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Boron Nutrition of Avocados

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ABSTRACT

Boron is an essential micronutrient for normal plant growth, but is deficient in many soils that support avocado cultivation. In avocado, deficiency symptoms include yellowing and deformation of leaves, thickening of nodal regions on branches, loss of geotropism, reduced root growth, branch and trunk lesions, reduced pollen viability, and deformed and smaller fruit. Avocado trees are particularly recalcitrant in respect to correcting deficiency problems and tolerate much higher soil levels of boron than other fruit trees such as citrus, macadamia and mangoes. Some foliar uptake of boron has been demonstrated, but when deficiency symptoms are present in trees, soil applications of boron fertilizers are the most effective method of correcting the problem. Supplemental foliar sprays during flowering have been shown to increase fruit set. Leaf boron concentrations of 40-60 mg/kg in mature summer flush leaves prior to inflorescence development are considered optimal for normal growth and development. Caution is required when using soil applications of boron fertilizers, especially on sandy soils, as toxicity can be induced. Observation of symptoms and monitoring of leaf concentrations are the most useful tools for managing this nutrient.

INTRODUCTION

There is increasing evidence pointing to the underestimation of boron nutrition of avocados in many countries where this crop is grown. This is indicated by mild to severe symptoms of boron deficiency not recognized as such, (as recently observed in Israel by the senior author) and by the widespread symptoms in South Africa in spite of repeated boron foliar applications. Where symptoms occur it is usually found that boron leaf concentrations are below 25 mg/kg, and they may be as low as 8-10 mg/kg. Often the condition is not recognized, because other crops nearby may have been diagnosed as having sufficient or toxic boron levels, engendering the belief that sufficient quantities of this nutrient will be present to satisfy the requirements of avocados. However, experience has shown that avocados are particularly poor in sourcing boron from the soil and world wide (with some exceptions, notably California) this is the most common nutrient deficiency found in this crop (A.W. Whiley, personal observations). This paper discusses the problem and causes, and concludes with a strategy of managing boron deficiency in avocados. However, the full picture remains incomplete and further research is required to develop effective and safe management of this essential micronutrient in avocado.

BORON — AN ESSENTIAL MICRONUTRIENT

Boron is one of the seven recognized micronutrients required for normal growth of most plants. Proof that it is an essential micronutrient is normally attributed to Warington (1923), who demonstrated that the absence of boron from the growth medium caused plant death and its reintroduction permitted regrowth. Nevertheless, some 70 years after its identification as an essential element for plants, the definitive primary function for boron is still unknown, making it the least understood of all plant nutrients (Hu & Brown, 1994). Marschner (1995) proposed primary roles in cell wall structure and metabolism, plasma membrane integrity, phenol metabolism, and in diffusible IAA; with a cascade of additional secondary effects if boron is deficient. Despite this lack of certainty on its primary role within plants, considerable progress has been made in documenting physiological functions, and there are many reports detailing the disruption to growth when boron is deficient. However, care is required in the management of this essential micronutrient; because the range between sufficient and toxic concentrations in plants is relatively narrow (Gupta *et al.,* 1985).

Uptake of boron from the soil is largely passive, the nutrient being transported through xylem tissues (Mengel & Kirkby, 1978). In the soil boron is available to plants as boric acid [$B(OH_3)$] the form in which it is absorbed by roots and transported (Clarkson & Hanson, 1980; Raven, 1980). High pH, high soil calcium and dry soils limit the availability of boron and induce deficiencies in crops grown under these conditions (Gupta 1979; Gupta & MacLeod 1981). Boron is also readily leached from soils (Gupta *et al.,* 1985) and should be regularly replaced in a programme commensurate with rainfall or irrigation, the retentive properties of the soil and the requirements of the crop (Harkness, 1959, A.W. Whiley, unpublished data). As primary transport is via xylem tissues, boron tends to accumulate in those organs with a transpiration function, i.e. leaves and, to a lesser extent, young fruit. Limited redistribution via phloem occurs and, coupled with xylem supply, appears sufficient to meet the demands of new growth in plants adequately supplied with boron (Shelp, 1993). There is an essential requirement for boron in all meristematic tissues. However, apparent limitations to phloem mobility make cell division and/or enlargement early casualties when deficiency occurs. This results in reduced growth of rapidly expanding organs such as new roots, shoots and young fruit (Jackson & Chapman, 1975; Dugger, 1983; Shelp, 1993). Boron is also required for floral development, pollen germination and pollen tube growth, and in deficient plants these processes may be severely impaired (Stanley & Lichtenberg, 1963; Vasil, 1963; Agarwala *et al.,* 1981).

