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Chapter 7

Boron mobility in plants

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Abstract

In the majority of plant species, B distribution between plant organs and the symptoms of B deficiency and toxicity indicate that B has restricted mobility. Nevertheless, B is present in phloem and is retranslocated in phloem, often in sufficient amounts to satisfy the demands of developing sink regions that do not readily transpire. In species that produce significant amounts of polyols in source leaves, boron is readily translocated as a consequence of the formation of B-polyol complexes. Boron is thus unique among the essential plant nutrients in that it has restricted mobility in many plant species and is freely mobile in others. No other element is known to vary so greatly in mobility.

The retranslocation of B has a profound effect on the expression of B deficiency and toxicity symptoms, and the approaches needed to diagnose and correct B imbalances. Examples of the impact of B mobility on B uptake, B diagnosis, B toxicity and the breeding of species for B tolerance, are discussed here and in the relevant chapters of this volume. In the following we provide a summary of current information on the mobility of B in plants and provide insights into the physiological and agronomic consequences of these findings.

Introduction

Boron deficiency in crops is more widespread than deficiency of any other micronutrient (Gupta, 1993a). Visual symptoms of B deficiency generally become evident in dicots, maize (*Zea mays*) and wheat (*Triticum aestivum*) at tissue concentrations of less than 20–30, 10–20 and 10 mg kg^{-1} dry wt, respectively (Anon., 1991; Gupta, 1993b). Nutritional disorders attributed to B deficiency are prevalent among vegetables, fruit and nut trees. These include brown heart in storage roots of rutabaga (*Brassica napus rapifera*), turnip (*Brassica rapa*) and radish (*Raphanus sativus*), and hollow stem in cauliflower (*Brassica oleracea* var. *botrytis*) and broccoli (*Brassica oleracea* var. *italica*) (Shelp and Shattuck 1987a, 1987b; Shelp et al., 1987, 1992a). In fruit and nut trees, B deficiency often results in decreased seed set even when vegetative symptoms are absent (Nyomora et al., 1997 and references therein). The occurrence of these disorders, even when B is in ample supply in the soil, suggests that B deficiency in plants is physiological in nature (e.g. induced by rapid growth resulting from favourable environmental conditions or high fertiliser nitrogen levels) and relates to B mobility within the plant. While there is little doubt that B is translocated in xylem to sites of greatest water loss, there has been considerable controversy regarding the role that the phloem plays in providing B to sites that do not lose water readily. In this article, we review evidence for the mobility of B in phloem, highlighting the strategies used to study its translocation.

It is now clear that species differ dramatically in the extent of B mobility. Species can thus be classified into those having restricted B mobility and those in which B is highly mobile. Given the dramatic differences in the behaviour of B in these two classes of species, they are considered separately in the following text. For each, we present a review of current information and a perspective on future research directions. This is followed by a discussion of the impact of differential B mobility on the diagnosis and management of B status in plants, and is concluded with a discourse on the potential uses for species that differ in B mobility to help define the function of B in plants.

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Dynamics of boron in species with restricted boron mobility

In plants, the long distance translocation of nutrient elements takes place in the vascular system consisting of the xylem and phloem; water is the translocating agent in these tissues. Upward movement from the roots to the shoots occurs in the nonliving cells of the xylem and is driven predominantly by the gradient in water potential resulting from surface water loss (transpiration) during the day. Thus, primary xylem translocation is directed mainly to the sites of highest transpiration (the large source leaves), which are not usually the sites of highest demands for nutrients (Pate, 1975). In contrast, long distance translocation in the phloem, with its living cells, occurs in both upward and downward directions. Phloem translocation is independent of transpiration and supplies the major proportion of nutrient requirements for actively growing areas, such as young leaves, fruits and seeds: organs that do not lose water readily.

During translocation, nutrients are transferred between xylem and phloem by extensive exchange processes. In the stem and leaf veins, xylem and phloem are separated by only a few cell layers, and direct exchange of unmetabolised nutrients between these two pathways may occur (DaSilva and Shelp, 1990; Pate, 1975; Shelp and DaSilva, 1990; van Bel, 1984). Indirect transfer occurs when nutrients are transformed in the leaf and immediately exported in the phloem, or stored and exported at a later stage of development. The latter process is often associated with leaf senescence during the growth of reproductive structures (flowers and fruits) and involves the translocation of reserve materials such as protein and carbohydrates. It is less associated with vegetative growth unless the plant has experienced a period of insufficient nutrient supply. Throughout this review, the term retranslocation will comprise both intraveinal exchange and the longer route involving solute movement between xylem and phloem via the mesophyll.

Nutrient distribution within plant shoots may be explained in terms of retranslocation, which has been assessed in a variety of ways including: the ratios of concentrations in younger to older parts, fruits and leaves, and in phloem exudate and xylem sap; the uptake pattern into fruit and inflorescences during growth; and the mobility of soil and foliar applied isotopes (Pate, 1975; Shelp, 1993).

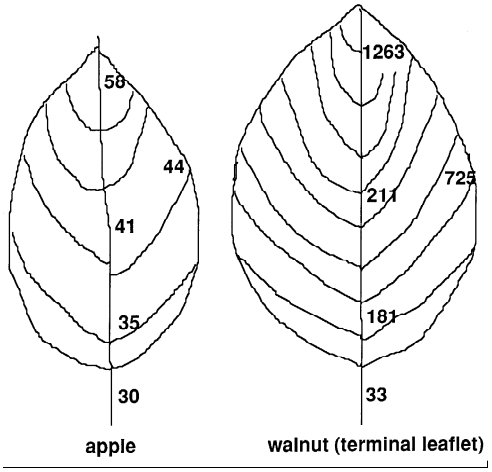

Figure 1. Leaf-B concentration (mg kg^{-1} dry wt) in field grown apple and walnut. Leaves were collected at the end of the growing season in 1995 in the Pomology orchard, Davis, California, USA. The two species were grown in close proximity and received the same irrigation.

Evidence against boron retranslocation

Boron uptake across the root plasma membrane is probably passive, involving the unassisted permeation of $B(OH)_3$ and subsequent formation of *cis*-diol complexes (Brown and Hu, 1994; Seresinhe and Oertli, 1991; Shelp, 1993). Once in the xylem, the translocation of B is related to the loss of water from shoot organs, as shown by the decreasing acropetal concentration gradient in response to increasing developmental maturity (e.g. Table 1, *Isomems* and *Ulmus*) (Bowen, 1972; Kohl and Oertli, 1961; Shelp et al., 1987; Shelp et al., 1992b; von Michael et al., 1969). Even within a particular leaf, a steep gradient in B concentration (petioles and midribs < middle of lamina < margins and tips (Oertli, 1994; Oertli and Roth, 1969; Figure 1) may result from an excessive supply of B. Furthermore, the concentration of B in leaves is higher than in phloem exudate (Marentes et al., 1997; Shelp, 1987, 1988; Shelp et al., 1996, Tammes and van Die, 1966), and this is discussed below. Symptoms of B deficiency in shoots typically occur in meristematic tissue (e.g. terminal buds and young leaves), whereas symptoms of B toxicity occur first in the margins of mature leaves, generally at the end of the transpiration stream (Marschner, 1995; Oertli, 1994; Oertli and Roth, 1969; Shelp et al., 1995). In young squash (*Cucurbita* sp.) and tomato (*Lycopersicon esculentum*) plants, B deficiency symptoms develop rapidly when the B supply is interrupted

Table 1. The relationship between sugar alcohols and B concentration (mg B kg^{-1} dry wt) in the leaf. Samples were collected from plants growing in a natural environment in Davis, California on 20 Sept., 1995. Leaves were washed for one min in deionised water. After dry ashing, B was analysed by Inductively Coupled Plasma-Mass Spectrometry (ICP-MS)

Sugar alcohol[1]	Species	B concentration		
		Expanding leaf	Mature leaf	Old leaf
None[2]	*Isomems arborea*	35	178	216
None[2]	*Ulmus parvifolia* (Chinese elm)	98	180	205
Sorbitol	*Eriobotrya deflexa*	292	285	76
Sorbitol	*Prunus elysifolia*	86	64	38
Mannitol	*Apium graveolens* (celery)	175	173	41
Mannitol	*Osmanthus fragrans* (fragrant olive)	428	144	68
Mannitol	*Phillyrea latifolia*	65	147	248

[1]Sugar alcohol information from Bourne (1958) and Bieleski (1982).
[2]No reported occurrence of sugar alcohols in this species.

