Boron Uptake and Effects on Growth and Carbohydrate Partitioning of Pistachio Seedlings

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Abstract. Seedlings of three pistachio rootstock (*Pistacia atlantica* Desf., *P. terebinthus* L., and *P. integerrima* Stewart × *atlantica*) and of the pistachio scion cultivar Kerman (*P. vera* L.) were grown in calcareous sandy loam irrigated with B solutions (0 to 15 mg·liter⁻¹) in a greenhouse. After 10.5 months of B treatment, rootstock seedling growth (root + stem weight and leaf dry weight, area, and number per plant) had decreased linearly with B application, which provided up to 48.9 mg B/liter in the soil saturation extract. Growth of *P. terebinthus* was greater than *P. atlantica* throughout the concentration range, but species sensitivity to B did not differ. Nine months of B at concentrations up to 10.7 mg·liter⁻¹ in the saturation extract did not alter the growth of *P. vera* seedlings. Leaf B concentrations of all species increased linearly with saturation extract B concentration after each of two growing periods and were higher in leaves of *P. terebinthus* than *P. atlantica*. From 62% to 75% of B was present in leaf tissue of the rootstock seedlings, with lower quantities in roots and stems. Boron toxicity appeared initially as interveinal chlorosis and apical necrosis of 1-month-old, fully expanded leaflets of the rootstock species. By 4 months, symptoms in some treatments advanced to severe necrosis of leaflets. Boron addition increased the concentrations of total leaf sugars (glucose, fructose, and sucrose) and root starch, decreased root glucose concentrations, and had no effect on other root carbohydrates of *P. vera* seedlings. Leaf carbohydrate supply limitations and altered root carbohydrate status may be consequences of high B in *P. vera* seedling leaves.

The presence of excess B in soils and irrigation waters has been a persistent concern in irrigated areas of the western United States (Mikkelsen et al., 1988; Wilcox, 1948). However, data on high B responses of pistachio, an important tree crop of the area, are limited. A greenhouse study established a high correlation between B concentration in soils and in leaves of some Iranian pistachio cultivars, but a concentration producing growth reduction was not determined (Parsa and Wallace, 1980b). Ashworth et al. (1985) imply a relationship between leaf marginal necrosis of *P. vera* 'Kerman' and high accumulation of B. We could find no data on pistachio seedling rootstock responses to excess B in soil solutions. The identification of growth and B uptake characteristics is essential for selecting seedling rootstock suitable for high B soils. For example, differences in B uptake were observed with citrus rootstocks (Cooper et al., 1955) and tomato cultivars (Brown and Jones, 1971).

There is also limited knowledge of plant metabolic dysfunctions resulting from B excess (Francois, 1986). Supraoptimal tissue B levels may alter the structure or function of the phloem (Canny, 1973; Epstein, 1973), which might be expected to impede the mobilization of soluble metabolites.

This study evaluated the effects of high B on the growth and B uptake of *Pistacia* spp. rootstock seedlings and on the carbohydrate status of *P. vera* seedlings.

Materials and Methods

General methods Two greenhouse studies were made between May 1986 and June 1988 using seedlings of three rootstock species and a scion cultivar. The seedlings were cultured in plastic pots containing the A horizon of Hueco sandy loam (calcareous, coarse silty, mixed, thermic, petrocalcic Paleargid). In both studies, the lower half of the pots was filled with soil that had been pretreated with dissolved boric acid solution to complement the sorption deficit according to the method of Ryan et al. (1977). During the experiments, B was applied to the soil through irrigation (boric acid in tap water) at the following concentrations: trace B (tap water only), 2.5, 5.0, 7.5, 10.0, and 15.0 mg·liter⁻¹. All irrigation solutions contained 0.66-strength Hoagland nutrient solution #1 without B (Hoagland and Arnon, 1950; Parsa and Wallace, 1980a). The tap water control contained ≈0.2 mg B/liter. Solutions were applied in amounts to cause a 0.45 to 0.55 leaching fraction (drainage/application volume) when the soil moisture in the pots, measured gravimetrically, was depleted to 0.15 m³·m⁻³, or half of the total storage capacity. The greenhouse was maintained between 16C at night and 32C during the day. For winter months, the daytime maximum was reduced to 27C.

