Occurrence of Sugar Alcohols Determines Boron Toxicity Symptoms of Ornamental Species

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ABSTRACT. The phloem mobility of boron (B) in plants varies dramatically among species. Variations in phloem B mobility occur as a consequence of the presence of sugar alcohols (polyols) in some species but not in others, and these differences in phloem B mobility profoundly affect the expression of B toxicity symptoms. Twenty-four species including common ornamental species varying in sugar alcohol content, were selected to test their response to B toxicity. Species that do not produce sugar alcohols exhibited previously described B toxicity symptoms that include accumulation of high concentrations of B in, and burning of, the tip and margin of old leaves. In the sugar-alcohol-producing species these symptoms were absent, and B toxicity was expressed as meristematic dieback and an accumulation of B in apical tissues. These symptoms have not previously been associated with B toxicity in these species and hence may have been frequently misdiagnosed.

The typical pattern of B accumulation in plants is for a higher concentration of B to be found in oldest leaves with progressively lower B concentrations in younger tissues and fruits. This distribution of B is typical of an element with limited phloem mobility and results in the development of leaf tip and margin burn of the oldest leaves as a consequence of the high B concentrations in these tissues (Brown and Shelp, 1997). Eaton et al. (1941) reported, however, that the leaf symptoms of B toxicity, so characteristic in many plants, are frequently absent in stone fruit trees. In support of these observations, other workers have also demonstrated that species of *Malus*, *Prunus*, and *Pyrus* do not accumulate high concentrations of B in their leaves, and that B toxicity is expressed as twig dieback and gum exudation in leaf axils and buds (Choe et al., 1986; El-Motaïum et al., 1994; Hansen, 1948, 1955; Maas, 1984; Woodbridge, 1955). These unusual symptoms of B toxicity are the result of the high phloem mobility of B in these species (Brown and Hu, 1996), which occurs as a result of the formation and phloem transport of a B-sorbitol complex (Brown and Hu, 1996; Hu et al., 1997). Because sugar alcohols (dulcitol, mannitol, sorbitol, etc.) can easily form complexes with boric acid with no enzymatic requirement (Makkee et al., 1985), and because they represent primary products of photosynthesis in these species, we predict that the B-sugar alcohol complex will be readily transported to active sinks such as apical tissues (Brown and Hu, 1996; Hu et al., 1997). As a result, B will be accumulated in the meristematic regions or fruit, but not in the mature leaves of species in which sugar alcohols are present. In these species, B toxicity will likely appear in apical and meristematic tissues, while the typical symptoms of B toxicity will not be observed.

As good-quality water for irrigation becomes less abundant, water previously rejected because of high B content will have to be used to meet future agricultural needs (Francois, 1991). Excess B and salinity are significant problems in California, where >150,000 ha in the San Joaquin Valley have been impacted by salinity (Croughan and Rains, 1982). Boron and salt accumulation

are also a potential concern in containerized plant production whenever water with a significant B load is used.

Descriptions of B toxicity symptoms in most modern texts reflect the patterns common in species with limited B mobility and have ignored the unique dieback symptoms of B toxicity expressed in species that produce sugar alcohols (Choe et al., 1986; El-Motaïum et al., 1994; Hansen, 1948, 1955; Maas, 1984; Woodbridge, 1955). As a result, the identification of B toxicity in many species is difficult. The present study was initiated to describe B toxicity symptoms in some common ornamentals that vary in sugar alcohol production.