(Hu and Brown, 1994; Oertli, 1993). While these data are the basis for the historical classification of B as an immobile element, they do not exclude the possibility of B translocation in phloem.

Evidence for boron retranslocation

Greenhouse grown broccoli and soybean (*Glycine max*) plants have a decreasing acropetal gradient of B concentration when grown with luxury or adequate B supply. However, in plants grown with deficient B, this gradient from old to young tissues disappears or is reversed (Al- Molla, 1986; Marentes et al., 1996; Shelp et al., 1992b). If B is mobile only in the xylem, tissue B should always be highest in old organs.

Shelp and coworkers reported that ratios of tissue B in developing sinks to old leaves of radish (Shelp et al., 1987), rutabaga (Shelp and Shattuck, 1987a), cauliflower (Shelp and Shattuck, 1987b) and broccoli (Shelp, 1988) are higher with a continuous supply of limiting B than with sufficient B. With each plant species studied, the relative element composition and, in particular, the low Ca, Mn and B contents of the sinks match what is generally known about the composition of phloem exudate (Pate, 1975; van Die and Tammes, 1975), indicating that phloem rather than xylem transport is quantitatively the most important route for nutrients.

Boron retranslocation is suggested from the decreased B concentration in mature leaves of grape (*Vitis vinifera*) (Scott and Schrader, 1947), broccoli (Benson et al., 1961; Shelp, 1988), cotton (*Gossypium hirsutum*) and turnip (McIrath, 1965), and its unchanging concentration in fruits of peanut (*Arachis hypogaea*) and subterranean clover (*Trifolium subterraneum*) (Campbell et al., 1975) when plants are subjected to B deficiency. Liu et al. (1993) investigated the B distribution in two broccoli cultivars, grown under irrigation with and without supplemental B, at three locations which differed in extractable B. A decreasing tissue B gradient up the shoot is only found in plants supplied with supplemental B. Furthermore, floret B concentration and content are rarely affected by the B treatments. Thus, in spite of the accumulation of B in transpiring organs, these studies provide circumstantial evidence for B translocation under conditions of low B supply (i.e. conditional mobility).

Recently, Marentes et al. (1997) supplied ^{10}B to the root systems of broccoli and lupin (*Lupinus albus*) plants to provide a quantitative picture of B distribution during early reproductive development. Plant B status and external B supply does not markedly influence the specific allocation to broccoli florets of ^{10}B acquired during inflorescence development; this newly acquired ^{10}B accounts for 68–99% of the floret B at 14 days after inflorescence emergence (DAIE), whereas the remainder is derived from previously acquired B (Figure 2). Boron acquired during inflorescence development is transiently accumulated in the stem, and middle and upper portions of the canopy (data not

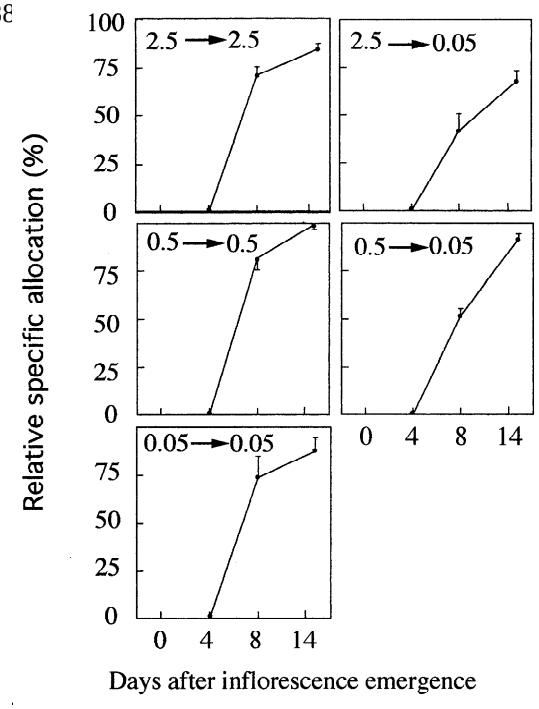

Figure 2. Relative specific allocation (proportion of B atoms that are ^{10}B labelled) in broccoli florets of ^{10}B acquired after inflorescence emergence. Arrows in the panel indicate a shift from various B concentrations supplied at natural abundance to those enriched in ^{10}B at inflorescence emergence. Data represent the mean ± SE (n = 5); where smaller than the symbol, SE is not shown. From Marentes et al. (1997).

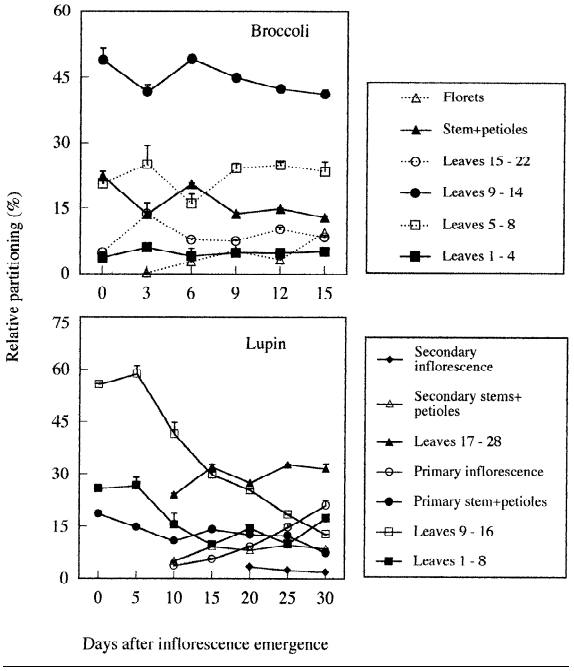

Figure 3. Relative partitioning among shoot strata during inflorescence development of ^{10}B acquired in the 10-day period before inflorescence emergence in broccoli (upper panel), and ^{10}B acquired in the 15-day period just before primary inflorescence emergence in lupin (lower panel). With the exception of the 10- or 15-day periods when broccoli and lupin plants were supplied with enriched ^{10}B at 0.5 and 0.3 mg L^{-1} respectively, they received enriched ^{11}B at the same concentration. The key indicates the various strata. Data represent the mean + SE (n = 5); where smaller than the symbol, SE is not shown. From Marentes et al. (1997).

shown). In another experiment, 8% of the ^{10}B acquired by broccoli in the 10 day period immediately prior to inflorescence emergence is recovered in the florets at 15 DAIE (Figure 3). Twenty one percent of the ^{10}B acquired by lupin in the 15 day period immediately prior to inflorescence emergence is recovered in fruits at 30 DAIE. Therefore, both newly and previously acquired B can contribute to the B requirements of reproductive structures. It is tempting to speculate that B, like N (DaSilva and Shelp, 1990; Pate, 1975; Shelp and DaSilva, 1990; van Bel, 1984), undergoes direct as well as indirect xylem to phloem transfer.

