

The effect of salinity and high boron on growth, photosynthetic activity and mineral contents of two ornamental shrubs

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Abstract

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Simultaneous salinity and boron (B) excess often occur due to irrigation with water containing high levels of salts, including B. The effects of excess of NaCl and B in the nutrient solution on some agronomical and physiological parameters of *Viburnum tinus* (laurustinus) and *Metrosideros excelsa* (metrosideros) were studied. Potted plants were grown in a factorial combination of B (1 and 6 mg/l) and NaCl (2 and 6 dS/m). B toxicity (6 mg/l) caused tip/edge burn in the lower leaves of laurustinus, while these symptoms were absent in metrosideros. Toxicity by B reduced dry biomass in the two species, particularly the aerial part in metrosideros and the roots in laurustinus. *Metrosideros* accumulated a similar content of B in all leaves, while the laurustinus tended to accumulate more B in the lower leaves. The leaf B content in laurustinus was reduced by salinity to a greater extent than in metrosideros; however, this was not sufficient to prevent injuries to the laurustinus photosynthetic system.

Keywords: boron toxicity; NaCl; laurustinus; metrosideros; chlorophyll fluorescence

The use of marginal waters containing high salt and B concentrations is common in many areas of the world, especially in arid and semiarid environments (YERMIYAHU et al. 2008). Although boron (B) is an essential element for plant growth, it can be toxic for plants when its concentration in the soil solution exceeds a given threshold value. Plant tolerance to B differs widely among species and cultivars (WU, DODGE 2005), and depends on the concentrations of B in the irrigation water applied to the root zone, which may cause growth reduction

or leaf injury. Saline groundwater often has a high B content (1–6 mg/l) and, in recent years, B toxicity has become a problem due to the use of desalinated water, which often has high concentrations of B (1 mg/l). The addition of desalinated water to municipal water in the Iberian Peninsula is gradually increasing the B content in reclaimed sewage.

In gardening and landscaping in Mediterranean areas it is very common to use ornamental shrubs adapted to local climatic conditions. Among these, metrosideros from New Zealand and laurustinus

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from the Mediterranean are widely known. The latter has been classified as a salt-sensitive while *metrosideros* as salt-resistant (AZZA et al. 2007). Levels of B above to the optimum range cause significant changes in the metabolism of higher plants. Thus, sensitivity to high B apparently involves reduced expansion in meristematic regions (causing loss of leaf area (LA)) and the development of necrotic regions in leaves (reducing the photosynthetic capacity and overall quality). Toxic levels of B have also been shown to cause root growth inhibition (CERVILLA et al. 2009). The exact mechanism of B uptake by plant roots is controversial, since experimental findings suggested both active and passive uptake (BROWN, SHELPS 1997). While the boron tolerance mechanism of plants shows similarity to the salt tolerance mechanism, the combined effect of salt and B in plant tissues appears to be very complex (BASTÍAS et al. 2010). Also, although the effects of B toxicity on gas exchange, ion distribution and plant morphology were studied in several species, less is known about the stress effect of excess B on the photosynthetic system.

The objective of this work was to determine the effects of B excess under saline conditions in two ornamental species with different degrees of salinity tolerance. The response in terms of plant growth, gas exchange, photosynthesis and ion accumulation were evaluated in order to elucidate whether salinity enhances or reduces the effects of B in these species.

MATERIAL AND METHODS

Plant material and growing conditions. Seedlings of one year old *metrosideros* (*Metrosideros excelsa*) and *laurustinus* (*Viburnum tinus*) were transplanted to black PVC pots of 2.8 l volume. The pots were filled with a mixture of coconut fiber-bark and perlite (4:1 v/v), and were introduced into holes (16 cm × 16 cm) of a metal grid made up of corrugated iron Ø 10 mm, which was 80 cm off the ground. The distance between pots was 32 cm × 48 cm, resulting in 6.5 pots/m² of metal grid bench. Transplantation of seedlings to cultivation pots was performed on 4 March 2009, and the experiment finished on 29 September 2009. The experiment took place in a greenhouse covered totally with polycarbonate sheets and located at the Experimental Agro Food Station of the Polytechnic University of Cartagena, Spain. The plants were ir-

rigated using computer-controlled automated programmable equipment (Agrónic 4000; Progés, s.a., Bellpuig, Spain) to control four pumps connected to four 1,000 l tank. Each pot had one emitter (2 l/h) connected to two spaghetti tubes (one each side of the pot). During the irrigation the doses and frequency differed for each species. The irrigation volume was determined by noting when the leaching fraction reached 15–20%, and the irrigation frequency by taking into account when pots lost between 70 and 90% of easily available water in the substrate, determined by weight.