Materials and Methods

Species commonly used as ornamentals were selected based upon known sugar alcohol production or their taxonomic relationship to other species known to produce sugar alcohols (Bielecki, 1982; Bourne, 1958; Plouvier, 1963; Wallaart, 1980; Zimmermann and Ziegler, 1975). Twenty-three species were purchased from local nurseries in Spring 1997: *Angelica gigas* L., *Antirrhinum* L. 'Liberty Mix', *Coprosma × kirkii* Forster & Forster f., *Cotoneaster dammeri* Medikus. 'Lowfast', *Digitalis purpurea* L. 'Alba', *Eryngium eburneum* L., *Forsythia × intermedia* Vahl. 'Lynwood', *Fragaria* L. 'Selva', *Galium odoratum* L., *Gardenia augusta* Ellis. 'Veitchiana', *Ligustrum japonicum* L. 'Texanum', *Maytenus boaria* Molina., *Olea europaea* L. 'Skylark', *Osmanthus heterophyllus* Lour., *Petroselinum crispum* Hill., *Potentilla alba* L. 'Snow White', *Punica granatum* L. 'Nana', *Pyracantha crenatoserrata* M. Roemer. 'Graberi', *Raphiolepis indica* Lindley. 'Pinkie', *Spiraea prunifolia* L., *Syringa vulgaris* L. 'Lavender Lady', *Trachelospermum jasminoides* Lemaire., and *Veronica austriaca* L. subsp. *teucrium* 'Crater Lake Blue'. In addition, *Lycopersicon esculentum* Mill. 'Roma VF', a species in which B is immobile (Oertli, 1994) and in which sugar alcohols are absent was included as a control. With the exception of *O. europaea*, which was 2 years old, the woody species used in this experiment were 1-year-old plants. Nonwoody species were 2-month-old plants. In this report, we also include photographs of two species, almond [*Prunus amygdalus* B. Syn. *P. dulcis* (Mill.)] and walnut (*Juglans regia* L.), as they develop typical B toxicity symptoms in the field.

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All plants were grown outdoors in a medium of 3 humus : 2 peat moss : 3 perlite : 2 sand (by volume) in 19-L pots at Davis, Calif. (38°33' N latitude, 121°46' longitude) from 5 Apr. until 16 Oct. 1997. During this period only 3.3 cm of rain was recorded. Temperature ranged from 4 °C minimum to 37 °C maximum in April to June, 11 °C minimum to 40 °C maximum in July to August, and 5 °C minimum and 37 °C maximum in Sept. to Oct. Full-strength Hoagland's solution no. 1 (Hoagland and Arnon, 1950) was applied to the plants once a week beginning on 11 Apr. Iron was supplied at 1.4 mg·L⁻¹ as Fe chelate (Sequestrene-138 Fe), and solution pH was adjusted to 6.0. The B treatment was started on 16 May when all the plants were vigorously growing, and was terminated after 5 months of treatment. Boric acid at 0.5 (control), 5, or 25 mg·L⁻¹ B, was applied once a week in each nutrient application. At each fertilization, 1 L of nutrient solution was applied per pot. Each treatment was replicated three times with one plant in each pot, so that each of the 24 species had nine pots. Pots were arranged in a randomized block design. Irrigation with deionized water was made every day except the day of the nutrient application and 1 d after the application. Visible B toxicity symptoms were recorded as they appeared. Photographs were taken on 8 July and 7 Aug., respectively, depending on the appearance of B toxicity symptoms.

Samples from the organs with B toxicity as well as leaves displaying no toxicity were collected on 25 July or 19 Aug. 1997 from each plant for B determination. Leaf samples of various age categories (from basal to apical) were collected from each plant on 23 Sept. 1997 in the 0.5 mg·L⁻¹ B treatment. Boron concentration in leaves along a shoot was used as an indicator of B mobility (Brown and Hu, 1996, 1998; van Goor and van Lune, 1980). For the purpose of this report, leaves in the lowest portion of a shoot were defined as basal leaves, these were all fully matured, relatively old leaves, recently fully expanded leaves were defined as middle leaves; and young, expanding leaves at the top of a shoot were defined as apical leaves. In a few species (see Results and Discussion), all the leaves were fully mature at the time of sampling, in these cases, apical leaves were simply those at the top of a shoot. Leaf samples were collected but were not washed because B is easily leached from leaves during washing procedures (Nyomora et al., 1997). Leaves were dried at 70 °C for 3 d. Except for the apical tissue, leaf samples were ground to pass 30-mesh screen. All the samples were ashed at 500 °C for 4 h. After ashing, samples were digested in 1% nitric acid. Boron concentration in the samples was determined with inductively coupled plasma-mass spectrometry (ICP-MS) as described previously (Brown and Hu, 1994). Throughout the analysis, borosilicate glass was avoided. Because the primary goal of this experiment was to identify the unique symptoms of B toxicity in these species, fresh weight or dry weight was not measured.