Foliar applied ^{10}B is also translocated to broccoli florets primarily via the phloem (Shelp et al., 1996), although some ^{10}B is recovered in xylem sap, presumably after transfer from phloem in roots (Pate, 1975). The florets of plants grown with a deficient, sufficient or luxury supply of B receive 25, 10 and 4%, respectively of its B from foliar fertilisation; this corresponds with 30, 29 and 16% of the ^{10}B distributed throughout the shoot. Thus, the partitioning of foliar applied B to florets is inversely related to plant B status. This translocated ^{10}B significantly enhances floret yields, regardless of plant B status, but is most effective in plants with relatively lower B status.

Schon and Blevins (1987) used a stem infusion technique to inject boric acid solutions directly into soybean stems throughout the reproductive phase of the plant. This methodology allows for a slow, but continual supply of B directly into the stem, throughout the reproductive phase of the plant. Boron treatment significantly increases the number of pods/branch and total seed yield, a result that is most likely attributed to the xylem to phloem transfer of B (Grabau et al.,1986).

Boron in phloem

From data on shoot B accumulation and water usage, Kitheka and Shelp (unpublished data) estimated that the B concentration of xylem sap from intact broccoli and lupin plants grown with sufficient B is about 5 μM;

this value is an order of magnitude lower than the B concentration found in root bleeding sap. In contrast, phloem exudate from attached inflorescences and fruits of these plants contain about 0.3 m*M* B (also Shelp, 1987, 1988). Furthermore, broccoli plants supplied with a sufficient supply of B (45 m*M*) have old leaves and florets with B concentrations of 4.6 and 0.4 m*M*, respectively (Shelp et al., 1992b), assuming 15% dry wt (Shelp, 1988). Tammes and van Die (1966) reported that in yucca (*Yucca flaccida*), B concentrations of source leaves, inflorescence and phloem exudate are 1.0 m*M* (32% dry wt), 0.3 m*M* (16% dry wt) and 0.2 m*M* (18% dry wt), respectively. Thus, the B concentration in phloem exudate is lower than that in source leaves but similar to that in young shoot tissues.

Shelp (1987) has estimated the contribution of selected nutrients from phloem to the developing sinks of broccoli grown with sufficient B. A comparison of the relative proportion by weight of all elements suggests that the phloem stream provides B to an equal or greater extent than it does N, P and K, nutrients which are generally classified as phloem mobile. The phloem supply of Zn is the only one exceeding B; the relative Ca supply is the lowest. Together, these studies suggest that phloem, rather than xylem, is the predominant source of B for developing sinks.

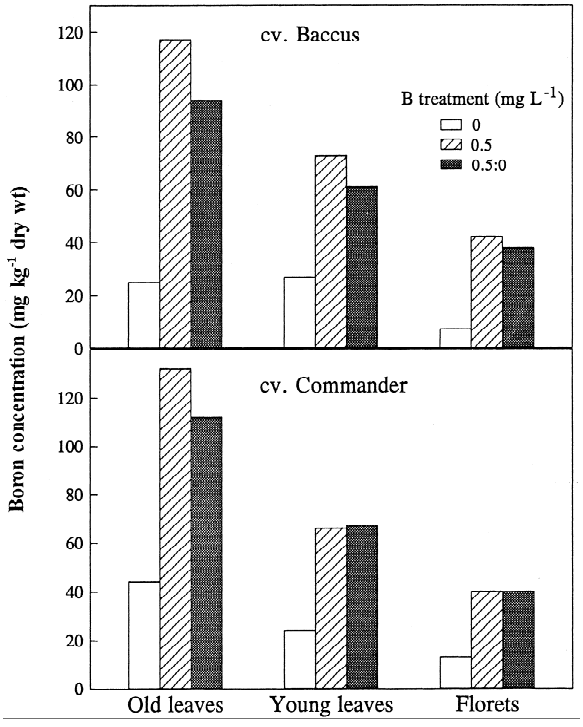

Figure 4. Boron concentrations of different parts of two broccoli cultivars grown to commercial maturity in a greenhouse. In the 0.5:0 treatment, the B supply was removed at initiation of inflorescence development. Based on Shelp et al. (1992a).

Genetic variation

Shelp and Shattuck (1987a) conducted a detailed comparison under controlled environmental conditions of two rutabaga cultivars, Laurentian (most widely grown North American cultivar) and Wihelmsberger (a European cultivar with low susceptibility to B deficiency; Shelp and Shattuck, 1987a). With sufficient B, the ratio of tissue B in storage root to old leaves is considerably less than the ratio for nitrogen and higher than that for calcium. Removal of B supply when roots are 1.0 to 1.5 cm in dia. does not markedly affect root yields, but does increase the B ratio by 110% in Laurentian and 190% in Wihelmsberger. Thus, the lower susceptibility of Wihelmsberger to B deficiency is attributed to its greater capacity for retranslocation of B to developing sinks from source leaves.

Another study determined the relative susceptibility of four broccoli cultivars including Commander, which possesses low susceptibility to the hollow stem disorder (Shelp et al., 1992a). In all cultivars, B retranslocation within the shoot is implicated from high tissue B in florets and young leaves, sinks which develop after the B supply is interrupted (Figure 4). Commander is the only cultivar that has tissue B in sinks equivalent to those in plants receiving sufficient B continuously. This is accompanied by a small but significant decline in tissue B of old leaves. Furthermore, in response to continuous B at a deficient level, the tissue B of florets from Commander is highest among the cultivars and shows the lowest percent decline relative to the controls. The stability of floret B concentration supports the view that Commander has a greater retranslocation capacity than the other cultivars examined. It is noteworthy that the authors were careful to compare the broccoli cultivars at similar developmental age. Earlier, Benson et al. (1961) provided evidence with another cultivar (Puyallup Ploycross 2) for the retranslocation of B from all except the basal leaves and youngest tissues. Together, these studies provide convincing evidence for a genetic basis for the ability of plants to retranslocate B during the reproductive growth phase and suggests that further research on the impact of plant development is required.

Summary

Considerable evidence suggests that B is supplied to sink tissues of many species in the phloem. Regardless of this apparent mobility of B in phloem, B deficiency often occurs rapidly in growing sink tissues upon withdrawal of B, and B accumulates in source tissues when B is present in adequate or excessive amounts. This is indicative of restricted B mobility. These apparent contradictions demonstrate the limitations of the term 'phloem mobility'. It is important to recognise that this term is qualitative and not quantitative, and that various xylem to phloem transfer processes are involved in the movement of an element. Retranslocation is a term that encompasses the various transfer processes.

It can be concluded, therefore, that B is supplied to growing tissues through the phloem and that B present in the phloem may be derived indirectly from developed leaves or directly from the xylem. The rapid occurrence of B deficiency in sink tissue following withdrawal of B from the growth medium suggests that the rate of phloem B movement is closely determined by current B uptake.

