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Growth, Morphological, and Biochemical Responses of Four Native Species to Salinity Stress

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Abstract. **Native plants are of great value in landscape maintenance. Despite their importance in the landscape, the salt tolerance of most native plants has received little attention. The present research was designed to assess morphological, physiological, and biochemical responses of four Utah-native plants [*Arctostaphylos uva-ursi* (kinnikinnick), *Cercocarpus ledifolius* (curl-leaf mountain mahogany), *Cercocarpus montanus* 'Coy' (alder-leaf mountain mahogany), and *Shepherdia* ×*utahensis* 'Torrey' (hybrid buffaloberry)] at different salinity levels. Each species was irrigated with a nutrient solution at an electrical conductivity (EC) of 1.2 dS·m^{-1} (control) or saline solutions at ECs of 5.0 or 10.0 dS·m^{-1} for 8 weeks. The experiment was a randomized complete block design with 10 replications. At 8 weeks after the initiation of the experiment, *A. uva-ursi* and *C. montanus* 'Coy' had slight foliar salt damage with an average visual score of 3.7 (0 = dead, 5 = excellent with no sign of foliar salt damage) when irrigated with saline solution at an EC of 5.0 dS·m^{-1} and were dead at an EC of 10.0 dS·m^{-1}. Similarly, *C. ledifolius* had an average visual score of 3.2 when irrigated with saline solution at an EC of 10.0 dS·m^{-1}. However, almost no foliar salt damage was observed on *S.* ×*utahensis* 'Torrey' during the experimental period. In addition, the shoot dry weight of all species was reduced with elevated salinity levels in the irrigation water. Salinity stress also reduced gas exchange rates of plants and affected their mineral content. Proline accumulated in the leaves of native plants but was species-dependent. In conclusion, *S.* ×*utahensis* 'Torrey' was tolerant to salinity stress followed by *C. ledifolius*; *A. uva-ursi* and *C. montanus* 'Coy' were sensitive to salinity stress.**

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Salinity in both irrigation water and soil is one of the major abiotic factors responsible for soil degradation. Nearly 6% of all lands worldwide are affected by salinity (Munns 2005). Salinity stress in plants is caused by excessive amounts of water-soluble salts. Some of the most common deleterious salts in soil include sodium sulfate (Na_2SO_4), sodium nitrate ($NaNO_3$), sodium chloride (NaCl), sodium bicarbonates ($NaHCO_3$), sodium carbonate (Na_2CO_3), potassium sulfate (K_2SO_4), calcium sulfate ($CaSO_4$), magnesium sulfate ($MgSO_4$), and magnesium chloride ($MgCl_2$) (Sazzad 2007). With salinity-affected areas and ever-increasing competition for potable water, planting salt-tolerant ornamental plants has become a sustainable strategy for urban landscape development.

In a saline environment, morphological and physiological processes in plants are disturbed, leading to an inhibition of growth (Alvarez and Sanchez-Blanco 2014). High concentrations of salts in soil or water affect stomatal conductance, photosynthesis, and ion balance in plants (Navarro et al. 2008). In addition, when sodium (Na^+) and chloride (Cl^-) are present in the soil, they can interfere with enzymatic transporters and disrupt the uptake of nutrients such as potassium (K^+) (Tester and Davenport 2003). If accumulated and not compartmentalized in vacuoles, Na^+ and Cl^- become metabolically toxic, causing leaf damage, nutritional disorders, stunted growth, and reduction in photosynthesis (Shannon and Grieve 1999; Zhang et al. 2014).

Plant salinity tolerance is the ability to tolerate high salt concentrations in the root zone without adverse effects (Shannon and Grieve 1999). Salinity tolerance differs among species with different mechanisms to cope with the detrimental effects of salinity stress (Munns and Tester 2008). Salt-tolerant ornamental plants may accumulate less Na^+ and Cl^- in their leaves when compared with salt-sensitive plants (Munns 2002). Sodium uptake is usually reduced or transporting sodium from roots to shoots is restricted in salt-tolerant plants (Munns 2002). On the other hand, some plants can tolerate accumulated Na^+ and Cl^- in shoot tissue (Munns and Tester 2008). There is a compartmentalization of Na^+ and Cl^- at cellular and intracellular levels to avoid the toxic concentrations within the cytoplasm, especially in mesophyll cells in the leaf (Munns and Tester 2008). Similarly, osmotic adjustment is an important adaptation of plants to salinity, as it helps to maintain cell turgor and volume. Osmolytes or compatible solutes in the cytoplasm are among the major compounds for halophytes to tolerate salt stress (Flowers 2004). Compatible solutes include compounds such as proline, betaine, polyols, sugar alcohols, and soluble sugars (Chinnusamy et al. 2005).

Native plants occur naturally in a region without direct or indirect human actions. Native plants are of great value in low-water landscapes (Rupp and Wheaton 2014). The use of native plants has gained popularity in ecological landscape design, green building construction, and urban habitat development. Consumers are increasing their interest in natural landscapes and showing a willingness to pay a premium price for native plant products (McCoy 2011); however, limited information exists on salinity stress responses of native plants.

In this study, we compared the salinity tolerance of four Utah-native plants, *A. uva-ursi* (kinnikinnick), *C. ledifolius* (curl-leaf mountain mahogany), *C. montanus* 'Coy' (alder-leaf mountain mahogany), and *S.* ×*utahensis* 'Torrey' (hybrid buffaloberry). *A. uva-ursi* is a drought-tolerant and winter-hardy evergreen plant and found as a pioneer plant on disturbed sites (Wood et al. 2013). It is a groundcover adaptable to infertile soils and requires very little maintenance once established. *C. ledifolius* is an evergreen shrub or small tree that is adapted to low-water landscapes (Rupp and Wheaton 2014). *C. montanus* 'Coy' is a dwarf evergreen cultivar with nitrogen-fixing ability and low water demand (Paudel et al. 2020). *S.* ×*utahensis* 'Torrey' is an interspecific hybrid of *S. argentea* (silver buffaloberry) and *S. rotundifolia* (roundleaf buffaloberry) (Sriladda et al. 2016). *S.* ×*utahensis* 'Torrey' is a nitrogen-fixing plant that tolerates disturbed soil and drought stress (Chen et al. 2021; Sriladda et al. 2016). Limited research has been conducted regarding

the salinity tolerance of these four plant species. Young et al. (2012) investigated the effect of NaCl at concentrations of 10, 30, 70, and 140 mM (~0.9, 2.7, 5.1, and 10.2 dS·m^{-1}) on the survival and growth of *A. uva-ursi* and claimed that it can tolerate up to 70 mM NaCl (~5.1 dS·m^{-1}). In addition, Qin et al. (2010) reported that *S. argentea* subjected to 200, 400, and 600 mM NaCl solutions (~14.6, 29.2, and 43.8 dS·m^{-1}) is tolerant to salinity levels tested in this study. Further research is required to understand the salinity stress responses of these native plants and select tolerant species for salt-affected landscapes.