The ion concentrations (mg/l) in the irrigation water were: Na⁺ (90.75), K⁺ (9.66), Ca²⁺ (95.89), Mg²⁺ (54.02), chloride (152.03), sulfate (305.55), carbonates (< 5), bicarbonate (78.26), nitrates (114.54), ammonia (0.18), phosphate (4.26), boron (0.34), manganese (< 0.02), iron (0.042), zinc (0.072), copper (< 0.04). Nutrients were provided at constant concentrations in the irrigation water. Nutrient solution contained 100 N, 30 P₂O₅, 120 K₂O, 60 CaO (ppm). It was made by mixing KNO₃, Ca(NO₃)₂, NH₄(NO₃), K(HPO₄) and HNO₃, the pH was adjusted to 6. The added fertilizers increased the EC approximately by 0.7 dS/m. Before fertilization the irrigation water had the EC of 1.3 dS/m and the pH of 7.3. The temperature and relative humidity were recorded continuously during the experiment by a datalogger (HOBO H08-004-02; MicroDAQ.com, Ltd., Contoocook, USA). Weather conditions were 10.3°C (min.), 24.7°C (average) and 36.9°C (max.); min. relative humidity was 22.4%, and the max. 100%, with a mean of 65.5%.

Salinity and boron treatments. Four treatments started on 6 April 2009: (1) irrigation with saline water and low B (6 dS/m and 1 mg/l); (2) irrigation with non-saline water and excess B (2 dS/m and 6 mg/l); (3) irrigation with saline water and B excess (6 dS/m and 6 mg/l); and (4) irrigation with non-saline water and low B (control irrigation, 2 dS/m and 1 mg/l). Fifteen plants per treatment were cultivated. In each treatment, one pot (or plant) was a replicate. Salinity and B were supplied as sodium chloride and boric acid, respectively, in the base nutrient solution of each 1,000 l tank.

Measurements of growth, leaf area and defoliation. At the end of the experiment, leaf area (LA) and the dry weight (DW) of roots and aerial part were determined. The substrate was gently washed from the roots (with pressurized water using a hose with flat tip). To calculate the DW, the aerial part or roots were introduced in envelopes clearly identified and placed in a natural convection bac-

teriological stove (model 2002471; JP Selecta, S.A., Barcelona, Spain) at 60°C until constant weight was reached. Finally, the DW was determined by weighing with a GRAM ST balance (sensitivity of 10 mg and up to 1,200 g; Gram Precision S.L., Barcelona, Spain). The growth index determined was the shoot DW/root DW (shoot/root). Blade area was determined with a leaf area meter (LI-3100C; LI-COR Biosciences, Lincoln, USA). Leaf fall was collected during the growing season and the cumulative area of these leaves per plant was recorded and calculated as a percentage of the LA (blade surface of leaves non-drop and drop per plant).

Mineral ions determination. To determine the total contents of B, tissue samples (lower and upper leaves, shoots and roots) were prepared by ashing 0.25 g of each sample in a furnace at 500°C for 5 h. Five ml of 1M HCl were added to the cooled ash, and the solution was filtered after 15 min and analysed. The B concentration was determined by inductively coupled plasma-mass spectrometry (Agilent 7500ce ICP-MS; Agilent Technologies, Santa Clara, USA). Dry matter samples of leaves were used to determine sodium (Na^+) and chloride (Cl^-) concentrations. Leaves were taken from all parts of the plant. Dry tissue samples were ground and three sub-samples of 0.2 g were analysed after extraction in 50 ml of distilled water by ion chromatography (model 861; Metrohm AG, Herisau, Switzerland).

