Ion-specific Limitations of Sodium Chloride and Calcium Chloride on Growth, Nutrient Uptake, and Mycorrhizal Colonization in Northern and Southern Highbush Blueberry

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ABSTRACT. Excess salinity is becoming a prevalent problem for production of highbush blueberry (*Vaccinium* L. section *Cyanococcus* Gray), but information on how and when it affects the plants is needed. Two experiments, including one on the northern highbush (*Vaccinium corymbosum* L.) cultivar, Bluecrop, and another on the southern highbush (*V. corymbosum* interspecific hybrid) cultivar, Springhigh, were conducted to investigate their response to salinity and assess whether any suppression in growth was ion specific or due primarily to osmotic stress. In both cases, the plants were grown in soilless media (calcined clay) and fertigated using a complete nutrient solution containing four levels of salinity [none (control), low (0.7–1.3 mmol·d⁻¹), medium (1.4–3.4 mmol·d⁻¹), and high (2.8–6.7 mmol·d⁻¹)] from either NaCl or CaCl₂. Drainage was minimized in each treatment except for periodic determination of electrical conductivity (EC) using the pour-through method, which, depending on the experiment, reached levels as high as 3.2 to 6.3 dS·m⁻¹ with NaCl and 7.8 to 9.5 dS·m⁻¹ with CaCl₂. Total dry weight of the plants was negatively correlated to EC and, depending on source and duration of the salinity treatment, decreased linearly at a rate of 1.6 to 7.4 g·dS⁻¹·m⁻¹ in ‘Bluecrop’ and 0.4 to 12.5 g·dS⁻¹·m⁻¹ in ‘Springhigh’. Reductions in total dry weight were initially similar between the two salinity sources; however, by the end of the study, which occurred at 125 days in ‘Bluecrop’ and at 111 days in ‘Springhigh’, dry weight declined more so with NaCl than with CaCl₂ in each part of the plant, including in the leaves, stems, and roots. The percentage of root length colonized by mycorrhizal fungi also declined with increasing levels of salinity in Bluecrop and was lower in both cultivars when the plants were treated with NaCl than with CaCl₂. However, leaf damage, which included tip burn and marginal necrosis, was greater with CaCl₂ than with NaCl. In general, CaCl₂ had no effect on uptake or concentration of Na in the plant tissues, whereas NaCl reduced Ca uptake in both cultivars and reduced the concentration of Ca in the leaves and stems of Bluecrop and in each part of the plant in Springhigh. Salinity from NaCl also resulted in higher concentrations of Cl and lower concentrations of K in the plant tissues than CaCl₂ in both cultivars. The concentration of other nutrients in the plants, including N, P, Mg, S, B, Cu, Fe, Mn, and Zn, was also affected by salinity, but in most cases, the response was similar between the two salts. These results point to ion-specific effects of different salts on the plants and indicate that source is an important consideration when managing salinity in highbush blueberry.

Soil salinity is becoming an increasing problem for production of blueberry (*Vaccinium* section *Cyanococcus*), particularly in arid and semiarid regions. Under such conditions, salts, which

can originate from soil parent material (weathered rocks and minerals) or the soilless media in which the plants are grown, irrigation water, fertilizers, and amendments such as elemental sulfur (often used to reduce soil pH), manures, and composts, are not readily leached (Richards, 1954). As a result, salts accumulate in the soil or growing media and affect many processes, including vegetative and reproductive growth, soil physical properties, and sufficiency and toxicity of nutrients (Munns, 1993). Although options to reduce salinity are available, knowing exactly at what level salts will limit growth and production of a crop is critical for developing cost-effective salt management programs (Horneck et al., 2007).

Like most perennial fruit crops, blueberry has a low salt tolerance (Bernstein, 1964) and tends to be most susceptible to

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salinity during establishment (Bryla and Machado, 2011; Vargas and Bryla, 2015). Patten et al. (1989) suggested maintaining the EC (or amount of salts) in the saturation extract (EC_e) at $<1.5 \text{ dS}\cdot\text{m}^{-1}$ to produce optimum growth in rabbiteye blueberry (*Vaccinium virgatum* Aiton). Machado et al. (2014) recommended a similar threshold for northern highbush blueberry (*V. corymbosum*), after they examined the effects of salinity induced by application of ammonium sulfate fertilizer under controlled conditions in a greenhouse. However, Messiga et al. (2018) found that yield declined at EC_e levels as low as $0.8 \text{ dS}\cdot\text{m}^{-1}$ as a result of fertilizing with K_2SO_4 under field conditions in northern highbush blueberry. Salinity also reduced photosynthesis when EC_e was at $0.7 \text{ dS}\cdot\text{m}^{-1}$ when K_2SO_4 was used in cranberry [*Vaccinium macrocarpon* Aiton (Samson et al., 2017)]. The preceding discrepancies may originate from differences among the plant species, the texture and water capacity of the soil, and the composition of the salts.

Plant response to salinity appears to occur in two distinct phases, including an osmotic phase that over time is followed by an ion-specific phase (Munns and Tester, 2008). During the osmotic phase, salt concentrations surrounding the roots reach a threshold level that negatively impacts plant water relations and reduces leaf expansion and new shoot growth. Curiously, shoot growth is more sensitive than root growth to salinity, a phenomenon that also occurs when plants are exposed to drying soils and for which there is no mechanistic explanation yet. The ion-specific phase is slower to develop and begins when salts accumulate to toxic levels in leaves, which eventually become necrotic and die. When leaf necrosis exceeds new leaf production, the photosynthetic capacity of the plant decreases and its growth is reduced even further. Ionic stress usually impacts plant growth much later than osmotic stress, especially at low to moderate salinity levels. In many crops, salinity tolerance during the ionic phase depends on the ability of the root system to exclude and limit translocation of toxic ions such as Na^+ and Cl^- to above-ground parts of the plant (Munns, 2002). However, blueberry plants appear to be poor excluders of Na^+ and Cl^- and rapidly accumulate toxic levels of these ions in the leaves (Ballinger, 1962; Muralitharan et al., 1992; Wright et al., 1993, 1995).

Depending on the composition of the solution in the root environment, ion toxicities or nutritional deficiencies may arise in plants because of predominance of specific ions or competition among these ions (Shannon et al., 1994). Most research on salinity effects on horticultural crops has focused on NaCl. However, $CaCl_2$ and its ionic form also can be prevalent in soils and irrigation water, as well as in road runoff from deicers, soilless substrates, and fertilizers and pesticides (Grattan and Grieve, 1999). Although both NaCl and $CaCl_2$ can cause salinity issues, supplementing plants with $CaCl_2$ can reduce damage from NaCl under certain circumstances (Cramer et al., 1986). This happens because Ca uptake is inhibited by high concentrations of Na in the soil, and adding more Ca can mitigate this issue. However, application of $CaCl_2$ and $CaSO_4$ did not ameliorate the negative effects of NaCl in rabbiteye blueberry or southern highbush blueberry (*V. corymbosum* interspecific hybrid) (Wright et al., 1993). In fact, the Ca salts in this case reduced photosynthesis more than NaCl alone, suggesting that different types of salt may alter the manner in which blueberry plants respond to salinity.

