

INTERRELATIONSHIPS BETWEEN PLANT GROWTH REGULATORS AND FRUIT TREE
MINERAL NUTRITION

J. Tromp

Department of Horticulture¹
Agricultural University
P.O. Box 30
6700 AA Wageningen

Research Station for Fruit Growing
4475 AN Wilhelminadorp
The Netherlands

Abstract

Information is presented for fruit trees to show the effect of applied growth substances on mineral uptake and tissue mineral levels. The effects of nutrient supply to the roots on hormone synthesis and levels in the plant are also considered. The data are discussed in terms of a direct effect of applied growth substances on the actual nutrient absorption occurring in the roots, and of an indirect influence occurring via growth effects induced by growth substances which weaken or strengthen sink demand and consequently affect mineral nutrition. In a few cases, the evidence for a direct effect on mineral uptake by the root is quite sound, but most experiments are inconclusive with respect to the explanation of the observed phenomena.

1. Introduction

This contribution deals with both the effect of growth-regulating compounds on mineral nutrition and, conversely, the influence of mineral supply on the synthesis and levels of endogenous hormones. The amount of relevant information is not large, certainly not when only fruit trees are considered. Thus Robinson (1975), reviewing the literature on the present topic and restricting himself to whole plants with emphasis on woody perennials, could provide only about 50 references. Moreover, the more widely studied topic of mineral nutrition of the fruit falls beyond the scope of this paper; it will be discussed by Drs. Faust and Miller as a contribution to this conference.

Although in the discussion below the interest will be focused on fruit trees, this restriction is not absolute. When information for fruit trees is not available, relevant references on other plants will be used in a few cases. The role of endogenous hormones in the ion-absorption process will not be considered.

Finally, two remarks concerning terminology and data expression should be made. The term growth substances or compounds will be used when no specification is needed. Hormones are defined herein as naturally occurring growth substances, while the term regulators is reserved exclusively for synthetic growth substances.

The second point concerns the expression of the analytical data for mineral elements. Dry weight is generally used, but it will be evident that when changes in dry weight occur due to e.g. applied growth substances, data expressed in terms of dry (or fresh) weight, i.e. concentration data, are not very informative. Especially when conclusions must be drawn on effects of treatments on mineral uptake, expression of the results on a whole plant basis is required. For

¹ Publication No. 551

trees, this requirement is rarely satisfied, and if so, the experiments involve young seedlings. An alternative method of measuring mineral element uptake is by growing plants in water culture, then calculating the absorption of minerals from the reduction of concentration in the nutrient solution. However, for practical reasons, this technique is restricted to experiments with relatively small plants.

2. Effect of growth substances on mineral uptake

This effect may occur via two principally different ways:

- directly, where the growth substances are involved in the absorption process, itself, occurring in the roots;
- indirectly, where the growth regulating substances in their effect on vegetative growth weaken or strengthen sink demand for various compounds including minerals.

The effect of growth substances on mineral uptake is mainly studied on excised tissue, including roots, storage tissue and leaf slices. There is no doubt that growth compounds do have an effect on ion absorption, but it remains uncertain whether results from excised tissue are representative of intact plants. Growth substances have been found to influence various physiological phenomena related to mineral uptake, e.g. the proton-pump mechanism, membrane conductance, and metabolic utilization of ions. Much work has been done on the effect of auxins and abscisic acid; the role of gibberellins has received less attention. These more fundamental aspects will not be discussed in this review, especially since there is no information available for fruit trees. The field has been reviewed in detail by Van Steveninck (1976) and Karmoker (1985).