There are numerous reports on genetic variability within a crop species with respect to boron requirements for normal growth (Gorsline *et al.,* 1968; Brown & Jones, 1971; Brown & Ambler, 1972; Shelp & Shattuck, 1987; Shelp, 1993). In some crops cultivars differ little in their uptake of boron by roots, but subsequent translocation to aerial organs is genetically controlled (Brown & Ambler, 1972).

The early literature suggested that boron was not redistributed from mature to actively growing plant tissues (Raven, 1980). More recent tracer studies with the isotope ^{10}B have conclusively shown that boron is phloem-translocated from fully grown leaves to sites of meristematic activity (Dugger, 1983; Shelp, 1993). There is, however, still some dispute on how much of the boron requirements of actively growing tissues can be supplied from remobilized sources, with some evidence of genotypic variation (Shelp, 1993; Zu *et al.,* 1993; Picchioni *et al.,* 1995).

AVOCADOS AND BORON

The earliest report of boron deficiency in avocado was from seedlings grown in culture solution studies in California where boron was withheld from plants (Haas, 1943). This resulted in the death of the terminal growing point, which subsequently released axillary buds. Ensuing growth was stunted and the terminal buds soon died. Leaves on affected trees were distorted and developed necrotic areas of tissue, while root growth declined significantly with most of the feeder roots disintegrating. Within a short time following the addition of boron to these trees, new healthy growth was evident.

A subsequent study was carried out with grafted Taylor & Lulu (West Indian race cultivars) trees grown in sand culture (Furr *et al.,* 1946). In addition to the symptoms reported by Haas (1943) it was found that stunted shoots partially defoliated and the nodal areas became swollen giving shoots a knobby appearance. In some cases shoots died back for several centimeters from their tips.

Further research on another West Indian race cultivar Booth 8 found that 30-100% of fruit from field-grown trees with less than 15 mg/kg of leaf boron had seeds with brown necrotic areas (Harkness, 1959). In some instances seeds were completely brown and dead. Trees that had received a soil application of boron, increasing leaf concentrations to 50 mg/kg, had fruit with completely healthy seed. In recent studies in Queensland with field-grown Hass, fruit from boron-deficient trees also produced seed with brown necrotic areas (T.E. Smith, unpublished results).

In two field studies with Hass growing in boron-deficient soils in Australia, Smith *et al.,* (1995) reported an 11-15% increase in fruit size (219-246 g and 222-261 g respectively), when trees were treated with soil applications of borax. There was no effect from boron applications on fruit numbers or yield. However, leaf boron concentrations were directly correlated with increased fruit size (22-56 mg/kg and 23-43 mg/kg), respectively. While the reasons for this increase have not been elucidated, it could be that soil-applied boron improved the general health of roots thereby alleviating tree stress, or increased cell division during the early stages of fruit ontogeny. Beneficial effects of mulching with composted pine bark in KwaZulu-Natal are probably also due, at least in part, to improved boron nutrition.

We have already noted that boron deficiency affects floral development, pollen viability and pollen tube growth of plants. Robbertse and co-workers (South Africa) have conducted a thorough study on the effects of boron on the floral biology of avocado over the past ten years. They have clearly demonstrated that boron deficiency in avocado reduces pollen viability, pollen tube growth down pistils and the potential for ovule fertilization (Coetzer & Robbertse, 1987; Robbertse & Coetzer, 1988; Robbertse *et al.,* 1990). In their studies, optimum pollen tube growth down pistils was obtained in flowers with boron concentrations between 50 and 75 mg/kg (Robbertse *et al.,* 1990). Coetzer *et al.,* (1993) found that in avocado ^{10}B was remobilized from mature leaves to developing inflorescences. Remobilization of boron in avocados is also supported by Whiley & Schaffer (1994) who found a significant decline of boron concentrations in mature avocado leaves adjacent to developing inflorescences (figure 1).