The objective of the present study was to investigate the response of highbush blueberry to salinity and assess whether growth suppression in the plants was ion specific or primarily

due to osmotic stress from the salts. To attain this goal, northern and southern highbush blueberry cultivars were grown in various isosmotic levels of salinity by adding either $CaCl_2$ or NaCl to a basic nutrient solution. Southern highbush blueberry has much lower chilling requirements (200–300 h) than the northern highbush type ($>800 \text{ h}$) and was developed for production in regions with warmer winters, such as Florida and California (Retamales and Hancock, 2018). Currently, it is unknown whether salinity tolerance differs between them, and we hypothesized that salinity limitations would differ depending on salt type in both types of highbush blueberry. We also examined the percentage of root length colonized by ericoid mycorrhizal fungi in each salinity treatment. These fungi commonly form symbiotic associations with roots of ericaceous plants, including blueberry, and often improve growth by increasing the ability of the plants to acquire immobile soil nutrients such as $NH_4\text{-N}$, P, and Zn (Smith and Read, 2008). To our knowledge, there is currently no information on how ericoid mycorrhizal fungi are affected by salinity.

Materials and Methods

PLANT MATERIAL AND GROWTH CONDITIONS. Experiments were conducted in a glasshouse using ‘Bluecrop’ northern highbush blueberry (Expt. 1) and ‘Springhigh’ southern highbush blueberry (Expt. 2). The plants in Expt. 1 were obtained from a commercial nursery (Hartmann’s Plant Company, Lacota, MI) and transplanted individually into 1.2-L containers [constructed from white polyvinyl chloride (PVC) pipe ($0.5 \text{ m tall} \times 5.5 \text{ cm i.d.}$)] filled with an inert, calcined, nonswelling illite and silica clay soilless media (Turface; Profile Products, Buffalo Grove, IL). The bottom of each container was covered with fiberglass window screen (secured with a PVC ring cut to fit inside the bottom of the pipe). The plants in Expt. 2 were also obtained from a commercial nursery (Fall Creek Farm & Nursery, Lowell, OR) but, in this case, were transplanted individually into black, 3.8-L buckets (S-179443BL; Uline, Pleasant Prairie, WI) filled with the calcinated clay media. Three holes (5.4-cm diameter) were drilled in the bottom of each bucket and covered inside with a circular piece of fiberglass window screen. Each bucket was then nested inside another bucket without holes in a pot-in-pot configuration. A plastic tube (19 mm o.d.) was inserted in the space between the inside and outside buckets to facilitate collection of leachate (see later in this article). Calcinated clay was used in the experiments to reduce confounding soil factors such as changes in availability of soil nutrients at different salinity levels (Grattan and Grieve, 1999) and to facilitate root harvest (roots do not penetrate the particles). Once transplanted, the plants were placed in racks on a greenhouse bench and allowed to become established for 13 d in Expt. 1 and 65 d in Expt. 2 before any treatments were applied. Plants were actively growing when they were transplanted in Expt. 1 (July) but not in Expt. 2 (February), and therefore, we waited until new leaves emerged and were fully expanded before initiating the treatments in the second experiment. The plants produced no flowers or fruit during either of the experiments.

Supplemental photosynthetically active radiation (400–700 nm) was provided from seven 330-W light-emitting diode lamps (ES330; Lumigrow, Novato, CA) over the bench and measured using a quantum light sensor (LI-190SA; LI-COR Biosciences, Lincoln, NE). Air temperature and relative humidity were measured using a shielded temperature/relative humidity sensor

(1400–104, LI-COR Biosciences). Readings from each sensor were recorded every 15 min using a data logger (LI-1400; LI-COR Biosciences). In Expt. 1, photosynthetic photon flux density (*PPFD*) averaged a maximum of $1375 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a total of $20.5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, and temperature and relative humidity averaged 23.9°C and 49.9% , respectively. The maximum temperature reached on any given date was 32.7°C , and the mean minimum temperature was 14.7°C . Relative humidity ranged from 15.8% to 72.4% . In Expt. 2, *PPFD* averaged a maximum of $1006 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a total of $24.1 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Temperature averaged 26.4°C and reached a maximum of 43.7°C and a minimum of 19.4°C . Relative humidity averaged 46.4% and ranged from 21.9% to 72.6% .

EXPERIMENTAL DESIGN. The salinity treatments were run for 125 d in Expt. 1 and 111 d in Expt. 2. In both cases, the treatments were applied to the plants using a multi drip-line injection system (Aragues et al., 1999), whereby fertilizer solution was added through one drip line and NaCl and CaCl_2 treatments mixed with fertilizer solution were added through two other lines. The system consisted of three water-drive chemical injectors (D14M22; Dosatron International, Clearwater, FL). The first injector was used to inject concentrated fertilizer solution into a main line at a 1:50 (v/v) ratio. The solution contained $4.5 \text{ mM NH}_4\text{-N}$, 0.8 mM P , 0.9 mM K , 0.05 mM Ca , 0.02 mM Mg , 1.9 mM S , $2.8 \mu\text{M B}$, $0.5 \mu\text{M Cu}$, $2.7 \mu\text{M Fe}$, $0.9 \mu\text{M Mn}$, $0.1 \mu\text{M Mo}$, $0.8 \mu\text{M Zn}$, and $5 \mu\text{M Cl}$, and, in Expt. 1 only, was adjusted to a pH of 5.4 using 5 mM HCl . The main line was then divided into three secondary lines, including one that supplied fertilizer solution to drip emitters in each plant container directly and two others that were used to inject concentrated NaCl and CaCl_2 solutions into tertiary lines with additional drip emitters [see Bryla and Scagel (2014) for details]. Different combination of emitters (2, 4, and $8 \text{ L}\cdot\text{h}^{-1}$; The Toro Co., Bloomington, MN) were selected to provide each salinity treatment with the same volume of fertilizer solution and varying concentrations of NaCl or CaCl_2 in the solution (Table 1). Stock solution molarities, injection ratios, and run times were assessed weekly and altered to address plant growth and changing water needs. The treatments were arranged in a randomized complete block design with six replicates per treatment on each of three destructive harvest dates, for a total of 144 plants (2 salt types $\times$ 4 salinity levels $\times$ 3 harvest dates $\times$ 6 replicates) in both experiments. The plants were fertigated daily with minimal amount of drainage, and water content of the media was maintained near container capacity to expose the plants to constant level of EC_e in each treatment.