At the end of B treatments, harvested seedlings were separated into leaves, stems, and roots. Total leaf number and fresh weight of roots plus stem were determined after washing soil from roots. Total leaf area was measured using a portable area meter (LI-COR 3000; LI-COR, Lincoln, Neb.). For B analyses, all leaves (fully expanded with petioles) were cleaned, dried, weighed, and ground (Picchioni et al., 1990). Subsamples (0.25 to 0.50 g) were ashed in a muffle furnace for 12 h at 550C, then B was extracted from the ash using 6 N HCl (Hatcher and Wilcox, 1950) and measured using a plasma emission spectrometer (Applied Research Laboratories, Sunland, Calif.).

Soil saturation extract B concentrations (Richards, 1954) were measured in each pot of each trial, as described above, midway

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and at the end of each experimental period. The average of the two readings represented soil B concentrations.

Rootstocks (Expt. 1). Seedlings of *P. atlantica* (PI 246336), *P. terebinthus* (PI 246341), and *P. integerrima* × *atlantica* (PG II) were prepared as described by Picchioni et al. (1990). Following a 2-month growing period in the greenhouse, seedling tops were 10 to 15 cm tall (≈2 g seedling fresh weight). Seedlings then were planted 30 May 1986 into 12-liter pots at the rate of four per pot (two each of *P. atlantica* and *P. terebinthus*). Because of a limited supply, PG II seedlings were planted individually in separate pots with three buffer seedlings of *P. terebinthus* and were exposed only to 5, 10, and 15 mg B/liter irrigation solutions. Previous data showed that PG II seedlings had a higher growth rate than *P. atlantica* and *P. terebinthus* (Picchioni et al., 1990); thus, we were primarily interested in the B uptake characteristics of this hybrid.

Boron treatments began 14 July; on 1 Nov., pots were moved to an unheated shadehouse to impose dormancy. On 5 Jan., leaves from trace, 5, 10, and 15 mg B/liter irrigation treatments were collected and pooled separately to allow sufficient dry weight for B analyses. On 2 Feb., defoliated plants were returned to the greenhouse, irrigated with B solutions during the second growth period, and prepared for analyses 1 June (10.5-month treatment). Stems and roots (woody and nonwoody) of three replicate seedlings of the 10 mg B/liter irrigation solution were also dried, ground, and analyzed for B as described for leaves.

Scion cultivar (Expt. 2). Seed of *P. vera* 'Kerman' were stratified 6 weeks in perlite at 5C, then planted 10 July 1987 in 8-liter pots. Boron treatments (identical to Expt. 1) began 31 Aug. after thinning to one seedling per pot (tops 10 to 15 cm tall, ≈5 g seedling fresh weight). On 17 Feb., leaves were ≈5.5 months old and were collected for B analyses for the first growing period. Boron treatments were maintained, and a second shoot growth period began within 2 weeks. By 1 Apr., terminal buds had formed and most leaves were fully expanded. Treatments were stopped on 7 June (9-month treatment); at midday, *P. vera* seedlings grown with trace, 5, and 15 mg B/liter irrigation solutions were harvested (second growth period). After recording root plus stem weight, three to four basal leaves, located at about the bottom one-third of the stem axes, and detached root systems were rinsed with distilled water, dried with paper towels, and preserved for carbohydrate determination by a method modified from Weimberg (1987) and Crane et al. (1976). Tissues were placed initially in a drying oven at 105C for 30 min, followed by 60C to constant dryness. Preliminary tests showed that tissue sugar concentrations were not significantly altered using this method (Picchioni, 1989). After drying, basal leaf weight was added to that of the remaining leaves to obtain a total dry weight. Boron analyses were also made on the basal leaves of this growing period.