Gas exchange, leaf chlorophyll and chlorophyll fluorescence. Stomatal conductance (g_s) and net photosynthesis rate (P_n) were measured at midday. P_n and g_s were measured using a CIRAS-2 Portable Photosynthesis System (PP Systems, Amesbury, USA). Chlorophyll fluorescence of the same leaves was measured using a Pulse Modulated Fluorimeter FMS-2 (Gomensoro Scientific Instrumentation, S.A., Madrid, Spain). The relative content of chlorophyll was measured with a SPAD-502 chlorophyll meter (Konica Minolta Sensing, Inc., Osaka, Japan). A shot in the middle of the limbo leaf was made on six leaves (facing south and mid-height) per plant, and for each plant the average of six shots was determined.

Statistical analysis. Two factors (B and salinity) and their interaction were analysed by two-way analysis of variance using Statgraphics Plus for Windows (Manugistics Inc., Rockville, USA). Treatment means were separated by the LSD test ($P < 0.05$). Ratios and percentages were arcsine (x)^{1/2} transformed before statistical analysis to ensure homogeneity of variance.

RESULTS AND DISCUSSION

Boron toxicity leaf symptoms and plant growth

The growth and development of the plants of metrosideros and laurustinus irrigated with water of 6 mg/l was clearly affected (Table 1), although differently in each case. Visual leaf symptoms due to B toxicity in laurustinus were tip/edge burn of old leaves, while in metrosideros red and necrotic spots appeared in the middle and edge of blade. B excess reduced plant DW by 11% (laurustinus) and 24% in metrosideros (Table 2), which indicates metrosideros growth was more affected by B toxicity. Salt stress decreased plant DW in laurustinus and metrosideros by 60 and 27%, respectively (Table 2). ALPASLAN and GUNES (2001)

Table 1. Level of signification from the two-way ANOVA conducted to determine the effects of boron (B), NaCl and interaction NaCl \times B on the studied parameters

Parameters	Metrosideros			Laurustinus		
	NaCl	B	NaCl \times B	NaCl	B	NaCl \times B
Plant dry weight (g)	**	***	**	***	***	ns
Leaf fall (%)	***	***	***	***	**	***
Shoot/root	**	**	ns	**	*	ns
Leaf area (dm ²)	**	***	***	***	***	ns
Upper leaf B (mg/kg DW)	**	**	ns	**	**	ns
Lower leaf B (mg/kg DW)	***	***	***	**	***	***
Shoot B (mg/kg DW)	**	***	ns	**	***	ns
Root B (mg/kg DW)	*	***	*	*	***	***
Leaf Na ⁺ (mg/g DW)	***	**	***	***	ns	ns
Leaf Cl ⁻ (mg/g DW)	ns	ns	ns	***	ns	ns
g_s (mmol/m ² s)	**	*	ns	***	**	**
P_n ($\mu\text{mol/m}^2\text{s}$)	**	**	*	**	**	**
SPAD readings	ns	ns	ns	**	*	*
F_v/F_m	ns	ns	ns	**	**	ns
ϕPSII	ns	ns	ns	**	**	*
NPQ	*	ns	ns	*	***	**

ns – non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; g_s – stomatal conductance, P_n – net photosynthesis rate, SPAD – chlorophyll content, ETR – apparent electron transport rate, F_v/F_m – maximum photochemical efficiency of photosystem II, NPQ – nonphotochemical quenching, ϕPSII – quantum yield of PSII linear electron transport, DW – dry weight

Table 2. Effects of salinity and boron (B) on growth parameters

Parameters	Salinity (dS/m)	Metrosideros B (mg/l)		Laurustinus B (mg/l)	
		1	6	1	6
Leaf fall (%)	2	1.80 ^{a*}	29.88 ^{b*}	0.65 ^{a*}	11.86 ^{b*}
	6	8.04 ^a	12.01 ^b	23.43 ^a	24.44 ^a
Plant dry weight (g)	2	169.52 ^{b*}	128.97 ^a	242.02 ^{b*}	216.19 ^{a*}
	6	123.41 ^a	123.22 ^a	99.41 ^b	78.76 ^a
Shoot/root	2	3.56 ^{b*}	3.02 ^{a*}	2.77 ^{a*}	3.08 ^{b*}
	6	2.78 ^b	2.33 ^a	3.33 ^a	3.54 ^b
Leaf area (dm ²)	2	51.67 ^{b*}	27.99 ^a	73.22 ^{b*}	64.95 ^{a*}
	6	39.80 ^b	33.31 ^a	39.92 ^b	31.28 ^a

