Boron and Salinity
The Relative Tolerance of Six Prunus Rootstocks to Boron and Salinity

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Abstract. The influence of B and salinity [3 Na2SO4 : 1 CaCl2, (molar ratio)] on B toxicity and the accumulation of B, sodium, and SO4 in six Prunus rootstocks was evaluated. High salinity reduced B uptake, stem B concentrations, and the severity of toxicity symptoms in five of the six rootstocks. Forward and backward stepwise regression analyses suggested that stem death (the major symptom observed) was related solely to the accumulation of B in the stem tissue in all rootstocks. The accumulation of B and the expression of toxicity symptoms increased with time and affected rootstock survival. No symptoms of B toxicity were observed in leaf tissue. The Prunus rootstocks studied differed greatly in stem B accumulation and sensitivity to B. The plum rootstock ‘Myrobalan’ and the peach–almond hybrid ‘Bright’s Hybrid’ were the most tolerant of high B and salinity, whereas the peach rootstock ‘Nemared’ was very sensitive to high B and salinity. In all rootstocks, adding B to the growth medium greatly depressed stem SO4 concentrations. In every rootstock except ‘Nemared’ peach, adding salt significantly depressed tissue B concentrations. A strong negative correlation between tissue SO4 and B was observed. Grafting experiments, in which almond was grafted onto ‘Nemared’ peach or ‘Bright’s Hybrid’, demonstrated the ability of rootstocks to influence B accumulation and scion survival.

Boron is an essential micronutrient that is often found in high concentrations in association with saline soils and saline well water (Dhankhar and Dahiya, 1980). Although B toxicity is closely associated with salinity problems (Nicholaichuk et al., 1988), it is not known whether B and salinity interact to impair the growth of fruit tree species.

Stone fruit trees are classified as relatively sensitive to salinity (Greenway and Munns, 1980; Maas, 1986). Hoffman et al. (1988) and Catlin et al. (1993) have demonstrated that growth of ‘Santa Rosa’ plum on ‘Myrobalan’ rootstock was not significantly reduced by exposure to soil conductivities of 4 and 8 dS·m–1 for one season, but continued exposure to these salinity levels resulted in yield declines in the second season. Catlin et al. (1993) calculated that 3 years of growth of ‘Santa Rosa’ plum in soils with an electrical conductivity >2.5 dS·m–1 would reduce production measurably. 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). This region produces more than $1 billion a year in almonds and stone fruit.

Published studies on the accumulation of toxic ions and the development of symptomology in plant species exposed to a combination of high B and salinity are limited. Eaton (1944) described a range of symptoms associated with B toxicity and emphasized that species differ greatly in their response to excess B. In Prunus, B toxicity has been associated with stem dieback, gum formation, and cracking and splitting of the bark (Woodbridge, 1955). Leaf symptoms of B toxicity have not been described for Prunus, and, as a result, the recognition of B toxicity in the field is severely inhibited.

Rootstock can greatly affect the scion’s tolerance to salinity (Bernstein et al., 1956; Hayward et al., 1946) or high B concentration (Hansen, 1948, 1955). For example, almond and peach scions grafted onto ‘Marianna’ plum rootstock consistently had lower Cl accumulation and less growth inhibition than those grafted onto ‘Lovell’ peach (Bernstein et al., 1956). In a comparison of rootstock effects on B tolerance, Hansen (1948, 1955) observed that French prune on ‘Marianna’ plum or peach roots showed more stem injury than those on almond or ‘Myrobalan’ plum rootstocks. None of these studies, however, considered interactions between B, salinity, and rootstock, and few have adequately discussed the accumulation of ions in plant tissues and its association with tree performance (Bernstein et al., 1956). Furthermore, information is required on the response of fruit trees to a combination of Na2SO4, CaCl2, and B of typical many areas of the western San Joaquin Valley of California and many similar areas in the world.

The objectives of this study were to 1) investigate the interactions of Na2SO4, CaCl2, salinity and B supply on the accumulation of B, Na, and SO4 in various plant parts, 2) study the relationship between the concentration of these ions, plant growth, and the expression of toxicity symptoms in six rootstocks, and 3) determine if rootstock can influence scion tolerance to excessive B or salinity stresses in the root environment.