Dynamics of boron in species with significant boron mobility

It has recently been demonstrated that B exhibits rapid and significant phloem mobility in species for which sorbitol is a primary photosynthetic product (Brown and Hu, 1996). This conclusion was made on the basis of our experimentation, a review and reanalysis of previous work and observations drawn from plants growing in natural environments. Brown and Hu (1996) suggested that B should be phloem mobile in any species for which sorbitol, mannitol, or dulcitol are the primary photosynthates since these polyols can effectively complex B. Subsequently, this hypothesis was verified through the isolation and characterisation of B–polyol complexes from celery (*Apium graveolens*) and peach (*Prunus persica*) (Hu et al., 1997).

In the following, we review the information that led to the identification of significant species differences in phloem B mobility. This will be followed by a discussion of the physiological and biochemical mechanism of B mobility, and a description of species and environmental conditions in which this mechanism is likely to occur. The implications of B mobility for the selection and development of B efficient species and the diagnosis and correction of B disorders will then be considered.

Historic evidence for phloem boron mobility

Distribution of boron within leaves

In their classic studies, Kohl and Oertli (1961) and Oertli and Kohl (1961) demonstrated that "the patterns of B distribution in plants, and symptoms of B toxicity, are correlated with leaf venation and are consistent with the hypothesis that B moves with the transpiration stream". Further, they concluded that "once B enters a leaf it remains, with little or none moving elsewhere" (Oertli and Richardson, 1970). Thus, in a species in which B is immobile, B will accumulate at the sites of termination of leaf veins.

This principle is illustrated in Figure 1 in which the distribution of B within a mature leaf of walnut (*Juglans regia*) and apple (*Malus domestica*) is contrasted. Both species were of similar age and were growing adjacent to each other under identical management and environmental conditions. In walnut, the highest B accumulation occurred at the leaf tip and leaf margin. Boron concentration at the leaf base was less than 14% of the tip value while the petiole represented only 2% of the leaf tip value. Walnut represents a striking example of B immobility. There are many examples of species with B distributions similar to those present in walnut, while, to our knowledge there are no published exceptions to this rule (Asen and Davidsen, 1950; Eaton, 1944; Kohl and Oerli, 1961; Oertli, 1960, 1993, 1994).

Leaves of apple are distinctly different from those of walnut (Figure 1). Leaf B concentrations were significantly lower than in walnut (40 mg B kg^{-1} dry wt in contrast to 600 mg B kg^{-1} dry wt leaf average) and there was very little difference in B accumulation across the leaf. This uniform low distribution of B in apple does not correlate with leaf venation pattern and is not consistent with the hypothesis that B distribution is determined solely by transpiration. This same leaf distribution was observed in almond (*Prunus amygdalus*), peach, and plum (*Prunus salicina*) (Hu and Brown, unpublished data).

Boron distribution in plant tissues

Evidence of B mobility can also be found in the distribution of B within different organs of a species. For example, under field conditions pistachio (*Pistacia vera* cv. Kerman) had highest B concentration in

Table 2. Boron distribution (mg B kg^{-1} dry wt) in leaf and fruit organs of four tree species. Samples were collected on 23 Sept., 1994. Values are means ±SE of three replicates

Organ	Almond (*Prunus amygdalus*)	Apple (*Malus domestica*)	Pistachio (*Pistacia vera*)	Walnut (*Juglans regia*)
Leaf	42 ± 1	41 ± 2	130 ± 8	295 ± 23
Hull	170 ± 19	51 ± 2*	33 ± 1	40 ± 1
Kernel	43 ± 1	54 ± 1†	1 ± 0	4 ± 3
Shell	34 ± 2	34 ± 1#	2 ± 1	9 ± 3

Note: * = peel, † = core, # = pulp.

leaves and lowest in fruit and seed tissue (Table 2). In contrast, almond grown at the same site, had highest B concentration in hull (fruit tissue) with much lower B in the leaves (Table 2). The same contrast can be seen between apple and walnut (Table 2). Similar results were observed by Eaton et al. (1941) who reported 1300 mg B kg^{-1} in leaves of walnut, 123 mg B kg^{-1} in the hull and 14 mg B kg^{-1} in the kernel, while leaves of apricot (*Prunus armeniaca*) (grown at the same site) contained 118 mg B kg^{-1}, fruit flesh had 441 mg B kg^{-1} while the kernel contained 85 mg B kg^{-1}.

The distribution of B seen in pistachio and walnut are indicative of limited phloem B mobility in these species, whereas B is clearly phloem mobile in almond and apricot. Examples of apparent B mobility based upon the presence of relatively high B concentrations in fruit and flower tissue can be found for pear, apple, cherry (*Prunus* sp.) (Crandall et al., 1981; Eaton, 1944; Woodbridge et al., 1971), apricot (Dye et al., 1983) as well as celery (Eaton, 1944) and olive (*Olea europa*) (Delgado et al., 1994).

The concentration of B in leaves of different age within a species can also provide evidence of B mobility. The authors examined seven species growing in close proximity under similar soil and environmental conditions. The occurrence of higher B concentrations in old or mature leaves in comparison to younger leaves is evidence of B immobility while higher B concentrations in younger leaves is an indication of B mobility since these leaves have transpired less water than older leaves. Boron concentrations in fruit or apical tissues that equal or exceed leaf B concentrations also indicate phloem B mobility (van Goor and van Lune, 1980). The results presented in Table 1, suggest that B is phloem mobile in species in which sorbitol is a primary photosynthetic product (*Eriobotrya deflexa* and *Prunus elysifolia*). Species known to produce mannitol as a primary photosynthetic product [celery, fragrant olive (*Osmanthus fragrans*) and *Phillyrea latifolia*] were more variable with some clearly transporting B (celery and fragrant olive) while others did not (*P. latifolia*). The relationship between sugar alcohols and B mobility will be addressed below.

Boron toxicity symptoms

The occurrence of B toxicity symptoms in leaf margins of old leaves has long been interpreted as an indication of the immobility of B in plants (Oertli, 1993). Nevertheless, as early as 1941 evidence was available to suggest that some plant species did not express this symptom of B toxicity (Eaton et al., 1941). Eaton observed that in stone fruit trees such as prune (*Prunus domestica*) and apricot, the typical symptoms of B toxicity are absent. Unusual symptoms of B toxicity in the *Prunus*, *Malus* and *Pyrus* species have also been observed by many subsequent authors. In almond and prune (Hansen, 1948, 1955), pear, apple and cherry (Woodbridge, 1955), peach (Kamali and Childers, 1970), apricot (Dye et al., 1983), and almond, peach, plum and hybrid species (almond × peach) (El-Motaium et al., 1994), a lack of leaf symptomology in plants suffering from B toxicity has been observed. Instead of the marginal leaf burn so typical of B toxicity, these species exhibit B toxicity as tip die back in young shoots, profuse gumming in the leaf axil and the appearance of brown corky lesions along stems and petioles. In apple, apricot and pear, bud abscission and death is also observed (Crandall et al., 1981; Dye et al., 1983; Hansen, 1974). Other researchers also reported similar findings and have shown that B does not accumulate in leaves of these species to any significant extent even when trees are grown at excessive levels of B (El-Motaium et al., 1994; Hansen, 1955; Woodbridge, 1955). Further comparison of the symptoms of B toxicity is presented in Chapter 12 of this volume.

