Mineral Composition of Young Rabbiteye and Southern Highbush Blueberry Exposed to Salinity and Supplemental Calcium

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Abstract. ‘Tifblue’ and ‘Brightwell’ rabbiteye blueberry (*Vaccinium ashei* Reade) and ‘Sharpblue’ southern highbush blueberry (primarily *V. corymbosum*) were treated with 0, 25, and 100 mM Na⁺ as Na₂SO₄ or NaCl, and 0, 1, 3, and 10 mM supplemental Ca²⁺ in sand culture in the greenhouse. For rabbiteye plants salinized with Na₂SO₄, leaf Na⁺ concentrations increased 54-fold and the percentage of total plant Na⁺ found in the leaves increased from 9% to 63% with increasing external Na⁺. Calcium supplementation reduced the Na⁺ concentrations in leaves by up to 20%. Leaf Ca²⁺ concentrations increased with Ca²⁺ supplementation, but accounted for a decreasing percentage of the total Ca²⁺ found in the plant, since root Ca²⁺ concentrations were much higher. Root Na⁺ concentrations increased with increasing Na⁺ treatments to a smaller extent than in the leaves and were also reduced by Ca²⁺ supplements. Potassium concentrations in leaves and roots decreased with increasing Na⁺ treatment levels, particularly in roots, where K⁺ concentration was about half at 100 mM Na⁺ (as Na₂SO₄). Leaf Na⁺ concentrations were up to two times greater when Na⁺ was supplied as NaCl compared to Na₂SO₄. For plants salinized with NaCl, leaf Na⁺ levels increased to 1.1% and did not decrease when supplemental Ca²⁺ was applied. Leaf Cl⁻ concentrations also increased greatly with NaCl, reaching >1.0% (dry weight basis). Root Cl⁻ concentrations also increased with increasing salinity and were not affected by Ca²⁺ supplements. Ca²⁺ supplementation led only to a greater Ca²⁺ concentration in leaves and roots, but this did not alter Na⁺ concentrations. Nutrient concentrations in ‘Sharpblue’ leaves, stems, and roots were greater than those of the rabbiteye cultivars, but were influenced by salinity and Ca²⁺ in essentially the same way. Excess Na⁺, Cl⁻, or both, together with lowered K⁺, were likely the cause of extensive leaf necrosis and may be indicative of a lack of a mechanism to control Na⁺ influx into blueberry leaves.

Rabbiteye and southern highbush blueberries require optimum-quality water to thrive and produce. Water pH levels >7.0, total bicarbonates (HCO₃⁻) >1.5 mM, total Na⁺ >2.0 mM, and total Cl⁻ >4.0 mM indicate poor-quality water (Haby and Pennington, 1988). While the nutrient composition of rain and surface water seldom exceeds these thresholds, it is often inadequate during midsummer and early fall, when irrigation demands are high. Lower-quality groundwater, which sometimes exceeds the thresholds, must then be used. Groundwater in eastern Texas may contain NaCl or NaHCO₃ salts or both, and often exceeds 15 mM Na⁺, 6 mM Cl⁻, and 10 mM NaHCO₃ (Texas Department of Health, 1990).

The most damaging effects of saline water on rabbiteye blueberry growth are reported to be due to high concentrations of Na⁺ rather than HCO₃⁻ (Haby et al., 1986). Fresh weight gain of potted plants irrigated with well water containing 7.83 mM Na⁺ was only

65% of the gain of plants irrigated with surface water (Haby et al., 1986). Similarly, Bush et al. (1990) compared field-grown plants treated with pond and saline well water. After 5 months, 39% of the plants irrigated with well water died, and, after 12 months, the mortality rate was 60%. None of the plants irrigated with pond water died. Wright et al. (1992) found that 100 mM Na⁺ reduced growth of ‘Tifblue’ rabbiteye shoots and roots by 62% and 57%, respectively, compared to unsalinized controls. Growth of southern highbush blueberries was more severely affected by salinity. Additionally, saline water treatment reduced gas exchange of rabbiteye and southern highbush blueberries, and high concentrations of Cl⁻ also seemed to damage the photosynthetic mechanism of blueberries (Wright et al., 1993).

Supplemental Ca²⁺ improves growth of many species exposed to salt stress. LaHaye and Epstein (1969) showed that adequate Ca²⁺ was a requirement for shoot and root growth in salt-stressed bean (*Phaseolus vulgaris* L.) plants. Similar results have been reported in shoots, roots, or both of maize (*Zea mays*) (Cramer et al., 1988; Maas and Grieve, 1987) and citrus (Ben-Hayyim et al., 1987; Bañuls et al., 1991). Additional Ca²⁺ seems to exclude Na⁺ from roots and leaves (Marschner, 1986). Although blueberries are calcifuges, plants that have low leaf Ca²⁺ concentration and thrive in soils low in Ca²⁺, we found that low concentrations of Ca²⁺ ameliorated the Na⁺ effects on growth and gas exchange of blueberry plants when exposed to Na₂SO₄ and, to a lesser extent, NaCl (Wright et al., 1992, 1993).