Fine roots (<2 mm in diameter) were separated from the dry root masses and analyzed along with basal leaves for carbohydrates and B. Tissues were ground as above and stored in sealed jars at -25C. Subsamples (0.50 g) were extracted for glucose, fructose, and sucrose four times (20 min each) in boiling ethanol (10 ml, 80% v/v) with refluxing (McBee et al., 1983). Starch was hydrolyzed from the ethanol-insoluble material following 24-h incubation at 38C (Na-acetate buffer, pH 4.6) with amyloglucosidase (Sigma, St. Louis). The residue was then extracted three times (5 min each) in 60C water. Five-milliliter aliquots of all extracts were passed through 0.45-μm membrane

filters to remove particulate matter, stored at 5C, and analyzed within 24 h.

Determination of sugars and starch (after hydrolysis) was made using a spectrophotometer at 340 nm (Spectronic 21 UV-D; Bausch and Lomb, Rochester, N. Y.) according to the enzymatic method outlined by Sturgeon (1990). Enzymes for the assays were obtained from Boehringer Mannheim (Indianapolis). Recovery of known sugars added before extraction of leaf samples averaged 99.8% and 98.5% as internal standards in assays of ethanol extracts (average cv = 3.7%).

Statistical analyses. Pots of Expt. 1 were arranged in a split plot, with B solution concentrations (main plot) randomized completely within each of five blocks. The subplots (rootstock species) were the average of two seedlings of *P. atlantica* and *P. terebinthus* per pot and one for PG II. The analysis of variance was made for the split plot according to Little and Hills (1978), excluding PG II seedling data. Experiment 2 was a one-way randomized complete block with two to three, four, or five replicates (B, carbohydrate, and growth analyses, respectively).

Orthogonal contrasts were partitioned from the main effects of B saturation extract values using polynomials for unequally spaced treatments (F.J. Hills, personal communication). Linear regressions were evaluated by slope and intercept comparisons (Snedecor and Cochran, 1989) using MSTAT-C statistical software (Michigan State Univ., East Lansing). In both studies, the B concentrations reported are those measured in the soil saturation extract.

Results

Seedling growth. Boron application decreased seedling growth of *P. atlantica* and *P. terebinthus* significantly (Table 1), with linear contrasts accounting for 74% to 86% of the B treatment variation (higher order contrasts were not significant). On average, the growth of *P. terebinthus* was 1.3 to 2.4 times greater than *P. atlantica*, depending on growth characteristic, with significantly greater intercepts in each comparison. However, there were no significant differences in species sensitivity to increasing saturation extract B concentration (decreasing slopes) with any of the growth characteristics. Root plus stem growth of *P. terebinthus* was highly variable at low B concentrations, particularly in controls (cv = 48%). In addition, mean growth of roots plus stem changed inversely between the species with each increase in B concentration. These factors contributed to the B × rootstock interaction, even though the slopes were nearly identical. Fresh root plus stem weight consisted of ≈70% roots (data not shown); thus, B effects were attributed mainly to root growth reduction.

At high B, the combined leaf dry weight averages declined 74% below controls. This reduction resulted mostly from a decrease in leaf number per seedling (53% reduction), with parallel losses in measured leaf area (54%). Specific leaf weights and leaf area per leaf were unaffected by B application (data not shown). Leaf area measurements included necrotic tissue at 20.9 mg B/liter in the saturation extract and higher; thus, functional leaf area was reduced more than the data indicate.

In Expt. 2, saturation extract B up to 10.7 mg·liter⁻¹ (15 mg·liter⁻¹ irrigation solution) did not reduce leaf dry weight, size, total area, root fresh weight, or root plus stem fresh weight of *P. vera* seedlings (data not shown). Final height of seedling tops ranged from 50 to 60 cm, and root plus stem fresh weight from 60 to 70 g.

Boron toxicity symptoms. There were no foliar disorders on

Table 1. Growth responses of *P. atlantica* and *P. terebinthus* rootstock seedlings to increasing B concentrations in the soil saturation extract (Expt. 1, second growing period). Irrigation solutions containing trace, 2.5, 5.0, 7.5, 10.0, or 15.0 mg B/liter correspond to increasing saturation extract B concentrations.