Results and Discussion

There was a great diversity in sensitivity to B toxicity among the species used. *Coprosma*, *Maytenus*, *Olea*, *Punica*, and *Trachelospermum*, were very tolerant of high B supply, and no B toxicity symptoms were observed for the duration of the experiment (5 months) even though the highest B treatment (25 mg·L⁻¹) was sufficient to kill other species. In contrast, other species such as *G. odoratum* were so sensitive that within 1 month of the treatment, B toxicity symptoms were observed even in the 5 mg·L⁻¹ B treatment. In this species whole plant death occurred before the end of the experiment in the 25 mg·L⁻¹ B treatment.

There were two distinct and species-specific expressions of B

toxicity. Classical B toxicities, such as those described in most current textbooks, are exhibited as tip/margin burn in the old leaves. This type of toxicity was observed in *Angelica*, *Eryngium*, *Forsythia*, *Fragaria*, *Galium*, *Lycopersicon*, and *Potentilla*. However, B toxicity was expressed as death of the apex in species of genera such as *Cotoneaster*, *Digitalis*, *Gardenia*, *Ligustrum*, *Osmanthus*, *Pyracantha*, *Rhaphiolepis*, and *Veronica*. *Angelica* (Fig. 1), *Juglans* (Fig. 2), and *Fragaria* (Fig. 3) showed leaf tip burn in oldest leaves. As exposure to B increased, greater portions of the oldest leaves became symptomatic, and symptoms began to appear in leaves of progressively lesser age. In contrast, *Gardenia* (Figs. 4–5), *Prunus* (Figs. 6–7), *Pyracantha* (Fig. 8), *Rhaphiolepis* (Fig. 9), and *Ligustrum* (Fig. 10) all showed meristem injury due to B toxicity, and B toxicity in the oldest leaves was only observed in the most advanced stages of toxicity. In *Gardenia*, the earliest symptom of B toxicity was severe curling of young, growing leaves only (Fig. 4). Leaf tip burn in the older leaves of *Gardenia* was not observed until B toxicity was advanced and only after significant meristematic damage had occurred (Fig. 5). In almond, B toxicity was exhibited as stem dieback (Figs. 6–7) or gum formation along the main stem; no leaf tip burn was observed. Death of young, growing leaves followed by defoliation of these young leaves was also observed in *Pyracantha* (Fig. 8), while mature leaves appeared normal. *Rhaphiolepis* (Fig. 9) resembled *Gardenia* in symptom expression with B toxicity evidenced by tip burn and defoliation of the youngest leaves. Dieback of shoot tips was also found in *Ligustrum* with no symptoms evident in mature leaves (Fig. 10).

Table 1 shows the B concentration in leaves expressing moderate B toxicity symptoms and leaves of the same age from control plants. The position of leaves showing B toxicity are also shown. The leaves in which B toxicity was first observed differed among species and were either basal or apical leaves. In no instance were symptoms first expressed in leaves of intermediate position.

In control plants, with no B toxicity symptoms, the B concentrations ranged from 35 to 752 µg·g⁻¹ dry weight after 3 to 4 months of 0.5 mg·L⁻¹ B treatment (Table 1). In most species, B toxicity symptoms were observed when tissue B concentrations ranged from 600 to 1600 µg·g⁻¹ dry weight, however in some species B toxicity was exhibited at relatively low leaf B concentrations (315 µg·g⁻¹ dry weight on a whole leaf basis in *S. prunifolia*), while in others very high concentrations of B were present in leaves exhibiting toxicity, such as 2184 µg·g⁻¹ dry weight in *L. esculentum* resulted in almost whole leaf death of all the old leaves. These differences in B concentration at which B toxicity occurs depended not only on the species, but also on the stage of tissue sampling, and the type of tissue sampled. Boron concentrations vary within leaves in many species (Brown and Shelp, 1997). For example, in blue dracaena [*Cordyline indivisa* (G. Forst) Steud.] the burned leaf tip contained 8615 mg·kg⁻¹ B, whereas the remaining tissue contained only 68 mg·kg⁻¹ B (Francois and Clark, 1979).