The aim of this study was to determine the effect of a range of concentrations of Na₂SO₄ and NaCl, with and without supplemen-

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tal Ca^{2+} , on the ionic relations of salt-stressed rabbiteye and southern highbush blueberries. Sodium sulfate was applied to provide insight into the specific effect of Na^+ , since SO_4^{2-} is absorbed slowly by plants (Marschner, 1986) and does not reduce blueberry growth (Spiers and Braswell, 1992). Salinization with NaCl was an alternative treatment to Na_2SO_4 and was designed to help understand the additional effect of Cl^- on nutrient content of blueberry plants.

Materials and Methods

Na_2SO_4 experiment. Dormant 1-year-old 'Tifblue' and 'Brightwell' rabbiteye blueberries were potted in sand in the greenhouse on 15 Mar. 1988. Watering was by drip irrigation. Details of potting method and pretreatment irrigation were reported by Wright et al. (1992).

Treatments on 144 plants began on 15 May 1988 and consisted of 0, 25, and 100 mM Na^+ (0, 12.5, and 50 mM Na_2SO_4) and 0, 1, 3, and 10 mM Ca^{2+} applied with the remaining essential elements in the nutrient solution. Calcium and Na^+ levels were crossed, forming 12 total treatments. Because of only moderate solubility of CaSO_4 , only 70% of each Ca^{2+} treatment was CaSO_4 ; the remainder was made up of 20% $\text{Ca}(\text{NO}_3)_2$ and 10% CaCl_2 . All treatments contained equimolar amounts of NO_3^- , NH_4^+ , and K^+ . Plants received ≈ 400 or 500 ml solution daily, and sufficient nutrient solution was applied so that some solution leached from the containers. Solution pH and electrical conductivity (EC) (corrected to 25°C) were recorded when solutions were prepared and each time they were replenished. These values, along with solution composition and sodium adsorption ratio (SAR), are reported in Table 1.

Plants were destructively sampled on 30 July 1988 after 76 days of treatment. Leaves and stems were separated from the roots, and roots were washed with distilled water to remove sand particles, then were blotted dry. Leaves, stems, and roots were dried at 60°C for 48 h and ground to pass through a 1-mm sieve. Samples were digested using a procedure developed by Parkinson and Allen (1975). Nitrogen was analyzed colorimetrically using an autoanalyzer (Technicon Instruments Corp., Tarrytown, N.Y.). Sodium, Ca^{2+} , and K^+ were analyzed using an inductively coupled plasma spectrophotometer (Allied Research Laboratories, Sunland, Calif.).

NaCl experiment. Dormant, 1-year-old, bare-root 'Tifblue' and 'Brightwell' rabbiteye blueberries and 'Sharpblue' southern highbush blueberries were planted on 15 Mar. 1989. The rabbiteye blueberries were handled in the same manner as in 1988, while the 'Sharpblue' plants were transplanted into sterilized 2750-ml pots containing sand and lined with fiberglass insulation (to prevent loss of media). 'Sharpblue' plants were pruned to a height of 20 cm. The irrigation regime was the same as that for 1988.

Plants were maintained with the complete nutrient solution until 15 May 1989, when treatments commenced. All plants except controls received NaCl, but otherwise the compositions of the 12 nutrient solutions were the same as those of 1988 (Table 1). Solution pH and EC were again measured when the solutions were made and replenished. 'Sharpblue' plants were only treated with those solutions containing 0 and 10 mM Ca^{2+} because sufficient plants were not available to test all Ca^{2+} levels. Plants were destructively sampled on 17 July 1989 after 63 days of treatment. Sampling and analysis protocols were the same as those of the Na_2SO_4 experiment. Chloride was measured in addition to the other nutrients mentioned above and was extracted from ground tissue using a hot water extraction method (Ghosh and Drew, 1991), then analyzed coulombimetrically with a chloridometer (Haake Buchler Instruments, Saddle Brook, N.J.).

The experimental design for both sand culture experiments was a randomized complete block. Experiments involving 'Tifblue' and 'Brightwell' were $4(\text{Ca}^{2+} \text{ levels}) \times 3(\text{Na}^+ \text{ levels}) \times 2(\text{cultivars})$ factorials with 6 replications, for a total of 144 plants. The experiment involving 'Sharpblue' was a 2×3 factorial with 4 replications, for a total of 24 plants. Data were analyzed using SAS' General Linear Model procedure (PROC GLM; SAS Institute, Cary, N.C.).

Results

Each cultivar responded differently to salinization with Na_2SO_4 and NaCl, so data could not be averaged. The main effects of salinity and Ca^{2+} supplementation on nutrient concentration and distribution (as a percentage of total plant nutrient content) are described below and some interactions between salt concentration and Ca^{2+} are given graphically. Leaf N averaged 1.5% and was not influenced by Ca^{2+} or Na^+ treatments (data not shown).