The occurrence of these 'unusual' symptoms of B toxicity are not however restricted solely to the members of the *Prunus*, *Malus* and *Pyrus* families. Francois and Clark (1979) studied B tolerance of 25 species of ornamental shrubs in sand culture. More than 20 of the species showed the typical symptoms of B toxicity, including marginal or tip leaf burn and/or leaf drop. Of the species that do not exhibit leaf burn only the growth of wax-leaf privet (*Ligustrum japonicum*) was inhibited by the B concentrations used. In this species, B toxicity is expressed as terminal stem death with no leaf burn. The symptoms described by Francois and Clark closely resemble those described for *Prunus* by El-Motaium et al. (1994). In a subsequent study, Francois (1988) contrasted the response of lettuce (*Lactuca sativa*) and celery to toxic levels of B in the medium. Whereas leaf margin and tip burn is evident in the oldest leaves of lettuce, in celery these symptoms are absent. Rather, celery responds to B toxicity by producing deformed young leaves, 'bitter' and misshapen stems.

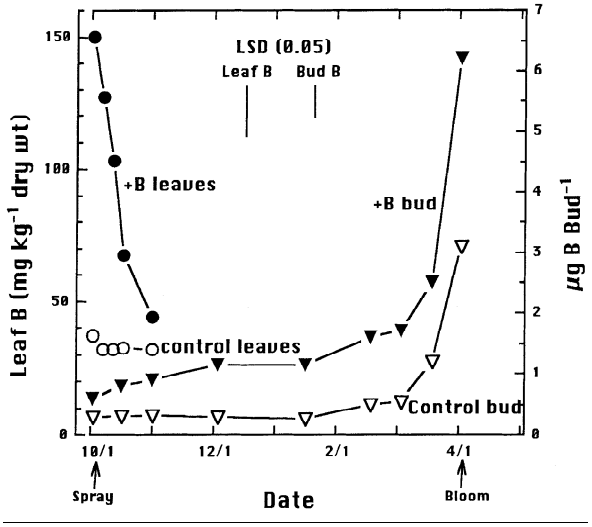

Figure 5. Changes in B levels in flower buds and leaves of 'Italian' prune following 500 mg L^{-1} B sprays applied on 3 Oct., 1978. Redrawn from Hanson et al. (1985).

Movement of foliar applied boron

If B is immobile in a species then application of foliar B fertilisers will result in enrichment of the treated leaf but will not result in enhanced B content of leaves formed after treatment or of tissues supplied primarily by the phloem (e.g. fruit). Evidence that foliar B is not readily transported to other tissues is readily available as has been discussed above (also Brown and Hu, 1996). Foliar B applications, however, have long been known to be an effective means of enhancing bud and flower B concentrations resulting in increased fruit set and yield in *Prunus*, *Malus* and *Pyrus* species (Batjer et al., Callan et al., 1978; Chaplin et al., 1977; Hanson, 1991b; Hanson et al., 1985; Johnson et al., 1995, and references therein).

The application of B in autumn results in enhanced B concentrations in buds and flowers in the subsequent spring. In plum, Hanson and Breen (1985) determined that dormant buds contain about 18% of the B present in senescent leaves, the remainder of this B is supplied from bark and wood of nearby branches. Boron applied to leaves of these trees in autumn apparently increases pools of B in these subtending tissues and plays a critical role in supplying the B requirements of flowers in the spring. In almond, B applied in autumn (1.7 kg B ha^{-1}) is the most effective timing of application and generally results in the highest increases in flower B concentrations in the following spring when compared to sprays applied at other times (Nyomora et al., 1997). Similar results have been observed for a number of *Prunus* species as well as *Malus* and *Pyrus* (Hanson, 1991a, 1991b). In most *Prunus* species, flowering precedes significant soil nutrient uptake; hence, nutrient demands for the critical periods of flowering and seed set are supplied from storage.

The mobility of autumn applied foliar B is illustrated in Figure 5 for prune. Autumn B application (October) increases leaf B concentrations 400% within 24 h of B application; over the subsequent 30 days this B concentration decreases dramatically, such that at leaf senescence (November) both treated and untreated leaves have similar B concentrations. During this period, and continuing through to early bud swell (February), buds on branches that received autumn foliar B have significantly higher B concentrations than control branches. As buds swelled during early spring, and up until flowering (April), this difference in bud B concentrations increases such that at flowering, flowers on treated branches have B concentrations 200% higher than control flowers.

The most compelling and detailed information demonstrating rapid and extensive mobility of foliar applied B followed from the introduction of isotopically enriched B isotopes into plant physiological research in the early 1990's (Brown and Hu, 1996; Brown et al., 1992; Hanson, 1991a, 1991b; Picchioni et al., 1995).

Using foliar application of ^{10}B, Hanson (1991b) reported a rapid export of isotope from the spur leaves

of sour cherry (*Prunus cerasus*) 3 to 9 days after treatment, the largest concentration of isotope is subsequently found in buds subtending the treated leaves. The possibility of earlier export was not evaluated in that study. On the basis of the results of Hanson and co-workers, Picchioni et al. (1995) conducted a series of experiments on the solution retention and the kinetics of uptake and export of foliar applied, labelled B by apple, pear, and sweet cherry (*Prunus avium*) leaves. Foliar uptake of labelled B is 88–96% complete within 24 h of application. Uptake proceeds to near completion within 24 h and is limited solely by the amount of B which can be retained by the leaf surfaces. Export, in turn, is closely related to the quantity of B absorbed and is 50% complete within 6 h of B application. This rapid rate of B uptake and export is equal to or greater than the rates observed for foliar urea (Klein and Weinbaum, 1985). This is likely to be due to similarities in physiochemical properties of B (as boric acid) and urea (urea and boric acid are both non-charged and are of similar molecular weight).

In these experiments, the sink demand of nearby, mature apple fruit does not affect the rate of export of labelled B from adjacent spur leaves, but the fruit imports 16% of their total B from the solution applied during a 10 day period. Picchioni et al. (1995) also detected significant quantities of ^{10}B in the phloem sap of apple and prune 2 h after foliar ^{10}B application, further suggesting that B is transported in the phloem.

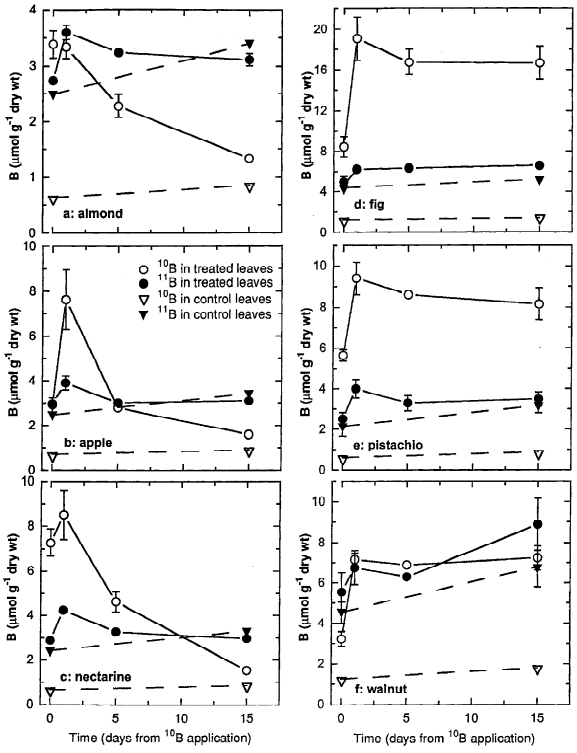

Figure 6. Changes in leaf B concentration during the 2 weeks following application of ^{10}B (50 m*M*) to leaves of six tree species. Treatments were applied on 19 May, 1995. Each point is a mean of three replicates ± SE. Where smaller than the symbol, SE is not shown. Reproduced from Brown and Hu (1996) with permission.