In studies in California Jaganath & Lovatt (1996) reported that foliar sprays of boron at the early expansion stage of inflorescence development (cauliflower stage) increased the numbers of pollen tubes that reached the ovules, while foliar sprays of boron at the beginning of anthesis resulted in the greatest increase in avocado fruit set in Australia (T.E. Smith, unpublished results). Robbertse *et al.,* (1991; 1992) were also able to increase fruit set of avocados substantially by foliar sprays of boron during floral development.

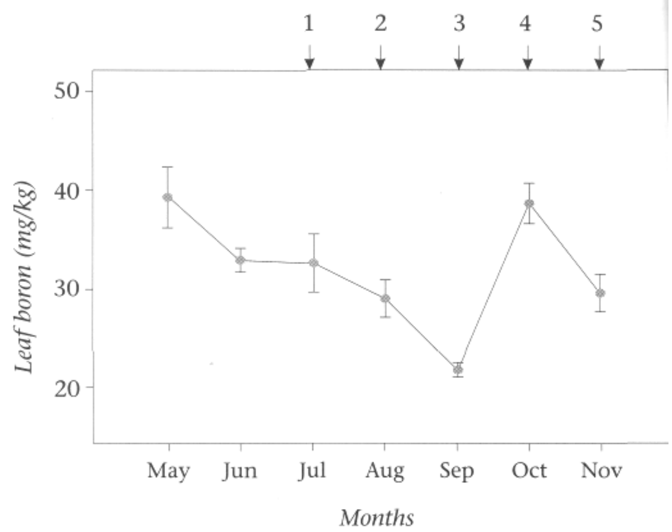

Figure 1
Changes in boron concentrations in the youngest mature leaves on summer-grown shoots of Hass avocado in relation to inflorescence development, flowering and fruit set.
(1 = floral bud burst; 2 = inflorescence development; 3 = anthesis; 4 = fruit set; 5 = leaf senescence.)

Data are mean values from 4 trees ± SEs.
Redrawn from Whiley & Schaffer, 1994.

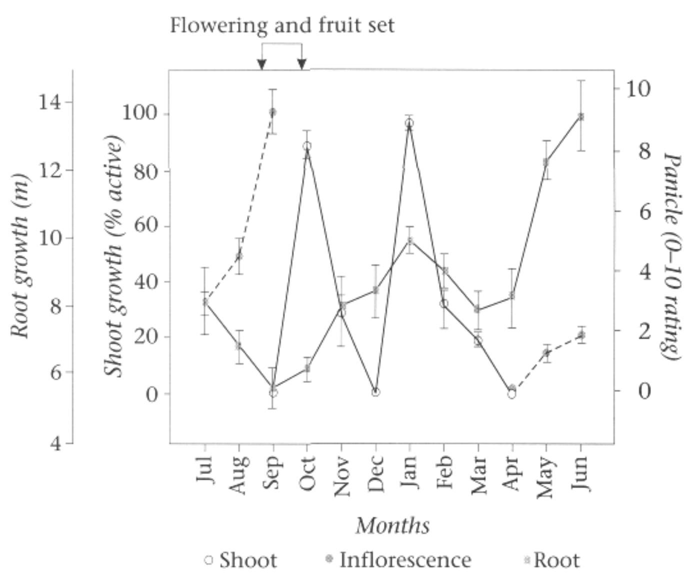

Figure 2
Sesonal growth of components of Hass avocado trees in SE Queensland, Australia. Data are means from 4 trees ±SEs.