Materials and Methods

Plant materials and growth condition. This study was conducted at the Utah State University (USU) Research Greenhouse in Logan, UT, USA (lat. 41°45′28″N, long. 111°48′48″W, elevation 1409 m). Native plants, *A. uva-ursi*, *C. ledifolius*, *C. montanus* 'Coy', and *S. ×utahensis* 'Torrey' in 3.8-L injection molded polypropylene containers (No. 1, Nursery Supplies, Orange, CA, USA) were used in this study. *A. uva-ursi* was purchased from J&J Nursery and Garden Center (Layton, UT, USA). *C. montanus* 'Coy' and *S. ×utahensis* 'Torrey' were vegetatively propagated via cuttings and grown for 8 months. *C. ledifolius* seedlings were collected from the USU campus in Jun 2019 and grown for 2 years. The plants were transplanted into 7.6-L injection molded polypropylene containers (No. 2B; Nursery Supplies) filled with Metro-Mix® 820 (Canadian Sphagnum peatmoss, 35% to 45% composted pine bark, coir, coarse perlite, and dolomitic limestone; SunGro Horticulture, Agawam, MA, USA) on 9 Jun 2021. The plants were kept in the research greenhouse. Logan City potable water [EC = 0.35 ± 0.01 dS·m^{-1}; pH = 7.7 ± 0.2, mean ± standard deviation] was applied when needed and water-soluble fertilizer (Peters Excel 15–5–15 Cal-Mag Special; ICL Specialty Fertilizers, Dublin, OH, USA) was applied twice before the treatments. Before treatments started, *C. montanus* 'Coy' and *S. ×utahensis* 'Torrey' were pruned to 30 cm high. *A. uva-ursi* and *C. ledifolius* were 23.2 ± 5.5 and 20.9 ± 5.8 cm high, respectively. The experiment started on 23 Aug 2021 and ended on 23 Oct 2021. The mean air temperature inside the greenhouse was maintained at 25.9 ± 0.3 °C during the day and 22.0 ± 0.3 °C at night. Daily light integral inside the greenhouse was 26.6 ± 3.6 mol·m^{-2}·d^{-1}. When light intensity inside the greenhouse was less than 500 µmol·m^{-2}·s^{-1}, supplemental light at 225.5 ± 86.5 µmol·m^{-2}·s^{-1}, measured using a Quantum Flux Meter (MQ-200X, serial # 1006; Apogee Instruments, Logan, UT, USA), was provided using 1000-W high-pressure sodium lamps at plant canopy level from 0600 to 2200 HR.

Treatments. Two salinity treatments were subjected to *A. uva-ursi*, *C. ledifolius*, *C. montanus* 'Coy', and *S. ×utahensis* 'Torrey' that included irrigation solutions at an EC of 5.0 or 10.0 dS·m^{-1}. The control group received only a nutrient solution at an EC of 1.2 dS·m^{-1}. Uniform plants were selected and randomly assigned to the treatments. The nutrient (control) solution was prepared by adding 0.8 g·L^{-1} 15N–2.2P–12.5K water-soluble fertilizer to potable water in a 100-L tank. The saline solution treatments at ECs of 5.0 and 10.0 dS·m^{-1} were prepared using sodium chloride (NaCl; Fisher Scientific, Waltham, MA, USA) and dihydrate calcium chloride ($CaCl_2·2H_2O$; Hi Valley Chemical, Centerville, UT, USA) at a molar ratio of 2:1 to the nutrient solution (Table 1). Calcium chloride was added to reduce salinity-induced calcium deficiency (Guo et al. 2021). The initial pH of treatment solutions was adjusted to 6.0 to 6.5 using 88% potassium hydroxide pellets (Sigma-Aldrich, St. Louis, MO, USA) or 1M nitric acid (Fisher Chemical, Fair Lawn, NJ, USA) as necessary. The sodium adsorption ratio (SAR) and elemental analysis were confirmed by the USU Analytical Laboratory (Table 1). Treatment solutions, 1200 mL per pot, were applied manually once per week for 8 weeks. The leaching fraction was targeted to ~25%. In-between treatments, plants were watered with an additional 250 to 500 mL distilled water, as necessary, to avoid the confounding effect of drought conditions.

Leachate and substrate EC. Leachate EC was measured weekly following the pour-through method described by Cavins et al. (2008) using an EC meter (LAQUA Twin, Horiba, Kyoto, Japan). Briefly, a saucer was placed under the container at least 30 min after each irrigation treatment and 100 mL of distilled water was poured from the top surface. Afterward, EC was measured from the leachate. Substrate EC was measured using the saturated paste method explained by Gavlak et al. (2005) with minor modifications. In brief, the pots containing soilless media were left to dry in the greenhouse after harvest. A 10 g sample of the substrate was taken from the top 5 cm surface, as salts move upward during the drying process. Then, 100 mL of deionized water was added to the substrate sample in a flask to make a paste. All samples in the flask were covered with parafilm® (American National Can™, Menasha, WI, USA), stored overnight at room temperature, and EC measurements were taken the following day.

Survival rate and visual quality. Dead plants were recorded at the end of the experiment and the survival rate was calculated. A visual score of 0 to 5 was assigned for each plant weekly to assess foliar salt damage without considering plant size. A visual score was assigned as 0 = dead (plants died because of salinity stress), 1 = severe foliar damage (> 90% burnt leaves, tip burn, or necrosis), 2 = moderate foliar damage (90% to 50%), 3 = slight foliar damage (50% to 10%), 4 = good quality with minimal foliar damage (<10%), and 5 = excellent without foliar damage (Sun et al. 2015).

Growth parameters. The number of shoots was recorded for each plant at the beginning and end of the experiment. Shoots longer than 5 cm were included in the count. At harvest, leaf area was measured using a leaf area meter (LI-3100; LI-COR® Biosciences, Lincoln, NE, USA). In addition, the shoot dry weight and root dry weight of plants were obtained by drying the samples in an oven at 60 °C for 1 week.

Gas exchange. Net photosynthesis rate (P_n), transpiration rate (E), and stomatal conductance (g_s) of the native plants in each treatment were measured 2 d before harvest using a portable LI-6800 photosynthesis system (LI-COR® Biosciences). Fully expanded, healthy leaves without damage were used. All measurements were taken within a range of 1000 and 1400 HR on sunny days. Environmental conditions in the cuvette were controlled at 25 °C, 1000 µmol·m^{-2}·s^{-1} photosynthetic photon flux (895.5 µmol·m^{-2}·s^{-1} red and 99.5 µmol·m^{-2}·s^{-1} blue) and 400 µmol·mol^{-1} carbon dioxide concentration. All plants were watered sufficiently 1 d before the measurements to avoid water stress.

Mineral analyses. Four plants of each native plant species were selected randomly

Table 1. The mineral content, sodium adsorption ratio (SAR), and electrical conductivity (EC) of nutrient and saline solutions used to irrigate container-grown plants native to Utah.