Materials and Methods

Six commercial Prunus rootstocks—‘Lovell’, ‘Nemaguard’ and ‘Nemared’ peach (Prunus persica Batsch), ‘Marianna 2624’ and ‘Myrobalan’ plum (P. salicina Lindl), and ‘Bright’s Hybrid’ (almond–peach hybrid) [P. amygdalus Batsch syn. P. dulcis (Mill.) D.A. Webb ‘Mission’ x P. persica ‘Nemared’]—were used in this experiment. ‘Marianna 2624’ cuttings and seeds of ‘Myrobalan’, ‘Nemaguard’, and ‘Nemared’ were obtained from the U.S. Dept. of Agriculture Germplasm Repository, Davis, Calif. ‘Marianna 2624’ cuttings were rooted in Fall 1990 and ‘Myrobalan’, ‘Nemaguard’ and ‘Nemared’ seeds were planted in April 1991 after 2 months of chilling at 5°C. ‘Lovell’ and ‘Bright’s Hybrid’ seedlings were obtained in April and May 1991 from Bright’s nursery near LeGrand, Calif. All rootstocks were transplanted into pots in May 1991 and grown at a field site near Davis. Plants were grown in 11-liter pots filled with perlite. Each pot contained two plants. Boron (H3BO3) was supplied at 0.025, 0.5, and 1.0 mm and salinity was provided as 3 Na2SO4 : 1 CaCl2 (molar ratio) to the growth medium to a final electrical conductivity of 2, 6, or 12 dS·m–1. The experiment was a three (B) × three (salinity) × six
Boron toxicity in the shoots was estimated as percentage length of dead shoots vs. total shoot length. The total dry weight for each pot was determined at the end of the experiment.

All samples were oven-dried at 70°C to a constant weight, weighed, ground to pass a 30-mesh screen, and ashed at 500°C for 16 h. After ashing, samples were digested in 1% nitric acid, and ion concentration was determined by inductively coupled plasma spectroscopy (Thermo Jarrell Ash Corp., Menlo Park, Mass.). Sulfate-S was extracted and analyzed according to Littlefield et al. (1990). Chloride was determined by a chloridometer (Haake Buchler, Saddle Brook, N.J.).

**Statistical analysis.** Statistical analysis was performed using SAS’s general linear models and stepwise procedures (SAS Institute, 1982). Percentage data were arcsin-transformed (Fernandez, 1992; Gomez and Gomez, 1984). Stem B concentration was log-transformed, and dry weight was cubic-root-transformed according to the criteria outlined by Fernandez (1992). Forward and backward stepwise regression was performed using nontransformed stem death as the dependent variable and B, Na, and SO4-S in the leaf and stem as independent factors. Analysis of treatment effects indicated that stem death, dry weight, and stem B concentration were affected by two- and three-way interactions between B, salinity, and rootstock. Statistical comparisons of main effect are therefore not valid. Results for the first and second year of the experiment were similar. Only second year results are presented here.

### Results

**Plant growth and symptoms.** Toxicity symptoms were observed 4 months after treatment and persisted into the second year of the experiment. The most significant toxicity symptom occurred in the stem and included shoot die back, gummy exudates, or necrotic spots along the lower or middle part of a stem and finally whole shoot death. This toxicity symptom was caused solely by B, as no symptoms were observed with salinity treatments alone. There were no apparent leaf symptoms in any treatments.

Stem death was affected by a three-way interaction ($P < 0.01$) between B, salinity, and rootstock (Table 1). The results indicate that, under low salt (2 dS·m$^{-1}$), ‘Marianna’, and ‘Lovell’ were least tolerant of high B (1 mm) (98 and 91 stem death, respectively) (Table 2), while ‘Myrobalan’ was very resistant to high B (13%

### Table 1. General linear models procedure analysis of percentage stem death after arcsin transformation. Stem death was determined 14 months after exposing six Prunus rootstocks to varying B and salinity treatments.

| Source | df | Mean square | F value |
|--------|----|-------------|--------|
| B      | 2  | 40,000      | 257**  |
| Salinity (S) | 2  | 933         | 6.01** |
| Rootstock (R) | 5  | 10,900      | 70.4** |
| B × S   | 4  | 1,460       | 9.41** |
| B × R   | 10 | 2,370       | 15.3** |
| S × R   | 10 | 430         | 2.77** |
| B × S × R | 20 | 405         | 2.61** |
| Error   | 258| 155         |        |

*Significant at $P < 0.01$.