Mean saturation extract B (mg·liter ⁻¹) ^a	Root + stem fresh wt (g)	Leaf dry wt (g)	Total leaf area (cm ²)	Leaves/plant
<i>P. atlantica</i>				
3.0 (control)	31.0	1.5	98.1	23.7
15.5	17.6	1.0	67.9	16.1
20.9	19.6	1.2	79.8	20.3
25.2	22.5	0.8	54.2	13.7
44.7	15.6	0.7	45.6	11.9
48.9	17.0	0.5	27.6	9.3
<i>P. terebinthus</i>				
3.0 (control)	27.5	2.7	187.4	28.8
15.5	40.3	3.0	209.9	24.2
20.9	34.3	2.3	151.6	29.6
25.2	22.7	3.3	224.5	36.0
44.7	26.1	1.7	122.7	21.0
48.9	13.0	0.6	102.8	15.6
Significance				
B solution	L**	L**	L**	L**
Rootstock	**	**	**	**
Rootstock × B	*	NS	NS	NS

^aValues are the means of five replicates, each the average of two seedlings per species.

**,*,NS Linear (L); significant at $P = 0.01$, 0.05 , or nonsignificant at $P = 0.05$, respectively.

the rootstock seedlings after the first growing period, although some leaves contained up to 2000 mg B/kg dry weight. By January, all leaves had senesced. One month after resumption of B application in Expt. 1 (2 Mar.), interveinal chlorosis and tip necrosis appeared on fully expanded leaflets at 20.9 mg B/liter in the saturation extract. Leaves <1 month old were not visibly affected. By 1 June, most sampled leaves were ≈4 months old, and toxicity symptoms had progressed to marginal and interveinal necrosis, affecting a greater proportion of leaves, which increased with B application. On average, necrosis was present on 47% of *P. terebinthus* leaflets from seedlings exposed to 20.9 mg B/liter and higher in the saturation extract, compared to only 30% for *P. atlantica*, although this difference was highly variable. Boron-affected seedling leaves contained >1300 mg B/kg dry weight, but toxicity was not observed with leaf concentrations <1000 mg·kg⁻¹.

With *P. vera* leaves, chlorosis and tip necrosis did not appear initially, although some marginal necrosis was evident on seedlings exposed to 5.3 mg B/liter in the saturation extract after the first growing period (17 Feb.). These leaves contained ≥1200 mg B/kg and were ≈5.5 months old at the bottom third of the stem axes. With 10.7 mg B/liter in the saturation extract, slight marginal necrosis was observed on 99-day-old leaves (≈2500 mg B/kg) from the second growing period (7 June), whereas no disorders were, observed with lower B rates. Necrotic areas comprised <5% of the total leaf weight at sampling.

Tissue B concentrations. Linear contrasts accounted for 94% to 97% of the B effect on leaf B concentrations of *P. atlantica*, *P. terebinthus*, and *P. vera*. After the first growing period, B levels in rootstock seedling leaves (≈5 months old, pooled samples) had increased linearly with B treatment ($R^2 = 0.88$ to 0.94) and reached as high as 2000 mg·kg⁻¹, but were not species-dependent (data not shown). However, with further B ap-

plication, leaf B of *P. terebinthus* increased at a significantly higher rate ($P = 0.05$) than that of *P. atlantica* following the second growth period (Fig. 1). When all three species were compared, only in 5-, 10-, and 15-mg·liter⁻¹ irrigation treatments ($n = 12-20$ at common saturation extract B levels) were there no regression differences, and there was a poor correlation for PG II ($R^2 = 0.09$). However, *P. atlantica* and PG II had similar slopes (49.5 and 36.3, respectively), with *P. terebinthus* much higher (98.0).

Fig. 1. Leaf B concentrations (dry-weight basis) of *Pistacia* spp. seedling rootstock (Expt. 1) as affected by B in the soil saturation extract. The line for PG II points (open triangles) is not included. Data are mean values of five replicates for leaf and saturation extract B concentrations after the second growing period. Regression data shown for 28 observations per species. (At 48.9 mg B/liter in the saturation extract, leaves of two replicates of each species provided insufficient dry weight for B analysis.)