		Saline solution[iii]	
Item[i]	Nutrient solution[ii]	5.0 dS·m^{-1}	10.0 dS·m^{-1}
Ca^{2+} (mg·L^{-1})	95.90	561.40	1,140.00
Mg^{2+} (mg·L^{-1})	37.60	32.00	30.00
Na^{+} (mg·L^{-1})	3.30	450.90	1,029.00
SO_4^{2-} (mg·L^{-1})	13.10	14.30	16.40
Cl^{-} (mg·L^{-1})	4.40	1,380.00	3,160.00
B (mg·L^{-1})	0.17	0.19	0.19
SAR	0.07	5.00	8.20
Adjusted SAR	0.13	11.67	21.33
EC (dS·m^{-1})	1.21 ± 0.03[iv]	5.09 ± 0.09	10.15 ± 0.10

[i] Calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^{+}), sulfate (SO_4^{2-}), chloride (Cl^{-}), and boron (B).
[ii] The nutrient solution at an EC of 1.2 dS·m^{-1} was made by mixing 0.8 g·L^{-1} 15N–2.2P–12.5K water-soluble fertilizer (Peter Excel 15–5–15 Ca-Mag Special) in potable water.
[iii] Sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2·2H_2O$) were used to prepare the saline solution. The nutrient solution was supplemented with NaCl at 0.92 g·L^{-1} and $CaCl_2·2H_2O$ at 1.17 g·L^{-1} to obtain the saline solution at an EC of 5.0 dS·m^{-1}, and 2.27 g·L^{-1} NaCl and 2.88 g·L^{-1} $CaCl_2·2H_2O$ was added to the nutrient solution to make the saline solution at an EC of 10.0 dS·m^{-1}.
[iv] Mean ± standard deviation.

from each treatment and leaf samples were ground with a grinder (Model 80393; Hamilton Beach, Glen Allen, VA, USA). The chloride (Cl^-) analysis was performed using a chloride analyzer (Model 926; Nelson-Jameson, Marshfield, WI, USA) and reported on a dry plant basis ($mg \cdot g^{-1}$). Briefly, 0.3 g of powdered leaf samples was extracted in 15 mL of 2% acetic acid (Fisher Chemical) in a conical tube placed on a platform shaker (Innova 2100; New Brunswick Scientific, Edison, NJ, USA) for 30 min and allowed to stand for 60 min. The extracted solution was filtered and retained for further analysis. Solution (500 µL) was added to the acid buffer (Nelson-Jameson) and Cl^- content was quantified. Furthermore, powder samples were analyzed at the USU Analytical Laboratories for other mineral contents. In brief, sodium (Na^+), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), manganese (Mn^{2+}), sulfur (S), phosphorus (P), iron (Fe), and zinc (Zn^{2+}) contents were quantified using nitric/hydrogen peroxide following the protocol described in Gavlak et al. (2005). A total of 0.5 g of powder samples and 6 mL of nitric acid (HNO_3) were added into a digestion tube followed by incubation in a digestion block for 10 min at 80 °C and subsequently cooled for 2 min. A total of 2 mL of 30% hydrogen peroxide (H_2O_2) was added into the digestion tube and then incubated again in the digestion block at 130 °C for 1 h. Tubes were placed in a vortex stirrer for mixing, cooled down, and diluted to the final volume. Then the digestion tube was cooled at room temperature, and the contents of the digestion tube were transferred into a 25-mL volumetric flask. The digest was analyzed using an Inductively Coupled Plasma-Optical Emission Spectrometry (iCAP 6300 ICP-AES; Thermo Scientific, Waltham, MA, USA) and reported on a dry plant basis ($mg \cdot g^{-1}$).

Proline. Proline in the leaves was estimated by the acid-ninhydrin method (Bates et al. 1973; Claussen 2005; Rakesh et al. 2021). Leaf samples were directly collected in liquid nitrogen on 28 Sep 2021 (after the sixth irrigation event) and stored at −80 °C until further use. The leaf samples (0.1 g) were ground in 5 mL of 3% sulfosalicylic acid (Spectrum Chemical, Gardena, CA, USA) and centrifuged at 5000 rpm for 5 min at room temperature using a benchtop centrifuge (Spectrafuge™ Labnet 6C Centrifuge, Edison, NJ, USA). Then 200 µL of supernatant, 200 µL of glacial acetic acid (Fisher Chemical), and 200 µL of acid ninhydrin (Sigma-Aldrich) were mixed in a tube and incubated in a boiling water bath at 95 °C for 1 h. After 1 h, tubes were immediately placed in an ice-bath to arrest the reaction. Thereafter, 400 µL of toluene (Fisher Chemical, Ottawa, ON, Canada) was added to each tube, vortexed well, and allowed to settle for 10 min. The upper pinkish color layer was separated and 200 µL of the sample was pipetted into the well of a microplate reader (Cellstar, F-bottom; BMG LabTech, Cary, NC, USA). Absorbance at 520 nm was recorded using a spectrophotometer (Spectra max M2; Molecular Devices, San Jose, CA, USA). Proline (L-Proline, St. Louis, MO, USA) was used to generate a standard curve that was used to estimate the proline content in the samples.

Experimental design and data analyses. The experiment was conducted in a randomized complete block design with four species, three treatments, and 10 replicates. An experimental unit consisted of one pot containing one plant. An analysis of variance was conducted to test the effect of saline solution irrigation and species on plant growth, gas exchange, and mineral nutrients. All data were subjected to log transformation. Because of different growth habits of each species, means separation among treatments was adjusted using Tukey's method for multiplicity at $\alpha = 0.05$. In addition, means separation among species was performed for visual score and proline content. Correlation analyses were carried out for Na^+ and Cl^- contents, and K^+/Na^+ ratio in plant tissue was compared with visual scores and gas exchange parameters. All statistical analyses were conducted using SAS (Version 14.1; SAS Institute, Cary, NC, USA) with PROC MIXED procedure.

Table 2. A summary of analysis of variance for the effects of treatments and their interactions with plant species on visual score (VS), number of shoots, leaf area (LA), shoot dry weight (DW), root DW, net photosynthesis rate (P_n), transpiration rate (E), stomatal conductance (g_s), and proline content of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 $dS \cdot m^{-1}$, control] or saline solution (EC = 5.0 $dS \cdot m^{-1}$ or 10.0 $dS \cdot m^{-1}$) in a greenhouse for 8 weeks.