*indicates significant differences as a result of salt; different letters indicate significant differences between boron (B) content, both according to the LSD test ($P < 0.05$)

reported growth reduction in other species due to high levels of B. B toxicity affects different aspects of vascular plants, altering metabolism, reducing root cell division, lowering the leaf chlorophyll contents and photosynthetic rates, and decreased lignin and suberin levels, among others (NABLE et al. 1997). Accordingly, reduced plant growth is typical of plants exposed to high B levels. Laurustinus root growth was more sensitive to B toxicity than aerial part growth, while the contrary was true in metrosideros (Table 2). This was due to metrosideros dropped damaged leaves to eliminate the B, so that fewer damaged leaves remained on the plant (Table 2). This avoidance mechanism did not occur in laurustinus as only the totally damaged leaves fell and many damaged leaves, including those with almost the whole blade burnt, remained. This response resulted in a loss of ornamental quality and therefore of commercial value. Moreover, laurustinus plants irrigated with excess B probably decrease their capacity to absorb water and nutrients, because a high shoot/root ratio means that the plant is more likely to suffer from water stress (MIRALLES et al. 2009). YERMIYAHU et al. (2008) and CERVILLA et al. (2009) found that excess B increased the shoot/root ratio in bell pepper and tomato plant, respectively. Salinity \times B interaction was significant for leaf fall in both species (Table 1), meaning that salinity mitigated leaf fall in high B conditions; this effect was more marked in laurustinus, in which saline conditions suppressed leaf fall due to B toxicity (Table 2).

Concentrations of boron, sodium and chloride in the plants

BROWN et al. (1998) demonstrated that patterns of B accumulation and B toxicity symptoms differ dramatically between species commonly used in the ornamental industry. In the majority of species, B toxicity symptoms were observed in tissues with a B concentration ranging from 600 to 1,600 mg/kg DW after five months of 25 mg/l B treatment. In species with no B toxicity symptoms, the B concentrations ranged from 100 to 400 mg/kg DW after five months of 0.5 mg/l B treatment. Although different concentration of B was applied in this experiment, the results of BROWN et al. (1998) suggest that the leaves of metrosideros or laurustinus exhibit of toxicity symptoms when the leaf B content exceeds a threshold value. According to the Table 3, the leaves of metrosideros exhibited toxicity symptoms when the leaf B contents exceeded 400 mg/kg DW (about 800 mg/kg DW caused leaf drop), while B contents of around 1,384 mg/kg would be necessary to produce strong necrosis in the leaves of laurustinus.

Laurustinus plants accumulated less B in shoots and roots than metrosideros, which points to a

Table 3. Effects of salinity and boron (B) on concentrations of (B) (mg/kg DW), sodium (Na⁺) (mg/g DW) and chloride (Cl⁻) (mg/g DW) in the plants

Parameters	Salinity (dS/m)	Metrosideros B (mg/l)		Laurustinus B (mg/l)	
		1	6	1	6
Upper leaf B	2	57.78 ^a	404.41 ^{b*}	60.12 ^a	214.23 ^{b*}
	6	66.27 ^a	319.98 ^b	54.46 ^a	198.78 ^b
Lower leaf B	2	63.79 ^a	428.59 ^{b*}	58.32 ^a	1,384.23 ^{b*}
	6	72.89 ^a	335.23 ^b	71.36 ^a	424.78 ^b
Shoot B	2	75.32 ^a	93.62 ^{b*}	18.80 ^a	61.96 ^b
	6	68.05 ^a	84.01 ^b	16.59 ^a	51.75 ^b
Root B	2	48.05 ^a	352.58 ^{b*}	19.27 ^a	139.53 ^{b*}
	6	51.40 ^a	126.39 ^b	27.78 ^a	88.75 ^b
Leaf Na ⁺	2	0.74 ^{a*}	0.72 ^a	0.92 ^{a*}	0.73 ^{a*}
	6	5.29 ^b	0.88 ^a	19.84 ^a	20.44 ^a
Leaf Cl ⁻	2	2.70 ^a	2.75 ^a	5.52 ^{a*}	4.44 ^{a*}
	6	3.02 ^a	2.80 ^a	34.93 ^a	35.21 ^a