MEASUREMENTS. EC and pH of the fertigation solutions were measured weekly at 25°C using a combination pH/conductivity meter (SevenGo Pro; Mettler-Toledo, Columbus, OH). Leachate EC and pH were also measured weekly, beginning after 8 d of

treatment in Expt. 1 and 5 d of treatment in Expt. 2. Leachate was collected in both experiments using a pour-through extraction method (Torres et al., 2010). The bottom of each container was fit with a plastic funnel before the pour-through to collect leachate in Expt. 1, and syringes were connected to the tubes installed between the pots to collect leachate in Expt. 2. Distilled water ($125\text{--}150 \text{ mL}$) was poured evenly by hand over the surface of each container 30 min after fertigation, and the extract was allowed to drain for 30 min into holding vessels. An average of 117 mL of leachate was collected from eight replicate containers per treatment on each date in Expt. 1, and an average of 110 mL of leachate was collected from six replicate containers per treatment on each date in Expt. 2. A subsample (25 mL) of each volume was taken for the EC and pH measurements.

Leaves on the plants were evaluated for salt damage beginning at 54 d of treatment in Expt. 1 and at 1 d of treatment in Expt. 2. The plants did not show much sign of leaf damage early on in the first experiment, and therefore, evaluations of damage were initiated later in the first than in the second experiment. Symptoms of salt damage included leaf tip burn and marginal necrosis. Leaves showing *any* signs of these symptoms were considered to have salt damage. The total number of healthy and damaged leaves was counted periodically to calculate the percentage of leaves with salt damage in each treatment.

Plants were harvested destructively after 62, 91, and 125 d of treatment in Expt. 1 and after 33, 67, and 111 d of treatment in Expt. 2. On each date, leaves were removed from the stems, and each stem was cut into $\approx 10\text{-cm}$ -long pieces. The root system was gently removed from the growing substrate, rinsed with water, and cleaned with tweezers to remove any remaining debris. Approximately 1 g of fresh roots were randomly sampled from each root system and stored in lactoglycerin solution. The leaves, stems, and remaining roots were then oven-dried at 60°C for at least 4 d and weighed. Once weighed, each part was ground to pass through a 40-mesh ($425\text{-}\mu\text{m}$) screen and analyzed for N using a combustion analyzer (TruSpec CN; Leco Corp., St. Joseph, MI); for P, K, Ca, Mg, S, B, Cu, Fe, Mn, Zn, and Na using inductively coupled plasma optical emission spectrometry (Optima 3000DV; PerkinElmer, Waltham, MA) following microwave digestion in 70% (v/v) nitric acid (Gavlak et al., 2005); and for Cl using an ion-selective electrode (perfection 51344706, Mettler-Toledo) following extraction in nitric acid (Rieger and Litvin, 1998). Nutrient content was calculated by multiplying the dry weight of each plant part by the concentration of a given nutrient (Chapin and Van Cleve, 1989). Roots stored in lactoglycerin solution were cleared and stained following procedures outlined in Scagel et al. (2005), and examined under a light microscope ($40\times$) for the presence of ericoid mycorrhizal fungi. Mycorrhizal colonization was quantified

Table 1. Amount of NaCl or CaCl_2 applied to ‘Bluecrop’ and ‘Springhigh’ blueberry plants exposed to four levels of salinity in Expts. 1 and 2, respectively.

Salinity level	Expt. 1				Expt. 2	
	NaCl ($\text{mmol}\cdot\text{d}^{-1}$)		CaCl_2 ($\text{mmol}\cdot\text{d}^{-1}$)		NaCl ($\text{mmol}\cdot\text{d}^{-1}$)	CaCl_2 ($\text{mmol}\cdot\text{d}^{-1}$)
	Day 0–91	Day 92–125	Day 0–91	Day 92–125	Day 0–111	Day 0–111
Control	0.0	0.0	0.0	0.0	0.0	0.0
Low	0.7	1.3	1.0	1.7	0.9	0.9
Medium	1.4	2.5	1.9	3.4	1.7	1.7
High	2.8	5.0	3.8	6.7	3.4	3.4

using a modified grid-line intersect technique and expressed as the percentage of the total root length with internal mycorrhizal structures such as internal hyphae and hyphal coils (Giovannetti and Mosse, 1980).

STATISTICAL ANALYSES. All data were analyzed using analytical software (Statistica version 12; StatSoft, Tulsa, OK). The data were checked for normality using the Komogorov-Smirnov test at $P \leq 0.01$, and tested for homogeneity of variance using Levene's test. Biomass allocation and root colonization data were arcsine-transformed before analyses and presented as back-transformed means.

Differences between salt types and among salinity levels were assessed on leaf necrosis using analysis of variance (ANOVA) in a complete factorial design with salt type and salinity level as main effects. Means from ANOVA were separated using Tukey's honestly significant difference test ($P \leq 0.05$). Differences between salt types and among salinity levels were assessed on EC of pour-through leachate using analysis of covariance (ANCOVA) in a complete factorial design with salt type and salinity level as main effects and leachate volume as a covariate. Adjusted means are presented for each salt type and salinity level, and these means were used as a covariate in analyses of plant response variables (described as follows).

Effects of salt type and EC on plant growth, biomass allocation, mycorrhizal colonization, and nutrient uptake and concentration were assessed separately for each harvest date using ANCOVA in a complete factorial design with salt type as a categorical effect and EC as continuous predictor variable. Based on significant ANCOVA results ($P \leq 0.05$), adjusted means are presented for the two salt types at an EC of $2 \text{ dS}\cdot\text{m}^{-1}$, and regression coefficients (β) are presented for relationships between EC and the response variables. EC determined by the pour-through method is $\approx 30\%$ greater than EC_e (Fisher et al.,

2006) and at $2 \text{ dS}\cdot\text{m}^{-1}$ is equivalent to the level of salinity at which plant production is reduced by at least 10% in salt-sensitive species such as blueberry (Maas and Grattan, 1999). In all regression analyses, the influence of salt type on relationships between EC and response variables was assessed using best subsets regression with the Mallows CP technique as the criterion for choosing the best subset of predictor effects from linear and quadratic models (Mallows, 1973). Differences in β between salt types were compared using Z-tests (Paternoster et al., 1998).

Results

LEACHATE EC AND pH. At any given level of salinity, the EC of leachate from the containers and buckets in Expts. 1 and 2, respectively, was greater with CaCl_2 than with NaCl (Fig. 1A and B). This difference was expected given that EC is a measure of milliequivalents of charge per liter, and at each concentration, CaCl_2 has twice as many ions as NaCl . Leachate EC also increased over time in Expt. 2, which indicates salt ions accumulated in the lower and wider containers used in the second experiment. By the final harvest, EC was as high as 3.2 and 6.3 $\text{dS}\cdot\text{m}^{-1}$ with NaCl and CaCl_2 , respectively, in Expt. 1, and as high as 7.8 and 9.5 $\text{dS}\cdot\text{m}^{-1}$ with NaCl and CaCl_2 , respectively, in Expt. 2. In contrast, EC of control treatments ranged from 0.4 to $0.7 \text{ dS}\cdot\text{m}^{-1}$ on each harvest date in either experiment.