Redrawn from Whiley & Schaffer (1994)

Despite an increase in fruit set with foliar sprays of boron during flowering, there has been no convincing evidence of increased final yield. This suggests that there are other yield-limiting factors between fruit set and final harvest. Root growth requires boron, and in deficient trees it is unlikely that sufficient nutrient from foliar applications would be translocated via phloem to the roots. Whiley (1994); Whiley & Schaffer (1994) and Thorp & Anderson (1996) have reported that, during flowering and fruit set, the total length of unsuberized feeder roots of avocados is substantially reduced (figure 2). This may be due either to stronger competition for resources by flowers and setting fruits, or to remobilization of carbon from roots to reproductive organs. A root system weakened by boron deficiency could expect to have proportionally fewer roots with a greater potential for development of internal stress in trees. It is also noteworthy that boron deficiency symptoms (inflorescence and twig dieback, shot-hole, fruit deformation) are most strongly expressed during spring — the most active growth period of the year when demand is greatest for resources from a feeder root system that has suffered severe attrition associated with flowering.

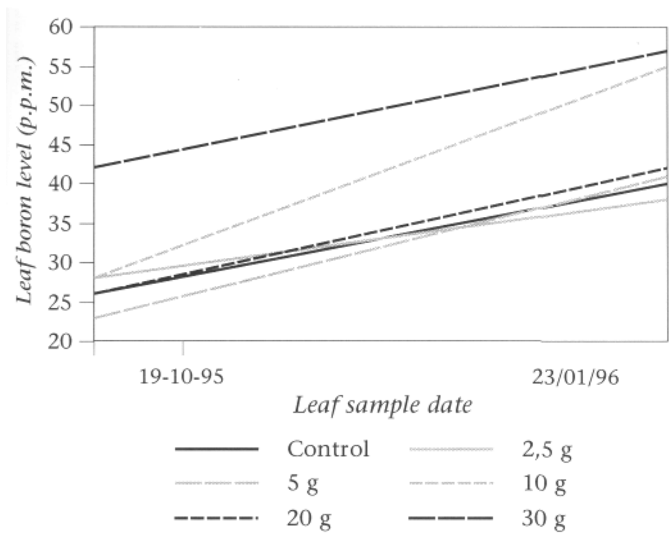

Figure 3
The effect of soil-applied boron on leaf boron concentrations in Hass grafted on Duke 7 (Mexican race) and Velvick (Guatemalan race) clonal rootstocks. Application rates are in kg/ha of elemental B.
T.E. Smith, upublished results

Preliminary results indicate that boron may influence postharvest performance of fruit. However, more studies are required to establish the importance of boron on storage of fruit (T.E. Smith, unpublished results; P.J. Robbertse, personal communication). In this regard, boron physiology has many parallels with calcium, which has been strongly implicated in fruit physiology disorders.

Avocados show obvious genotypic differences in sensitivity to boron, the Australian-developed Sharwil being one of the most susceptible to deficiency. Hass and Reed fall in to the middle range of sensitivity to boron deficiency, and Fuerte is reasonably tolerant. Rootstocks also differ in their ability to provide boron to grafted scions. In general, rootstocks of the Guatemalan race (e.g. Edranol, Nabal, Velvick) are more efficient than those of the Mexican race (e.g. Duke 7, Topa Topa, Mexicola). In a study in Australia, field-grown Sharwil trees grafted to Mexicola seedling rootstocks were only half the size of Sharwil grafted to Velvick seedling rootstocks two years from planting. The Sharwil/Mexicola trees were pale yellow, prostrate, and developed severe shothole symptoms in leaves and cankers on branches and the tree trunk. Flowering also occurred 6-8 weeks earlier than in Sharwil/Velvick trees, indicating a condition of prolonged stress. Boron leaf concentrations in Sharwil/Mexicola trees were lower than 10 mg/kg, whereas in Sharwil/Velvick trees boron leaf concentrations were about 24 mg/kg and growth was relatively normal. Soil applications of borax resulted in the resumption of normal growth (A.W. Whiley, unpublished data). In glass-house studies over a range of soil boron concentrations Hass grafted to Velvick had boron leaf levels approximately 30% higher than Hass grafted to Duke 7 rootstock (figure 3) (T.E. Smith, unpublished data).

