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Effect of Salt Stress on the Growth, Physiology, and Mineral Nutrients of Two Penstemon Species

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Abstract. **Penstemons are a diverse group of flowering plants valued for their ability to enhance the visual appearance of urban landscapes. *Penstemon barbatus* (Cav.) Roth 'Novapenblu' (rock candy blue® penstemon) and *Penstemon strictus* Benth 'Rocky Mountain' (rocky mountain beardtongue) are widely used in landscapes, but their tolerance to soil salinity remains poorly understood. This study aimed to investigate the effects of salinity levels at electrical conductivities (ECs) of 1.0 (nutrient solution), 2.5, 5.0, 7.5, and 10.0 dS·m^{-1} on two penstemons (*P. barbatus* and *P. strictus*). Penstemons were irrigated with nutrient or saline solution for 8 weeks and various growth and physiological data were recorded before harvest. Salinity stress degraded the visual quality of penstemon species and led to a reduction in the growth rate and biomass production. Leaf burn and necrosis were observed in penstemons because of salinity stress. The visual score of *P. barbatus* and *P. strictus* decreased with increasing EC levels in the saline solution. When irrigated with saline solution at an EC of 7.5 dS·m^{-1}, *Penstemon barbatus* and *P. strictus* had severe-to-moderate foliar salt damage with average visual scores of 1.7 and 2.5, respectively (0 = dead plant; 5 = excellent plant without any foliar damage). The two penstemon species had severe foliar salt damage or were dead when irrigated with saline solution at an EC of 10.0 dS·m^{-1}. There were 87% and 92% decreases in the leaf area of *P. barbatus* and *P. strictus*, respectively, when irrigated with saline solution at an EC of 10.0 dS·m^{-1} compared with those in the control. Although not statistically significant, there were 7% to 18% decreases in shoot dry weight of *P. barbatus* when irrigated with saline solutions at ECs of 2.5 to 10.0 dS·m^{-1} compared with control. However, *P. strictus* displayed declines of 13% to 31% in shoot dry weight as the salinity levels of the irrigation solution increased. As the salinity levels increased, the net photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration (E) rates decreased. Furthermore, sodium (Na^+) and chloride (Cl^-) contents of *P. barbatus* and *P. strictus* increased with the increase in salinity levels of the treatment solution. Consequently, *P. barbatus* and *P. strictus* demonstrated sensitivity to salinity stress at ECs of 7.5 and 10.0 dS·m^{-1}. This study provides important insights for their effective utilization in landscaping practices within saline-prone areas.**

Ornamental plants play a significant role in the horticultural industry because they are widely used in landscaping to create visually appealing outdoor environments. Traditionally, homeowners have used good-quality water to irrigate landscape plants because of the primary importance of their external appearance. However, landscape plants consume a substantial amount of water. The water requirement for producing 1 kg of dry matter in ornamental plants ranges from 100 kg to 350 kg, depending on the plant species, cultivation system, and growing environment (Fornes et al. 2007).

As the population and agricultural production increase, there is a growing competition for good-quality water. Although recycled water can be used to irrigate landscape plants, it often contains a higher salt content, which can lead to soil salinity (Carter and Grieve 2008). Recycled or reclaimed water is being used to irrigate landscape plants in many parts of the world, which can be a significant factor contributing to soil salinity in urban landscapes (Gorji et al. 2015). Ornamental plants are sold in potted containers filled with substrates such as peatmoss and grown under field conditions (Reid and Jiang 2012). Whether grown in pots or in landscapes, ornamental plants are influenced by soil salinity and irrigation water quality (Gracia-Caparros and Lao 2018).

The presence of excessive salts reduces the availability of water to plants by decreasing the soil water potential. As a result, plants experience limited access to water, hindering essential physiological processes such as nutrient uptake, photosynthesis, and cellular expansion (Munns 2002; Zhang et al. 2013). Excessive salt levels disrupt the ionic balance and impose osmotic stress on plants, resulting in severe damage to their morphology, biomass, and biochemical processes (Rahneshan et al. 2018; Zhang et al. 2013). Soil salinity leads to increased sodium (Na^+) and chloride (Cl^-) contents in plants, which affect the normal ionic activities in plants (Singh et al. 2014).