Leachate pH decreased over time in both experiments but was similar among the salinity treatments (data not shown). In Expt. 1, pH averaged 5.0 at 62 d of treatment, 4.1 at 91 d, and 3.9 at 125 d. In Expt. 2, pH averaged 5.7 at 33 and 67 d of treatment and 5.1 at 111 d. As mentioned, the fertilizer solution was acidified with HCl in the first experiment, which explains why pH was lower in Expt. 1 than in Expt. 2.

Fig. 1. Relationship between the amount of NaCl or CaCl_2 applied and electrical conductivity (EC) of the pour-through leachate after 62, 91, and 125 d of treatment on (A) 'Bluecrop' blueberry in Expt. 1 and after 33, 67, and 111 d of treatment on (B) 'Springhigh' blueberry in Expt. 2. Data were fit using second-order polynomials. Each symbol represents the mean of six replicates, and error bars indicate the least significant difference at the 5% level.

Fig. 2. Relationship between electrical conductivity (EC) of the pour-through leachate and total dry weight of the plants after 62, 91, and 125 d of treatment with NaCl or CaCl₂ on (A) 'Bluecrop' blueberry in Expt. 1, and after 33, 67, and 111 d of treatment with NaCl or CaCl₂ on (B) 'Springhigh' blueberry in Expt. 2. Each symbol represents the mean of six replicates, and error bars indicate the least significant difference at the 5% level. Regression coefficients (β) are presented for significant linear relationships between leachate EC and total dry weight ($P < 0.01$). One β is shown when the response to NaCl and CaCl₂ is similar on a given day, and two are shown when the response is different.

PLANT GROWTH AND BIOMASS ALLOCATION. Total dry weight of the plants was negatively correlated to EC of the pour-through leachate and, depending on the source and duration of the salinity treatment, decreased linearly at a rate of 1.6 to 7.4 g·dS⁻¹·m⁻¹ in 'Bluecrop' (Expt. 1) and 0.4–12.5 g·dS⁻¹·m⁻¹ in 'Springhigh' (Expt. 2) (Fig. 2A and B). In both cultivars, reduction in total dry weight was similar between the two salinity sources initially, but by 91 d or later, reductions were greater with NaCl than with CaCl₂ in each part of the plant, including in the leaves, stems, and roots (Table 2). In most cases, differential effects of the two salt sources on tissue dry weight occurred at higher salinity levels and were mostly absent when EC of the leachate was ≤ 2 dS·m⁻¹.

Salinity reduced allocation of biomass to leaves (in favor of stems and/or roots) at each harvest date in 'Bluecrop' and at the final harvest date in 'Springhigh' (Table 2). However, with a few exceptions, allocation of biomass among each organ was generally similar between the two salt sources. Exceptions included relationships between leachate EC and allocation of biomass to leaves and roots at 91 d in 'Bluecrop' and to leaves, stems, and roots at 111 d in 'Springhigh'. In the first case, 'Bluecrop' allocated less biomass to roots in favor of leaves when plants were treated with NaCl and less biomass to leaves in favor of roots when plants were treated with CaCl₂. In the second case, 'Springhigh' allocated less biomass to leaves and roots in favor of stems when plants were treated with NaCl, but allocation was unaffected by CaCl₂. Furthermore, when EC was normalized to 2 dS·m⁻¹ in 'Springhigh', plants treated with NaCl allocated less biomass to leaves at 33 d than those treated with CaCl₂.

MYCORRHIZAL COLONIZATION. Mycorrhizal colonization was affected by salinity at 91 and 125 d of treatment in 'Bluecrop' and at 111 d of treatment in 'Springhigh' (Table 2). On these

dates, the percentage of root length that was colonized by the fungi declined with increasing levels of salinity in 'Bluecrop' and, when EC was normalized to 2 dS·m⁻¹, was lower by an average of 10% with NaCl than with CaCl₂ in both cultivars.

NUTRIENT UPTAKE AND CONCENTRATIONS. As expected, uptake of Na was greater in both cultivars when plants were treated with NaCl than with CaCl₂, whereas uptake of Ca was greater when the plants were treated with CaCl₂ than with NaCl (Table 3). Furthermore, CaCl₂ salinity had no effect on uptake or concentration of Na in the plant tissues, but NaCl salinity reduced Ca uptake in both cultivars and resulted in lower concentrations of Ca in the leaves and stems of 'Bluecrop' and in each part of the plant in 'Springhigh'. By the end of the experiment for 'Bluecrop', Na concentrations averaged 75.8, 1.4, and 1.8 mg·g⁻¹ in the leaves, stems, and roots, respectively, of plants treated with the highest level of NaCl but was <0.2 mg·g⁻¹ in each tissue of those treated with the highest level of CaCl₂. Calcium concentrations, on the other hand, averaged 2.1, 3.6, and 1.6 mg·g⁻¹, respectively, in each tissue of plants treated with the highest level of NaCl and 11.0, 12.6, and 3.3 mg·g⁻¹, respectively, in those treated with the highest level of CaCl₂. Similar differences were observed by the end of the experiment for 'Springhigh'. In this case, Na concentrations averaged 18.9, 4.5, and 4.8 mg·g⁻¹, respectively, in plants treated with the highest level of NaCl and <0.6 mg·g⁻¹ in each tissue in those treated with the highest level of CaCl₂. Calcium concentrations averaged 3.3, 1.6, and 1.7 mg·g⁻¹, respectively, in plants treated with the highest level of NaCl and 17.2, 6.4, and 3.4 mg·g⁻¹, respectively, in those treated with the highest level of CaCl₂.

Both of the salts increased Cl uptake, particularly when NaCl was applied (Table 3). In many cases, NaCl salinity resulted in higher concentrations of Cl in the plant tissues than CaCl₂ in

both cultivars. This was partially because twice as much Cl^- was applied with NaCl than with an equivalent mmol addition of CaCl_2 . By the end of the experiments, the concentration of Cl in ‘Bluecrop’ averaged 2.2, 2.4, and 3.5 $\text{mg}\cdot\text{g}^{-1}$ in the leaves, stem, and roots, respectively, in plants treated with the highest

level of NaCl and 6.8, 4.1, and 3.7 $\text{mg}\cdot\text{g}^{-1}$, respectively, in those treated with the highest level of CaCl_2 . In ‘Springhigh’, Cl concentrations averaged 19.3, 7.2, and 3.0 $\text{mg}\cdot\text{g}^{-1}$ with the highest level of NaCl, and 19.8, 6.7, and 4.6 $\text{mg}\cdot\text{g}^{-1}$ with the highest level of CaCl_2 .