Oertli (1960) suggested that B toxicity symptoms reflect the patterns of B accumulation, and that the occurrence of B toxicity symptoms in old leaves and specifically in the margins and tips of these leaves corresponded to the site of maximal B accumulation. The data presented here support the conclusion that toxicity is related to the local, high B concentration, but in contrast to Oertli (1960) we have demonstrated that this can occur in leaves either in basal or apical positions, and that this is species dependent. There did not appear to be differences in relative tolerance of apical or basal leaves to B accumulation, because toxicity symptoms were expressed at similar B concentrations in either location.

Figs. 1–10. Boron toxicity symptoms. 1), *Angelica gigas*, 2), *Juglans regia*, 3), *Fragaria* 'Selva', 4–5), *Gardenia augusta* 'Veit-chiana', 6–7), *Prunus dulcis*, 8), *Pyracantha crenatoserrata* 'Gra-beri', 9), *Raphiolepis indica* 'Pinkie', 10), *Ligustrum japonicum* 'Texanum'.

Table 1. Boron concentration in leaves of control and those expressing B toxicity symptoms. Samples were collected on 25 July or 19 Aug. 1997 as B toxicity occurred. Boron concentration was analyzed by inductively coupled plasma-mass spectrometry.

Species	B concn ($\mu\text{g}\cdot\text{g}^{-1}$ dry wt)		
	Leaf displaying toxicity symptoms	Control leaf ²	Leaf position
<i>Angelica gigas</i>	1252 a ³	209 b	Basal
<i>Eryngium eburneum</i>	885 a	195 b	Basal
<i>Fragaria</i> 'Selva'	1676 a	487 b	Basal
<i>Galium odoratum</i>	1373 a	267 b	Basal
<i>Lycopersicon esculentum</i>	2184 a	752 b	Basal
<i>Potentilla alba</i> 'Snow White'	971 a	186 b	Basal
<i>Cotoneaster dammeri</i> 'Lowfast'	637 a	110 b	Apical
<i>Digitalis purpurea</i> 'Alba'	1686 a	374 b	Apical
<i>Gardenia augusta</i> 'Veitchiana'	745 a	169 b	Apical
<i>Ligustrum japonicum</i> 'Texanum'	924 a	293 b	Apical
<i>Pyracantha crenatoserrata</i> 'Graberii'	736 a	315 a	Apical
<i>Raphiolepis indica</i> 'Pinkie'	1566 a	392 b	Apical
<i>Veronica austriaca</i> subsp. <i>teucrium</i> 'Crater Lake Blue'	370 a	115 b	Apical
<i>Antirrhinum</i> 'Liberty Mix'	1458 a	126 b	Basal
<i>Forsythia</i> $\times$ <i>intermedia</i> 'Lynwood'	1465 a	100 b	Basal
<i>Osmanthus heterophyllus</i>	964 a	227 b	Apical
<i>Spiraea prunifolia</i>	315 a	95 b	Apical
<i>Syringa vulgaris</i> 'Lavender Lady'	594 a	35 b	Apical

²Leaves displaying toxic symptoms were sampled from the 25 mg·L⁻¹ B treatment, while the control leaves were sampled from 0.5 mg·L⁻¹ B treatment of the same position as those showing toxic symptoms.

³Means were compared within a species according to Fisher's protected LSD. Means with different letters differed significantly ($p < 0.05$).

Table 2 shows the B concentration in the leaves along a single shoot. An increasing concentration from young to old leaves is typical of a phloem-immobile element, while the opposite is true of a phloem-mobile element (van Goor and van Lune, 1980). In several species, the highest B concentration occurred in the basal leaves, while lowest B concentration occurred in the apical leaves, indicating that B is phloem-immobile in these species. In contrast, in other species, the opposite concentration gradient was found; the lowest B concentration occurred in the basal leaves, while the highest B concentration occurred in the apical leaves, indicating that B is phloem-mobile in these species.