	Analysis of variance								
Source	VS	No. of shoots	LA	Shoot DW	Root DW	P_n	E	g_s	Proline
Plant	****[i]	****	****	****	***	****	NS	NS	****
Treatment	****	****	****	**	NS	****	***	****	*
Plant × Treatment	****	NS	*	NS	NS	****	NS	NS	*

[i] NS, *, **, ***, **** Nonsignificant or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

Results

Visual quality and Survival rate. A. uva-ursi irrigated with saline solution at ECs of 5.0 and 10.0 $dS \cdot m^{-1}$ started showing foliar salt damage (necrosis and burnt leaves) at 5 and 4 weeks after treatment initiation, respectively (data not shown). *C. ledifolius* at an EC of 10.0 $dS \cdot m^{-1}$ exhibited foliar salt damage (tip burn and burnt leaves) at 4 weeks after treatment initiation (data not shown). Moreover, *C. montanus* 'Coy' started showing foliar salt damage (tip burn and burnt leaves) at 6 and 4 weeks after treatment initiation (data not shown) when irrigated with saline solution at ECs of 5.0 and 10.0 $dS \cdot m^{-1}$, respectively. Saline solution irrigation had significant effects on the visual score of native plants at 8 weeks and there were significant interactive effects between species and treatment ($P < 0.0001$, Tables 2 and 3). At 8 weeks, all four species survived when they were irrigated with saline solution at an EC of 5.0 $dS \cdot m^{-1}$ (Table 3). *C. ledifolius* and *S. ×utahensis* 'Torrey' plants also survived with saline solution at an EC of 10.0 $dS \cdot m^{-1}$, but *A. uva-ursi* and *C. montanus* 'Coy' plants were dead. *A. uva-ursi* had visible foliar salt damage with an averaged visual score of 3.7 when irrigated with saline solution at an EC of 5.0 $dS \cdot m^{-1}$ (Table 3, Fig. 1). *C. ledifolius* had minimal to no foliar salt damage when irrigated with saline solution at an EC of 5.0 $dS \cdot m^{-1}$ but plants at an EC of 10.0 $dS \cdot m^{-1}$ had foliar salt damage with an averaged visual score of 3.2. Similarly, *C. montanus* 'Coy' had averaged visual score of 3.6 when irrigated with saline solution at an EC of 5.0 $dS \cdot m^{-1}$. However, *S. ×utahensis* 'Torrey' was healthy without foliar salt damage when plants were irrigated with saline solution at an EC of 5.0 and 10.0 $dS \cdot m^{-1}$ throughout the experiment.

Plant growth. The number of shoots and leaf area varied with treatments and species ($P < 0.0001$, Table 2). Compared with the control, the number of shoots was reduced by 26% and 37% for *A. uva-ursi* and *C. montanus* 'Coy' treated with saline solution at an EC of 5.0 $dS \cdot m^{-1}$, respectively (Table 4).

Table 3. Visual score and survival rate of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 $dS \cdot m^{-1}$, control] or saline solution [EC = 5.0 $dS \cdot m^{-1}$ (EC 5) or 10.0 $dS \cdot m^{-1}$ (EC 10)] in a greenhouse for 8 weeks.

	Visual score (0–5)[i]			Survival (%)		
Plants	Control	EC 5	EC 10	Control	EC 5	EC 10
Arctostaphylos uva-ursi	5 a[ii]A[iii]	3.7 bB	0 cC	100	100	0
Cercocarpus ledifolius	5 aA	4.9 aA	3.2 bB	100	100	100
Cercocarpus montanus 'Coy'	5 aA	3.6 bB	0 cC	100	100	0
Shepherdia ×utahensis 'Torrey'	5 aA	5 aA	4.9 aA	100	100	100

[i] 0 = dead (plants died because of salinity stress), 1 = severe foliar damage (>90% burnt leaves, tip burn, or necrosis), 2 = moderate foliar damage (90% to 50%), 3 = slight foliar damage (50% to 10%), 4 = good quality with minimal foliar damage (<10%), and 5 = excellent without foliar damage (Sun et al. 2015).

[ii] Means with same lowercase letters within species are not different among treatments by Tukey's method for multiplicity at $\alpha = 0.05$.

[iii] Means with same uppercase letters within column are not different among species by Tukey's method for multiplicity at $\alpha = 0.05$.

Similarly, *S.* ×*utahensis* 'Torrey' treated with saline solution at an EC of 10.0 dS·m^{-1} had a 32% reduction in the number of shoots. In addition, the leaf area of *A. uva-ursi* treated with saline solution at an EC of 5.0 dS·m^{-1} was 52% less than the control. *C. montanus* 'Coy' had 26% less leaf area than control plants when treated with saline solution at an EC of 5.0 dS·m^{-1} but was not different. *C. ledifolius* had 44% less leaf area than control plants when treated with saline solution at an EC of 10.0 dS·m^{-1}. Although the leaf area of *S.* ×*utahensis* 'Torrey' tended to decrease with saline solutions, there were no differences among treatments.

Shoot dry weight varied with treatments and species ($P < 0.01$, Table 2). Compared with control, although there were no significant differences, there was a trend of reduced shoot dry weight of *A. uva-ursi* and *C. montanus* 'Coy' treated with saline solution at an EC of 5.0 dS·m^{-1} and *C. ledifolius* treated with saline solution at an EC of 10.0 dS·m^{-1} (Table 5). More replications might be needed to improve the statistical power of the analysis and show significant differences. In addition, the shoot dry weight of *S.* ×*utahensis* 'Torrey' was reduced by 32% compared with the control when treated with saline solution at an EC of 10.0 dS·m^{-1}. Similarly, root dry weight differed among species but was unaffected by salinity treatments (Tables 2 and 5).

These results indicate that plants experienced significant salinity stresses, which attribute to the salts accumulated in the soilless growing substrate. Leachate EC or substrate EC is an indirect or direct way to measure salinity levels in soil and growing substrate. In this study, leachate EC increased over time with saline solution irrigation (Fig. 2). The highest leachate EC was 1.9, 11.3, and 17.3 dS·m^{-1} for the control or saline solutions at ECs of 5.0 and 10.0 dS·m^{-1}, respectively, during the experiment. Similarly, the higher the salinity of irrigation water, the more salts accumulated in the substrate (Fig. 3). By the end of the experiment, average ECs of the substrate were 7.1 ± 2.4 and 15.1 ± 1.0 dS·m^{-1} when irrigated with saline solution at ECs of 5.0 or 10.0 dS·m^{-1}, respectively, reflecting salt accumulation in soilless media.

Gas exchange. With the increase of salinity levels in irrigation water, the net photosynthesis rate (P_n) of four native plants decreased ($P < 0.0001$, Table 2, Fig. 4). In addition, P_n varied with species and had interactive effects between treatment and species ($P < 0.0001$). Net photosynthesis rate of *A. uva-ursi* and *C. montanus* 'Coy' decreased from 3.8 and 9.2 μmol·m^{-2}·s^{-1} to 2.2 and 1.5 μmol·m^{-2}·s^{-1} when treated with saline solution at an EC of 5.0 dS·m^{-1}, respectively. Similarly, P_n decreased from 11.1 and 16.2 μmol·m^{-2}·s^{-1} to 0.6 and 4.2 μmol·m^{-2}·s^{-1} for *C. ledifolius* and *S.* ×*utahensis* 'Torrey', respectively, when treated with saline solution at an EC of 10.0 dS·m^{-1}.