### Table 2. Mean percentage stem death of six Prunus rootstocks grown under varying B and salinity treatments. Plants were exposed to treatments for 14 months.

| B (mM) | HY | LO | M  | MA | NG | NR |
|--------|----|----|----|----|----|----|
| 0.025  | 3 ± 1 | 18 ± 1 | 2 ± 1 | 16 ± 6 | 5 ± 1 | 16 ± 3 |
| 0.5   | 7 ± 2 | 40 ± 8 | 15 ± 8 | 42 ± 7 | 33 ± 7 | 52 ± 5 |
| 1     | 71 ± 4 | 91 ± 8 | 13 ± 3 | 98 ± 1 | 62 ± 7 | 78 ± 13 |
| 0.025/6 | 2 ± 1 | 17 ± 3 | 3 ± 1 | 28 ± 7 | 14 ± 2 | 12 ± 6 |
| 0.5/6 | 7 ± 3 | 35 ± 2 | 3 ± 2 | 24 ± 11 | 21 ± 1 | 24 ± 3 |
| 1/6    | 43 ± 11 | 56 ± 8 | 5 ± 2 | 100 ± 0 | 52 ± 11 | 99 ± 0 |
| 0.025/12 | 2 ± 1 | 13 ± 2 | 6 ± 1 | 14 ± 8 | 33 ± 9 | 30 ± 7 |
| 0.5/12 | 4 ± 2 | 17 ± 1 | 4 ± 3 | 19 ± 2 | 24 ± 3 | 25 ± 3 |
| 1/12   | 12 ± 1 | 66 ± 19 | 3 ± 1 | 63 ± 5 | 40 ± 15 | 100 ± 0 |

*HY = ‘Bright’s Hybrid’, LO = ‘Lovell’, M = ‘Myrobalan’, MA = ‘Marianna’, NG = ‘Nemaguard’, NR = ‘Nemared’. Values are untransformed original means ± SE.

†Only four to five observations, all others had six observations.
stem death only). At the intermediate salt concentration (6 dS·m⁻¹), the relative sensitivities of the six rootstocks differed slightly from sensitivities at the low salt concentration. Thus 'Marianna' and 'Nemared' were most sensitive, 'Myrobalan' was least sensitive, and 'Lovell', 'Nemaguard', and 'Bright’s Hybrid' were intermediate in their response. At the highest B level (1 mM), increasing salinity (2 to 12 dS·m⁻¹) decreased shoot death by 80%, 30%, 70%, 30%, and 30% in 'Bright’s Hybrid', 'Lovell', 'Myrobalan', 'Marianna', and 'Nemaguard', respectively (Table 2).

Only in 'Nemared' did increasing salinity increase shoot death percentages (78% to 100%). A similar trend was apparent at intermediate B levels with increasing salinity. Thus, increasing salinity reduced B toxicity in all species except 'Nemared'. The rootstocks 'Marianna', 'Lovell', 'Nemaguard', and 'Nemared' were the most sensitive to high B and high salinity, while 'Myrobalan' and 'Bright’s Hybrid' were least sensitive. 'Bright’s Hybrid' is relatively tolerant of B, particularly if salinity is high, while 'Myrobalan' is tolerant of B at all salt levels used here.

Dry weight accumulation also depended on a three-way interaction between B, rootstock, and salt (P < 0.05) (Table 3). Under low salt, adding high B greatly decreased dry weight accumulation in all species except 'Myrobalan' (Table 4). Under the highest B concentration, increasing salt level increased dry weight accumulation in 'Bright’s Hybrid'. Thus, increasing salt mitigated the effects of B on 'Bright’s Hybrid'. Intermediate salt levels also partially mitigated the effects of B in 'Marianna' and 'Myrobalan'. Under high B and high salt, 'Myrobalan' and 'Bright Hybrid' maintained 60% to 80% of control growth (low B and low salt) compared to 20% to 30% growth in the other rootstocks.