Boron concentrations in leaves of *P. vera* were markedly higher than those in the rootstock species at equivalent saturation extract B levels (Fig. 2). Leaf B concentrations increased at a higher rate during the second growing period ($P = 0.05$), which may have resulted from the long-day conditions compared to short days for the first growing period. However, this difference was observable only at the highest B concentration.

The percentage of total plant B in seedling organs (the product of organ dry weight and the corresponding B concentration) was highest in leaves, with much smaller but similar values in roots and stems (Table 2). PG II contained the lowest percent total plant B in leaves, but there was no rootstock effect on B quantity in nonfoliar portions. Boron concentrations in roots and stems (rootstock averages) were 252 and 271 $\text{mg}\cdot\text{kg}^{-1}$, respectively.

There were also much smaller B concentrations in nonwoody *P. vera* roots on the final sampling date, despite the large increases in leaf B (root averages of 77, 193, and 289 $\text{mg}\cdot\text{kg}^{-1}$ for 0.4, 3.9, and 10.7 mg B/liter saturation extract concentrations, respectively). Lower B concentrations were found in woody roots (data not shown).

Carbohydrate levels. Boron applications altered the balance of carbohydrates in leaf and root tissues of *P. vera* without affecting total carbohydrates measured (Table 3). Raising the B concentration in the saturation extract resulted in a linear in-

crease in leaf sucrose concentration. Total leaf sugars increased 54% with 10.7 mg B/liter in the saturation extract, even though changes in concentrations of reducing sugars in leaves were inconsistent.

High B also caused a significant increase in the ratio of leaf : root sugars (1.0 vs. 0.5 in controls), whereas 3.9 mg B/liter in the saturation extract had no effect (data not shown). Linear but opposite B effects on root glucose and starch levels were greatest at 3.9 mg B/liter, followed by marginal changes with 10.7 $\text{mg}\cdot\text{liter}^{-1}$. Control roots had 54% lower starch and 64% higher glucose concentrations than high-B-treated roots.

Discussion

Although 20.9 mg B/liter in the saturation extract caused prolonged leaflet necrosis of *P. atlantica* and *P. terebinthus* seedlings, higher B concentrations were required to bring about observable root plus stem growth reductions when averaged for both species. This observation is similar to a report of B-affected barley (*Hordeum vulgare* L.) seedlings in which B toxicity symptoms were expressed before shoot and root weights decreased (Riley, 1987). Leaf weights seemed to be more B-sensitive than root plus stem weights (reductions of 74% vs. 48% for high B, respectively), which may ultimately affect total plant weight with longer treatment duration or in environments of higher evaporative demand, which intensify the movement of B to leaves (Oertli and Kohl, 1961). The greenhouse relative humidity rarely dropped below 23%, whereas in outdoor conditions of far-western Texas, midday relative humidity is frequently less than half of this value during the growing season.

There were no B effects on shoot elongation rates or shoot mortality after the first growing period of Expt. 1 (data not shown), indicating that reductions in leaf weight and number were caused only after sufficient duration of B treatment (10.5 months) by the end of the second growing period. In an earlier study, we found that after 8 months, saturation extract B ≥ 3 $\text{mg}\cdot\text{liter}^{-1}$ caused death of axillary and terminal buds of young pecan trunks [*Carya illinoensis* (Wangenh.) C. Koch], which limited new shoot and leaf production (Picchioni et al., 1991).

The differences in B uptake and distribution patterns between PG II, *P. atlantica*, and *P. terebinthus* may be important for high B soils. However, we are uncertain whether the higher rate of increase in seedling leaf B concentrations of *P. vera* compared to the rootstock seedlings reflects inherent characteristics or differences in experimental conditions. These findings indicate that further study is needed to determine whether the rootstock can alter B accumulation rates of *P. vera* scion leaves in high B areas.

