surface. Incomplete nutrient solutions - only N,P,K, and Mg - can distrub the required ionic balance in the soil. And an applied balanced solution may ultimately result in imbalance due to the unequal absorption of the elements and thus different amounts remaining (83). In as far as trickle irrigation increases growth rates, e. g. for lettuce, it may be deleterious to the required calcium distribution (17).

Although primarily applied to obtain improved soil conditions and eradication of weeds around the plant, mulching may result in nutritional side-effects. Especially grass-mulch - often applied in orchards - contains relatively much potassium. The same holds for straw mulch. Enchanced root development in the improved superficial soil layers may thus contribute towards a certain dominance of potassium uptake (38, 67) and restriction of calcium nutrition. Mulches consisting of dicotyledonous species may enchance calcium supply.

Reasonable, and often even high levels, of organic matter are considered favourable for crop production, especially in intensive cropping systems. At the correct pH its stock of absorbed calcium and its regular slow release of nitrogen, which can be oxidized to nitrate, can be considered favourable for calcium nutrition. But there has been a report that drought could result in formation of more ammonium - as a result of the reducing capacity of a high organic matter content - which would reduce calcium intake (19).

Soil temperature is an important factor, which can be influenced through organic matter content, mulching and heating. A rise in temperature to levels of between 293 - 298° K will speed up many processes in soil and plant. As potassium uptake is generally more sensitive to increased metabolic activity in contrast to the more passive calcium absorption, lower soil temperatures would favour the relative calcium status (63). Higher soil temperatures may become deleterious, depending on the level of susceptibility to temperature damage of the plant involved.

The result of the general immobility of calcium in the plant is that most plant-analysis data may demonstrate high contents, without the certainty that this fact indicates a reasonable rate of its supply to susceptible plant parts at the moment of sampling(33). Thus, it is advisable to provide conditions for a continuous adequate uptake of calcium, especially during periods when the susceptible parts develop.

B. Climatic conditions

Light and temperature are the two main factors directly affecting the performance of the above-ground parts of a plant. As a source of energy and in governing the rate of chemical and physical processes they greatly affect growth. The overall growth rate of a plant will not have a large effect on general calcium uptake and level, but different parts of the plant could be unevenly affected. High assimilation and growth rates usually result in some decrease in mineral contents of the whole plant, and can bring about stronger reductions in calcium content of fruits, etc.

Far more important for our discussion is the fact that these two factors - along with rainfall - govern both evaporation and transpiration. A negative water balance for the soil will result in an increase in pF, with its concomitant effect on calcium supply. In the plant itself, increasing water stress will be accompanied by a change in movement of water in the xylem and a shift in the distribution pattern. Also, with adequate soil water the most intensively transpiring parts, where the highest suctions will develop, will then obtain a relatively larger part of the available water. Sometimes the leaves may even attract water from other organs, e.g. fruits, where it is less firmly held. The already described shift between the contributions of xylem and phloem in the provision of calcium will result. By means of this response the competition for water by the more highly transpiring leaf surface will diminish the calcium supply to the storage tissues and enclosed young centers of growth.

A number of practical measures aim at reducing high transpiration of the crop. Reducing of wind speed by means of shelterbelts is often practised and shading can be used. Also overhead sprinkling will affect both plant and soil favourably (45, 64), although some calcium may be lost by leaching (78). Application of antitranspirant oil sprays has been able to reduce bitter pit incidence (58). Under special conditions this reduced transpiration can result in development of root pressure and forcing of xylem water into plant parts otherwise receiving little or none(48).

In glasshouse culture, however, the regulation of the internal water balance of the plant may be slightly difficult. The usually moist atmosphere may require increased ventilation to prevent excessive heating of the leaves (reduced transpiration) under high light intensity. Shading may then be practised and it could have the additional advantage of slowing down photosynthesis. This latter fact could contribute to a slower supply of assimilates plus the accompanying water to the sinks (storage tissues). This retarded phloem supply, along with slower growth, would enhance xylem water influx and thereby a higher supply of calcium (27, 77).