Na_2SO_4 experiment: nutrient concentration of leaves. In gen-

Table 1. Mineral composition, sodium adsorption ratio (SAR), pH, and electrical conductivity (EC) of nutrient solutions.^z

Total Na^{x+}	Total Ca^{2+}	Mineral composition (mM)						SAR	pH ^y		EC (dS·m ⁻¹)	
		CaSO_4	$\text{Ca}(\text{NO}_3)_2$	CaCl_2	KNO_3	$(\text{NH}_4)_2\text{SO}_4$	K_2SO_4		Na_2SO_4	NaCl	Na_2SO_4	NaCl
0	0	0.0	0.0	0.0	4.0	4.0	0.0	0.0	6.1	5.4	1.22	1.18
0	1	0.7	0.2	0.1	3.6	4.0	0.4	0.0	5.4	5.3	1.30	1.38
0	3	2.1	0.6	0.3	2.8	4.0	1.2	0.0	5.2	5.0	1.62	1.81
0	10	7.0	2.0	1.0	0.0	4.0	4.0	0.0	5.1	5.1	2.37	2.49
25	0	0.0	0.0	0.0	4.0	4.0	0.0	31.0	5.5	6.4	3.23	3.80
25	1	0.7	0.2	0.1	3.6	4.0	0.4	19.4	5.6	5.0	3.34	3.75
25	3	2.1	0.6	0.3	2.8	4.0	1.2	13.0	6.1	5.1	3.72	3.80
25	10	7.0	2.0	1.0	0.0	4.0	4.0	7.6	6.0	4.9	4.00	4.53
100	0	0.0	0.0	0.0	4.0	4.0	0.0	124.0	6.7	5.3	8.87	8.80
100	1	0.7	0.2	0.1	3.6	4.0	0.4	77.8	6.0	5.4	8.08	9.35
100	3	2.1	0.6	0.3	2.8	4.0	1.2	52.3	6.2	5.0	8.92	9.55
100	10	7.0	2.0	1.0	0.0	4.0	4.0	30.6	5.9	5.1	8.72	8.48

^zAdditionally, solutions contained 0.1 mM KH_2PO_4 , 0.65 mM MgSO_4 , 0.125 mM $\text{FeNa}(\text{O}_2\text{CCH}_2)_2\text{NCH}_2\text{CH}_2\text{N}(\text{CH}_2\text{CO}_2)_2$, 10.9 μM MnSO_4 , 1.2 μM H_3BO_3 , 0.2 μM CuSO_4 , 0.076 μM ZnSO_4 , and 15 μM $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$.

^ypH and EC values are means of at least three replications.

^xTotal Na^+ as Na_2SO_4 or NaCl.

eral, there was a significant influence of Na^+ , Ca^{2+} , and the $\text{Na}^+ \times \text{Ca}^{2+}$ interaction on 'Tifblue' leaf mineral concentration and nutrient ratios (Table 2). There was an 54-fold linear increase in leaf Na^+ when Na^+ in the external solution increased from 0 to 100 mM. These increases in leaf Na^+ were diminished when Ca^{2+} was applied (Fig. 1). At 25 mM Na^+ , plants receiving supplemental Ca^{2+} had lower leaf Na^+ concentrations. At 100 mM Na^+ , plants that received 1 mM Ca^{2+} had $\approx 20\%$ lower Na^+ concentration.

The percentage of total plant Na^+ found in the leaves increased as Na^+ concentration in the external solution increased [Fig. 1 (inset), Table 3]. For those plants subjected to 100 mM Na^+ , the percentage of Na^+ found in leaves also increased with increasing Ca^{2+} concentration in the external solution. The percentage of total plant Na^+ found in the leaves of plants salinized with 100 mM Na^+ but no additional Ca^{2+} was $\approx 50\%$, while 70% of the Na^+ was found in leaves of plants given 3 or 10 mM Ca^{2+} .

'Tifblue' leaf Ca^{2+} concentrations decreased slightly as Na^+ levels in the nutrient solution increased (Fig. 2). For unsalinized plants or for those given 25 mM Na^+ , any level of Ca^{2+} supplementation led to higher leaf Ca^{2+} levels, but for plants given 100 mM Na^+ , only 10 mM Ca^{2+} led to the greatest leaf Ca^{2+} concentrations.

The percentage of total plant Ca^{2+} found in the leaves did not vary with Na_2SO_4 (36% to 39%), but it decreased as Ca^{2+} concentration in the external solution increased (Table 3). For plants supplied with 10 mM Ca^{2+} , the percentage of total plant Ca^{2+} found in the leaves was less than half that of plants supplied with lesser amounts of Ca^{2+} . Thus, while leaf Ca^{2+} concentrations increased with increasing Ca^{2+} treatment levels (Table 2), these levels accounted for a decreasing percentage of the total Ca^{2+} in the plant, a result indicating that a greater percentage of the Ca^{2+} remained in the root.

Leaf K^+ concentrations generally decreased with increasing Na^+ . No clear effects of Ca^{2+} addition on leaf K^+ concentration were apparent with unsalinized plants (Fig. 3). Leaf K^+ concentrations decreased in salinized plants supplied with Ca^{2+} . The percentage of total plant K^+ found in the leaf was $\approx 50\%$ and did not vary significantly with Na^+ or Ca^{2+} treatment (Table 3).

Nutrient concentration of stems. The concentrations of Na^+ and Ca^{2+} in 'Tifblue' stems were less than in leaves, but, as with leaves, stem Na^+ concentrations increased with increasing Na^+ concentrations (Table 2), and showed small reductions (up to 23%) after Ca^{2+} addition (data not shown). The percentage Na^+ found in stems was

less than in the corresponding leaves (Table 3) and ranged from 6% to 12% of the total.