Transpiration rate (E) decreased as salinity levels in the irrigation water increased for *C. ledifolius* and *C. montanus* 'Coy' (Fig. 4). However, E was not significantly reduced for *S.* ×*utahensis* 'Torrey'. The g_s also decreased with increasing salinity levels. The g_s of *C. montanus* 'Coy' decreased from 125.5 to 20.9 mmol·m^{-2}·s^{-1} when treated with saline solution at an EC of 5.0 dS·m^{-1}. Similarly, g_s decreased from 119.4 and 170 mmol·m^{-2}·s^{-1} to 18.4 and 25 mmol·m^{-2}·s^{-1} for *C. ledifolius* and *S.* ×*utahensis* 'Torrey', respectively, when treated with saline solution at an EC of 10.0 dS·m^{-1}.

Mineral contents. For all four native plants, leaf Na^+ content was lower than Cl^- content ($P < 0.0001$) but varied with species. Salinity treatments significantly increased Na^+ contents in the leaves of native plants

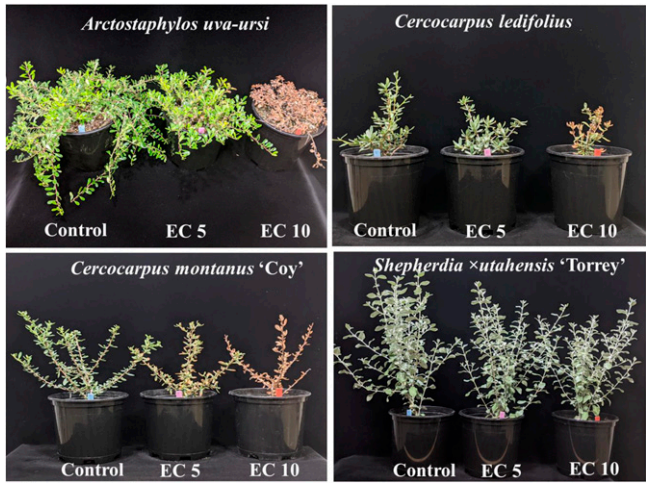

Fig. 1. Photos of representative container-grown plants native to Utah after irrigating with a nutrient solution (EC = 1.2 dS·m^{-1}; control) or a saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks.

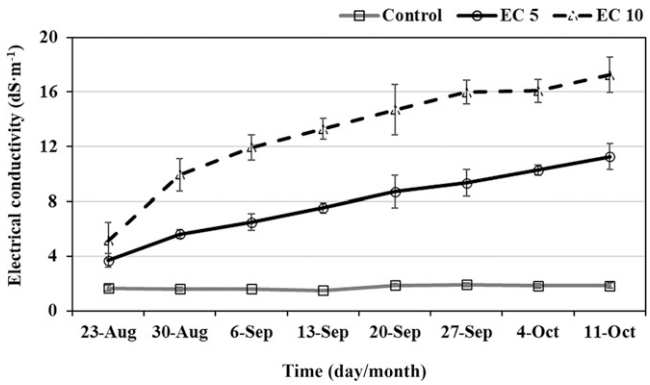

Fig. 2. Electrical conductivity (EC) of leachate solution collected after irrigating container-grown plants native to Utah with a nutrient solution (EC = 1.2 dS·m^{-1}, control) or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] over the course of the experiment. Vertical bars represent standard errors of four measurements.

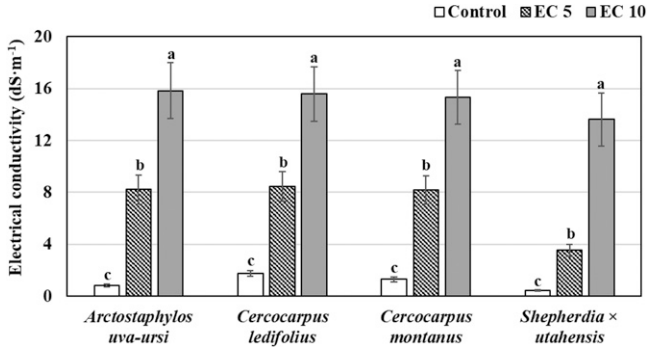

Fig. 3. Electrical conductivity (EC) of soil extraction from container-grown plants native to Utah after irrigating with a nutrient solution (EC = 1.2 dS·m^{-1}, control) or a saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks. Vertical bars represent standard errors of five measurements. The same letters above column bars within species represent no significance among treatments as determined by Tukey's method for multiplicity at $\alpha = 0.05$.

($P < 0.0001$, Table 6). The highest level of Na^+ at 8.3 mg·g^{-1}, 35 times higher than that in the control, was found in the leaves of *A. uva-ursi* when treated with saline solution at an EC of 10.0 dS·m^{-1}. Similarly, Na^+ content in the leaves of *C. ledifolius*, *C. montanus* 'Coy', and *S. ×utahensis* 'Torrey' when treated with saline solution at an EC of 10.0 dS·m^{-1} was 4.1, 5.5, and 5.2 mg·g^{-1}, respectively, which increased by 81, 78, and 21 times compared with the control. Furthermore, there was an increase in Cl^- content with increasing salinity levels ($P < 0.0001$, Table 6). The highest level of Cl^- at 51.89 mg·g^{-1}, which was 44 times higher when compared with the control, was found in the leaves of *C. montanus* 'Coy' when treated with saline solution at an EC of 10.0 dS·m^{-1}.

Calcium content in leaves of the native plants was significantly affected by salinity ($P < 0.0001$, Table 6); however, increase in Ca^{2+} content was less pronounced when compared with Na^+ and Cl^- contents. Compared with the control, there was less than 2 times increment of the Ca^{2+} content in the leaf tissue when plants were treated with saline solution at an EC of 10.0 dS·m^{-1}. Salinity treatments had no effects on K^+ content in the leaves of native plants, except *S. ×utahensis* 'Torrey', of which the K^+ content decreased when they were irrigated with saline solution at an EC of 10.0 dS·m^{-1}, compared with the control and those with saline solution at an EC of 5.0 dS·m^{-1} (Table 6). However, salinity stress dramatically decreased the K^+/Na^+ ratio in all plants ($P < 0.0001$). Similarly, Mg^{2+} content increased with increasing salinity levels in the irrigation water for *A. uva-ursi*, *C. ledifolius*, and *C. montanus* 'Coy'. Manganese content increased in *A. uva-ursi*, *C. montanus* 'Coy', and *S. ×utahensis* 'Torrey' at higher EC levels. Elevated salinity led to a slight decrease in S content of *C. ledifolius*, *C. montanus* 'Coy', and *S. ×utahensis* 'Torrey' (data not shown). However, the P, Fe, and Zn^{2+} contents of native plants did not vary among salinity treatments tested in this experiment (data not shown).

Proline content. Leaf proline content observed in the experiment was mostly species-dependent ($P < 0.0001$, Tables 2 and 7). *C. montanus* 'Coy' had the highest proline content of 16.2 µmol·g^{-1} when treated with saline solution at an EC of 10.0 dS·m^{-1} without differences among treatments. The proline content of *S. ×utahensis* 'Torrey' was the highest when treated with saline solution at an EC of 10.0 dS·m^{-1} compared with the lower salinity treatments.