Exposure of fruits themselves to light and wind may also be of influence. The higher their own transpiration is the more water inflow through the xylem is apt to occur. Avoidance of very dense planting and using a pruning method directed towards prevention of much leaf, could then be measures to consider. In as far as dense planting reduces vigour and results in slower growing and slightly smaller fruit, it tends to have a favourable effect.

As long as transpiration is not impaired, high light intensity and temperatures up to a range of about 298 - 308°K will stimulate photosynthesis, metabolism, and growth. Generally, one would not expect any specific influence on the primary calcium supply as a result of this higher rate of activity. But if increased metabolism were to be accompanied by alterations in organic-acid production or other shifts in binding capacities for divalent cations an indirect effect could occur. As yet, indications for these possibilities do not seem to exist, but we should keep them in mind.

Fast growth, as a result of increased assimilation or metabolsim, should result in increased export of organics from leaves to the sinks. It thus increases phloem transport. This increased phloem transport is detrimental to the calcium influx through the xylem. It may thus be advantageous to avoid temperature, light, and moisture conditions which are conducive to very high growth and production rates(63). These phenomena are to be taken into account in relation to spacing. Wide spacing goes with much light, which is favourable for fast growth, along with a high transpiration, which entails competition for water.

The last point to consider is whether climatic factors, mainly temperature, may affect redistribution of stored calcium. This stored calcium is mainly found in stems and roots of woody perennials and in bulbs and tubers. For trees, there is evidence that stored calcium can be released to the xylem in analogy to reserve carbohydrates (37). Early spring bleeding sap may thus contain calcium released from storage. Whether the same type of mobilization occurs in sprouting tubers and bulbs does not seem to have been investigated. In tulips, however, where conditions favouring fast growth can lead to "toppling", the lack of calcium provision to the elongating stem can most likely be ascribed to dominance of phleom supply with its low calcium content.

For phloem-fed potato sprouts and young peanuts an external supply of calcium from the soil can be of importance (15, 79) in ensuring healthy development, because transpirational pull on xylem water (plus its calcium) may be lacking.

CULTURAL PRACTICES

One of the first measures to consider is the choice of cultivar, as it can help to evade problems in calium nutrition. Within species, variations in uptake, translocation and fixation of calcium have been demonstrated (14, 52). Differences in uptake may be related to variations in root C.E.C., while differences in translocation may correspond to differences in fixation through varying oxalate content. Selection to obtain cultivars insensitive to distrubances in their calcium nutrition can, thus, partly be based on examination of the phenomena just mentioned.

Of much importance from a practical point of view are the stock/scion interrelationships as budded or grafted plants are much used(23). Differences in the supply of potassium and calcium to the scion have been observed in the Malling rootstocks(45).

Knowledge concerning the relative affinity for calcium of the roots of the stock is by no means sufficient to forecast its value. As the stock also has an effect on numerous growth and development characteristics of the scion, and the graft union can interfere with certain translocation processes the uptake alone is often not the decisive factor in regulating the total calcium supply and its distribution in the plant. The effects brought about through variations in fruiting and leaf; fruit ratios may be of more importance. The choice of certain stocks and scions (cultivars) is, however, quite often based on other required characteristics than insensivity to calcium disorders.

Pruning, pinching of buds, and other methods to reduce branching are often used to influence growth and production. They can be used for quite different purposes.

Removal of buds of young side-shoots can be useful to obtain less numerous but larger salable products, such as flowers or fruits. Fruit-thinning serves the same purpose. The source: sink ratio is raised, resulting in faster and larger development of the required products. It will result in relative dominance of phloem supply, with its low calcium influx.

But pruning can also be used to achieve a higher fruitfulness and a more open type of plant. Again the source: sink (leaf/fruit) ratio is affected, but now in a manner favouring supply. This is especially the case if regular yearly bearing and avoidance of "on-and-off-years" can be promoted through these manipulations.

The favourable effect of summer pruning to diminish leaf surface of apples somewhat, thereby reducing bitter pit incidence (65,77), fits in well with the relationships described earlier. There is also quite an amount of evidence that in fruit growing, steady fruit growth should be preferred and that fast fruit growth - especially in the earlier and intermediate stages - can be detrimental to optimal calcium supply.