**Table 3.** General linear models procedure analysis of dry weight after cubic-root transformation. Dry weight was determined 14 months after exposing six *Prunus* rootstocks to varying B and salinity treatments.

| Source          | df | Mean square | F value |
|-----------------|----|-------------|---------|
| B               | 2  | 32.7        | 146**   |
| Salinity (S)    | 2  | 2.39        | 10.6**  |
| Rootstock (R)   | 5  | 25.3        | 112**   |
| B × S           | 4  | 2.13        | 9.47**  |
| B × R           | 10 | 1.04        | 4.66**  |
| S × R           | 10 | 0.53        | 2.36*   |
| B × S × R       | 20 | 0.517       | 2.29**  |
| Error           | 244| 0.224       |         |

Correlation of stem death with elemental concentrations. A stepwise regression analysis (SAS Institute, 1982) was used to determine which independent variable—B, Na, or SO₄—in the leaf and stem was most likely to contribute to stem death (Table 5). Chloride data are not shown because Cl⁻ did not accumulate to significant levels in any treatment (Cl⁻ concentrations in leaves ranged from 150 to 600 µg·g⁻¹ and were not significantly affected by treatment or rootstock effects). Stem B was the only variable that was significantly correlated with stem death. Further analysis of individual rootstocks and elemental concentrations suggests that there was no interactive effect between Na and SO₄ in leaf tissue and the sensitivity of a plant to B toxicity. Thus, B accumulation in the stem tissue is the sole determinant of B toxicity. Any apparent effect of salinity on stem death may be attributed to the effect of salinity on stem B concentrations.

As with stem death and dry weight accumulation, B accumulation in the stem depended on a three-way interaction between B, salinity, and rootstock (P < 0.01) (Tables 6 and 7). The relationship between treatment, stem B concentration, and stem death can be easily recognized by comparing Tables 2 and 7. The B concentrations in stems of the various rootstocks varied with treatment and correlated well with stem death (Table 5). Thus, under high salinity, rootstocks with the highest stem B concentrations ('Nemared', 'Lovell') typically had the highest percentage of stem death, while 'Myrobalan' and 'Bright’s Hybrid' had lower stem death and lower stem B concentrations (Tables 2 and 7). When B was supplied at its highest concentration, increasing salt level markedly decreased stem death at all species except 'Nemared' (Table 2). This decrease in stem death coincided with a salinity-induced decrease in stem B concentration (Table 2 vs. 7). During the experiment, the plum rootstock 'Myrobalan' exhibited remarkable tolerance to B and salinity (Table 2), which corresponded to the restricted accumulation of B in its stem (Table 7).

The relationship between stem B concentrations and stem death was also apparent in experiments with grafted plants. The effect of rootstock ('Bright’s Hybrid' and 'Nemared') on stem death and B accumulation is illustrated in Fig. 1. Plants grafted onto 'Bright’s Hybrid' rootstock suffered considerably less stem death under low salinity and high B and high salinity and high B than those grafted to 'Nemared'. This difference was most marked at the highest salinity and B combination (Fig. 1, top). Here again, increasing salinity decreased the toxic effects of B when 'Bright’s Hybrid' was used as the rootstock. The difference of stem death was due largely to the difference in B concentration in stem tissue of the scion that was as much as 75% less in plants grafted on.

**Table 4.** Total dry weight (roots, leaves, and stems (g/pot)) of six *Prunus* rootstocks grown under varying B and salinity treatments.

| B (mM) | Rootstock |
|--------|-----------|
| salt (dS·m⁻¹) | HY | LO | M | MA | NG | NR |
| 0.025/2 | 265 ± 23³ | 95 ± 4³ | 103 ± 6³ | 142 ± 22² | 166 ± 25 | 96 ± 10³ |
| 0.5/2   | 178 ± 17³ | 50 ± 5 | 87 ± 18³ | 98 ± 22 | 79 ± 11 | 89 ± 17 |
| 1/2     | 102 ± 6 | 33 ± 4 | 93 ± 25³ | 48 ± 5 | 26 ± 3 | 39 ± 2 |
| 0.025/6 | 253 ± 23³ | 96 ± 8 | 109 ± 19³ | 154 ± 11³ | 126 ± 16 | 81 ± 3³ |
| 0.5/6   | 240 ± 15³ | 62 ± 5 | 133 ± 5³ | 181 ± 27³ | 60 ± 17³ | 70 ± 8 |
| 1/6     | 141 ± 18 | 43 ± 8 | 106 ± 21 | 61 ± 6 | 35 ± 11 | 30 ± 6 |
| 0.025/12 | 193 ± 8³ | 52 ± 6 | 90 ± 11³ | 125 ± 17³ | 51 ± 7 | 61 ± 10 |
| 0.5/12  | 173 ± 3 | 63 ± 8 | 135 ± 39 | 109 ± 15 | 81 ± 12 | 70 ± 7 |
| 1/12    | 163 ± 10 | 29 ± 3 | 77 ± 5 | 54 ± 9 | 42 ± 2 | 20 ± 3 |

³HY = 'Bright’s Hybrid', LO = 'Lovell', M = 'Myrobalan', MA = 'Marianna', NG = 'Nemaguard', NR = 'Nemared'. Values are untransformed original means ± se.