Discussion

Landscape plant species have different abilities to tolerate salts in irrigation water. It is therefore necessary to evaluate and distinguish them for salt tolerance. In this study, four Utah-native plants with potential landscape use were investigated to determine their salinity tolerance. The salinity levels tested in this research were above 4.0 dS·m^{-1}, which is reported to cause soil salinity problems and affect plant productivity and quality (Chinnusamy et al. 2005; Shrivastava and Kumar 2015).

In the present study, several parameters were studied to evaluate the salinity tolerance of Utah-native plants. Aesthetic value is an important component when screening ornamental plants for salt tolerance, as foliar salt damage is problematic for many landscape plants (Cassaniti et al. 2012; Niu and Cabrera 2010; Veatch-Blohm et al. 2014). Researchers use visual ratings to compare relative salt tolerance among plant species (Cameron et al. 2004; Fox et al. 2005; Sun et al. 2015). Leaf burn and necrosis were observed on *A. uva-ursi*, *C. ledifolius*, and *C. montanus* 'Coy', but not on *S. ×utahensis* 'Torrey', which corresponds to the increasing salinity levels (Tables 3 and 8). According to these results, *S. ×utahensis* 'Torrey' was the most salt-tolerant species followed by *C. ledifolius*, whereas *A. uva-ursi* and *C. montanus* 'Coy' performed similarly and were relatively salt sensitive. Similarly, Young et al. (2012)

Table 4. Number of shoots and leaf area of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 dS·m^{-1}, control] or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks.

	No. of shoots			Leaf area (cm^2)		
Plants	Control	EC 5	EC 10	Control	EC 5	EC 10
Arctostaphylos uva-ursi	105.2 a[i]	77.8 b	–[ii]	1648 a	791 b	–
Cercocarpus ledifolius	8.4 a	7.1 a	6.7 a	180 a	173 a	101 b
Cercocarpus montanus 'Coy'	10.7 a	6.7 b	–	285 a	211 a	–
Shepherdia ×utahensis 'Torrey'	19.8 a	16.6 ab	13.4 b	1559 a	1230 a	1028 a

[i] Means with same lowercase letters within species and dependent variable are not different among treatments by Tukey's method for multiplicity at $\alpha = 0.05$.
[ii] *A. uva-ursi* and *C. montanus* 'Coy' were dead when treated with saline solution at an EC of 10 dS·m^{-1}.

Table 5. Shoot and root dry weight of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 dS·m^{-1}, control] or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks.

	Shoot dry wt (g)			Root dry wt (g)		
Plant	Control	EC 5	EC 10	Control	EC 5	EC 10
Arctostaphylos uva-ursi	52.4 a[i]	34.6 b	–[ii]	11.5 a	8.9 a	–
Cercocarpus ledifolius	10.1 a	11.1 a	8.5 a	5.3 a	5.6 a	4.9 a
Cercocarpus montanus 'Coy'	17.0 a	14.1 a	–	6.7 a	6.2 a	–
Shepherdia ×utahensis 'Torrey'	37.4 a	28.1 ab	25.6 b	12.8 a	10.9 a	11.5 a

[i] Means with same lowercase letters within species and dependent variable are not different among treatments by Tukey's method for multiplicity at $\alpha = 0.05$.
[ii] *A. uva-ursi* and *C. montanus* 'Coy' were dead when treated with saline solution at an EC of 10.0 dS·m^{-1}.

Table 6. Leaf mineral content and potassium to sodium (K^+/Na^+) ratio of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 dS·m^{-1}, control] or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks.

		Ion content (mg·g^{-1})[i]						
Plant	Treatment	Na^+	Cl^-	Ca^{2+}	K^+	K^+/Na^+	Mg^{2+}	Mn^{2+}
Arctostaphylos uva-ursi	Control	0.23 c[ii]	0.95 b	8.34 c	10.27 a	44.83 a	2.06 b	0.03 b
	EC5	4.80 b	22.49 a	11.9 b	9.83 a	2.05 b	2.48 ab	0.05 a
	EC10	8.32 a	22.94 a	16.81 a	10.95 a	1.32 b	3.04 a	0.07 a
Cercocarpus ledifolius	Control	0.05 c	0.88 c	8.70 b	12.47 a	272.80 a	2.49 b	0.02 a
	EC5	0.39 b	6.56 b	10.33 b	10.79 a	27.89 b	2.72 b	0.03 a
	EC10	4.11 a	47.13 a	15.30 a	11.95 a	2.91 c	3.45 a	0.03 a
Cercocarpus montanus 'Coy'	Control	0.07 c	1.16 c	11.55 b	13.79 a	189.34 a	2.11 b	0.04 b
	EC5	0.42 b	23.77 b	18.65 a	15.33 a	36.29 b	2.89 a	0.06 a
	EC10	5.54 a	51.89 a	21.88 a	14.43 a	2.61 c	3.13 a	0.08 a
Shepherdia ×utahensis 'Torrey'	Control	0.24 c	1.54 c	11.64 b	21.33 a	88.62 a	5.69 a	0.07 b
	EC5	1.92 b	6.65 b	19.00 a	20.74 a	10.78 b	6.36 a	0.12 a
	EC10	5.17 a	29.11 a	22.05 a	17.29 b	3.34 c	5.21 a	0.11 a
Plant		****[iii]	**	****	****	****	****	****
Treatment		****	****	****	NS	****	****	****
Plant × Treatment		****	****	NS	*	****	**	NS

[i] Sodium (Na^+), chloride (Cl^-), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), and manganese (Mn^{2+}) ions.
[ii] Means with same lowercase letters within a column and species are not different among treatments by Tukey's method for multiplicity at $\alpha = 0.05$.
[iii] NS, *, **, ***, **** Nonsignificant or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