Plants have developed various strategies to combat these challenges, including osmotic adjustment, compartmentalization, which helps store excess Na^+ in the vacuole, and the synthesis of osmolytes (Queiros et al. 2009; Rahneshan et al. 2018; Silva et al. 2015). Osmolytes, such as proline, protect plant cells, aiding in osmotic adjustment and increasing salinity tolerance (Rahneshan et al. 2018). Additionally, high salt levels can affect the metabolism of sensitive plants and cause the accumulation of toxic ions, disrupting normal cellular processes (Munns and Tester 2008). The effects of salinity in various ornamental plants have been previously studied. For example, *Sedum telephium* (autumn joy) and *Sedum reflexum* (blue spruce) were considered relatively salt-tolerant, whereas *Sedum rupestre* (angelina) and *Evolvulus glomeratus* (blue daze) were found to be less tolerant (Hooks and Niu 2019). Similarly, *Tetraneuris acaulis* cultivar arizonica (arizona four-nerve daisy) was reported as a salt-tolerant species (Paudel et al. 2019).

Among the diverse array of ornamental plants, penstemons stand out as one of the most attractive native flowers of North America, with high aesthetic importance in urban landscape, leading to their increasing popularity. Penstemon represents America's largest endemic genus within the Plantaginaceae family, encompassing more than 270 species (Kramer 2009). These plants are commonly used in gardens because of their showy flowers during spring and summer (Lattier 2016) and have been used in ecological restoration efforts (Howe et al. 2006). Most penstemon species are drought-tolerant and thrive in well-drained soils (Kratsch 2011). In the United States, the annual sales of potted penstemon for garden and landscape uses are estimated at $3.2 million (US Department of Agriculture 2020).

Penstemon species are listed as herbaceous plants that have medium tolerance to saline soil (Jull 2009). Previous research of the salinity tolerance of penstemons is limited. Niu and Rodriguez (2006) investigated the salt tolerance of *Penstemon eatonii* A. Gray (firecracker penstemon), *Penstemon pseudospectabilis* M.E. Jones (desert beardtongue), and *Penstemon strictus* Benth. up to an electrical conductivity (EC) of 12.0 dS·m^{-1} and found that these plants exhibited low salt tolerance. Niu and Rodriguez (2006) studied the effect of salinity stress on plant growth, osmotic potential, and mineral nutrient content. However, they did not investigate the gas exchange rate of penstemons, which has been recorded in this present study. Similarly, Zollinger et al. (2007) reported that *Penstemon palmeri* A. Gray (palmer penstemon) showed intermediate levels of salt tolerance, whereas *Penstemon ×mexicali* 'Red Rocks' (red rocks penstemon) was relatively intolerant to salinity stress at 3000 mg·L^{-1} (~4.7 dS·m^{-1}). Zollinger et al. (2007) tested penstemons up to 5000 mg·L^{-1} (~6.3 dS·m^{-1}). However, during the present study, penstemons were tested for salinity levels up to an EC of 10.0 dS·m^{-1}. The present study aimed to access the morphological and physiological responses of two penstemon species, namely *Penstemon barbatus*

(Cav.) Roth 'Novapenblu' (rock candy blue® penstemon) and *Penstemon strictus* 'Rocky Mountain' (rocky mountain beardtongue), under salt stress. By examining their response to elevated salt levels, this research contributes to our understanding of the salt tolerance of penstemon species and inform their potential use in landscape and gardening practices. We hypothesized that *P. barbatus* and *P. strictus* irrigated with higher salinity levels exhibit foliar salt damage, decreased plant growth, and altered plant physiological status.

Materials and Methods

To assess the salinity tolerance of penstemons across varying salinity levels, a greenhouse study was conducted. The experiment was focused on investigating the morphological, physiological, and biochemical attributes of the penstemons under controlled conditions.

Plant materials and culture conditions. The experiment was conducted at the Utah State University Research Greenhouse in Logan, UT, USA. *Penstemon barbatus* (Cav.) Roth 'Novapenblu' (rock candy blue® penstemon) and *Penstemon strictus* 'Rocky Mountain' (rocky mountain beardtongue) in 2.8-L injection molded polypropylene containers (Pro-Cal™; South Gate, CA, USA) were purchased from Perennial Favorites (Layton, UT, USA). The plants were transplanted into 7.6-L injection molded polypropylene containers (No. 2B; Nursery Supplies, Orange, CA, USA) filled with a soilless growing medium (Metro-Mix® 820; Canadian sphagnum peatmoss, 35% to 45% composted pine bark, coir, coarse perlite, and dolomitic limestone; SunGro Horticulture, Agawam, MA, USA) on 2 May 2022. Logan City potable water (EC = 0.35 ± 0.01 $dS \cdot m^{-1}$; pH = 7.7 ± 0.2, mean ± *SD*) was applied to plants when needed. Penstemons were pruned to 12 cm tall, and flowers were removed. Uniform plants that were free from any visible signs of stress or disease were then selected for the salinity study. A shadecloth (60%) was placed at the top of the greenhouse during the research period. The experiment started on 16 Jun 2022 and ended on 12 Aug 2022. Plants were grown in the greenhouse with day temperatures of 26.2 ± 0.5 °C, night temperatures of 22.8 ± 0.6 °C, and a daily light integral of 13.0 ± 2.9 $mol \cdot m^{-2} \cdot d^{-1}$.