*significant differences as a result of salt; different letters indicate significant differences between boron (B) content, both according to the LSD test ($P < 0.05$); for abbreviations see Table 1

greater restriction of B uptake in the latter species. We suggest that metrosideros developed two effective mechanisms against B toxicity: (1) removing excess B by dropping leaves and (2) preventing B from entering the plant by retaining it in the roots. These mechanisms enabling it to maintain a suitable commercial aspect, avoiding leaf necrosis. NABLE et al. (1997) indicated that the leaves of species susceptible to B toxicity generally have higher B concentrations than tolerant species, so that metrosideros could be considered a species resistant to B toxicity, while laurustinus is sensitive. Metrosideros was also more salt-resistant than laurustinus (Table 2), which could be related with the different degrees of resistance of both species to B toxicity, since their salinity resistance mechanisms also control the excessive uptake of B (ALPASLAN, GUNES 2001).

B toxicity symptoms in laurustinus may be attributed to the low mobility of B in the plant (BROWN, SHELP 1997). After being loaded into the xylem, B is transported through the vascular system to the shoots by the transpiration stream (BROWN et al. 1998), resulting in a high accumulation of B in the mature leaves which had the highest transpiration levels. However, the mobility of B is drastically divergent in different plant species (TAKANO et al. 2008). In this experiment, the lower leaves of laurustinus accumulated much more B than those of metrosideros, the highest levels being observed in the non-salinated plants exposed to excess B (Table 3). BROWN and SHELP (1997) suggested that B can also be transported via phloem, improving its mobility and provoking other symptoms such as die back in young shoots. This behaviour was not observed in metrosideros plants, in which the main B toxicity symptom was leaves falling, especially mature leaves from any part of the plant. Possibly, the growth characteristics of this species (globose shaped plant with many lateral shoots) could improve B mobility through the plants; consequently the leaves of all parts of the plant would present similar B concentrations (Table 3).

An antagonistic interaction for the B content in the tissues studied was found, being stronger in salt-sensitive laurustinus than in salt-resistant metrosideros (Tables 1 and 3), which led to leaf B being reduced in saline conditions, especially in laurustinus. GRATTAN et al. (2005) and EDELSTEIN et al. (2005) also observed this interactive effect in broccoli and tomato, respectively. In this sense, ALPASLAN and GUNES (2001) suggested that tolerance to B toxicity in saline conditions may involve dif-

ferential B uptake and transport within the plants. Decreasing B uptake in saline conditions could have had three main causes: (1) salinity reduces B uptake because this stress decreases growth; (2) a decrease in transpiration, perhaps as a result of osmotic effect of salinity; (3) the higher content of saline ions in water leads to physiological damage to the plant, which consequently diminishes B uptake. As regards the third point, in saline conditions, laurustinus tended to accumulate more Cl^{1-} and Na^{1+} in leaves than metrosideros (Table 3), which is consistent with their different degree of sensitivity to salinity. Decreasing Na^{+} uptake in the face of increased B would indicate a competition between Na^{+} and B for absorption in metrosideros plants, which possibly contributed to decreasing leaf fall in salinity and excess B conditions. Controlling the uptake and distribution of Na^{+} is a major trait in resistance to salinity. Thus, the combination of salinity and excess B reduced the negative effects of salt through competition between B and Na^{+} in metrosideros, which did not occur in laurustinus (Table 3).