Comparing the leaf types exhibiting B toxicity (Table 1) with the patterns of B accumulation (Table 2), we can find that in the majority of species, B accumulation patterns matched very well with the leaf types exhibiting B toxicities. In other words, if the highest B concentration is found in the basal (oldest) leaves in a species indicating that B is phloem-immobile, then leaf tip/margin burn will occur on old leaves when this species is subject to high B treatments. On the other hand, if highest B concentration is found in the apical (youngest) leaves in a species, indicating that B is phloem-mobile, then dieback of the meristem will occur when this species is subject to high B treatment. The appearance of B toxicity symptoms is therefore determined solely by the patterns of B distribution in the plant.

There were few species that did not strictly fit this general classification. *Antirrhinum* and *Forsythia* both exhibited basal leaf tip burn and would be expected to have a decreasing acropetal concentration gradient (i.e., lowest B concentration in the apical leaves) according to our predication. However, they showed no gradient (Table 2). This may have occurred because at the time of sampling, all the leaves of these two species were fully mature, and no young tissues were present. *Osmanthus*, *Spiraea*, and *Syringa* not only showed death of apical leaves in the 25 mg·L⁻¹ B treatment, but also some unusual symptoms when provided B at 0.5 mg·L⁻¹. As a result, for these species whether B toxicity will

exhibit as death of apical leaves or burn of tip/margin of old leaves are uncertain.

Symptoms of B toxicity have been described previously for many other species. Whereas the majority of plant species show the typical symptoms of B toxicity including leaf tip and margin burn in old leaves (Brown and Shelp, 1997; Eaton, 1944), several species do not. Stem dieback as a result of B toxicity has been reported in several species of *Prunus* by Eaton et al. (1941), Hansen (1948, 1955), Woodbridge (1955), Dye et al. (1983), and El-Motaum et al. (1994). Dieback of apical or lateral shoots and cracked fruit have also been found in pear [*Pyrus pyrifolia* (Burm.f.) Nakai (syn. *P. Serotina* Rehd.)] by Choe et al. (1986). Both *Prunus* and *Pyrus* transport sorbitol (Loescher, 1987), and hence a high B accumulation in the meristem or fruit can be expected in these species due to the high mobility of B (Brown and Hu, 1996, Brown and Shelp, 1997). The B-toxicity-induced dieback in *L. japonicum* 'Texanum' described in this experiment has also been reported in the same species by Francois and Clark (1979). *Ligustrum* transports mannitol in its phloem (Zimmermann and Ziegler, 1975), and hence B should be highly mobile (Brown and Hu, 1996). Francois (1988) also found B toxicity in young growing leaves in celery (*Apium graveolens* var. *dulce* (Mill.) Pers.] but not in old leaves. This is consistent with the results presented here because mannitol is the primary photosynthetic product and the major form of translocated carbon in celery (Davis et al., 1988). As a result, B is highly mobile in celery (Hu et al., 1997).

Some of the species we studied did not exhibit B toxicity, however the tissue in which toxicity would ultimately occur can be predicted from information of B distribution, if B accumulation patterns reflect B toxicity patterns in all species. *C. ×kirkii* and *T. jasminoides* will probably show leaf tip/margin burn in old leaves, while *P. crispum* and *P. granatum* 'Nana' will probably show stem dieback. In *M. boaria* and *O. europaea* 'Skylark' stem dieback is likely to occur given the higher B concentrations in

Table 2. Boron concentration in leaves of different ages along a shoot. Samples were collected on 23 Sept. 1997 from the 0.5 mg-L⁻¹ B treatment. Boron concentration was analyzed by inductively coupled plasma-mass spectrometry.