Stem Ca^{2+} increased as Ca^{2+} concentration in the external solutions increased and declined as salinization increased. Because the dry weight of stems was less than the weight of leaves (Wright et al., 1992), the stem Ca^{2+} represented a lesser percentage of total Ca^{2+} found in the plant. Stem K^+ concentrations declined with increasing Na^+ (Table 4) and were not affected by Ca^{2+} treatments.

Nutrient concentration of roots. Root Na^+ concentrations increased only 2-fold with increasing Na_2SO_4 treatments (Table 2), relative to the 50-fold increase in leaf Na^+ over the same treatment range (Table 2). Root Na^+ concentrations of plants receiving 100 mM Na^+ were about one-third less than Na^+ concentrations in leaves of the same plants. Additionally, a smaller percentage of total plant Na^+ was found in the roots of these plants (Table 3) compared to the leaves, despite the greater dry mass of the roots (Wright et al.,

Fig. 1 Leaf Na^+ concentration and percentage of Na^+ found in the leaves (inset) of 'Tifblue' rabbiteye blueberry exposed to Na_2SO_4 and supplemental Ca^{2+} . Vertical bars indicate SE.

Table 2. Influence of Na_2SO_4 and Ca^{2+} treatments on leaf, stem, and root mineral nutrient concentration ($\mu\text{g}\cdot\text{g}^{-1}$ dry weight) of 'Tifblue' rabbiteye blueberry plants.

Treatment (mM)	Na^+			Ca^{2+}			K^+		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Ca^{2+}									
0	3122	948	4218	940	795	957	7066	5260	4430
1	2621	800	3410	1356	1307	1645	5682	5607	5108
3	3355	846	3137	1408	1388	2273	5583	5667	5346
10	2849	735	2359	1575	1543	15694	6261	5787	4448
	**	L**	L**	L**	L**	L**	Q**	NS	Q**
Na^+ (Na_2SO_4)									
0	119	144	2144	1502	1377	7622	7158	6573	6099
25	2072	885	3027	1353	1282	6106	5838	5611	4902
100	6467	1042	4482	1143	1151	2874	5532	4662	3578
	L**	L**	L**	L**	L**	L**	L**	L**	L**
Interaction									
$\text{Ca}^{2+} \times \text{Na}_2\text{SO}_4$	**	**	NS	**	**	NS	**	NS	**

NS, ** Nonsignificant or significant at $P \leq 0.01$, respectively; L = linear, Q = quadratic.

Table 3. Influence of Na_2SO_4 and Ca^{2+} treatments on Na^+ , Ca^{2+} , and K^+ distribution (percentage of total) to leaves, stems, and roots of 'Tifblue' rabbiteye blueberry plants.

Treatment (mM)	Na^+			Ca^{2+}			K^+		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Ca^{2+}									
0	35	9	56	44	26	30	53	26	21
1	41	9	50	46	25	29	49	28	23
3	45	9	47	43	25	32	49	28	23
10	43	10	47	19	11	70	50	29	21
	**	NS	**	**	**	**	NS	NS	NS
Na^+ (Na_2SO_4)									
0	9	6	84	36	18	47	50	26	24
25	48	12	40	39	22	39	49	28	23
100	63	9	27	39	26	36	50	28	19
	**	**	**	NS	**	**	NS	*	**
Interaction									
$\text{Ca}^{2+} \times \text{Na}_2\text{SO}_4$	**	**	NS	NS	NS	NS	NS	NS	NS

NS, *, ** Nonsignificant or significant at $P \leq 0.05$ or 0.01 , respectively.

Fig. 2. Leaf Ca^{2+} concentration of 'Tifblue' rabbiteye blueberry exposed to Na_2SO_4 and supplemental Ca^{2+} . Vertical bars indicate SE.

Fig. 3. Leaf K^+ concentration of 'Tifblue' rabbiteye blueberry exposed to Na_2SO_4 and supplemental Ca^{2+} . Vertical bars indicate SE.

1992). Sodium concentrations and the percentage of total plant Na^+ found in the roots decreased with increasing Ca^{2+} treatment levels. This contrasts with the increased percentage of Na^+ found in leaves of plants treated with Ca^{2+} .

Calcium concentration and percentage of total plant Ca^{2+} in the roots of salinized plants decreased with increasing Na^+ treatment. Root Ca^{2+} concentration and percentage of total plant Ca^{2+} found in roots increased with added Ca^{2+} (Tables 2 and 3). For plants subjected to 3 and 10 mM Ca^{2+} , root Ca^{2+} concentration was up to 10 times greater than in the leaves (Table 2). This increase coincided with the decreased Ca^{2+} found in the leaves.

Potassium concentrations and percentage of total plant K^+ in roots were less than K^+ concentrations in 'Tifblue' leaves and stems, and both declined with increasing external Na_2SO_4 (Fig. 3, Table 3). Three mM Ca^{2+} treatments led to the greatest root K^+ concentrations, but Ca^{2+} treatments had no effect on the percentage of total plant K^+ found in the roots (Table 3).