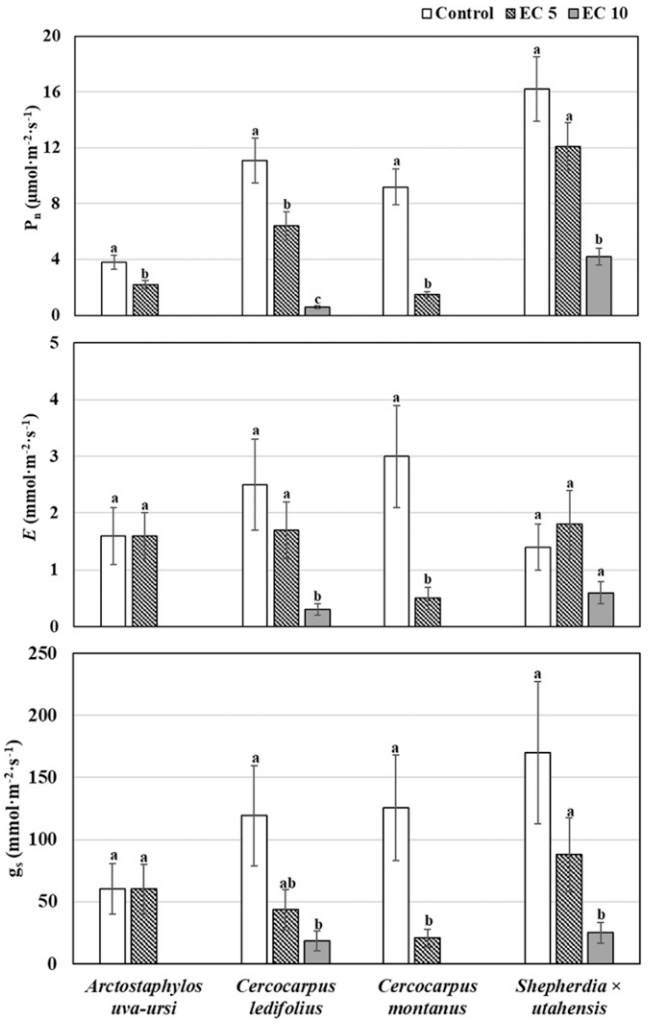

Fig. 4. Net photosynthesis rate (P_n), transpiration rate (E), and stomatal conductance (g_s) of container-grown plants native to Utah after irrigating with a nutrient solution (EC = 1.2 dS·m^{-1}, control) or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks. Vertical bars represent standard errors of five measurements. The same letters above column bars within species represent no significance between/among treatments as determined by Tukey's method for multiplicity at $\alpha = 0.05$. *Arctostaphylos uva-ursi* and *Cercocarpus montanus* 'Coy' died when treated with saline solution at an EC of 10.0 dS·m^{-1} so gas exchange data were not taken.

reported that *A. uva-ursi* became more brittle and drier with increasing NaCl concentration in irrigation water. *S. argentea* was described as highly tolerant to salinity, as it survived at the salinity level of 600 mM (~43.8 dS·m^{-1}) for at least 30 d (Qin et al. 2010).

Salinity stress is a critical factor that affects plant growth and metabolism. In the present study, salinity stress depressed plant growth and biomass, and affected survival of the native plants. Salt accumulation leads to leaf necrosis and senescence, which decreases the supply of carbohydrates and/or growth hormones to meristematic parts and inhibits plant growth (Acosta-Motos et al. 2017). Furthermore, leaf area was reduced with increasing salinity levels in irrigation solution in previous studies (Niu et al. 2012; Paudel et al. 2019; Sun et al. 2018), and in *A. uva-ursi*, *C. ledifolius*, and *C. montanus* 'Coy' in this current study. There was no difference in the leaf area of *S.* ×*utahensis* 'Torrey' among salinity treatments. In contrast, the leaf area of *S. argentea* significantly reduced at all tested salinity levels with 200, 400, and 600 mM NaCl solutions (~14.6, 29.2, and 43.8 dS·m^{-1}) (Qin et al. 2010). In our study, NaCl and $CaCl_2$ were used to prepare saline solution, but only NaCl was used in the study conducted by Qin et al. (2010). It is also possible that salt tolerance may have increased in the hybrid *S.* ×*utahensis* 'Torrey' compared with the parent *S. argentea*. In previous studies, hybrids were observed to be more salt tolerant than parents (Koonce et al. 2020; Zeng et al. 2015).

Biomass changes are parameters normally used to determine plant tolerance to salinity (Bastias et al. 2004; Gama et al. 2007). Plant growth and dry matter accumulation are often reduced in ornamental species under salinity stress (Alvarez et al. 2012; Cassaniti et al. 2012); however, these changes vary among species. In this study, there was a decreasing trend in the shoot dry weight of all four species but relatively lower reductions in root dry weight for *C. ledifolius*, *C. montanus* 'Coy', and *S.* ×*utahensis* 'Torrey'. This reflects that plants spend more photosynthetic energy on root production under salinity stress to maintain a relatively high water relation (Cheeseman 1988; Iqbal 2005).

During the experiment, leachate ECs from the substrate and EC of the substrate increased throughout the duration. Similarly, Paudel et al. (2019) and Xing et al. (2021) reported that leachate and substrate EC increased with saline water irrigation over time. Salt accumulation in the soilless substrate mainly depends on irrigation leaching fraction, salinity of irrigation water, irrigation frequency and amount, and substrate properties (Martinez and Clark 2009; Sharma and Minhas 2005). In field conditions, salt concentration in the soil can vary due to evaporation, irrigation water quality, rising water tables, rainfall, and soil properties (Munns and Tester 2008; Shrivastava and Kumar 2015).

Plants under salinity stress have reduced photosynthetic rates, which are mainly due to reductions in water potential. Accumulation of high Na^+ and/or Cl^- ions also inhibits P_n and directly interferes with plant growth (Zhang et al. 2014). In the present study, P_n of the native plants was reduced in response to salinity and negatively correlated with Na^+ and Cl^- contents in the leaf tissue ($P = 0.006$ and $P < 0.0001$, respectively, Table 8). Likewise, P_n of *S. argentea* was reduced when irrigated with saline solution of 600 mM (~43.8 dS·m^{-1}) NaCl (Qin et al. 2010). Furthermore, P_n was positively correlated with the visual scores of native plants ($P = 0.0002$, Table 8). *S.* ×*utahensis* 'Torrey', the most salt tolerant among the four native plants, and has higher P_n than the other three species, which suggests the more

Table 7. Proline content in leaves of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 dS·m^{-1}, control] or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks.[i]

	Proline content (μmol·g^{-1})		
Plant	Control	EC 5	EC 10
Arctostaphylos uva-ursi	0.6 a[ii]B[iii]	0.4 aB	0.3 aC
Cercocarpus ledifolius	1.3 aB	2.6 aA	2.2 aB
Cercocarpus montanus 'Coy'	10.3 aA	7.3 aA	16.2 aA
Shepherdia ×*utahensis* 'Torrey'	0.7 bB	2.6 bA	15.1 aA

[i] Leaves were harvested after the sixth irrigation event for proline estimation.
[ii] Means with same lowercase letters within species are not different among treatments by Tukey's method for multiplicity at $\alpha = 0.05$.
[iii] Means with same uppercase letters within a column are not different among species by Tukey's method for multiplicity at $\alpha = 0.05$.

Table 8. Correlation probability (upper triangular) and coefficients (lower triangular) for sodium (Na^+), chloride (Cl^-), potassium to sodium ratio (K^+/Na^+), visual score (VS), net photosynthesis rate (P_n), transpiration rate (E), and stomatal conductance (g_s) of container-grown plants native to Utah after irrigating with a nutrient solution [electrical conductivity (EC) = 1.2 dS·m^{-1}; control] or saline solution [EC = 5.0 dS·m^{-1} (EC 5) or 10.0 dS·m^{-1} (EC 10)] in a greenhouse for 8 weeks.