Table 2. Effects of salinity from NaCl or CaCl_2 on plant tissue dry weight, biomass allocation, and mycorrhizal colonization in ‘Bluecrop’ (Expt. 1) and ‘Springhigh’ (Expt. 2) blueberry.

Salinity treatment ^z	Tissue dry wt (g/plant)			Biomass allocation (% total dry wt)			Mycorrhizal colonization (% root length)
	Leaves	Stems	Roots	Leaves	Stems	Roots	
Bluecrop							
62 d of treatment							
Mean at 2 dS·m ⁻¹							
NaCl	3.9	1.4	1.0	62	22	16	7
CaCl ₂	4.6	1.3	1.1	63	21	15	8
<i>P</i> value	0.3637	0.9191	0.5973	0.7866	0.9190	0.7983	0.6458
β (per dS·m ⁻¹)							
NaCl							
CaCl ₂	−1.3	−0.2	−0.2	−3.0	2.7	NS	NS
<i>P</i> value	<0.0001	0.0014	0.0159	0.0098	0.0401	0.5076	0.2719
91 d of treatment							
Mean at 2 dS·m ⁻¹							
NaCl	7.5	2.9	1.6	62	24	14	13
CaCl ₂	8.6	3.7	2.2	58	26	16	27
<i>P</i> value	0.9171	0.7823	0.6864	0.6527	0.8017	0.2258	0.0093
β (per dS·m ⁻¹)							
NaCl	−2.1	−0.8	−0.7	0.6		−1.0	−12
CaCl ₂	−1.6	−0.5	−0.3	−2.2	0.5	1.2	−6
<i>P</i> value	<0.0001	<0.0001	<0.0001	0.0080	0.0191	0.0036	0.0151
125 d of treatment							
Mean at 2 dS·m ⁻¹							
NaCl	15.3	7.1	3.7	58	28	14	25
CaCl ₂	16.5	7.8	4.3	57	27	16	32
<i>P</i> value	0.0739	0.1342	0.5426	0.3507	0.5849	0.6028	0.0409
β (per dS·m ⁻¹)							
NaCl	−4.4	−2.0	−1.0				−9
CaCl ₂	−2.3	−0.5	−0.5	−0.8	0.4	0.6	−4
<i>P</i> value	<0.0001	<0.0001	<0.0001	0.0188	0.0312	0.0441	0.0207
Springhigh							
33 d of treatment							
Mean at 2 dS·m ⁻¹							
NaCl	4.1	2.4	1.5	51	30	19	2
CaCl ₂	5.7	2.8	1.8	55	27	18	3
<i>P</i> value	0.0044	0.4820	0.2664	0.0309	0.0753	0.3020	0.6247
β (per dS·m ⁻¹)							
NaCl							
CaCl ₂	−0.8	NS	−0.2	NS	NS	NS	NS
<i>P</i> value	0.0007	0.4373	0.0084	0.0961	0.0792	0.4937	0.6247
67 d of treatment							
Mean at 2 dS·m ⁻¹							
NaCl	20.2	10.8	5.2	56	30	14	9
CaCl ₂	20.1	11.4	5.1	55	31	13	7
<i>P</i> value	0.8536	0.5080	0.9767	0.9730	0.5550	0.4525	0.6983
β (per dS·m ⁻¹)							
NaCl							
CaCl ₂	−1.2	−0.6	−0.4	NS	NS	NS	NS
<i>P</i> value	0.0001	0.0011	<0.0001	0.3786	0.4943	0.1101	0.8798

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Table 2. (Continued) Effects of salinity from NaCl or CaCl₂ on plant tissue dry weight, biomass allocation, and mycorrhizal colonization in ‘Bluecrop’ (Expt. 1) and ‘Springhigh’ (Expt. 2) blueberry.

Salinity treatment ^z	Tissue dry wt (g/plant)			Biomass allocation (% total dry wt)			Mycorrhizal colonization (% root length)
	Leaves	Stems	Roots	Leaves	Stems	Roots	
111 d of treatment							
Mean at 2 dS·m ⁻¹							
NaCl	47.1	33.5	10.6	50	38	11	12
CaCl ₂	43.8	31.0	12.6	51	37	13	20
<i>P</i> value	0.0425	0.4920	0.3195	0.1897	0.1591	0.8313	0.0081
β (per dS·m ⁻¹)							
NaCl	-6.8	-3.7	-2.0	-1.4	2.0	-0.6	NS
CaCl ₂	-4.2	-3.1	-1.4	NS	NS	NS	
<i>P</i> value	<0.0001	<0.0001	<0.0001	0.0101	0.0004	0.0141	

^zMeans (n = 24) of NaCl and CaCl₂ were estimated at a leachate electrical conductivity (EC) of 2 dS·m⁻¹. Regression coefficients (β) are presented for significant linear relationships between leachate EC and tissue dry weight, biomass allocation, and mycorrhizal colonization. One β is shown when the response to NaCl and CaCl₂ is similar on a given day, and two are shown when the response is different.

^{NS}Nonsignificant.

Other nutrients were also affected by salinity (Table 4). In one or both cultivars, the concentration of N, P, Cu, and Zn in the plants increased with salinity on at least one harvest date, whereas the concentration of K, Mg, S, Fe, and Mn often declined with salinity. Boron was the only nutrient that

responded differently to salinity in the two cultivars. In this case, the concentration of B increased with salinity in ‘Bluecrop’ and, with one exception (i.e., CaCl₂ salinity at 111 d), declined with salinity in ‘Springhigh’. In most cases, the response of these nutrients to salinity was similar between the two salts; however,

Table 3. Effects of salinity from NaCl or CaCl₂ on total uptake and plant tissue concentrations of Na, Ca, K, and Cl in ‘Bluecrop’ (Expt. 1) and ‘Springhigh’ (Expt. 2) blueberry.