Varietal differences in mineral nutrient concentration. Effects of Na_2SO_4 and Ca^{2+} on leaf and stem mineral nutrient concentra-

tions of 'Brightwell' plants were usually similar to the effects on 'Tifblue' leaves and stems (data not presented). However, leaf Na^+ of 'Brightwell' supplied with 100 mM Na^+ was $\approx 30\%$ higher than in 'Tifblue'. Similarly, the leaf Ca^{2+} concentration of 'Brightwell' was usually greater than that of 'Tifblue', but the interaction effect was similar.

The effects of Na_2SO_4 and Ca^{2+} treatments on 'Brightwell' root element concentrations were also comparable to the effects on 'Tifblue' (data not presented), but root Ca^{2+} concentrations in 'Brightwell' were less than in 'Tifblue', while root Na^+ was greater. Root K^+ concentrations in both cultivars were similar. Distribution of Na^+ , Ca^{2+} , and K^+ to leaves, shoots, and roots (%) of 'Brightwell' plants was similar to their distribution in 'Tifblue'.

NaCl experiment: nutrient concentration of leaves. Increasing NaCl concentrations in the nutrient solution led to increases in 'Tifblue' leaf Na^+ and Cl^- concentrations and decreases in leaf Ca^{2+} and K^+ (Table 4). These trends are comparable to the effects of Na_2SO_4 salinity on 'Tifblue'. However, leaf Na^+ concentrations of plants given 25 and 100 mM were nearly twice that of 'Tifblue'

Table 4. Influence of NaCl and Ca²⁺ treatments on leaf, stem, and root mineral nutrient concentration (µg·g⁻¹ dry weight) of ‘Tifblue’ rabbiteye blueberry plants.

Treatment (mM)	Na ⁺			Cl ⁻			Ca ²⁺			K ⁺		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Ca ²⁺												
0	5307	1401	3940	5339	2546	2915	1519	1426	1449	7139	5538	5047
1	4628	1283	3390	3771	1886	2936	1576	1395	1948	6595	5722	5457
3	5457	1561	3486	6349	2234	3101	1705	1656	2976	6698	5949	5101
10	5844	1270	3145	6227	2217	3130	2001	1893	8791	6789	5437	5364
	NS	NS	NS	NS	NS	NS	L**	L**	L**	NS	NS	NS
Na ⁺ (NaCl)												
0	669	478	2015	917	928	1679	1864	1606	5541	7276	6395	6504
25	4234	1497	3702	2990	2452	3607	1644	1574	3620	6251	5457	5039
100	10979	2166	5019	12252	3340	3799	1592	1595	1985	6865	5123	3950
	L**	L**	L**	L**	L**	L**	L**	NS	L*	Q**	L**	L**
Interaction												
Ca ²⁺ × NaCl	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS, *, ** Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively; L = linear, Q = quadratic.

plants given equivalent levels of Na⁺ as Na₂SO₄. Leaves of these plants contained >50% of the total Na⁺ (Table 5), which was more than twice the percentage of total plant Na⁺ found in the leaves of unsalinized plants. Leaf Cl⁻ concentrations of plants given 100 mM NaCl were >1.2% (dry weight basis.). Leaf Ca²⁺ concentrations decreased linearly with increasing Na⁺. The percentage of total plant Ca²⁺ found in the leaves also declined in response to Na⁺ treatments as did the percentage of total plant K⁺. Supplemental Ca²⁺ treatments did not alter leaf nutrient Na⁺ or Cl⁻ concentrations, but led to increased leaf Ca²⁺ concentrations.

Nutrient concentration of stems. ‘Tifblue’ stem Na⁺ and Cl⁻ concentrations also increased with increasing Na⁺ in the external solution, but, in salinized plants, these concentrations were 60% to 70% less than in the leaves. Stem Na⁺ concentrations were not influenced by Ca²⁺ treatments. The percentage of total plant Na⁺ found in the stems was not influenced by Na⁺ or Ca²⁺ treatments (Table 5) and was ≈16%. ‘Tifblue’ stem Ca²⁺ level increased linearly with increasing Ca²⁺ in the external solution, but Ca²⁺ addition had no other effect on any other nutrients. Stem K⁺ concentration decreased in response to increasing NaCl in the irrigation solution.

Nutrient concentration of roots. Root Na⁺ and Cl⁻ concentrations increased with increasing Na⁺ treatments (Table 4) and were not affected by Ca²⁺ treatments. Root Na⁺ and Cl⁻ concentrations were less than one-half of the corresponding leaf Na⁺ and Cl⁻ concentrations when 100 mM NaCl was applied, a result suggesting that when salinity levels are high, both ions are preferentially transported to the leaves. Root Ca²⁺ concentration decreased with increasing Na⁺ treatments, but increased with increasing Ca²⁺ treatments. In plants supplied with 10 mM Ca²⁺, root Ca²⁺ concentration was more than four times the Ca²⁺ concentration of the leaves. This accumulation of Ca²⁺ in the roots is similar to the Ca²⁺ accumulation found in roots of plants treated with Na₂SO₄. Root K⁺ also decreased with increasing Na⁺ in the irrigation solution. Total plant Na⁺ in the roots decreased as Na⁺ treatment concentrations increased (Table 5) and was not affected by Ca²⁺ treatments, but roots contained an increasing percentage of total plant Ca²⁺ with increasing Ca²⁺ treatments. Sodium and Ca²⁺ treatments did not affect the distribution of K⁺ throughout the plants.