The linear relationship between leaf B and saturation extract B in Expts. 1 and 2 indicates that seedling B status of these species can be assessed by leaf or saturation extract B measurements. Also, B concentrations ≥ 1200 $\text{mg}\cdot\text{kg}^{-1}$ in 3- to 6-month-old leaves were well correlated with toxicity occurrence during both studies. Ashworth et al. (1985) found slightly less B (≈ 1000 $\text{mg}\cdot\text{kg}^{-1}$) in necrotic, B-affected leaves of *P. vera* trees at the end of a growing season. Saturation extract B increased linearly with B in the irrigation solutions, but soil B characteristics differed greatly between Expts. 1 and 2. This difference may have resulted from variation in leaching fractions between the studies. Minor variation in leaching water volume can greatly affect soluble soil B levels in the range of leaching fractions used in this study (Keren and Miyamoto, 1990).

Raven (1980) suggested that limited mobility of B is associated with toxicity of this element in the phloem. The injury

Fig. 2. Leaf B concentrations of *P. vera* 'Kerman' seedlings (Expt. 2) after the first and second growing periods, expressed as in Fig. 1. Data are mean values of two to three replicates for leaf and saturation extract B concentrations. Regression data shown for 18 and nine observations for periods 1 and 2, respectively. For period 2, leaf B only for 0.4, 3.9, 6.0, and 10.3 $\text{mg}\cdot\text{liter}^{-1}$ saturation extract B levels are included.

Table 2. Partitioning of B among seedling tissues of *Pistacia* spp. rootstock with 10 mg B/liter in the irrigation solution (Expt. 1, second growing period). Soil saturation extract B concentrations ($\text{mg}\cdot\text{liter}^{-1}$) were 44.5 ± 6.9 (*P. atlantica* and *P. terebinthus*) and 39.2 ± 8.6 (PG II).

Rootstock ^a	B distribution (%) ^b		
	Leaves	Stems	Roots
<i>P. atlantica</i>	75 a	14 a	11 a
<i>P. terebinthus</i>	74 a	11 a	15 a
PG II	62 b	20 a	18 a

^aMean separation in columns by Duncan's multiple range test ($P = 0.05$).

^bValues are the averages of three or five seedling replicates (nonfoliar and foliar portions, respectively) calculated as organ dry weight (kg) $\times$ B concentration ($\text{mg}\cdot\text{kg}^{-1}$ dry weight)/total seedling B (mg) $\times 100$.

Mean saturation extract B (mg·liter ⁻¹) ^z	Carbohydrate concn (mg·g ⁻¹)					
	Glucose	Fructose	Sucrose	Total sugars	Starch	Total
	<i>Leaves</i>					
0.4 (control)	4.9	4.0	7.8	16.7	17.4	34.1
3.9	2.2	2.0	12.0	16.2	20.9	37.1
10.7	6.1	6.5	13.1	25.7	14.5	40.2
Significance	NS	L*,Q*	L*	L*	NS	NS
	<i>Roots</i>					
0.4 (control)	9.2	7.8	14.8	31.9	3.8	35.6
3.9	6.9	6.9	12.3	26.1	7.9	33.9
10.7	5.6	7.3	12.0	25.0	8.3	33.2
Significance	L*	NS	NS	NS	L*	NS

*^{NS}Linear (L), quadratic (Q); significant or nonsignificant at $P = 0.05$, respectively.

A reduced supply of carbohydrates from B-affected leaves could have altered sink demand and carbon pools in roots, where starch increased as glucose decreased with leaf B concentration. A direct influence of B on roots should not be discounted, since Klein and Brown (1982) showed that high B arrests mitosis (thus carbon use) in pea (*Pisum sativum* L.) root tips. However, root plus stem growth reduction in Expt. 1 occurred with root B concentrations similar to those in Expt. 2 (with no root growth reductions), but with higher overall leaf B concentrations. Thus, a direct effect of B in leaves, followed by alterations in root carbohydrate status, and ultimately growth of roots seem to be consequences of high leaf B concentrations in these seedlings. Since *P. vera* root growth was unaffected, younger leaves that

Additional work is necessary to evaluate the effects of long-term, recurring high B conditions on growth and carbohydrate status of bearing pistachio trees. High leaf B concentrations, for example, may further alter carbohydrate status of trees with competing, reproductive sinks.

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