Salinity treatment ^z	Na uptake (mg/plant)	Na concn (mg·g ⁻¹)			Ca uptake (mg/plant)	Ca concn (mg·g ⁻¹)			Cl uptake (mg/plant)	Cl concn (mg·g ⁻¹)			
		Leaves	Stems	Roots		Leaves	Stems	Roots		Leaves	Stems	Roots	
Bluecrop													
62 d of treatment													
Mean at 2 dS·m ⁻¹													
NaCl	15	2.65	1.58	1.95	15	2.3	3.2	1.8	9	0.84	1.53	3.28	
CaCl ₂	1	0.14	0.35	0.21	27	3.7	6.3	2.5	8	1.17	1.52	2.73	
<i>P</i> value	0.0058	<0.0001	0.1587	0.6707	0.8725	0.4433	0.6977	0.9497	0.9703	0.0022	0.2191	0.0479	
β (per dS·m ⁻¹)													
NaCl	8	1.68	0.71	0.90	-8	-0.28	-0.82	NS	2.9	0.32	0.76	1.53	
CaCl ₂	NS	NS	NS	NS	NS	0.57	0.87	0.27		0.79		0.70	
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	0.0015	<0.0001	0.0005	0.0007	<0.0001	0.0003	<0.0001	0.0239	
91 d of treatment													
Mean at 2 dS·m ⁻¹													
NaCl	30	3.17	1.54	1.91	27	1.9	3.2	1.6	25	1.97	2.07	2.74	
CaCl ₂	2	0.01	0.19	0.17	50	3.5	5.6	2.2	14	0.93	1.34	2.17	
<i>P</i> value	0.0026	0.0003	0.0813	0.0198	0.0070	0.0405	0.4367	0.4874	0.0032	0.4500	0.0204	0.0391	
β (per dS·m ⁻¹)													
NaCl	19	2.32	0.84	1.03	-13	-0.28	-0.44	NS	16.1	1.54	1.34	1.41	
CaCl ₂	NS	NS	NS	NS	NS	0.98	1.21	0.15	5.3	0.87	0.69	0.74	
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0003	0.0127	<0.0001	0.0021	<0.0001	0.0014	
125 d of treatment													
Mean at 2 dS·m ⁻¹													
NaCl	28	1.99	0.87	1.02	69	2.3	3.7	1.6	26	1.23	1.35	2.02	
CaCl ₂	3	0.10	0.12	0.11	106	3.8	6.1	2.0	24	0.70	1.23	1.91	
<i>P</i> value	0.0059	<0.0001	0.0863	0.0561	0.0051	0.0406	0.0437	0.4874	0.6316	0.0231	0.0158	0.1119	
β (per dS·m ⁻¹)													
NaCl	14	1.81	0.39	0.50	-22	-0.15	-0.14	NS	12.1		1.07	0.98	
CaCl ₂	NS	NS	NS	NS	NS	1.35	1.31	0.21	9.2	1.28	0.62	0.64	
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0003	0.0339	<0.0001	<0.0001	0.0089	

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Table 3. (Continued) Effects of salinity from NaCl or CaCl₂ on total uptake and plant tissue concentrations of Na, Ca, K, and Cl in 'Bluecrop' (Expt. 1) and 'Springhigh' (Expt. 2) blueberry.

Salinity treatment ^z	Na uptake (mg/plant)	Na concn (mg·g ⁻¹)			Ca uptake (mg/plant)	Ca concn (mg·g ⁻¹)			Cl uptake (mg/plant)	Cl concn (mg·g ⁻¹)			
		Leaves	Stems	Roots		Leaves	Stems	Roots		Leaves	Stems	Roots	
Springhigh													
33 d of treatment													
Mean at 2 dS·m ⁻¹													
NaCl	20	1.42	2.44	5.62	23	3.3	2.7	2.2	31	3.29	3.51	5.01	
CaCl ₂	1	0.03	0.18	0.34	44	4.9	3.7	2.7	30	2.81	2.91	4.13	
<i>P</i> value	0.0061	0.0013	<0.0001	0.0738	0.3184	0.0414	0.8476	0.1396	0.5718	0.4897	0.0659	0.5072	
β (per dS·m ⁻¹)													
NaCl	14	1.11	1.55	1.01	-9	-0.29	-0.20	-0.27	17	1.89	2.38	1.78	
CaCl ₂	NS	NS	NS	NS	NS	0.93	0.34	0.17			1.74	1.78	
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	0.0013	<0.0001	0.0197	0.0017	<0.0001	<0.0001	0.0067	0.0028	
67 d of treatment													
Mean at 2 dS·m ⁻¹													
NaCl	100	3.92	1.79	2.36	129	4.1	2.9	2.5	130	4.63	2.89	4.06	
CaCl ₂	6	0.03	0.21	0.49	188	6.4	3.8	2.8	118	3.74	2.79	4.21	
<i>P</i> value	0.0014	0.0158	0.0563	0.0609	0.0059	0.0161	0.0009	0.0471	0.8786	0.4622	0.4670	0.7735	
β (per dS·m ⁻¹)													
NaCl	60	2.99	0.96	0.86	-12	-0.15	-0.07	-0.10	86	3.89	1.85	1.78	
CaCl ₂	NS	NS	NS	NS	13	1.20	0.41	0.07	38	2.09	0.78	1.05	
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0100	<0.0001	<0.0001	<0.0001	0.0033	
111 d of treatment													
Mean at 2 dS·m ⁻¹													
NaCl	147	2.34	1.54	1.72	289	4.0	2.1	2.0	167	2.66	1.86	3.10	
CaCl ₂	26	0.06	0.47	0.57	364	5.8	2.5	2.3	170	2.18	2.13	2.90	
<i>P</i> value	0.00861	0.0072	0.2306	0.0812	0.0552	0.0465	0.0291	0.4416	0.5524	0.4650	0.0291	0.4415	
β (per dS·m ⁻¹)													
NaCl	54	2.88	0.70	0.78	-43	-0.13	-0.08	-0.08	85	3.55	1.33	1.44	
CaCl ₂	NS	NS	NS	NS	15	1.67	0.57	0.18	65	2.69	0.86	1.08	
<i>P</i> value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	0.0185	0.0187	<0.0001	0.0110	

^zMeans (n = 24) of NaCl and CaCl₂ were estimated at a leachate electrical conductivity (EC) of 2 dS·m⁻¹. Regression coefficients (β) are presented for significant linear relationships between leachate EC and uptake and concentration of each nutrient. One β is shown when the response to NaCl and CaCl₂ is similar on a given day, and two are shown when the response is different.

^{NS}Nonsignificant.

there were a few exceptions. For example, in 'Bluecrop', concentration of K and S at 91 d and of K, Cu, and Mn at 125 d were either more affected by NaCl than by CaCl₂ or affected by NaCl only. This was also the case for the concentrations of B and Fe in 'Springhigh' at 111 d.

SALT DAMAGE IN THE LEAVES. Leaf damage increased with the level of salinity in both cultivars and was greater with CaCl₂ than with NaCl (Table 5). In 'Bluecrop', leaf damage differed between the salts beginning at 99 d of treatment but, on average, remained <5% with NaCl and reached only 10% with CaCl₂ (Fig. 3A). In 'Springhigh', leaf damage differed between the salts as early as 30 d and increased to an average of 25% with NaCl and 45% with CaCl₂ (Fig. 3B).