Varietal differences in mineral nutrient concentration. Effects of increasing NaCl salinity on leaf, stem, and root element concentrations were similar to that of ‘Tifblue’, except that Na⁺ and Cl⁻ concentrations were less in ‘Brightwell’ than in ‘Tifblue’. Chloride concentrations of ‘Brightwell’ leaves and roots were only 55%

and 32%, respectively, of the concentrations found in ‘Tifblue’. ‘Brightwell’ leaf and root Ca²⁺ increased with increasing Ca²⁺ in the solutions (data not presented). There were no other responses to Ca²⁺ addition. Percentage distribution of Na⁺, Ca²⁺, and K⁺ in ‘Brightwell’ plants was similar to that of ‘Tifblue’, except that ‘Brightwell’ plants seemed to contain more Na⁺ in the roots than in the leaves and stems.

‘Sharpblue’ leaf Na⁺ concentrations increased as solution Na⁺ increased (Table 6). Medium (25 mM) and high (100 mM) Na⁺ treatment levels increased ‘Sharpblue’ leaf Na⁺ to 0.8% and 2.3%, respectively. Corresponding leaf Cl⁻ concentrations were 0.2 and 1.5% (dry weight basis.) Extensive leaf necrosis was the result of these extremely high leaf Na⁺ and Cl⁻ concentrations. Percentage of total plant Na⁺ found in the leaves increased from 37% to 57% as Na⁺ concentrations in the irrigation solution increased from 0 to 100 mM (data not presented). Calcium treatments did not affect the percentage of Na⁺ found in the leaves.

‘Sharpblue’ leaf Ca²⁺ concentrations were not affected by Na⁺ treatments, but were greater in plants treated with 10 mM Ca²⁺ than in plants not supplied with Ca²⁺. Nonetheless, the percentage of total plant Ca²⁺ found in the leaves declined with increasing Ca²⁺ treatments (data not presented), a result indicating a greater accumulation of Ca²⁺ in the stems and roots when 10 mM Ca²⁺ was applied. Percentage of total plant Ca²⁺ in the leaves was not affected by Na⁺ treatments. Potassium concentrations in the leaf declined with increasing Na⁺ and Ca²⁺ treatments (Table 6).

Stem and root nutrient concentrations of ‘Sharpblue’ were usually less than leaf nutrient concentrations. Stem Na⁺ and Cl⁻ concentrations were greatest at 100 mM NaCl. Root K⁺ and Ca²⁺ decreased with additional NaCl, while root Na⁺ and Cl⁻ increased. However, the root Na⁺ and Cl⁻ concentrations were only 33% and 25%, respectively, of the Na⁺ and Cl⁻ concentration in the leaves. High (10 mM) Ca²⁺ treatment led to increased Ca²⁺ in the stem, compared to controls.

Discussion

Most crop species that can be characterized as glycophytes avoid salinity damage by salt exclusion (Greenway and Munns, 1980). At low salt concentrations, Na⁺ is excluded from the leaves by roots that actively pump Na⁺ out of cells into the external medium. Xylem parenchyma cells in the basal (older) zones of the

Table 5. Influence of NaCl and Ca²⁺ treatments on Na⁺, Ca²⁺, and K⁺ distribution (percentage of total) to leaves, stems, and roots of ‘Tifblue’ rabbiteye blueberry plants.

Treatment (mM)	Na ⁺			Ca ²⁺			K ⁺		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Ca ²⁺									
0	42	16	42	39	36	26	44	34	22
1	44	17	39	39	32	29	44	35	22
3	43	17	40	34	29	37	43	34	23
10	48	15	37	25	24	52	42	33	25
	NS	NS	NS	**	**	**	NS	NS	NS
Na ⁺ (NaCl)									
0	25	17	59	37	25	38	45	31	24
25	53	16	31	35	28	37	45	32	23
100	55	16	28	30	38	33	40	39	21
	**	NS	**	**	**	NS	**	**	NS
Interaction									
Ca ²⁺ × NaCl	NS	NS	NS	**	NS	**	NS	NS	NS

NS, **Nonsignificant or significant at $P \leq 0.01$, respectively.

Table 6. Influence of NaCl and Ca²⁺ treatments on leaf mineral nutrient concentration ($\mu\text{g}\cdot\text{g}^{-1}$ dry weight) of ‘Sharpblue’ southern highbush blueberry plants.

Treatment (mM)	Na ⁺			Cl ⁻			Ca ²⁺			K ⁺		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Ca ²⁺												
0	10966	4535	7214	5375	1572	3596	2739	2442	2645	10625	5229	7275
10	10848	6081	6509	7359	2229	4044	4025	3983	9548	9744	5079	7014
	NS	NS	NS	NS	NS	NS	**	**	**	*	NS	NS
Na ⁺ (NaCl)												
0	1460	1088	2657	1282	609	2884	3721	3236	8117	13226	6811	9233
25	8244	4990	9582	2173	1264	4228	2726	2220	5774	9186	4959	7893
100	23017	9847	8346	15646	3830	4349	3698	4151	4398	8143	3691	4308
	L**	L**	L**	L**	L**	L**	NS	Q**	L*	L**	L**	L**
Interaction												
Ca ²⁺ × NaCl	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively; L = linear, Q = quadratic.

roots also accumulate Na⁺ in the vacuole, thereby removing Na⁺ from the xylem sap.