Incidentally some other measures aimed at reducing vigorous vegetative growth, which is associated with relatively much leaf, have been used. One of them has been root pruning in apples, which, indeed, reduced bitter pit in some cases.

Another fact to consider is disease control. Its overall effect has been a general improvement of leaf condition and productive capacity. In this manner yields have been increased, but also growth rates and size of the product. In as far as the product belongs to those plant parts which have a relatively dominating sap supply through the phloem, this can have contributed to a diminished calcium supply.

Regulation of fruit set, which is often practised in order tc obtain constant good yields of high quality, can contribute to reduction of calcium disorders in the fruit. If the measures taken, e.g. pruning, hormone sprays, avoiding "off-years" by fruit thinning in "on-years", or training, result in reasonably high yields and a steady and not too fast growth rate of the fruit, the calcium supply will be more or less optimal. Heavy leaf competition for water and a strongly dominating phloem supply are then avoided, partly on account of the optimal leaf; fruit ratio achieved.

The fact that late picking has often proven to be of value in reducing bitter pit may be related to the fact that influx via the phloem diminishes in the full-grown fruit. As transpiration still goes on, the relative contribution of calcium influx via the xylem could increase, thus raising its content(47). But available data do not definitely confirm this possibility.

But nowadays there are ways of manipulating plant growth by application of any of a large array of growth regulators. We now have growth retardants such as CCC and maleic hydrazide at our disposal, as well as general or specific stimulating substances, such as the kinetins which could be used to stimulate growth of certain sinks. Their effect on calcium nutrition will probably most often be linked with changes induced in intensity of uptake(26) and changas in the xylem and phloem transports. Daminozide, a growth retardant, can indeed, produce smaller fruits containing somewhat more calcium (26,77). Clear evidencse of effects through altered metabolism, permeability or fixation are still extremely scarce. The effect of TIBA on lowering the calcium level in the apple fruit is an example(47, 62).

A number of difficulties might disappear if the calcium content of the phloem could be raised, thus effecting a raised general mobility. Raising the overall calcium level of the plant can have some effect as the phloem-sap content is correlated (85) with it, but one could also conceive of attempting to overcome its low solubility as an ion in this sap(72) by administering suitable chelating substances. Chelates could possibly also help to obtain more mobile calcium, with its possible entry into the phloem(41).

The existence of anti-transpirants is also something to consider. In as far as they can be effectively applied some effect on calcium distribution is to be expected. One could expect a slightly improved calcium supply to those parts of the plant which are sinks for assimilates. It could, in many respects, be compared to the effects of overhead sprinkling.

SUMMARY AND CONCLUSIONS

Assuming that liming and fertilizing have resulted in an adequate chemical fertility level, optimum calcium nutrition of the crop is not always guaranteed. To raise the availability of calcium for the plant, a number of measures can be taken. Tillage and drainage can result in better rooting and increased absorptive surface. Irrigation, mulching, and soil temperature can promote availability and increased absorption of calcium. But as generally the same holds for other ions, the antagonism by equally raised concentrations of K, Na, NH_4, Mg, etc. may counteract the primary uptake. Indirectly, soil factors may also influence calcium distribution in the plant.

Both climatic factors and plant treatments will primarily act on growth and development patterns. As these are linked with changes in xylem and phloem transport intensities, the calcium distribution is affected. Generally, xylem transport to a carbohydrate sink should not decrease too much as the phloem sap will often not supply adequate amounts of calcium. But in relation to metabolic factors, e.g. nitrate conversion, even xylem inflow may carry along insufficient calcium if its content is lost by fixation along this pathway.

Especially for fruits, all measures aiming at a good fruit set and reasonable leaf: fruit ratio seem favourable.

In general, much evidence points to the fact that a regular constant supply and regular steady growth rates of the plant parts susceptible to disorders favour the ultimate calcium content.

The fact that many cultural practices can have a bearing on different processes and links in the total uptake and distribution systems, which are often opposite in effect, makes forecasting and prescribing still somewhat unreliable(7). But nevertheless a number of measures to minimize the problems are coming into practice.

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