Phloem mobility of boron is species dependent

Despite the evidence provided by the preceding experimental results, that B is phloem mobile in *Prunus*, *Malus* and *Pyrus*, it is not evident from these studies that this is a general phenomenon or was merely a consequence of foliar B application. It was not until recently, that Brown and Hu (1996) proposed that the occurrence of significant phloem mobility of B is species dependent. Based upon the movement of isotopic B and a review of existing chemical data (Makkee et al., 1985 and references therein), they hypothesised that the apparent mobility of B in *Prunus*, *Malus* and *Pyrus* is a consequence of the use of sorbitol as a primary translocated photosynthate in these species.

Experimental verification of this hypothesis was provided in a series of experiments involving foliar and solution applied B isotopes and naturally acquired (soil) B. Three species in which sorbitol is a predominant photosynthate [apple, almond and nectarine (*Prunus persica* var. *nectarina*)] and three in which sorbitol is not known to occur [pistachio, walnut and fig (*Ficus carica*)] were contrasted. In sorbitol rich species, foliar applied ^{10}B is rapidly (0–15 days) translocated out of treated leaves to adjacent fruit. In the sorbitol poor species, by contrast, there is no evidence of ^{10}B translocation out of the leaf even though leaf B concentrations are increased by 200–500% in leaves receiving foliar B (Figure 6). Whereas foliar applied ^{10}B is rapidly and almost completely translocated out of the leaves of sorbitol rich species within 15 days, only a small percentage of the ^{11}B present in the leaf at the time of foliar application is retranslocated.

These results, though verifying the phloem mobility of foliar applied B, do not necessarily demonstrate that B, acquired from the soil, is phloem mobile. Evidence to support the notion that B is phloem mobile, irrespective of its original source, is available. The B distribution within organs, that is commonly observed in the sorbitol rich species, almond and apple, clearly suggest that soil acquired B is phloem mobile, where-

Table 3. Boron distribution in leaves of apple seedlings. Plants were grown for 36 days in complete nutrient solution (with 25 μM B), then transferred to modified nutrient solution containing either 25 μM B or 0 μM B. Foliar ^{10}B (50 mM) was applied to leaves 6–10 to half of the seedlings growing in 0 μM B treatment. Application was made every three days for 45 days. Plants were harvested after 49 days of treatment. Values are means ± SE of two replicates.

Leaf number	Solution B Foliar B	25 μM 0 mM	0 μM 50 mM	0 μM 0 μM
1–5		44 ± 4	28 ± 4	18 ± 1
6–10		41 ± 1	37 ± 2*	15 ± 2
11–15		44 ± 2	22 ± 0	12 ± 1
16–20		48 ± 1	22 ± 0	10 ± 1
21–25		45 ± 3	22 ± 1	12 ± 1
26–30		49 ± 6	25 ± 2	13 ± 2
31–35		47 ± 3	30 ± 1	11 ± 3
Meristem		73 ± 12	66 ± 31	17 ± 3

* Leaves receiving foliar ^{10}B application.

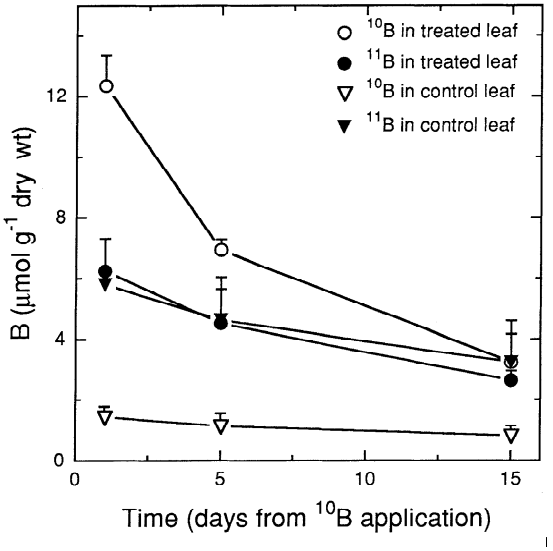

Figure 7. Changes in celery leaf B concentration following application of 50 mM ^{10}B enriched boric acid at time 0. Each point is a mean of two replicates ± SE. Reproduced from Hu et al. (1997) with permission.

as B distribution in walnut and pistachio are characteristic of B immobility (Table 2). The most striking evidence of B mobility, however, is provided by the growth of apple seedlings in solution cultures with either B supplied in the solution or as a foliar application to a limited number of mature leaves. Using this approach, Brown and Hu (1996) demonstrated that following removal of B from the rooting medium there is a gradual decline in B content of mature leaves and an apparent transfer of this B to maintain the growth of meristematic tissues. Only, when the majority of the leaves decline in B concentration to below 12 mg kg^{-1} dry wt are signs of B deficiency observed in root tissues. This does not occur until 4–6 weeks after removal of B from the root medium. Foliar B supply to leaves 6–10 (in the absence of B in the root medium), effectively maintains plant growth at control levels for the duration of the experiment (seven weeks) with no development of B deficiency symptoms in either roots or shoots (Table 3).

The ability of apple to grow normally in the absence of B in the root medium clearly demonstrates that B is freely phloem mobile in apple. Movement of B in the phloem occurs irrespective of the B source (soil, solution or foliar). Boron also appears to be phloem mobile in all species in which sorbitol is a primary translocated photosynthate and it has been suggested that B is also phloem mobile in any species in which the B binding polyols (sorbitol, mannitol or dulcitol) occur (Brown and Hu, 1996). Evidence to support phloem B mobility in other species is presented in Figure 7, which demonstrates the rapid export of foliar applied ^{10}B in celery. The distribution of B within tissues of various sorbitol and mannitol producing species further supports this hypothesis (Table 1). Boron is also freely phloem mobile in dulcitol producing species (results not shown).

Isolation and characterisation of soluble boron-polyol complexes from leaf tissue and phloem sap of celery and peach

Experimental verification of the hypothesis of Brown and Hu (1996) has recently been provided (Hu et al., 1997; Penn et al., 1997), utilising matrix assisted laser desorption Fourier transform mass spectrometry (MALDI-FTMS). This technique allows for the direct determination of mass and charge of molecules in liquid samples collected from plant tissues. This technique does not require any sample pretreatment and the vaporisation technique utilised does not disrupt the integrity of small molecular weight biological compounds. MALDI-FTMS has a mass resolution of 0.000001 atomic mass units which, in combination with known isotopic distributions, allows for the absolute identification of essentially all complexes with a molecular weight of less than 1000.