Sodium exclusion is an energy-dependent process, which, in some species, seems to be limited when external salt concentrations are high (Drew and Dikunwin, 1985). Ion transport processes at the plasmalemma can be inhibited in the presence of excess salt. Chung and Matsumoto (1989) found that K⁺–Mg²⁺ ATPase activity in the roots of cucumber exposed to 200 mM NaCl were always less than activities of control plants. Additionally, Van Steveninck et al. (1982) proposed that the inability of *Lupinus luteus* to restrict Na⁺ transport to leaves was because of an inability to sequester Na⁺ in the vacuoles of root cortical cells. Their research was supported by more recent work of Maathius and Prins (1990), who demonstrated that NaCl decreased the open probability of voltage- and Ca²⁺-dependent tonoplast channels in salt-sensitive plantago species.

When these exclusion systems are ineffective or fail due to high salinity, Na⁺ concentrations in the leaves can rise dramatically. Evidence of exclusion failure has been documented in pistachio (*Pistacia vera*), in which root Na⁺ concentrations were five times greater than leaf concentrations until soil solution Na⁺ surpassed 125 mM (Picchioni et al., 1990), and in bean (*P. vulgaris*), in which Na⁺ concentration of leaves gradually increased as external Na⁺ increased (Jacoby, 1964). In highbush blueberry (*Vaccinium*

corymbosum cv. Bluecrop) leaf Na⁺ concentrations gradually increased to a maximum of 5.4 mg·g⁻¹ in plants grown in 50 mM NaCl, a leaf concentration nearly twice that found in the roots (Muralitharan et al., 1992). In the present study with rabbiteye and southern highbush blueberries, leaf Na⁺ concentrations of rabbiteye plants provided with 100 mM NaCl increased to ≈10.9 mg·g⁻¹, and Na⁺ seemed to be accumulated in the leaves, because leaf Na⁺ concentration was also twice that of the roots (Table 4). Since the percentage of total plant Na⁺ found in the leaves also increased (to a maximum of 50% to 70%) with increasing Na⁺ treatment levels (Table 5), it can be concluded that Na⁺ exclusion failed. The accumulation becomes inevitable when transpiration draws salts up the xylem into the leaves in the absence of salt glands.

Similar differences between leaf and root Na⁺ concentrations occurred in rabbiteye plants provided 100 mM Na⁺ as Na₂SO₄, but there was little difference between leaf and root Na⁺ concentrations of rabbiteye plants given 25 mM Na⁺. High salt treatments led to leaf and root necrosis and reduced shoot growth and caused stunting and abnormal branching of roots (Wright et al., 1992). Thus, while our data partially support the findings of Spiers (1983), who concluded that rabbiteye blueberries lack a mechanism to restrict Na⁺ uptake to shoots, there is the possibility that such a mechanism exists, but is rendered ineffective at high external Na⁺ concentrations and may play a greater role at lower Na⁺ concentra-

tions such as the 25 mM concentration used in this study.

Our previous work suggests that salt damage to rabbiteye blueberries is more extensive with NaCl than with Na_2SO_4 (Wright et al., 1992, 1993). Data collected here showed that root and leaf Na^+ concentrations of plants subjected to Na_2SO_4 were often lower than Na^+ concentrations of plants subjected to NaCl salinity (Tables 2 and 4). These differences were not due to increased transpiration, because Na_2SO_4 -salinized plants transpired more than NaCl-salinized plants (Wright et al., 1993). 'Bluecrop' highbush blueberry exposed to Na_2SO_4 and NaCl showed similar differences in transpiration (Muralitharan et al., 1992). Manchanda and Sharma (1989) also found that, at higher salinity, the Na^+ concentration in chickpea shoots was greater in Cl^- -dominated than in SO_4^{2-} -dominated salinity. In contrast, Boursier and Luchli (1990) found that Na^+ concentrations in the leaf blade of sorghum was greater with Na_2SO_4 than with NaCl-treated plants. They suggest that the difference is because the accumulation of Na^+ in the vacuoles of root cells is limited by the relatively slower uptake of SO_4^{2-} into those vacuoles compared to Cl^- uptake. Differences in transport rate across the tonoplast and plasma membrane are likely to be determined in part by the presence of suitable co-ions (Marschner, 1986) and also by plant species.

Exclusion of Cl^- from blueberry leaves was no more effective than for Na^+ at high external NaCl. Leaf Cl^- concentrations were at least three times greater than root Cl^- concentrations after 63 days of treatment. Such high leaf Cl^- concentrations emphasize the possibility that Cl^- and Na^+ may both be damaging to growth and gas exchange of blueberries. Chloride is known to be damaging to bean (Lessani and Marschner, 1978) and a number of fruit species (Brown et al., 1958; Ehlig, 1965).