BORON DEFICIENCY SYMPTOMS IN AVOCADO

Boron deficiency symptoms on aerial structures of avocado trees are generally visible when mature leaf concentrations of boron fall below 30 mg/kg. Ideally, leaves from unsprayed trees should be analysed to eliminate the risk of surface contaminiaton of leaves by boron sprays. Chronic symptoms are seen in trees with mature leaf concentrations of boron below 15 mg/kg. These figures are only a guide — boron deficiency may be transient, and changes in soil conditions or root health may temporarily interrupt supply and induce symptoms in actively growing organs.

In general terms boron deficiency has the potential to reduce growth and modify tree architecture substantially. Newly planted trees in boron-deficient soils may have restricted growth rates, thereby extending the time to positive cash flow. Loss of apical dominance and geotropism resulting in weeping growth are attributed to boron deficiency in trees. The development of branch and trunk cankers, which in Australia are sometimes, colonized by the bacteria *Pseudomonas syringae,* and major limb dieback followed by the growth of strong water shoots which also may subsequently decline, are commonly associated with boron deficient avocado trees (Whiley *et al.,* 1988; Broadley *et al.,* 1991).

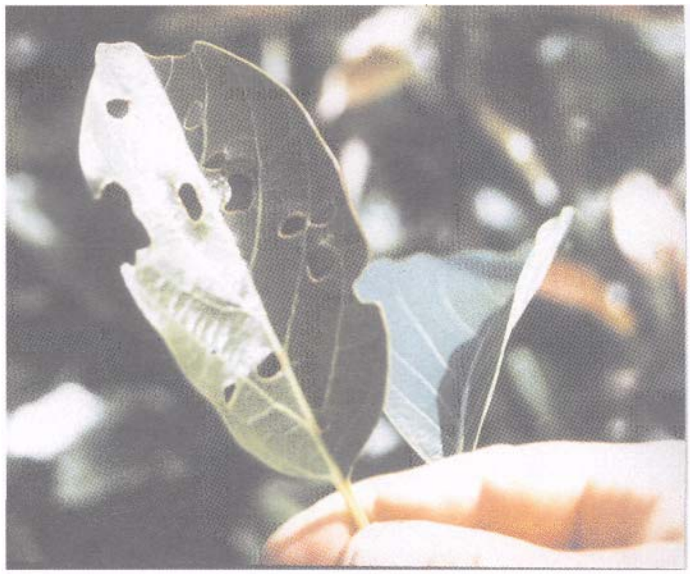

Figure 4
Typical shot-hole symptoms in spring flush leaves

Fruit distortion is another symptom, giving rise to the characteristic sickle-shaped fruit, often with a navel-like lesion on the concave side, increasing as boron leaf concentrations decline (Whiley *et al.,* 1988; Broadley *et al.,* 1991). In some cultivars fruits develop large bumps producing an irregular shape. Packhouse data indicate that in susceptible cultivars up to 20% of fruit may be downgraded or rejected due to distortion when leaf boron concentrations fall below 15 mg/kg, whereas from the same trees in subsequent seasons when boron leaf concentrations were increased to 40 mg/kg the rejection dropped to less than 2% (A.W. Whiley, unpublished data).

The most common symptom found in boron-deficient trees is shot hole of leaves. This is usually found in spring flush leaves that emerge after flowering — an event which depletes free boron from adjacent mature leaves (figure 1). During the rapid expansion stage of leaves, holes develop due to a collapse of cells giving rise to necrotic areas that abscise in the interveinal regions of the lamina. The yellowish halos around the margins of the holes give this symptom a unique appearance (figure 4). Another leaf symptom is deformity which occurs when cell expansion on one side of the leaf is retarded, followed by tissue necrosis in that region. This results in a crescent-shaped leaf.

In trees with advanced boron deficiency, leaves yellow in association with reduced growth (figure 5). Trees showing this symptom have generally lost most of their feeder roots, will flower up to six weeks earlier than healthy trees, and will substantially defoliate during flowering. This symptom should not be confused with *Phytophthora* root rot, because in boron-deficient trees leaves do not wilt during the day.