MALDI-FTMS analysis of celery phloem sap and vascular exudate as well as sap collected from phloem fed nectaries of peach, demonstrates that B forms sta-

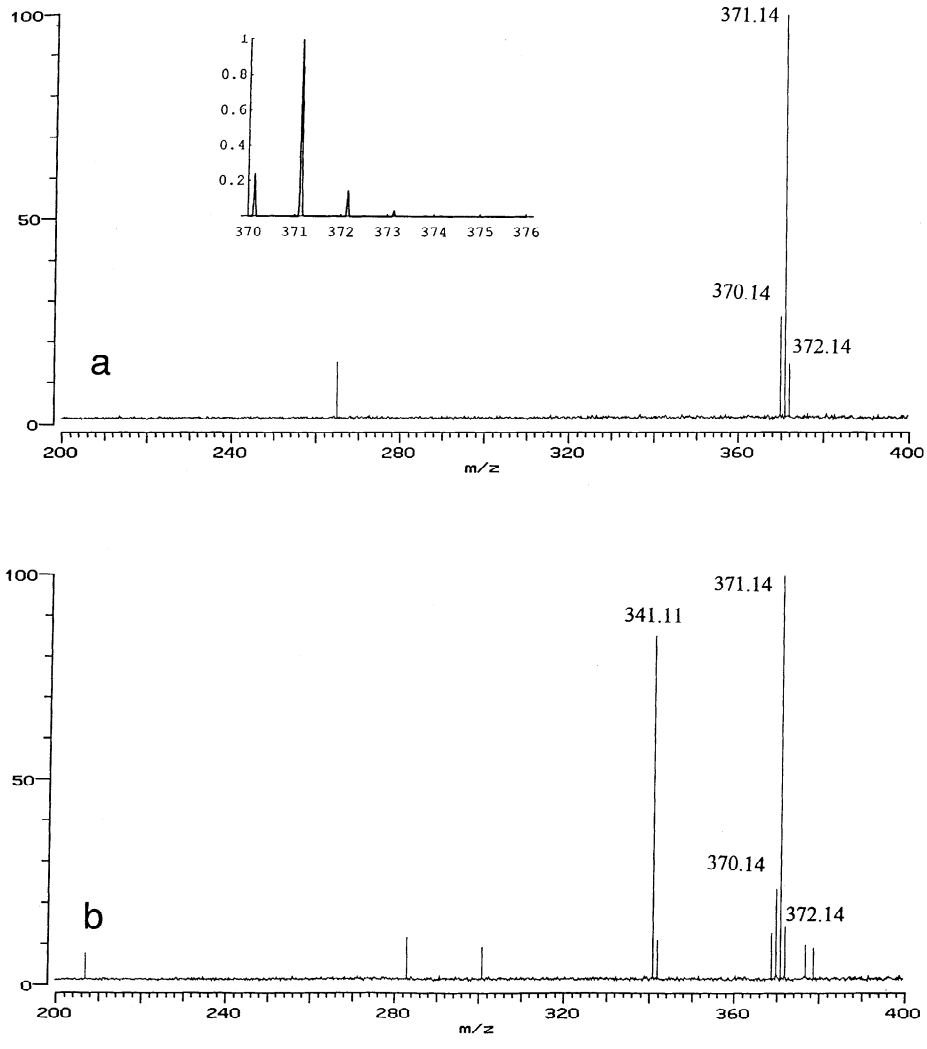

Figure 8. Spectra of matrix assisted laser desorption -Fourier transform mass spectrometry (MALDI-FTMS: (a) 10 m*M* mannitol/1m *M* boric acid. Insert: Predicted peak height of mannitol–B–mannitol complex based upon relative isotopic abundance: (b) celery phloem sap. Mass to charge ratio of B complexes is identified as following: 370.14, mannitol-^{10}borate-mannitol; 371.14, mannitol-^{11}borate-mannitol; 372.14, mannitol-^{11}borate-mannitol which contains one ^{13}C; 341.11, deprotonated disaccharide (sucrose). Reproduced from Hu et al. (1997) with permission.

ble complexes with the ligands (Lg) mannitol, sorbitol and fructose (Hu et al., 1997). A typical mass charge spectrum and peak allocation is presented in Figure 8. Presuming normal concentrations of both B (10 μM – 1 m*M*) and Lg (10–500 m*M*), and based upon the theoretical calculations of Makkee et al. (1985) it is predicted that essentially all B is present as the BLg_2 complex. This is verified by MALDI-FTMS. Additional peaks are also present at higher masses corresponding to various polymeric combinations of B with the predominant ligand i.e. B_2Lg_3, B_3Lg_4 etc. (Penn et al., 1997). No free B is observed in any collected sample, and this is predicted given the ratio of B to ligand in these samples (Makkee et al., 1985).

The distribution of polyols in higher plants

The demonstration of the occurrence of phloem mobile B–polyol complexes clearly provides a mechanistic explanation for the phloem mobility of B in celery and peach. Polyols are also known to be significant in other *Prunus*, *Malus* and *Pyrus* species as well as members of the Apiaceae [celery, carrot (*Daucus carota*)],

Table 4. List of economically important plants reported to produce polyols

Sugar alcohol[1]	Genus/species		
Dulcitol	*Catha* *Celastrus*	*Euonymus*	*Maytenus*
Mannitol	*Allium* (onion) *Apium graveoleus* (celery) *Asparagus* (asparagus) *Brassica* (cabbage, cauliflower)	*Coffea arabica* (coffee) *Daucus carota* (carrot) *Foeniculum vulgare* (fennel) *Fraxinus* (ash)	*Olea europaea* (olive) *Phaseolus vulgaris* (bean) *Pisum* (pea) *Punica granatum* (pomegranate)
Sorbitol	*Crataegus monogyna* (English hawthorn) *Cydonia oblonga* (quince) *Eriobotrya deflexa* *Eriobotrya japonica* (loquat) *Heteromyles arbutifolia* (Christmas berry) *Malus domestica* (apple)[2] *Osteomeles enthyllidifolia* *Osteomeles schwerinae*	*Prunus amygdalus* (almond)[2] *Prunus armeniaca* (apricot) *Prunus avium* (cherry)[2] *Prunus domestica* (prune)[2] *Prunus elysiforlia* *Prunus glandulosa* (flowering almond) *Prunus persica* (peach) *Prunus persica* var. *nectarina* (nectarine)[2]	*Prunus salisina* (plum)[3] *Prunus serotina* (black cherry) *Pyrus communis* (pear)[2] *Pyrus pyrifolia* (Asian pear) pear)[3] *Pyracantha buxifolia* *Vauquelinia californica*

[1]Information on sugar alcohols from Bieleski (1982), Bourne (1958), Plouvier (1963), Wallaart (1980).
[2]Boron mobility already demonstrated by Brown and Hu (1996), Hanson (1991a), Picchioni et al. (1995).
[3]Predicted to contain sorbitol from Bieleski (1982).

Oleaceae [olive and ash (*Fraxinus*)] and Celestraceae (*Celastrus* and *Euonymus*).

Sorbitol is characteristic of the woody Rosaceae, including members of the economically important genera, *Malus*, *Pyrus* and *Prunus* (peach, nectarine, cherry, plum and apricot) where it accounts for 60–90% of the carbon exported from the leaf (Loescher, 1987; Zimmermann and Ziegler, 1975). Mannitol is found in many important members of the family Scrophulariaceae [snapdragon (*Antirrhinum majus*)], Apiaceae [carrot, celery, caraway (*Carum* sp.), fennel (*Foeniculum vulgare*) and parsley (*Petroselinum crispum*)], Rubiaceae [coffee (*Coffea arabica*) and gardenia (*Gardenia augusta*)] and Oleaceae (olive and ash) (Bieleski, 1982; Bourne, 1958). Dulcitol is found in some species of the Lauraceae and Celastraceae (Bourne, 1958). Low and variable quantities of polyols, however, may be present in many species (Bieleski, 1982). A list of economically important species thought to produce polyols is presented in Table 4.