Accumulation of Na^+ , Cl^- , or both depended on species and cultivar. With Na_2SO_4 as the salt source, Na^+ concentrations in 'Brightwell' were usually greater than those in 'Tifblue', but visual damage appeared equivalent. Calcium and K^+ concentrations were also greater in 'Brightwell' than in 'Tifblue'. When NaCl was the salt, 'Tifblue' plants had higher Na^+ and Cl^- and lower Ca^{2+} than 'Brightwell'. There was little difference in salinity damage or in growth between the two rabbiteye cultivars (Wright et al., 1992). 'Sharpblue' southern highbush blueberries accumulated more Na^+ and Cl^- than either rabbiteye cultivar; 'Sharpblue' leaf Na^+ and Cl^- concentrations were 2.1 and 1.3 times greater than those of 'Tifblue'. These high concentrations of Na^+ and Cl^- likely caused the extensive leaf necrosis and rapid decline of photosynthesis in 'Sharpblue' compared to the rabbiteye cultivars (Wright et al., 1992, 1993). These differences in nutrient uptake may be due to differing characteristics of the parent material and, in the case of 'Sharpblue', to differing sensitivities of *V. corymbosum* and *V. darrowii*.

High Ca^{2+} treatments reduced accumulation of Na^+ in stems and roots of 'Tifblue' and 'Brightwell' plants subjected to 100 mM Na^+ as Na_2SO_4 (Fig. 1). These treatments also led to the greatest accumulation of Ca^{2+} in the roots (Table 2), a result suggesting that sodium exclusion from the roots relies on high Ca^{2+} levels (Marschner, 1986). This result possibly supports research by Rains and Epstein (1967), Jacoby and Hanson (1985) and Cramer et al. (1987) indicating that, at high external Na^+ concentrations, Na^+ influx into the roots was inhibited in the presence of adequate Ca^{2+} . However, for leaves, these high Ca^{2+} levels led to the highest Na^+ concentrations and the highest percentage of total plant Na^+ found in the leaves. For plants salinized with 100 mM Na_2SO_4 , growth and gas exchange was reduced in plants supplied with high levels of Ca^{2+} (Wright et al., 1992, 1993). This result indicates that Na^+ may simply pass through roots and stems and accumulate in leaves

when Ca^{2+} is high, thus leading to salinity damage. Our results also suggest that high concentrations of supplemental Ca^{2+} may damage mechanisms that limit Na^+ influx into blueberry leaves. We are unaware of any reports of this phenomena occurring in any other species, but it should be borne in mind that blueberry is essentially a calcifuge in its nutrition.

Adding NaCl increased leaf Na^+ and Cl^- , lowered leaf Ca^{2+} , and decreased the total percentage Ca^{2+} found in the leaves. Neither Na^+ or Cl^- concentrations of leaves, stems, or roots were altered by supplemental Ca^{2+} . This suggests that the greater concentrations of Na^+ found in plants treated with NaCl or the Cl^- anion may have masked the beneficial effects of Ca^{2+} or damaged mechanisms by which the plant might normally limit Na^+ uptake (Drew and Dikunwin, 1985). Possible sites of damage include the plasmalemma, in which high concentrations of Na^+ have been shown to displace Ca^{2+} (Cramer et al., 1985; Lynch et al., 1987; Suhayda et al., 1990), thus leading to decreased membrane resistance. High Na^+ concentrations also lower ATPase activity necessary for active efflux of Na^+ from the cytoplasm (Chung and Matsumoto, 1989).

The inability of Ca^{2+} to limit Na^+ uptake in plants treated with NaCl may involve metabolic damage due to Cl^- . Excessive Cl^- is known to inhibit growth (Ballinger, 1962; Manchanda and Sharma, 1989), and photosynthesis (Bongi and Loreto, 1989). However, the effects of high levels of Cl^- on other facets of plant metabolism have received little attention.

Increasing Na^+ also decreased K^+ concentrations in leaves, stems, and roots. Adequate Ca^{2+} has been shown to increase root K^+ levels in citrus (Bauls et al., 1991) and maintain K^+/Na^+ selectivity in cotton roots (Cramer et al., 1987). Potassium concentrations in leaves of highbush blueberries dropped as NaCl or Na_2SO_4 treatments increased (Muralitharan et al., 1992). But, in our study, leaf and root Na^+ increased and K^+ decreased with increasing Ca^{2+} in rabbiteye plants treated with NaCl. This again suggests that Ca^{2+} was ineffective in limiting Na^+ uptake in blueberry plants treated with NaCl.

In summary, these data suggest that a lack of Na^+ exclusion mechanism may be responsible for high leaf Na^+ concentrations in plants treated with 100 mM Na_2SO_4 or NaCl. Sodium chloride led to higher leaf Na^+ concentrations than Na_2SO_4 , possibly because Na^+ and Cl^- disrupt metabolism. Calcium effectively lowered leaf Na^+ concentration when Na_2SO_4 and not NaCl was the salt source. Sodium treatments also led to decreased K^+ and Ca^{2+} concentrations in the leaves. Excessive accumulation of Na^+ and Cl^- in leaves parallels the onset of growth retardation, slower photosynthesis, and leaf necrosis recorded earlier for these experiments.

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