Discussion

Salinity reduced the growth of highbush blueberry in the present study, but the response differed depending on the source of the salinity. Specifically, NaCl resulted in less plant growth than CaCl₂, which was expected given the known deleterious effects of Na⁺ on photosynthesis (Sudhir and Murthy, 2004), cell turgor (Munns 2002; Munns and Passioura, 1984), and uptake of

cations and other nutrients (Grattan and Grieve, 1999). However, CaCl₂ resulted in more leaf damage to the plants than NaCl when the plants were exposed to medium to high levels of salinity. This latter difference did not appear to be attributable to Cl⁻ from the salts, given that the concentration of Cl in the leaves was usually the same or lower in plants treated with CaCl₂ than with NaCl at a given isosmotic level and was well below the level considered toxic to highbush blueberry [26 mg·g⁻¹ (Muralitharan et al., 1992)]. Excessive accumulation of Ca²⁺, on the other hand, might have somehow increased leaf damage over time. In fact, when plants were treated with a high level of CaCl₂, leaf Ca concentrations were above the normal range for highbush blueberry [4.1–8.0 mg·g⁻¹ (Hart et al., 2006)]. Because blueberry is a calcifuge and is adapted to acidic soils with low Ca²⁺ concentrations, the plants tend to be efficient at Ca uptake and have relatively low requirements for the nutrient (Bryla and Strik, 2015). Thus, when a calcifuge plant such as blueberry is exposed to high concentrations of Ca²⁺ in the soil, they cannot regulate Ca²⁺ influx and consequently accumulate excessive amounts of the ion (Wacquant and Picard, 1992). Like blueberry, *Lupinus angustifolius* L. has a very low Ca requirement, and growth in this species is severely depressed by higher Ca content in its tissue (Islam et al., 1987). This behavior is

typical of calcifuges (Korcak, 1988) and might be related to insufficient capacity for compartmentation or physiological inactivation of Ca^{2+} (e.g., precipitation as calcium oxalate) (Marschner, 2002). High Ca concentrations are also known to inhibit stomatal regulation and lead to water stress in certain species, such as *Tripolium pannonicum* (Jacq.) Dobrocz. [= *Aster*

tripolium L. (Perera et al., 1995)] and *Gerbera jamesonii* Adlam (Albin-Garduño et al., 2007), and may likewise do so in blueberry.

Salinity also reduced root colonization by ericoid mycorrhizal fungi in the present study, particularly when we treated the plants with NaCl. Similar results have been observed in plants

Table 4. Effects of salinity from NaCl or CaCl_2 on total plant tissue concentrations of macro- and micronutrients in 'Bluecrop' (Expt. 1) and 'Springhigh' (Expt. 2) blueberry.

Salinity treatment ^z	Macronutrient concn ($\text{mg}\cdot\text{g}^{-1}$)					Micronutrient concn ($\mu\text{g}\cdot\text{g}^{-1}$)				
	N	P	K	Mg	S	B	Cu	Fe	Mn	Zn
Bluecrop										
62 d of treatment										
Mean at 2 $\text{dS}\cdot\text{m}^{-1}$										
NaCl	18.2	1.74	5.85	1.12	1.61	27	6.4	100	270	26
CaCl_2	17.9	1.70	6.15	0.93	1.59	28	5.4	119	203	22
P value	0.8472	0.7119	0.0762	<0.0001	0.2917	0.3500	0.0654	0.1080	0.0045	0.0591
β (per $\text{dS}\cdot\text{m}^{-1}$)										
NaCl										
CaCl_2	NS	NS	-0.51	-0.24	-0.22	2.5	NS	-18	-34	NS
P value	0.6043	0.3837	<0.0001	<0.0001	<0.0001	0.0054	0.6951	0.0106	0.0146	0.0823
91 d of treatment										
Mean at 2 $\text{dS}\cdot\text{m}^{-1}$										
NaCl	17.0	1.63	5.45	1.05	1.50	21	7.1	115	210	23
CaCl_2	17.2	1.71	6.16	0.91	1.59	21	6.9	137	179	21
P value	0.3863	0.3740	0.0011	0.0013	0.4998	0.9633	0.3985	0.4723	0.0767	0.0157
β (per $\text{dS}\cdot\text{m}^{-1}$)										
NaCl										
CaCl_2	NS	NS	-0.94	-0.18	-0.17	1.3	NS	-18	-32	NS
P value	0.8278	0.6323	<0.0001	<0.0001	0.0381	0.0112	0.3704	<0.0001	0.0102	0.7503
125 d of treatment										
Mean at 2 $\text{dS}\cdot\text{m}^{-1}$										
NaCl	17.9	1.85	6.15	1.14	1.58	19	9.6	140	205	23
CaCl_2	17.8	1.87	6.78	0.96	1.58	20	9.4	148	166	22
P value	0.5920	0.7746	0.0055	<0.0001	0.7854	0.4884	0.5139	0.4047	0.0036	0.0196
β (per $\text{dS}\cdot\text{m}^{-1}$)										
NaCl										
CaCl_2	NS	NS	-0.62	-0.09	NS	1.7	0.5	-12	-24	1.2
P value	0.5920	0.7746	<0.0001	<0.0001	0.1016	<0.0001	0.0159	0.0009	0.0438	0.0054
Springhigh										
33 d of treatment										
Mean at 2 $\text{dS}\cdot\text{m}^{-1}$										
NaCl	20	1.84	9.67	1.37	1.94	39	6.7	165	451	40
CaCl_2	20	1.86	9.37	1.53	1.95	37	6.6	178	489	37
P value	0.5525	0.7413	0.4730	0.0272	0.7256	0.6876	0.8688	0.8800	0.5054	0.3839
β (per $\text{dS}\cdot\text{m}^{-1}$)										
NaCl										
CaCl_2	NS	NS	NS	-0.12	-0.17	-1.5	0.7	-20	NS	5
P value	0.8582	0.9881	0.5405	<0.0001	0.0046	0.0176	0.0155	0.0686	0.9445	<0.0001
67 d of treatment										
Mean at 2 $\text{dS}\cdot\text{m}^{-1}$										
NaCl	15	1.43	6.80	1.46	1.65	34	4.5	201	478	29
CaCl_2	14	1.40	7.34	1.51	1.68	31	4.1	182	446	28
P value	0.2443	0.6724	<0.0001	0.5727	0.8002	0.3040	0.0362	0.1861	0.1796	0.3042
β (per $\text{dS}\cdot\text{m}^{-1}$)										
NaCl										
CaCl_2	NS	NS	NS	NS	-0.05	-0.4	0.2	-18	NS	2
P value	0.2561	0.3942	0.0528	0.0532	0.0039	0.0304	0.0007	0.0089	0.1137	0.0002

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Table 4. (Continued) Effects of salinity from NaCl or CaCl₂ on total plant tissue concentrations of macro- and micronutrients in 'Bluecrop' (Expt. 1) and 'Springhigh' (Expt. 2) blueberry.