³Only four to five observations, all others had six observations.
‘Bright’s Hybrid’ than in those grafted on ‘Nemared’ under 1 mM B and 12 dS·m⁻¹ salt (Fig. 1, bottom). This result indicated that the tolerance of a rootstock to B and salinity can influence the response of the scion.

**The effect of salinity and B on the accumulation of B in six Prunus rootstocks.** Accumulation of B in root tissue varied greatly and did not show any clear relationship between treatment and tissue concentration (data not shown). However, leaf B concentrations increased with increasing B in the growth medium in all rootstocks, which is typical in ‘Bright’s Hybrid’ (Fig. 2). Leaf B increased 50% to 80% and 100% to 150% over the control as B in the medium increased from 0.025 to 0.5 mM and 0.025 to 1.0 mM, respectively. There was no significant effect of salinity on leaf B concentration on any rootstock (Fig. 2). In all treatments and in all rootstocks except ‘Myrobalan’, tissue B concentrations were lower in leaves than in stems and did not differ consistently between rootstock and treatment. The much higher accumulation of B in stem than leaf tissue is a characteristic of Prunus rootstocks.

Compared with leaf B, stem B responded much more dramatically to changes in growth medium B, and significant interactions between rootstock, salinity, and B were evident. Stem B concentrations increased 100% to 300% and 200% to 1000% over the control as B increased from 0.025 to 0.5 mM and 0.025 to 1.0 mM, respectively (Table 7). Stem B levels in ‘Bright’s Hybrid’ ranged from 48 µg·g⁻¹ in the control to 558 µg·g⁻¹ at the highest B concentration in the medium. In all rootstocks except ‘Nemared’, increasing salinity significantly reduced B accumulation in stem tissues (Table 7). This effect was significant in ‘Bright’s Hybrid’, in which adding salt at 12 dS·m⁻¹ to the high B treatment reduced B accumulation by 80% (558 vs. 145 µg·g⁻¹). There was a strong negative correlation between B concentration in the stem and salt in the growth medium under high B for ‘Bright’s Hybrid’, ‘Myrobalan’, and ‘Nemaguard’ ($r = -0.888, -0.762, -0.781$, respectively).

**Effect of B and salinity on Na and SO₄ accumulation.** Regression analysis indicated that there was no significant correlation between B application and tissue Na levels. As such, we will only discuss the effect of salinity on tissue Na concentration at the low B treatments. Leaves contained the highest Na concentrations of all tissues, and leaf Na concentrations varied most significantly (and consistently) between rootstocks and treatments (Fig. 3). With the addition of salt, leaf Na concentrations increased dramatically in all rootstocks except ‘Marianna’, which had the lowest leaf Na concentrations. Highest concentrations of Na occurred in ‘Myrobalan’ followed by ‘Bright’s Hybrid’, ‘Nemared’, ‘Nemaguard’, and ‘Lovell’. Although leaf Na concentrations of up to 12000 µg·g⁻¹ dry weight (1.2%) were recorded in ‘Myrobalan’, the growth of this rootstock was not significantly affected by high salinity and leaves did not show symptoms of Na toxicity (data not shown).

In contrast to Na, a very significant correlation between B treatment and tissue SO₄ was observed and there were significant differences in SO₄ accumulation among rootstocks. Thus, SO₄ concentrations in leaves (and stems) decreased markedly in response to increasing B in the growth medium (Fig. 4 top vs. bottom). This correlation was marked in ‘Bright’s Hybrid’, in which, at the highest salt level, leaf SO₄ levels were reduced by 80% with the addition of 1.0 mM B (Fig. 4). Significant B-induced

| Variable | $R^2$ |
|----------|-------|
| Leaf     |       |
| B        | 0.0545|
| Na       | 0.0039|
| SO₄-S    | 0.0171|
| Stem     |       |
| B        | 0.4331***|
| Na       | 0.0006|
| SO₄-S    | 0.0003|

**Significant at $P < 0.001$. The forward selection of variables was in the following sequence: stem B, leaf B, stem SO₄-S, and leaf Na. For all other variables, $R^2$ was obtained from backward elimination.**