Treatments. This study exposed penstemons to either a nutrient or a saline solution at ECs of 1.0, 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$. The nutrient (control) solution was prepared in a 100-L tank by adding 0.8 $g \cdot L^{-1}$ 15N–2.2P–12.5K water-soluble fertilizer (Peters Excel 15–5–15 Cal-Mag Special; ICL Specialty Fertilizers, Dublin, OH, USA) to reverse osmosis water. The saline solutions were prepared by adding sodium chloride (NaCl; Fisher Scientific, Waltham, MA, USA) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$; Hi Valley Chemical, Centerville, UT, USA) to the nutrient solution at a molar ratio of 2:1 (Table 1). The initial pH of the treatment solutions was adjusted to 6.0 to 6.5 using 88% potassium hydroxide pellets (Sigma-Aldrich, St. Louis, MO, USA) or 1 M nitric acid (Fisher Chemical, Fair Lawn, NJ, USA) as needed. The EC, sodium adsorption ratio (SAR), adjusted SAR (Lesch and Suarez 2009), and elemental analysis results were confirmed by the Utah State University Analytical Laboratory (Logan, UT, USA) (Table 1). Treatment solutions of 1200 mL per pot were manually applied weekly, and 30% of the leachate volume was maintained. The treatment solutions were applied using a beaker through the top of the pot in the morning of each week. Plants were irrigated with 500 to 600 mL of reverse osmosis water when the top (~1 cm) soilless medium was dry to avoid the confounding effects of drought.

Leachate and substrate EC. The EC of the leachate was measured by the pour-through method as described by Cavins et al. (2008) using an EC meter (LAQUA Twin; Horiba, Kyoto, Japan) after applying the treatment solution. When the leachate EC was greater than that of the treatment solution, the substrate was washed with reverse osmosis water to maintain similar EC levels in the substrate over time. A single plant was chosen for the measurement of leachate EC in each treatment for each species. After harvest, the substrate EC was determined using the saturated paste extraction method with some changes (Gavlak et al. 2005) after the substrate was left to dry for 2 weeks. Five plants were chosen for measurement in each treatment. The leachate and substrate EC data were pooled across the species because there were no differences observed between species.

Visual quality. A visual score of 0 to 5 was assigned to each plant biweekly based on the percentage of leaves with burnt leaves or necrosis (Sun et al. 2015) (Table 2). A score of 0 indicated that the plant was dead. A score of 1 indicated severe foliar damage (>90%). A score of 2 indicated moderate foliar damage (51%–90%). A score of 3 indicated slight foliar damage (10%–50%). A score of 4 indicated good quality with minimal foliar damage (<10%). A score of 5 indicated excellent quality without any foliar damage. The plant growth was not considered while determining the visual score.

Growth parameters and plant harvest. Plant heights (centimeters) were recorded at the beginning and end of the experiment. At harvest, the area (square centimeters) of all leaves was measured for all the surviving plants using a leaf area meter (LI-3100; LI-COR® Biosciences, Lincoln, NE, USA). Additionally, the shoot dry weight (DW) (stem DW + leaf DW) and the root DW of plants were determined by drying the plants for 1 week at 60 °C.

Chlorophyll content, chlorophyll fluorescence, and leaf gas exchange. Relative chlorophyll content (or leaf greenness) of all plants was determined using a chlorophyll meter [Soil Plant Analysis Development (SPAD)-502; Minolta Camera, Osaka, Japan] before harvest. Eight mature leaves from each plant were measured, and the average value was recorded.