	Na^+	Cl^-	K^+/Na^+	VS	P_n	E	g_s
Na^+		<0.0001	<0.0001	<0.0001	0.0058	NS[1]	NS
Cl^-	0.7914		0.0002	<0.0001	<0.0001	0.0123	0.0157
K^+/Na^+	−0.5842	−0.5668		0.0023	0.0046	NS	NS
VS	−0.7821	−0.7622	0.4305		0.0002	NS	NS
P_n	−0.4341	−0.6440	0.4439	0.5550		NS	NS
E	−0.1709	−0.3973	0.1836	0.1864	0.1823		<0.0001
g_s	−0.1505	−0.3844	0.1470	0.1751	0.2196	0.9913	

[1] NS = nonsignificant.

tolerant species tended to have higher P_n than the more sensitive ones (Dong et al. 2019). According to our results, the increasing salinity levels decreased E and g_s of four native plants. This finding is consistent with a study for *S. argentea*, which had reductions in P_n, E, and g_s with the increase of salinity (Qin et al. 2010). It is believed that salinity-induced impairment in stomatal movement causes the reduction in E and g_s (Orzechowska et al. 2021). Limiting transpiration is an effective mechanism for plants using water efficiently, which further reduces the uptake of harmful salt ions (Hasegawa et al. 2000).

Nutrients have a role in the structure, metabolism, and osmoregulation of plant cells. Salinity disorders may result from nutrient availability, competitive uptake, transport, or partition within the plant. Sodium and Cl^- contents increased in leaves, stems, and roots of several ornamental plants treated with saline solutions (Alvarez et al. 2012; Paudel et al. 2020). In this study, Na^+ and Cl^- contents increased in the leaves of four native plants with increasing salinity levels. A negative correlation between visual score and Na^+ and Cl^- content was also observed ($P <$ 0.0001, Table 8). The Na^+ and Cl^- contents were highest in *A. uva-ursi* and *C. montanus* 'Coy', respectively, which might be responsible for their foliar injury. This suggests that *A. uva-ursi* and *C. montanus* 'Coy' might exhibit a low ability to exclude these ions from shoots and a low tolerance for Na^+ and/or Cl^- accumulation. The rapid increase of ions in the cell walls or cytoplasm when vacuoles can no longer sequester incoming salts causes salt injury in leaves (Acosta-Motos et al. 2017). In a saline environment, tolerating high salt concentrations in the upper parts of plants, restricting entry through the roots, and limiting transport to the shoots are important mechanisms that allow plants to survive under saline conditions (Colmer et al. 2005; Murillo-Amador et al. 2006). In this study, *S. ×utahensis* 'Torrey' showed tolerance to higher Na^+ and Cl^- content in the leaves.

Calcium helps in maintaining membrane integrity and ion-transport regulation and remediates the adverse effects of salinity on plants (Martinez-Ballesta et al. 2006; Nedjimi and Daoud 2009). Calcium uptake is generally disturbed under saline conditions (Alam et al. 2001), which leads to calcium deficiency similar to many horticultural crops under nonsaline conditions (Grattan and Grieve 1999). Reduced K^+ content in the roots due to salinity can be restored to adequate levels by an additional supply of Ca^{2+}, as it protects cell membranes from the adverse effects of Na^+ and minimizes the leakage of cytosolic K^+ (Tuna et al. 2007). Therefore, an adequate supply of Ca^{2+} in the solutions is important to control the severity of ion toxicities in the plants that are susceptible to NaCl injury (Qadir et al. 2001). In this study, $CaCl_2$ was added while preparing the saline solution (Table 1). Plants had higher Ca^{2+} content in leaf tissue under elevated salinity conditions.

Potassium has an important role in plant growth and development, and in maintaining cell turgor and membrane potential. In plants, K^+ is the major cation that counterbalances the negative charge of anions and plays an important role in the activation of enzymes responsible for metabolism, synthesis of proteins and carbohydrates, and regulation of stomatal movement (Rahneshan et al. 2018). The uptake of K^+ ions was not changed with increasing salinity levels during this experiment. However, the decrease in the K^+/Na^+ ratio with the increase in salinity levels suggests that Na^+ ions were transported in greater proportion to K^+ ions in leaves. Sodium competes with K^+ uptake through Na^+-K^+ cotransporters under salinity stress, as they have a similar chemistry (Jouyban 2012; Zhu 2003). A high cytosolic K^+/Na^+ ratio is essential for normal cellular functions in plants. Results from the current study suggest that there were no effective mechanisms in tested native plants to control the net uptake of Na^+ to leaf tissue.

Magnesium greatly contributes to the processes in chloroplasts including photosynthesis, where chlorophyll-bound Mg^{2+} accounts for 6% to 25% of the total Mg^{2+} content (Luczak et al. 2021). Furthermore, manganese is an essential element that acts as an enzyme cofactor or as a metal with catalytic activity in biological clusters (Andresen et al. 2018). It has been observed that salinity induces Mg^{2+} deficiency and affects plant growth (Khan et al. 2000). Conversely, Mg^{2+} and Mn^{2+} contents in the leaf tissue of four native plants remained the same or increased with increasing salinity levels (Table 6). Accumulation of these nutrients might be one of the strategies for these species to thrive in saline conditions. In addition, no effect on P, Fe, and Zn^{2+} content indicates that salinity stress was not imposing deficiency of these nutrients in these native plants.

Osmotic adjustment is another mechanism in plants for tolerating salinity stress. Solute accumulation helps plants to tolerate salinity by reducing the cellular solute potential (Hasegawa et al. 2000). Proline has a role in pH adjustment in the cytosol protecting cell membranes and proteins and brings reactive oxygen species into a normal range (Behzadi Rad et al. 2021). Proline is also known as a source of carbon and nitrogen for plant recovery after stress. In this study, the amount of proline in leaves remained similar for *A. uva-ursi*, *C. ledifolius*, and *C. montanus* 'Coy' in response to salinity stress; however, the amount of proline in *S. ×utahensis* 'Torrey' increased at high salinity levels. The high levels of proline in *S. ×utahensis* 'Torrey' may explain its higher tolerance to salinity compared with the other species. Many studies have demonstrated that higher proline content was observed in salt-tolerant than salt-sensitive species (Kumar et al. 2010; Mansour and Ali 2017). The reallocation of energy resources from cumulative growth to maintenance processes such as ion compartmentation and synthesis of proline could have contributed to a reduced biomass of *S. ×utahensis* 'Torrey' at high salinity levels.

Conclusions

Four Utah-native plants tested in this study showed some variations in response to salinity stress. *A. uva-ursi* and *C. montanus* 'Coy' had severe foliar salt damage and *C. ledifolius* had moderate to slight foliar salt damage at elevated salinity levels. However, *S. ×utahensis* 'Torrey' had no foliar salt damage. Saline solution irrigation reduced the growth and biomass of all four native species. Photosynthesis, E, and g_s of native plants also decreased after saline solution irrigation. Furthermore, salinity stress caused Na^+ and Cl^- uptake and accumulation. In addition, more proline was accumulated in leaves of *S. ×utahensis* 'Torrey' as a possible protective metabolic adaptation to prevent leaf tissue from damage under high salinity. Based on research results, *S. ×utahensis* 'Torrey' was considered salt tolerant, *C. ledifolius* was moderately salt tolerant, and *A. uva-ursi* and *C. montanus* 'Coy' were salt sensitive.

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