**Effect of B and salinity on Na and SO₄ accumulation.** Regression analysis indicated that there was no significant correlation between B application and tissue Na levels. As such, we will only discuss the effect of salinity on tissue Na concentration at the low B treatments. Leaves contained the highest Na concentrations of all tissues, and leaf Na concentrations varied most significantly (and consistently) between rootstocks and treatments (Fig. 3). With the addition of salt, leaf Na concentrations increased dramatically in all rootstocks except ‘Marianna’, which had the lowest leaf Na concentrations. Highest concentrations of Na occurred in ‘Myrobalan’ followed by ‘Bright’s Hybrid’, ‘Nemared’, ‘Nemaguard’, and ‘Lovell’. Although leaf Na concentrations of up to 12000 µg·g⁻¹ dry weight (1.2%) were recorded in ‘Myrobalan’, the growth of this rootstock was not significantly affected by high salinity and leaves did not show symptoms of Na toxicity (data not shown).

In contrast to Na, a very significant correlation between B treatment and tissue SO₄ was observed and there were significant differences in SO₄ accumulation among rootstocks. Thus, SO₄ concentrations in leaves (and stems) decreased markedly in response to increasing B in the growth medium (Fig. 4 top vs. bottom). This correlation was marked in ‘Bright’s Hybrid’, in which, at the highest salt level, leaf SO₄ levels were reduced by 80% with the addition of 1.0 mM B (Fig. 4). Significant B-induced

| Source     | df | Mean square | F value |
|------------|----|-------------|---------|
| B          | 2  | 3.60        | 253***  |
| Salinity (S)| 2  | 0.348       | 24.6**  |
| Rootstock (R)| 5  | 0.631       | 44.5**  |
| B × S      | 4  | 0.0787      | 5.6**   |
| B × R      | 10 | 0.0783      | 5.5**   |
| S × R      | 10 | 0.0548      | 3.9**   |
| B × S × R  | 20 | 0.0658      | 4.6**   |

**Significant at $P < 0.01$.**

Table 7. Stem B concentrations (µg·g⁻¹ dry weight) of six Prunus rootstocks grown under varying B and salinity treatments. Plots were exposed to treatments for 14 months.

| B (mM)¹/ | HY  | LO  | M   | MA  | NG  | NR  |
|----------|-----|-----|-----|-----|-----|-----|
| 0.025/2  | 48 ± 16² | 76 ± 18 | 45 ± 9 | 86 ± 14 | 62 ± 9 | 53 ± 10 |
| 0.5/2    | 152 ± 16² | 117 ± 14 | 69 ± 5  | 242 ± 44 | 182 ± 42 | 269 ± 75 |
| 1/2      | 558 ± 45² | 415 ± 115 | 126 ± 21 | 171 ± 41 | 312 ± 46 | 211 ± 22 |
| 0.025/6  | 136 ± 8³  | 68 ± 3  | 51 ± 4  | 54 ± 6  | 65 ± 8  | 83 ± 8  |
| 0.5/6    | 97 ± 6   | 157 ± 18 | 58 ± 14 | 97 ± 6  | 200 ± 12 | 134 ± 2  |
| 1/6      | 234 ± 7  | 277 ± 48 | 67 ± 8  | 127 ± 14 | 275 ± 33 | 268 ± 30 |
| 0.025/12 | 37 ± 6   | 90 ± 6  | 35 ± 1  | 48 ± 8  | 70 ± 8  | 60 ± 3  |
| 0.5/12   | 74 ± 12  | 137 ± 20 | 43 ± 7  | 77 ± 11 | 147 ± 26 | 91 ± 3  |
| 1/12     | 145 ± 44 | 253 ± 66 | 55 ± 4  | 197 ± 33 | 138 ± 39 | 416 ± 15 |

¹HY = ‘Bright’s Hybrid’, LO = ‘Lovell’, M = ‘Myrobalan’, MA = ‘Marianna’, NG = ‘Nemaguard’, NR = ‘Nemared’. Values are untransformed original means ± se.
²Duplicate observations, all others had three.
depression of leaf SO₄ concentrations was also observed in ‘Lovell’ and ‘Nemaguard’ rootstocks and probably also in ‘Nemared’ (Fig. 4). A negative correlation of \( r = -0.799, -0.940, \) and \(-0.672 \) for ‘Bright’s Hybrid’, ‘Lovell’, and ‘Nemaguard’, respectively, was observed.