Figure 5
Leaf yellowing associated with advanced boron deficiency

Figure 6
Loss of apical dominance resulting in multiple shoot growth and a weeping growth habit

Figure 7
Nodal swelling on shoots, leading to distorted growth

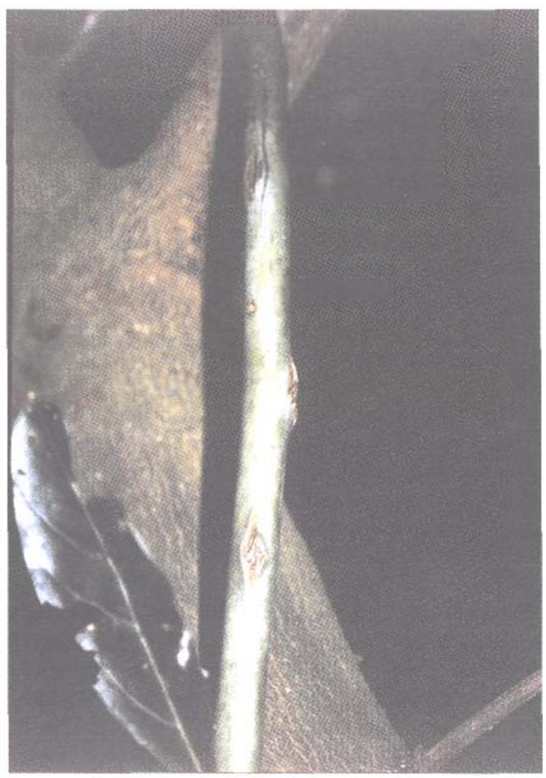

Figure 8
Splitting of stems associated with chronic boron deficiency

Reduced growth in trees is accompanied by loss of apical dominance which often stimulates growth from multiple epicormic buds, and the resultant loss of geotropism gives a weeping habit in the tree (figure 6).

Often partial or severe defoliation allows sunburn of limbs, which is a secondary effect. Nodal swelling on branches (figure 7) leading to distorted growth generally develops when boron deficiency reaches a chronic stage. Trees showing these symptoms usually develop splitting of stems (figure 8) which can lead to cankers in trees when leaf boron concentrations fall below 12 mg/kg (figures 9 and 10).

Inflorescence and twig die-back occur in the spring during flowering and growth of shoots (figure 11). This is more noticeable during years of heavy flowering when excessive attrition of roots during this period (Whiley, 1994) may reduce boron supply to the new growth.

In boron-deficient trees deformed fruit may develop during the first six weeks of growth (figure 12). This symptom is irreversible and in deficient trees of susceptible cultivars can result in substantial losses of marketable fruit.

MANAGEMENT OF BORON IN AVOCADOS

Leaf analyses together with the observation of visual symptoms in the tree are the most reliable tools for managing boron nutrition in avocados. There is no doubt that the avocado is particularly stubborn with respect to responding to foliar and soil applied boron, and tolerates soil applications up to 10 times greater than those which cause severe toxicity in other crops, e.g. citrus, macadamia, mango and papaya (Whiley *et al.,* 1988). This has been attributed to few root hairs (reduced absorption from the soil) and the accumulation of high boron concentrations in roots (poor translocation from roots to aerial parts of the tree) (Coetzer *et al.,* 1993; 1994).

Low remobilization of boron in plants is a problem compounding the management of this nutrient, and strategies should be aimed at applying a number of small amounts of boron throughout the growing season. Soil and foliar application as well as trunk injection are all used to supply essential nutrients to trees. Whiley *et al.,* (1991) reported that the use of trunk injection of boron in avocados is unsuitable for correcting a deficiency, due to the insolubility of boron. Robbertse and co-workers have fostered foliar application of boron (as Solubor) to enhance tissue concentrations, thereby improving pollination, ovule fertilization and fruit set. Evidence of foliar uptake of boron by avocados has been furnished (Coetzer *et al.,* 1993) though not quantified, and there is some doubt as to what concentrations are required in mature leaves before remobilization occurs. Whiley & Schaffer (1994) showed that remobilization of boron occurred in leaves with 40 mg/kg of boron whereas South African data suggested that this did not occur until leaf concentrations exceeded 70 mg/kg (Robbertse, personal communication). The discrepancy between these results may be due to sample contamination in the South African experiments, because foliar methods were used to apply boron, and it is known that avocado leaves absorb nutrients into waxy leaf cuticles which are not removed during standard sample preparation. Australian experience has shown that leaves sprayed with boron products and subsequently collected for leaf analysis, are unreliable as an indicator of boron status in trees even if they are carefully washed and prepared.