Any direct effect of growth substances on ion absorption can be demonstrated best when they are applied to the soil, or even better, to the nutrient solution when the plants are grown in water culture. A good example is seen from an experiment by Sweitlik and Miller (1984) on 1-year-old apple seedlings grown in water culture. During five successive periods of 4-7 days each, they followed growth, transpiration, and the uptake of Ca and K (calculated from the reduction of concentration in the nutrient solution) as affected by the growth retardant paclobutrazol added to the culture solution. In the first 7 days following the application of paclobutrazol, Ca uptake was reduced whereas fresh weight increase and transpiration were unaffected. In the later periods, growth and transpiration decreased, but the paclobutrazol treatment did not result in any significant correlation between Ca uptake on the one hand and transpiration and fresh weight increase on the other. In contrast, the reduction of K absorption occurring in the paclobutrazol-treated trees could be explained for the greater part by a decreased rate of transpiration. However, the relationship between K uptake and the reduction of fresh weight increase was rather weak. These observations suggest the occurrence of a direct effect of paclobutrazol on the uptake of Ca and K by the roots. Nevertheless, there remains doubt. Paclobutrazol is readily taken up by the roots and translocated to the above-ground parts (Lever, 1986; Tukey, 1986); its growth reducing effect is ascribed to inhibition of the synthesis of gibberellins (Daiziel and Lawrence, 1984; Hedden and Graebe, 1985). Therefore, the effect of paclobutrazol on mineral absorption actually may be due to a reduced gibberellin level.

The above serves to illustrate and emphasize the problems arising when an attempt is made to explain the effect of growth substances on mineral absorption in intact plants. When conclusions from even simple experiments (water culture, short duration, small plants, uptake data determined on a whole plant basis) are tentative, it is not surprising that many less "ideal" experiments on fruit trees in this area give little insight into the mechanisms of the observed effects. Most experiments on fruit trees are of rather long duration; the analytical data on the mineral content usually concern leaves collected only once — at the end of the experiment. Furthermore, growth responses occur that may greatly affect concentration ("dilution effect"). Thus, Swietlik and Miller (1985) applied paclobutrazol as a soil drench to apple seedlings, and 11 weeks later at the end of the experiment found a decrease in K and Ca content on a whole plant basis, but an increase in leaf concentration as compared to the untreated controls.

The indirect effect of growth compounds on mineral absorption, occurring through control of growth vigour, is based on the observed relationship between mineral uptake and growth demand. Tromp (1980) found for young apple trees that in spite of marked differences in shoot dry weight due to various experimental conditions, the uptake of K (and Ca to a somewhat lesser degree) per gram shoot dry weight to be unaffected. These findings fit with the concept of Russell (1978) that the long-term uptake of nutrients is determined mainly by metabolic demand. Richards and Rowe (1977b) and Richards (1978) varied the growth rate of peach seedlings by root manipulation treatments and with sprays of a cytokinin, benzylaminopurine, and found a linear relationship between uptake of Ca and K and dry weight increment. A similar relationship was reported for apple seedlings by Richards (1980).

2.1. Naturally occurring growth substances

Information on the effect of applied hormones on mineral absorption in fruit trees is relatively scanty. Only a few references could be found for gibberellins (GA) and indoleacetic acid (IAA).

There is little effect of gibberellins on mineral uptake in fruit trees. Thus K-gibberellate sprayed on mature apple trees did not affect the N and Mg concentration in leaves (Stahly and Benson, 1976). Steenkamp and De Villiers (1979) sprayed 6-week-old apple seedlings with GA₃ and determined its effect on Ca uptake from the nutrient solution during a period of 5 days. GA₃ tended to increase absorption slightly, but the effect did not reach statistical significance. In an experiment with young M.25 apple rootstocks, GA₃ applied to the soil decreased the shoot/root ratio somewhat, but had no effect on N, P, and K in leaves when expressed as concentration or on the basis of total leaves per plant (Atkinson and Crisp, 1982). In short term uptake studies with pea and bean seedlings, GA₃ clearly depressed uptake from the nutrient solution into the shoots but only slightly into the roots (per plant basis, Wieneke et al., 1971). In a similar experiment with sunflower seedlings, GA₃ increased the translocation of Rb (K) to the shoots, whereas accumulation in the root did not occur; it was suggested that GA₃ influences ion secretion into the xylem from the symplasm (Benlloch et al., 1983).