**Discussion**

Research on the response of *Prunus* rootstocks to salinity or B toxicity and their interaction is important because, in many arid regions, high levels of B and salt coexist (Dhankhar and Dahiya, 1980). Results presented here indicate that B and salinity interact to influence the expression of toxicity symptoms, plant growth and survival, and tissue ion concentrations in *Prunus*. In *Prunus*, B toxicity symptoms are correlated with stem B concentrations. *Prunus* leaves do not exhibit B toxicity symptoms and leaf B concentrations are not closely correlated with stem.
reduce B accumulation in the scion and reduce the impact of high
B to excess B than ‘Lovell’ peach (Hansen, 1955).

He observed that almond (no cultivar specified) was more resistant
and ‘Shalil’ peach (Hansen, 1948), while in a second experiment
tolerant than either apricot (no cultivar specified) or ‘Marianna’
and ‘Myrobalan’ as more
classified almond (no cultivar specified) and ‘Myrobalan’ as more
tolerant than either apricot (no cultivar specified) or ‘Marianna’
and ‘Shalil’ peach (Hansen, 1948), while in a second experiment
he observed that almond (no cultivar specified) was more resistant
to excess B than ‘Lovell’ peach (Hansen, 1955).

Results of grafting experiments demonstrate that rootstock can
reduce B accumulation in the scion and reduce the impact of high
B. Significantly, the B-tolerant rootstocks (‘Bright’s Hybrid’ and
‘Myrobalan’) had reduced B concentrations in their shoots and
roots. Thus, differential tolerance to B is associated with an ability
to limit B uptake by the plant. Recent work by Nable and co-
workers (Nable, 1988; Nable et al., 1990; Paull et al., 1992) and
earlier work by Brown and Jones (1971) has shown that tolerance
to high B is associated with an exclusion of B from the plant and
not a differential distribution of B within the plant. Thus, using
rootstocks with reduced B uptake can help maintain tree produc-
tion in high-B soils.

In the experiments described here, we found no direct correla-
tion between tissue B and tissue Na or Cl and the expression of B
toxicity. Nevertheless, the presence of salt in the growth medium
reduced stem tissue B accumulation (and B toxicity) in all rootstocks
except ‘Nemared’. In addition, there was a strong negative corre-
rlation between stem B and stem SO4 concentrations. There was no
correlation between stem SO4 concentrations and plant growth.
Thus, saline growth conditions can influence B toxicity in Prunus.

We observed a strong negative correlation between B concentra-
tions in the stem and salt concentrations in the growth medium
under high B in some rootstocks. As we did not apply differential
SO4 (i.e., without Na) we cannot conclude that the salinity-induced
reduction in B accumulation was directly due to SO4. Nevertheless,
the lack of any clear relationship between B and tissue Na or Cl and
the significant negative correlation between tissue B and tissue
SO4 suggests that SO4 could be responsible for the salinity-induced
decline in tissue B. The reason for this interaction is unclear, and
we are not aware of any previous evidence for this interaction. Leaf
SO4 concentrations were strongly reduced by high levels of B in the
growth medium, further suggesting that there is a specific B × SO4
interaction in Prunus.

Recently, we have shown that B uptake is a passive process
(P.H. Brown and H. Hu, unpublished data) in which the uncharged
H2BO3 molecule (kPa 9.24) passes freely through the root plasma
membrane. In contrast, SO4 is taken up as a divalent anion and
must, therefore, involve active uptake (since there is a net negative
charge inside the plasma membrane). As a result, direct competi-
tion for uptake with the passively assimilated, noncharged B is
unlikely. Given the large differences in B compared to SO4
concentrations in the growth medium, it is also unlikely that B is
competitively inhibiting SO4 uptake at the root surface. The
mechanism of this B × SO4 interaction remains unknown.

Prunus rootstocks differ significantly in their tolerance of
salinity and B, and using a tolerant rootstock can restrict B
accumulation in the grafted scion. Prunus also seems to be unique
in its expression of B toxicity and the accumulation of B in stems,
a result suggesting that stem tissue is the best indicator of B
toxicity. The strong negative correlation between B and SO4
observed in Prunus cannot be explained by our current understand-
ing of B plants. It is not known if this interaction is observed in
other species. Identifying Prunus rootstocks tolerant of high B and
salinity and recognizing the symptoms of B toxicity will help
manage almond production in arid and semi-arid regions.

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