Figure 9
Development of stem and trunk cankers associated with very low leaf boron levels

Figure 10
Development of stem and trunk cankers associated with
very low leaf boron levels

Figure 11
Twig and inflorescence dieback resulting from reduced boron supply from
a depleted root system in spring

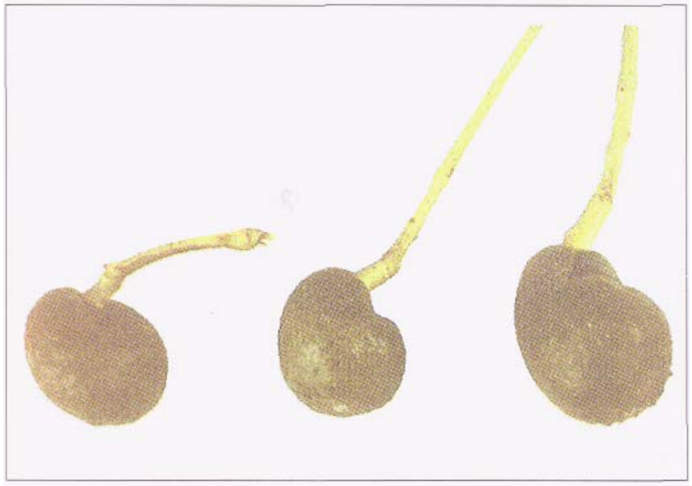

Figure 12
Development of determined fruit during the first six weeks of growth in boron deficient trees

Boron enrichment of mature summer leaves and developing inflorescence boron by foliar sprays is recommended by Coetzer *et al.,* (1993), while Smith *et al.,* (1995) have shown the benefits of foliar applied boron during inflorescence development. However, experience in Australia has shown that foliar applications are relatively ineffective when moderate to chronic deficiency symptoms (figures 4-12) are present in avocado trees.

Most avocado-producing coastal soils in eastern Australia are naturally boron deficient (Aitken *et al.,* 1987) and tree growth responds to soil-applied boron (Whiley *et al.,* 1988). Coetzer *et al.,* (1994) rightly point out the dangers of toxicity arising from soil applied boron, and there is no doubt that management of this nutrient when added to the soil requires careful monitoring. Under normal circumstances soil texture, pH, rainfall (presence of leaching events) and rootstock are the most important factors to consider with respect to management of soil boron, and programmes must be developed for each situation. Generally soil applied boron should be split into several applications each year, and leaf concentrations carefully monitored. If leaf levels exceed 60 mg/kg, then further soil applications should be substantially reduced until analysis verifies the direction in which tissue concentrations are moving.

With respect to boron requirements of avocados during flowering, Coetzer *et al.,* (1993) recommend sampling the youngest mature leaf from the summer growth (carries the inflorescences) which is consistent with the leaf position recommended for nutrient analysis in Australia.

CONCLUSIONS

Boron affects many aspects of avocado growth, and effective management under deficient situations has the potential of increasing yield, fruit size and fruit storage. However, to achieve maximum benefits from boron applications it is likely that a combination of soil and foliar sprays will be required. Foliar applications have the advantage that specific organs can be targeted to enhance their boron concentrations, but the disadvantage that insufficient boron can be absorbed through leaves to mediate chronic deficiency in trees. Soil applications have been shown to improve the health of boron-deficient trees dramatically, but careful management is required to ensure that toxic levels do not develop. Soil applications have been the norm in Australia for some 10 years, and a sophisticated computer program (AVOMAN) has been developed to give recommendations for a wide range of conditions.

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