With respect to the effect of IAA, Atkinson and Crisp (1982) could not find any effect of a soil application of this material on N, P, and K in leaves of M.25 apple rootstocks. In the uptake studies of Wieneke

et al. (1971), IAA sprayed on the leaves decreased the accumulation of Ca in pea shoots but increased it for bean.

2.2. Synthetic growth regulating substances

2.2.1. Growth retardants

Within this group of synthetic growth substances, the information on the growth retardants daminozide and paclobutrazol and their effect on nutrient absorption is relatively abundant.

Daminozide usually is applied as a leaf spray. Although Martin and Williams (1966) have shown that it is quite mobile and moves easily from the above-ground parts to the roots, the evidence in favour of a direct effect on mineral uptake by the roots is limited. Himelrick et al. (1976) found that apple seedlings sprayed with daminozide clearly absorbed more Ca than untreated controls during a 12-day uptake period. This suggests a real effect on absorption, the more so since Ca accumulation per unit of dry weight in the treated plants exceeded that of the untreated ones. Steenkamp and De Villiers (1979) found a tendency of increased Ca uptake by foliar applied daminozide to apple. Similarly, Ca absorption was stimulated by daminozide in bean plants, but reduced in pea (Wieneke et al., 1971). The positive effect of daminozide on nutrient uptake may be due to its effect on membrane permeability (Undurraga and Ryugo, 1970).

There are a number of reports of more practical experiments on mature apple trees where the effect of daminozide sprays on minerals present in leaves was determined. Southwick et al. (1968) found for apple a very limited influence of daminozide on the foliar levels of essential elements. In a similar experiment, daminozide did not affect leaf N but decreased the Mg concentration in leaves (Stahly and Benson, 1976). In a rather extensive experiment, Himelrick and Pollard (1977) followed the foliar concentration of a number of elements for apple trees that had received daminozide sprays for the preceding 5 or 6 years. An important result was that leaf Ca was significantly increased in the daminozide-treated trees; leaf N, however, was decreased. In contrast, Ashby and Looney (1968) found a lower foliar Ca level in daminozide-sprayed apple trees. In another experiment on young apple trees where Ca sprays were applied, daminozide also reduced the amount of Ca present in the leaves (Naumann, 1971).

Thus, the data with respect to the effect of daminozide on the foliar mineral level are not conclusive. The reason is a matter of conjecture, but since daminozide invariably reduced growth, growth effects may have been involved. In this respect it is interesting that daminozide applied to mature apple trees reduced the K and increased the Ca, Fe, and Mn concentration in leaves when sprayed at the time of maximum growth rate, but was unaffected when sprayed after growth termination or when growth was slow (Velarde and Salamanca, 1978). Bearing trees were used in most of these experiments. The growth retardation by daminozide may have changed the relative strength of the various sinks including growing shoots and fruits.

Although in commercial fruit growing the use of the rather recently developed growth retardant paclobutrazol is still very limited, its effects on growth and other aspects of plant physiology, including nutrient uptake, have been studied in a considerable number of experiments. In contrast to most other regulators, it is applied both as a soil drench and as a foliar spray. Atkinson and Crisp (1982,

1983), in their experiments on young apple rootstocks found that soil-applied paclobutrazol increased the total amount of N and P in the leaves and decreased that of K; leaf concentration showed the same pattern. In 2-year-old Cox's Orange Pippin apple trees on M.9 and M.26, foliar N concentration was higher but P and K lower in soil-treated trees than in the controls; Ca concentration was the same (Atkinson, 1986). Wieland and Wample (1985) applied paclobutrazol to 1-year-old apple trees by soil drenching or by stem application. No effect on the concentration of N, P, K, and Mg in either leaves or roots could be shown. Similarly, soil applied paclobutrazol to mature apple trees had only a minor influence on the P, K, Ca, and Mg concentration of new shoot leaves and no effect at all on spur leaves (Steffens et al., 1985b). In sour orange seedlings, foliar applied paclobutrazol affected neither the leaf concentration of macro elements nor that of the trace elements (Swietlik, 1986). In field grown nectarines, paclobutrazol did not influence leaf N content (DeJong and Doyle, 1984).