Species	B concn (µg·g ⁻¹ dry wt)		
	Leaf position		
	Basal	Middle	Apical
<i>Angelica gigas</i>	178 a ^z	134 a	78 a
<i>Eryngium eburneum</i>	250 a	95 b	64 b
<i>Fragaria</i> 'Selva'	512 a	176 b	68 c
<i>Galium odoratum</i>	399 a	177 b	92 b
<i>Lycopersicon esculentum</i>	721 a	318 b	94 c
<i>Potentilla alba</i> 'Snow White'	176 a	128 a	115 a
<i>Cotoneaster dammeri</i> 'Lowfast'	157 a	190 a	439 a
<i>Digitalis purpurea</i> 'Alba'	146 b	335 b	688 a
<i>Gardenia augusta</i> 'Veitchiana'	73 b	89 b	311 a
<i>Ligustrum japonicum</i> 'Texanum'	103 b	153 b	380 a
<i>Pyracantha crenatoserrata</i> 'Graberii'	50 b	66 b	268 a
<i>Rhaphiolepis indica</i> 'Pinkie'	85 b	171 b	425 a
<i>Veronica austriaca</i> subsp. <i>Teucrium</i> 'Crater Lake Blue'	59 a	61 a	199 a
<i>Antirrhinum</i> 'Liberty Mix'	347 a	312 a	390 a
<i>Forsythia ×intermedia</i> 'Lynwood'	437 a	387 a	401 a
<i>Osmanthus heterophyllus</i>	169 b	204 b	464 a
<i>Spiraea prunifolia</i>	58 b	51 b	339 a
<i>Syringa vulgaris</i> 'Lavender Lady'	40 a	42 a	60 a
<i>Coprosma ×kirkii</i>	489 a	238 b	66 b
<i>Maytenus boaria</i>	95 a	101 a	115 a
<i>Olea europaea</i> 'Skylark'	42 a	51 a	56 a
<i>Petroselinum crispum</i>	141 a	387 a	473 a
<i>Punica granatum</i> 'Nana'	38 b	40 b	155 a
<i>Trachelospermum jasminoides</i>	665 a	253 b	183 b

^zMeans were compared within a species according to Fisher's protected LSD. Means with different letters differed significantly ($p < 0.05$).

apical rather than basal leaves. However, leaves on these species are long lived, and changes in photosynthetic capacity with leaf age may alter sugar alcohol export, B distribution, and symptoms.

The identification by Brown and Hu (1996) and Hu et al. (1997) that phloem B mobility and tissue B distribution are a consequence of the formation and phloem mobility of a sugar alcohol-B complex provides an explanation for the symptom expression observed here. In species used here or reported elsewhere, for which B-complexing sugar alcohols have been experimentally determined, B is phloem-mobile, and toxicity symptoms occur in young tissues. We predict, based upon these results that the presence of B-complexing sugar alcohols in a species will result in apical B accumulation and expression of B toxicity in young tissues of that species. In species for which sugar alcohols have not been found in any member of that family, B is immobile, and symptoms appear in old leaves (*Lycopersicon*), we predict this will be true for all species in which sucrose is the sole transported sugar in the phloem.

For species and families in which sugar alcohol content has not been measured it is impossible to determine B transport and toxicity patterns. Hence, we included several species in the experiment because some members of that plant family have been reported to produce B-complexing sugar alcohols. Of the species in this group several (*G. augusta* 'Veitchiana' and *L. japonicum* 'Texanum') were clearly B transporters and exhibited apical B toxicity, while others (*A. gigas* and *E. eburneum*) were not and exhibited B toxicity in basal leaves. On the basis of this work and the results reported by others we conclude that B is phloem-mobile and hence B toxicity will be expressed in young tissues of species within the Rosaceae, Oleaceae, Rubiaceae, Scrophul-

ariaceae, Apiaceae, and Celastraceae. Not all species within these families necessarily exhibit B mobility and the consequent B toxicity symptoms, for example, *Fragaria* and *Potentilla* (Rosaceae), and *Angelica* and *Eryngium* (Apiaceae) do not exhibit B mobility while other members of the same family do [e.g., *Cotoneaster*, *Pyracantha* (Rosaceae) and *Petroselinum* (Apiaceae)].

Patterns of B toxicity in species with phloem B mobility would not be recognized by many horticulturists and could easily be mistaken for other diseases and physiological disorders. For example, the symptoms of B toxicity in the species of *Cotoneaster*, *Prunus*, *Pyracantha*, *Pyrus*, and *Rhaphiolepis* are similar to those caused by fire blight (*Erwinia amylovora*) and could only be definitively separated by B analysis of affected organs. In summary, this report provides new insight into the determination of B toxicity in diverse species and should help identify problems in commercial and residential horticultural practice.

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