The maximum photochemical quantum yield of photosystem II (PSII) [$F_v/F_m = (F_m - F_o)/F_m$] was measured on dark-adapted leaves using a chlorophyll fluorometer (PEA version 12.1; Hansatech Instrument Ltd., Norfolk, UK), where F_o denotes the minimum fluorescence at low-modulated light and F_m denotes the maximum fluorescence signal at saturating light. Six plants for each species and treatment were used for measurement. First, leaves were adapted in the dark for at least 30 min using leaf clips (diameter, 4 mm) (Hansatech Instrument Ltd.). Measurements were performed in the middle of fully developed leaves on both species. Additionally, the performance index (PI_{abs}) for energy conservation from photons absorbed by PSII was recorded.

Leaf gas exchange of five plants for each species and treatment was measured using a portable photosynthesis system (CIRAS-3; PP Systems, Amesbury, MA, USA) with an automatic universal leaf cuvette (PLC3; PP Systems). The leaf net photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration rate (E) of plants in each treatment were recorded based on the measured carbon dioxide (CO_2) and water vapor (H_2O) exchange on the youngest fully emerged leaves. All plants were watered 1 d before measurements to avoid water stress condition.

Mineral analyses. Dried penstemon leaves were ground with a stainless-steel Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) and allowed to pass through a 1-mm mesh screen. The powder samples were analyzed at the Utah State University Analytical Laboratories for mineral contents. In brief, the concentrations of Na^+, calcium (Ca^{2+}), potassium (K^+), boron (B), magnesium (Mg^{2+}), phosphorus (P), zinc (Zn^{2+}), and manganese

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Table 1. Calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^{+}), sulphate (SO_4^{2-}), chloride (Cl^{-}), and boron (B) contents, sodium adsorption ratio (SAR), adjusted SAR, and electrical conductivity (EC) of nutrient and saline solutions used to irrigate penstemon plants.

Item	Nutrient solution[i]	Saline solution[ii]			
		2.5 dS·m^{-1}	5.0 dS·m^{-1}	7.5 dS·m^{-1}	10.0 dS·m^{-1}
NaCl		30.9	91.7	145.0	226.5
$CaCl_2{\cdot}2H_2O$		39.5	116.7	183.0	280.4
Ca^{2+} (mg·L^{-1})	48.1	189.7	448.6	723.3	960.7
Mg^{2+} (mg·L^{-1})	17.8	18.9	18.6	14.2	15.4
Na^{+} (mg·L^{-1})	1.3	140.8	374.0	638.1	876.1
SO_4^{2-} (mg·L^{-1})	2.7	3.1	3.5	5.5	5.3
Cl^{-} (mg·L^{-1})	1.1	428.0	1360.0	2280.0	3050.0
B (mg·L^{-1})	0.2	0.2	0.2	0.2	0.2
SAR	0.04	2.6	4.7	6.4	7.7
Adjusted SAR	0.1	3.6	7.7	11.8	14.6
EC (dS·m^{-1})	1.0 ± 0.1	2.5 ± 0.1	5.1 ± 0.1	7.6 ± 0.2	10.1 ± 0.2

[i] The nutrient solution at an electrical conductivity (EC) of 1.0 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 reverse osmosis water.

[ii] Sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2{\cdot}2H_2O$) were added at a molar ratio of 2:1 to the nutrient solution to prepare the saline solution.

(Mn^{2+}) were determined using nitric/hydrogen peroxide following the protocol described by Gavlak et al. (2005). The concentration of Cl^{-} was measured using a Flow Injection Analysis and Ion Chromatograph System (QuikChem 8000; Lachat Instrument, Loveland, CO, USA) and expressed on a dry plant basis (mg·g^{-1}). To determine the levels of Na^{+}, Ca^{2+}, K^{+}, B, Mg^{2+}, P, Zn^{2+}, and Mn^{2+}, 0.5 g of powdered samples were mixed with 6 mL of nitric acid (HNO_3) in a digestion tube, which was then subjected to a digestion block for 10 min at 80 °C, followed by cooling for 2 min. A total of 2 mL of 30% hydrogen peroxide (H_2O_2) was added into the digestion tube that was again placed in the digestion block at 130 °C for 1 h. The digestion tubes were mixed using a vortex stirrer. 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 inductively coupled plasma-optical emission spectrometry (iCAP 6300 ICP-AES; Thermo Scientific, Waltham, MA, USA) and reported based on DW (mg·g^{-1}).