Indications that B is mobile in these species and families was presented earlier (Table 2). Currently, our knowledge of the occurrence and physiology of polyols is insufficient to predict the extent of B mobility in agricultural species. It is also likely that there are significant environmental and phenological effects on polyol production which might also influence B mobility. For example, Delgado et al. (1994) provided evidence to suggest that foliar applied B is retranslocated out of leaves of olive at only certain times of the year. This may be interpreted as evidence that mannitol is not always the primary translocated photosynthetic

Table 5. Comparison of B uptake (mg kg^{-1}) between wild type tobacco (*Nicotiana tobacum*) 'Strain SR1' and transgenic tobacco 'Strain S11' (genetically engineered with sorbitol dehydrogenase gene). Plants grown for three weeks with 3/4 strength Hoagland solution. ^{10}B was supplied as 95.91% enriched (atom%) boric acid to the roots. Values are means of 4 observations

Treatment ^{10}B	^{10}B in leaf		^{10}B in root	
(m*M*)	Wild type	Transgenic	Wild type	Transgenic
0.01	25	28	39	45
0.1	27	32	37	70
1	27	69	41	204

product of olive or that mannitol is converted to another sugar form prior to loading of the carbohydrate into the phloem. Recently it was demonstrated that stachyose, not mannitol, is the primary transported photosynthate in olive (Flora and Madore, 1993). If a significant fraction of the mannitol is converted to stachyose in the phloem companion cells, then B transport would be limited since stachyose does not complex B and is not expected to facilitate B transport. The extent of this interconversion may be environmentally or phenologically determined.

Summary

The research described above demonstrates that accepted dogma regarding the mobility of B in plants is incorrect for a broad range of important agricultural species. The evidence provided demonstrates that B is transported as a complex with polyols in species in which polyols are the primary photosynthetic product. Species that produce polyols include many important crop and forest species; however, we have insufficient information to fully determine the extent of polyol distribution in higher plants. Further, it is likely that environmental and phenological factors would influence the production and distribution of polyols and hence B mobility.

Impact of boron mobility on breeding and selection of crops for improved tolerance of boron toxicity and deficiency

Adequate B supply is essential to reproductive processes and the requirement for B in reproductive growth may be higher than the B requirement for vegetative growth (Nyomora et al., 1997). Thus, B deficiency may reduce fruit and seed set even when B concentrations in the tissue are adequate for optimal vegetative growth. As a result of the general immobility of B that is characteristic of most species, plants require a constant supply of B during all phases of plant growth. Even a short term decrease in B availability (as a result of drought, etc.) can influence plant growth. If B deficiency occurs during critical reproductive stages very significant crop losses can occur.

The short duration and variable nature of many B deficiencies makes prediction and correction of B deficiency difficult. Breeding and selection for tolerance to B deficiency (specifically short term deficiencies) has not been effective since (1) we did not understand the physiology of B movement and (2) the variable occurrence of B deficiency greatly complicates field screening techniques. The polyol transporting species we have identified are immune to short term deficiencies of B by virtue of their ability to retranslocate B within the plant. The selection or genetic manipulation of plants for improved ability to retranslocate internal B by increasing the production of polyols may, therefore, result in cultivars that are resistant to short term B deficiency.

Recently, Bellaloui and Brown (1997) demonstrated that tobacco plants genetically engineered to produce sorbitol have a significantly greater rate of B uptake than control plants. Increases in root and shoot B concentration of greater than 200% are observed (Table 5) suggesting that the expression of sorbitol is sufficient to affect B metabolism. It is significant that sorbitol concentrations in these early transformants are only relatively low (100–700 nmole g^{-1} fresh wt) which is approximately 0.1% of that present in species such as *Prunus*. Nevertheless, this amount of sorbitol is sufficient to influence B uptake. Interestingly, increasing B concentrations in the medium increased the production of sorbitol by these transgenic plants. One may speculate that the formation of the sorbitol–B complex

releases end product feedback facilitating additional sorbitol production. This has not been verified.

It may not, however, be necessary to genetically engineer species for enhanced polyol production to enhance B mobility. Many families of plants, including the economically important Brassicaceae are reported to have low but variable mannitol production (Bourne, 1958). It is plausible that *Brassica* genotypes with relatively high mannitol concentration may be selected from within wild or improved genotypes. Increased mannitol production may, in turn, be associated with B mobility and hence tolerance of short term B deficiency. This has not been experimentally verified.

Impact of boron mobility on management of boron in crops

Diagnosis of plant boron status

The mobility of B in polyol transporting species influences B diagnosis and correction. Currently practiced sampling techniques and symptom descriptions are based on the premise that B is not mobile. Selection of tissue samples and determination of critical nutrient concentrations are all fundamentally dependent on the phloem mobility of B. Table 1 illustrates that B does not accumulate in the older leaves of species in which B is mobile. Thus, old leaves are an inadequate tissue for determination of B toxicity as has been observed by El Motaium et al. (1994) and others (discussed previously). The B concentration of fruit tissues may be a superior indicator of B status in these species since B accumulates readily in these tissue (Table 2). This observation has led to the widespread use of hull B as a determinant of B status in almond in California (Nyomora et al., 1997).

Even within species that do not exhibit a high degree of B retranslocation the use of a recently matured leaf is inappropriate because the xylem has provided a significant portion of the B present in these leaves. The B concentration of a developed leaf may not, therefore, reflect the B status of growing tissues for which a constant B supply is most critical. Since tissue expansion is one of the first processes influenced by B deficiency it is clear that B diagnosis must reflect current B availability, this can only be achieved by sampling growing tissues. This is an inherently difficult and inconsistent process. By contrast, mature leaves are appropriate for assessing B deficiency in B mobile species (both annual and perennial) especially if remedial action is required. This issue is discussed in greater detail in Chapter 10 of this book.

Improved fertilisation strategies

The management of B fertilisation in plants is greatly influenced by patterns of B mobility. In general, foliar application of B has not been widely used in agriculture as it was believed that the immobility of B would limit its effectiveness. The mobility of foliar applied B in polyol transporters suggests that foliar application of B in those species can be used effectively at any time functional leaves are present to correct B deficiency, and to supply B to flower and fruit tissue (Brown and Hu, 1996; Nyomora et al., 1977; Picchioni et al., 1995). Since B deficiency dramatically affects fruit set and quality in many species this is a finding of significant importance.

The significant response to foliar B application on fruit set that has been observed in numerous tree species may be in part due to the limited mobility of B to the opening flowers. This may even occur when plants have adequate B for vegetative growth (Hanson, 1991b; Nyomora et al., 1997). In species in which B is phloem mobile, the enrichment of bud B concentrations can be ensured by supplying foliar B at a time when leaves are still photosynthetically active and buds represent the primary carbohydrate sink. This occurs after fruit harvest and prior to significant leaf senescence in early autumn. In species in which B is immobile, foliar B applications should be made directly to the swelling bud in the spring time. Earlier B applications may not be absorbed and may be leached in winter rains; soil B applications though potentially effective, may not be available to the plant at the critical stage of bud formation or expansion.

The demonstration that foliar B sprays can supply B to broccoli florets also suggests the utility of foliar B sprays (discussed in “Dynamics of boron in species with restricted boron mobility”). The amount of B supplied in this manner is, however, limited and the effectiveness of the spray is short lived. This approach is of most use in high value crops in which the reproductive structure is the organ of economic value.

Summary

Boron is unique amongst all essential mineral elements in that species differ dramatically in their ability to retranslocate B within the plant. This phenomenon fun-

damentally alters the manner in which B nutrition is managed and provides a direction for the selection of genotypes resistant to B deficiency. The great diversity that exists in the expression of B toxicity and the distribution of B between plant parts provides a striking example of the role of phloem mobility in nutrient management.

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