Swietlik and Miller (1985) estimated, in their experiments on apple seedlings, mineral uptake on a whole tree basis. Plants soil-treated with paclobutrazol absorbed less K, Ca, Mg and Mn than untreated controls. There were no treatment effects on N, Zn, and Cu. Since, due to reduced dry matter production, the foliar concentration for various minerals had increased in the treated seedlings, the paclobutrazol effect on mineral uptake could not easily be explained in terms of absorption controlled by growth. As already pointed out, paclobutrazol may influence directly the nutrient uptake by the roots (Swietlik and Miller, 1984).

Paclobutrazol has been found to reduce gibberellin synthesis. Therefore, it is not unexpected that GA₃ sprays could overcome the growth reduction induced by paclobutrazol in apple seedlings (Steffens et al., 1985a) and that it partially reversed the increased mineral concentration in leaves in the paclobutrazol treated plants (Wang et al., 1985).

The growth retardant chlormequat (CCC) is widely used to reduce growth vigour in pear in Western Europe. With respect to its effect on mineral uptake, Naumann (1971) found that foliar-applied chlormequat in apple trees appreciably decreased the amount of Ca accumulated in shoots and leaves. Chlormequat as a soil drench reduced the total amount of N present in leaves of the apple rootstock M.25, but did not affect P and K (Atkinson and Crisp, 1982).

The group of growth retardants also includes triiodobenzoic acid (TIBA), chiefly known as an inhibitor of auxin translocation in the plant. Its use for growth control in commercial fruit growing is limited. Data on possible effects on mineral absorption are scanty. In experiments on full-grown apple trees, TIBA did not affect foliar concentration of Ca, Mg, and N (Stahly and Benson, 1976). Soil application of TIBA to M.25 apple rootstocks also remained without response for N, P, and K in leaves (Atkinson and Crisp, 1982). Foliar-applied TIBA markedly promoted the basipetal movement of labeled Ca applied to terminal leaves of young apple trees; a similar positive effect was demonstrated for Fe (Kessler and Moscicki, 1958). However, for seedlings of lemon, no effect of TIBA applied to leaves or the soil on Fe uptake into the leaves and on Fe mobility could be shown (Bar-Akiva and Hewitt, 1959).

2.2.1. Auxins

Various growth regulators, including the synthetic auxin naphthalene-acetic acid (NAA), were found to direct the movement of labeled P (stem or leaf applied) to the point of regulator application in apple seedlings (Hatch and Powell, 1971). During a period of 15 days Himelrick et al. (1976) followed Ca uptake by apple seedlings sprayed with NAA. The Ca concentration for the plant as a whole was not increased over the control, but since growth was reduced by NAA, uptake per unit of dry weight was higher in the treated plants. This suggests a positive effect of NAA on root uptake. Furthermore, NAA appeared to have shifted the ratio of Ca between leaves and stem in favour of the stem. A similar promotive effect of the amide of NAA (NAAm) on the absorption of Ca by apple seedlings was reported by Steenkamp and De Villiers (1979). In mature apple trees, sprays of NAA and 2-(2,4,5-trichlorophenoxy) propionic acid (fenoprop) did not affect leaf mineral concentration (Stahly and Benson, 1976).