Gas exchange, photochemical efficiency and SPAD

In saline conditions, the addition of excess B increased g_s in laurustinus, which did not prevent a fall in P_n (Table 4). Decreases in P_n may be related to stomatal factors or non-stomatal factors. In our experiment, this decrease could be related to non-stomata factors, such as damage in thylakoids (PEREIRA et al. 2000), which can affect the transport of photosynthetic electrons. Furthermore, alterations in some metabolites as consequence of salinity and excess B in laurustinus plants could be involved, because these plants presented similar relative content of chlorophyll (SPAD) values to those submitted only to saline stress (Table 4) despite P_n under salinity and B excess was lower than just under salinity. Study of the photochemical efficiency of laurustinus showed that nonphotochemical quenching (NPQ) increased as a result of salinity or B toxicity (Table 4), which means an increase of radiant energy dissipated as heat in order to protect leaves from photooxidative damage (MAXWELL, JOHNSON 2000). However, when plants were subjected simultaneously to both stresses P_n but not ϵPSII (quantum yield of PSII (photosystem II) linear electron transport) fell sharply, which sug-

Table 4. Effects of salinity and boron (B) on gas exchange, chlorophyll fluorescence and leaf SPAD

Parameters	Salinity (dS/m)	Metrosideros B (mg/l)		Laurustinus B (mg/l)	
		1	6	1	6
g_s (mmol/m ² s)	2	46.63 ^{a*}	43.31 ^{b*}	32.08 ^{a*}	33.02 ^{a*}
	6	44.25 ^a	41.19 ^b	16.70 ^a	24.63 ^b
P_n (μmol/m ² s)	2	6.78 ^{a*}	6.05 ^b	5.34 ^{a*}	5.28 ^{a*}
	6	6.01 ^a	5.74 ^a	4.02 ^b	2.82 ^a
SPAD readings	2	53.90 ^a	51.22 ^a	56.92 ^{b*}	46.67 ^{a*}
	6	53.05 ^a	52.69 ^a	41.37 ^a	42.96 ^a
F_v/F_m	2	0.84 ^a	0.82 ^a	0.84 ^{b*}	0.81 ^{a*}
	6	0.83 ^a	0.83 ^a	0.81 ^b	0.76 ^a
èPSII	2	0.39 ^a	0.38 ^a	0.22 ^{b*}	0.19 ^a
	6	0.40 ^a	0.42 ^a	0.19 ^a	0.20 ^a
NPQ	2	2.34 ^{a*}	2.31 ^{a*}	2.62 ^{a*}	3.25 ^{b*}
	6	2.68	2.71 ^a	2.85 ^a	2.86 ^a

*indicate significant differences as a result of salt, and different letters indicate significant differences between boron (B) content, both according to the LSD test ($P < 0.05$); for abbreviations see Table 1

gests a disorder in electron transport and photorespiration (FRYER et al. 1998), resulting in a decrease of the maximum photochemical efficiency of PSII (F_v/F_m ratio) from 0.84 to 0.76 (Table 4). These findings support the conclusion that the combination of salinity and B toxicity harmed the photosynthetic system of laurustinus.

In metrosideros, B toxicity slightly decreased g_s , which was followed by proportional decreases in P_n (Table 4) confirming that any decrease in P_n can be mainly assigned to stomatal factors. Contrary to what occurred in laurustinus, salinity and B toxicity did not affect èPSII or F_v/F_m (Table 4), which indicates that the proportion of light absorbed by chlorophyll associated with photosystem II (PSII) used in photochemistry was maintained under stressful conditions. No change in èPSII indicates the absence of photoinhibition and no chlorophyll loss (FLOWERS et al. 2007), which was also observed to consider leaf chlorophyll levels (Table 4). The metrosideros plants exposed to salinity prevented photosynthetic damage increasing NPQ (nonphotochemical quenching), due to the èPSII was maintained and the P_n was reduced under such stressful conditions. Under salinity, excess B did not produce any effect; however, under non-saline conditions, both èPSII and NPQ did not change

while P_n decreased (Table 4). This supports the conclusion that these plants exposed to salinity did not present changes in the rate of photorespiration or electron transport, while under excess B there was photochemical dissipation. So, salt and excess B stressed metrosideros plants were photochemically healthy and the drop in P_n was a result of the reduction in g_s .

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