Salinity treatment ^z	Macronutrient concn (mg·g ⁻¹)					Micronutrient concn (μg·g ⁻¹)				
	N	P	K	Mg	S	B	Cu	Fe	Mn	Zn
111 d of treatment										
Mean at 2 dS·m ⁻¹										
NaCl	10	1.14	5.43	1.28	1.27	28	2.9	217	503	19
CaCl ₂	10	1.19	6.58	1.24	1.22	29	2.8	211	398	16
<i>P</i> value	0.0744	0.4241	0.0003	0.8248	0.8369	0.0414	0.9581	0.4680	<0.0001	0.2031
β (per dS·m ⁻¹)										
NaCl	0.43	0.04	-0.21	-0.04	-0.02	-0.6	0.3	-24	-13	2
CaCl ₂						0.8		-14		
<i>P</i> value	<0.0001	<0.0001	0.0287	0.0026	0.0274	0.0115	<0.0001	0.0213	0.0202	<0.0001

^zMeans (n = 24) of NaCl and CaCl₂ were estimated at a leachate electrical conductivity (EC) of 2 dS·m⁻¹. Regression coefficients (β) are presented for significant linear relationships between leachate EC and the concentration of each nutrient. One β is shown when the response to NaCl and CaCl₂ is similar on a given day, and two are shown when the response is different.

^{NS}Nonsignificant.

colonized by arbuscular mycorrhizal fungi (Evelin et al., 2009). Reduced colonization from salinity could be attributed to a number of factors, including osmotic effects of the salts on sporulation and hyphal development of the fungi (Estaun, 1990; Juniper and Abbott, 2006; McMillen et al., 1998), Na⁺ and Cl⁻ toxicity to the roots and/or fungi (Hirrel, 1981), and limited availability of carbohydrates to support the fungi brought about by the negative effects of salinity on plant growth (Thomson et al., 1990). Work is needed to determine which of these factors is affecting growth and activity of these fungi under saline conditions in blueberry.

As anticipated, high concentrations of NaCl reduced plant uptake of essential nutrients, including K⁺, Ca²⁺, and Mg²⁺, in both cultivars tested in the present study. In fact, leaf tissue analysis indicated that Ca was deficient in both cultivars [<4.0 mg·g⁻¹ (Hart et al., 2006)] when the plants were fertigated each day with nutrient solution containing 2.8–5.0 mmol NaCl. This result is similar to previous research by Wright et al. (1994), who found that increasing NaCl concentrations in the nutrient solution led to increases in leaf Na and Cl concentrations and decreases in leaf K and Ca concentrations in rabbiteye blueberry. Excess Na⁺ in the root zone often causes the development of

osmotic stress in fruit and vegetable crops and disrupts cell ion homeostasis by inducing both the inhibition in uptake of essential nutrients such as K⁺, Ca²⁺, and NO₃⁻ and the accumulation of Na⁺ and Cl⁻ (Machado and Serralheiro, 2017; Paranychianakis and Chartzoulakis, 2005). Likewise, excess Ca²⁺ may be problematic as well (Bernstein and Hayward, 1958; Nassery et al., 1979) and, in this study, resulted in lower concentrations of K, Mg, S, Fe, and Mn in both cultivars.

As mentioned, exposure to NaCl and CaCl₂ increased the amount of Cl⁻ in the shoot and root tissues of both cultivars, which like Na⁺ can be toxic to the plants. The damaging impact of Cl⁻ is described in the literature on blueberry (Wright et al., 1992, 1993, 1994) and other berry crops (Ehlig, 1965). Wright et al. (1994) found that excessive accumulation of Cl⁻ in blueberry leaves parallels the onset of growth retardation, reduced photosynthesis, and leaf necrosis. This work further identified that the effects of NaCl on growth were more severe than the effects of the higher concentration of Na₂SO₄ at equimolar concentrations of Na⁺ (Wright et al., 1992, 1993). In rabbiteye blueberry, leaf Cl concentrations were at least three times greater than root Cl concentrations after 63 d of treatment (Wright et al., 1994). We observed a similar response, but in our case, Cl concentrations were up to 42 times greater in the leaves than in the roots in the northern highbush cultivar, Bluecrop, and up to four times greater in the southern highbush cultivar, Springhigh. Such high Cl concentrations in the leaves emphasize the possibility that Cl⁻ may be at least partly as damaging as Na⁺ to growth and gas exchange of blueberry.

In summary, NaCl reduced plant growth more than CaCl₂ in both northern and southern highbush blueberry, but CaCl₂ resulted in greater leaf damage over time. Salinity also reduced root colonization by mycorrhizal fungi, which are beneficial to the plants for nutrient uptake. Mycorrhizal colonization was particularly affected when the plants were treated with NaCl. Salinity from NaCl also reduced plant uptake of essential nutrients such as K⁺ and Ca²⁺ more than salinity from CaCl₂, whereas both of the salts increased the amount of Cl⁻ in the plant tissue, which can be toxic to the plants. These results point to ion-specific effects of different salts on the plants and indicate that source is an important consideration when managing salinity in highbush blueberry. The information from this work will be

Table 5. Leaf damage (tip burn and/or marginal necrosis) from NaCl or CaCl₂ salinity in 'Bluecrop' (Expt. 1) and 'Springhigh' (Expt. 2) blueberry.

Salinity level ^y	Leaves with salt damage (% of all leaves) ^z					
	Bluecrop			Springhigh		
	NaCl	CaCl ₂	Difference	NaCl	CaCl ₂	Difference
Control	2 b ^x	2 b	0 ^{NS}	6 b	6 d	0 ^{NS}
Low	2 b	4 b	-2 ^{NS}	7 b	12 c	-5 ^{NS}
Medium	2 b	3 b	-1 ^{NS}	11 a	26 b	-15 ^{**}
High	5 a	16 a	-11 ^{**}	14 a	34 a	-20 ^{**}

^zData are pooled across seven dates measured between 52 and 120 d of treatment in 'Bluecrop' and 13 dates measured between 8 and 99 d of treatment in 'Springhigh'.

^ySee Table 1 for the daily amount of salt applied at each level of salinity.

^xMeans followed by a common letter within a column are not significantly different at $P \leq 0.05$.

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

Fig. 3. Development of leaf damage (tip burn and/or marginal leaf necrosis) from NaCl or CaCl₂ salinity in (A) 'Bluecrop' blueberry in Expt. 1, and (B) 'Springhigh' blueberry in Expt. 2. Data are pooled across three levels of salinity (see Table 1). Each symbol represents the mean of six replicates. An asterisk above the symbols on a given day indicates the means were significantly different at $P \leq 0.05$.

useful for developing better salt management practices for commercial blueberry production.

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