2.2.3. Cytokinins

The use of synthetic cytokinins to affect tree behaviour is limited in practical fruit growing, being restricted to stimulating branching of young trees in combination with GA₄₊₇. With respect to its possible role in nutrient absorption, in a split-root experiment with apple seedlings kept in water, Richards (1980) continually exposed one half of the root system to benzylaminopurine (BAP), and determined from nutrient depletion the uptake of various minerals by the treated half and the untreated control. Initially, BAP decreased the uptake of all the minerals considered, i.e. Ca, Mg, N, and K. Later, a recovery occurred for Ca, Mg, and N, but not for K. It was suggested that cytokinins affect absorption directly, i.e. by affecting the actual mechanism, or indirectly by changing root morphology. Using peach seedlings, a foliar spray of BAP reduced the leaf concentration of N and P, and to a lesser degree Ca, and increased that of K (Richards and Rowe, 1977a). In the same experiment, total N uptake could be determined from depletion of the nutrient solution. Uptake of N was the same for BAP-treated and untreated seedlings. Since BAP stimulated the growth of the top of the plants, the reduction of leaf N concentration may have been due to dilution. The ability of cytokinins to mobilize nutrients was shown for apple seedlings by Shear and Faust (1970) for Ca and by Hatch and Powell (1971) for P. Granger and Looney (1983) applied a mixture of BAP and GA₃ to axillary buds of 1-year-old apple trees kept in water culture and found a marked reduction of Ca uptake as estimated from nutrient depletion.

3. Effect of mineral nutrition on endogenous hormone levels

It is generally accepted that environmental factors affect plant behaviour through their effect on both metabolism and distribution of hormones, in this way changing the balance between various substances. Mineral supply is an environmental factor, and therefore it is not unexpected that fertilization, apart from increasing the nutrient level in the plant, has been shown to affect the hormone status of the plant as well (Marschner, 1983; Moorby and Besford, 1983). Even for trees, some information is available. The most important mineral factor seems to be nitrogen. Its relationship with the production of cytokinins in

particular has received attention. It should be borne in mind that root tips are the main sites of cytokinin synthesis and that the N/C ratio of the various cytokinins is high.

Horgan and Wareing (1980) exposed seedlings of birch and sycamore to N deficiency for various periods and found a reduced cytokinin level in deficient birch plants as compared with normally fertilized controls; this decline continued as the deficiency period increased. In contrast, the cytokinin level of sycamore leaves did not respond to N deficiency. In both species, N deficiency affected growth negatively. The form in which N is supplied may affect the cytokinin status, as was observed for leaf and root tissue of birch seedlings by Darrall and Wareing (1981). The highest activity occurred when N was given as ammonium nitrate, whereas no activity could be detected in trees fed with ammonium sulphate. Calcium nitrate occupied an intermediate position in this respect. In experiments with N deficient M.7 apple rootstocks, Buban et al. (1978) followed the zeatin content of xylem sap from trees that shortly before bud break had received N either as nitrate or as ammonium. One day after treatment, the zeatin content increased sharply in both cases, but especially with the ammonium treatment, as compared with the control trees. A week later the contents were back to their original low values, which at least partially may have been due to dilution by increased transpiration as buds leafed out.

Nitrogen fertilization also may affect the levels of other hormones. In mature peach trees nitrogen, as ammonium nitrate applied in February and August, increased the abscisic acid content of buds sampled throughout autumn and winter as compared with unfertilized controls (Reeder and Bowen, 1978). In a N fertilization experiment with cranberry, the heavier N application resulted in a reduced gibberellin concentration in stem and leaves (Luke and Eck, 1978). Since that treatment was most stimulatory of growth, dilution may have occurred.

Other minerals in addition to nitrogen may influence the hormone status of trees. For sycamore seedlings grown in water culture at a range of P concentrations, Dhillon (1978) observed that some P concentrations affected the cytokinin level of xylem sap. In a P deficiency experiment with sycamore, the cytokinin level in leaves did not respond to treatments, but P deficiency in birch brought about a clear decline of the foliar cytokinin level (Horgan and Wareing, 1980).

4. Concluding remarks

Our knowledge about the effect of applied growth substances on mineral absorption of fruit trees is very limited. The few studies where attention has focused on the absorption process itself have involved seedlings and these may not be representative of mature orchard trees. In addition, in many experiments the central theme concerns the influence of applied growth substances on flowering, shoot growth, yield, etc., and mineral analyses are restricted to a few samples of leaves only. Furthermore, the observed effects on the nutrient status of the tree are usually rather small, and are often contradictory, probably due to foliar vs root application, variations in applied concentration, time of application, tree age, etc.

The data suggest that there is little reason to apply growth substances to fruit trees merely to affect mineral absorption.

Nevertheless, their use may be appropriate for routing mineral elements to particular sinks, e.g., fruits. The topic of nutrition of the fruit, however, falls beyond the scope of the present paper. It is sufficient to note that experiments aimed at promoting the movement of calcium into fruits by application of growth substances has received much attention. This is not surprising in view of the relationship between calcium and the occurrence of storage disorders of fruits.

References

- Ashby, D.L., and Looney, N.E., 1968. Mineral content of fruit and leaves of Spartan apple trees treated with succinamic acid 2,2-dimethylhydrazide. *Can. J. Plant Sci.* 48:422-423.
- Atkinson, D., 1986. Effects of some plant growth regulators on water use and the uptake of mineral nutrients by tree crops. *Acta Hort.* 179:395-404.
- Atkinson, D., and Crisp, C.M., 1982. Prospects for manipulation of tree root systems using plant growth regulators: some preliminary results. *Proc. Brit. Crop Prot. Conf., Weeds*:593-599.
- Atkinson, D., and Crisp, C.M., 1983. The effect of a number of plant growth regulators on fruit tree root growth and mineral nutrition. *J. Sci. Food Agric.* 34:265.
- Bar-Akiva, A., and Hewitt, E.J., 1959. The effects of triiodobenzoic acid and urea on the response of chlorotic lemon (*Citrus limonia*) trees to foliar application of iron compounds. *Plant Physiol.* 34:641-642.
- Benlloch, M., Fournier, J.M., and Diaz de la Guardia, M., 1983. Effect of gibberellic acid on $K^+(Rb^+)$ uptake and transport in sunflower roots. *Physiol. Plant.* 57:79-84.
- Buban, T., Varga, A., Tromp, J., Knegt, E., and Bruinsma, J., 1978. Effects of ammonium and nitrate nutrition on the levels of zeatin and amino nitrogen in xylem sap of apple rootstocks. *Z. Pflanzenphysiol.* 89:289-295.
- Daiziel, J., and Lawrence, D.K., 1984. Biochemical and biological effects of kaurene oxidase inhibitors, such as paclobutrazol. In: R. Menhenett and D.K. Lawrence (Eds.) *Biochemical Aspects of Synthetic and Naturally Occurring Plant Growth Regulators.* *Brit. Pl. Growth Regul. Gr., Monogr.* 11:43-57.
- Darrall, N.M., and Wareing, P.F., 1981. The effect of nitrogen nutrition on cytokinin activity and free amino acids in *Betula pendula* Roth. and *Acer pseudoplatanus* L. *J. Exp. Bot.* 32:369-379.
- DeJong, T.M., and Doyle, J.F., 1984. Leaf gas exchange and growth response of mature "Fantasia" nectarine trees to paclobutrazol. *J. Amer. Soc. Hort. Sci.* 109:878-882.
- Dhillon, S.S., 1978. Influence of varied phosphorus supply on growth and xylem sap cytokinin level of sycamore (*Platanus occidentalis* L.) seedlings. *Plant Physiol.* 61:521-524.
- Granger, R.L., and Looney, N.E., 1983. Radio-calcium uptake by 'Spartan' and 'Delicious' apple as influenced by rootstock and BA + GA₃ to activate growth of lateral buds. *HortScience* 18:314-316.
- Hatch, A.H., and Powell, L.E., 1971. Hormone-directed transport of ³²P in *Malus sylvestris* seedlings. *J. Amer. Soc. Hort. Sci.* 96:230-234.
- Hedden, P., and Graebe, J.E., 1985. Inhibition of gibberellin

- biosynthesis by paclobutrazol in cell-free homogenates of *Cucurbita maxima* endosperm and *Malus pumila* embryos. *J. Plant Growth Regul.* 4:111-122.
- Himelrick, D.G., and Pollard, J.E., 1977. The effect of sampling date, and daminozide on the nutrient composition of 'McIntosh' apple leaves. *J. Amer. Soc. Hort. Sci.* 102:97-100.
- Himelrick, D.G., Pollard, J.E., and Estes, G.O., 1976. Effect of daminozide and NAA on Ca uptake and accumulation in 'McIntosh' apple seedlings. *J. Amer. Soc. Hort. Sci.* 101:713-715.
- Horgan, J.M., and Wareing, P.F., 1980. Cytokinins and the growth responses of seedlings of *Betula pendula* Roth. and *Acer pseudoplatanus* L. to nitrogen and phosphorus deficiency. *J. Exp. Bot.* 31:525-532.
- Karmoker, J.L., 1985. Hormonal regulation of ion transport in plants. In: S.S. Purovit (Ed.) *Hormonal Regulation of Plant Growth and Development*. Martinus Nijhoff/Dr. W. Junk, Dordrecht, Boston, Lancaster:219-263.
- Kessler, B., and Moscicki, Z.W., 1958. Effect of triiodobenzoic acid and maleic hydrazide upon the transport of foliar applied calcium and iron. *Plant Physiol.* 33:70-72.
- Lever, B.G., 1986. "Cultar" - a technical overview. *Acta Hort.* 179:459-466.
- Luke, N.C., and Eck, P., 1978. Endogenous gibberellin-like activity in cranberry at different stages of development as influenced by nitrogen and daminozide. *J. Amer. Soc. Hort. Sci.* 103:250-252.
- Marschner, H., 1983. General introduction to the mineral nutrition of plants. In: A. Läuchli and R.L. Bielecki (Eds.) *Encyclopedia of Plant Physiology N.S.*, Springer, Berlin, 15A:5-60.
- Martin, G.C., and Williams, M.W., 1966. Breakdown products of ¹⁴C labelled N-dimethyl amino succinamic acid (Alar) in the apple tree. *Proc. Amer. Soc. Hort. Sci.* 89:1-9.
- Moorby, J., and Besford, R.T., 1983. Mineral nutrition and growth. In: A. Läuchli and R.L. Bielecki (Eds.) *Encyclopedia of Plant Physiology N.S.*, Springer, Berlin, 15B:481-527.
- Naumann, W.D., 1971. Calciumverteilung in Apfelbäumen und Entwicklung von Stippigkeit unter dem Einfluss von Wachstumsregulatoren. *Gartenbauwiss.* 36:63-69.
- Reeder, B.D., and Bowen, H.H., 1978. Effect of nitrogen application on bloom delay and levels of abscisic acid, carbohydrates, and nitrogen in peach buds. *J. Amer. Soc. Hort. Sci.* 103:745-749.
- Richards, D., 1978. Root-shoot interactions: functional equilibria for nutrient uptake in peach (*Prunus persica* L. Batch.). *Ann. Bot.* 42:1039-1043.
- Richards, D., 1980. Root-shoot interactions: effects of cytokinin applied to the root and/or shoot of apple seedlings. *Scient. Hort.* 12:143-152.
- Richards, D., and Rowe, R.N., 1977a. Effects of root restriction, root pruning and 6-benzylaminopurine on the growth of peach seedlings. *Ann. Bot.* 41:729-740.
- Richards, D., and Rowe, R.N., 1977b. Root-shoot interactions in peach: the function of the root. *Ann. Bot.* 41:1211-1216.
- Robinson, J.B.D., 1975. The influence of some growth-regulating compounds on the uptake, translocation and concentration of mineral nutrients in plants. *Hort. Abstr.* 45:611-618.
- Russell, R.S., 1977. *Plant Root Systems: Their Function and*

- Interaction with the Soil, McGraw-Hill, London:62-89.
- Shear, C.B., and Faust, M., 1970. Calcium transport in apple trees. *Plant Physiol.* 45:670-674.
- Stahly, E., and Benson, N.R., 1976. Calcium levels of 'Golden Delicious' apples as influenced by calcium sprays, 2,3,5-triiodobenzoic acid, and other plant growth regulator sprays. *J. Amer. Soc. Hort. Sci.* 101:120-122.
- Steenkamp, J., and De Villiers, O.T., 1979. The effect of growth regulators on the uptake and distribution of calcium in 'Golden Delicious' apples. *Agroplantae* 11:79-81.
- Steffens, G.L., Byun, J.K., and Wang, S.Y., 1985a. Controlling plant growth via the gibberellin biosynthesis system. I. Growth parameter alterations in apple seedlings. *Physiol. Plant.* 63:163-168.
- Steffens, G.L., Wang, S.Y., Faust, M., and Byun, J.K., 1985b. Growth, carbohydrate, and mineral element status of shoot and spur leaves and fruit of 'Spartan' apple trees treated with paclobutrazol. *J. Amer. Soc. Hort. Sci.* 110:850-855.
- Southwick, F.W., Lord, W.J., and Weeks, W.D., 1968. The influence of succinamic acid 2,2-dimethylhydrazide (Alar) on the growth, production, mineral nutrition, and quality of apples. *Proc. Amer. Soc. Hort. Sci.* 92:71-81.
- Swietlik, D., 1986. Effect of gibberellin inhibitors on growth and mineral nutrition of sour orange seedlings. *Scient. Hort.* 29:325-333.
- Swietlik, D., and Miller, S.S., 1984. The effect of paclobutrazol on the growth and uptake of Ca and K by apple seedlings. *J. Plant Nutr.* 7:1555-1565.
- Swietlik, D., and Miller, S.S., 1985. The effect of paclobutrazol on mineral absorption of apple seedlings. *J. Plant Nutr.* 8:369-382.
- Tromp, J., 1980. Mineral absorption and distribution in young apple trees under various environmental conditions. In: D. Atkinson, J.E. Jackson, R.O. Sharples, and W.M. Waller (Eds.) *Mineral Nutrition of Fruit Trees*, Butterworth, London, Boston:173-182.
- Tukey, L., 1986. Plant growth regulator absorption through roots. *Acta Hort.* 179:459-466.
- Undurraga, M.J., and Ryugo, K., 1970. The effect of Alar on permeability, a possible explanation for its mode of translocation. *J. Amer. Soc. Hort. Sci.* 95:348-354.
- Van Steveninck, R.F.M., 1976. Effect of hormones and related substances on ion transport. In: U. Lüttge and M.G. Pitman (Eds.) *Encyclopedia of Plant Physiology N.S.*, Springer, Berlin, 2B:307-342.
- Velarde, F.G.-A., and Salamanca, F.M., 1978. Effects of N-dimethyl-aminosuccinamic acid on mineral nutrition of one-year-old apple trees. *Acta Hort.* 80:71-73.
- Wang, S.Y., Byun, J.K., and Steffens, G.L., 1985. Controlling plant growth via the gibberellin biosynthesis system. 2. Biochemical and physiological alterations in apple seedlings. *Physiol. Plant.* 63:169-175.
- Wieland, W.F., and Wample, R.L., 1985. Root growth, water relations and mineral uptake of young Delicious apple trees treated with soil- and stem-applied paclobutrazol. *Scient. Hort.* 26:129-137.
- Wieneke, J., Biddulph, O., and Woodbridge, C.G., 1971. Influence of growth regulating substances on absorption and translocation in pea and bean. *J. Amer. Soc. Hort. Sci.* 96:721-724.