Proline estimation. The acid-ninhydrin method was used for the quantification of proline in penstemons (Bates et al. 1973; Claussen 2005; Rakesh et al. 2021). In brief, leaf samples collected after the sixth irrigation event were frozen in liquid nitrogen and subsequently stored at −80 °C until use. Leaf samples (0.2 g) were ground in 5 mL of 3% sulfosalicylic acid (Spectrum Chemical, Gardena, CA, USA) and centrifuged for 5 min at room temperature using a benchtop centrifuge (Spectrafuge™ Labnet 6C Centrifuge; The Laboratory Depot, Dawsonville, GA, USA) with 5000 g_n. After centrifugation, 200 µL of supernatant, 200 µL of glacial acetic acid (Fisher Chemical, Fair Lawn, NJ, USA), and 200 µL of acid ninhydrin (Sigma-Aldrich, St. Louis, MO, USA) were combined 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, Colonnade Road, Ottawa, ON, USA) was added to each tube, and the mixture was vortexed and left to settle for 10 min. The upper layer of 200 µL of the resulting solution was pipetted to a microplate reader (Greiner bio-one; Cellstar, F-bottom, Monroe, NC, USA). Absorbance was recorded using a spectrophotometer (Spectra max M2; Molecular Devices, CA, USA) at 520 nm. Proline (L-Proline, St. Louis, MO, USA) was taken as standard, and a graph was plotted to estimate the proline content in the samples. The concentration of proline was calculated as follows:

$$\mu\text{mol}\cdot\text{g}^{-1}\ \text{tissue} = \mu\text{g proline}\cdot\text{mL}^{-1} * \text{mL toluene}/115.5 * 25\cdot\text{g}^{-1}\ \text{sample}$$

Experimental design and statistical analysis. The experiment was conducted using a randomized complete block design with 10 replications encompassing five treatments and two species. Each experimental unit consisted of one pot containing a single plant. Statistical analyses were conducted using SAS (version 14.1; SAS Institute, Cary, NC, USA) with PROC MIXED procedure. An analysis of variance (ANOVA) was performed to evaluate the effects of saline solution irrigation and species on various plant characteristics, including growth, gas exchange, and mineral nutrients. To normalize the data, logarithmic transformation was applied for all response variables to improve model performance. Dead plants were excluded from the data analysis of all parameters except for the visual score. Because of the diverse growth habits of each species, means separation among treatments was adjusted using Tukey's method for multiplicity at $\alpha = 0.05$. Furthermore, means separation between species was conducted for proline content. To explore relationships, correlation analyses were performed between visual scores, Na^{+} and Cl^{-} contents, and K^{+}/Na^{+} and Ca^{2+}/Na^{+} ratios. Correlation analyses of gas exchange parameters, Na^{+} and Cl^{-} contents, and K^{+}/Na^{+} and Ca^{2+}/Na^{+} ratios were performed. Additionally, linear and quadratic trend analyses of the plant growth data were performed.

Results

During this study, we delve into the effects of salinity stress on *P. barbatus* and *P. strictus*, with a focus on visual quality, plant growth, and physiological parameters. Understanding these responses is critical to formulating strategies to mitigate the adverse effects of salinity stress on urban landscapes.

Visual score and plant growth parameters. Salt damage was observed on penstemon species at higher salinity levels, mainly in the form of burnt leaves and necrosis (Fig. 1). After the second irrigation event, visual scores were affected by salinity ($P < 0.0001$) (Table 3), and an interaction was observed between species × salinity ($P = 0.004$). The

Table 2. Visual score of penstemon plants in response to salinity stress.

Visual score	Salt damage[i]	Percentage of foliar salt damage (%)
0	Dead plants because of salinity stress	100
1	Severe foliar salt damage	>90
2	Moderate foliar salt damage	51–90
3	Slight foliar salt damage	10–50
4	Minimal foliar salt damage	<10
5	No foliar salt damage	0

[i] Burn and necrosis symptoms of penstemon leaves.

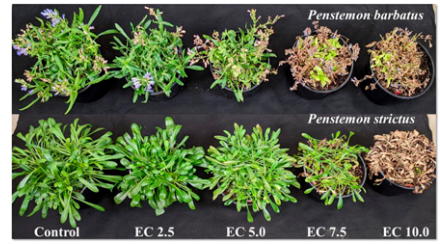

Fig. 1. Photos of representative penstemons after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} (control) and saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse.

Table 3. Summary of the analysis of variance of the effects of species, treatments, and their interactions on visual score (VS) of *Penstemon barbatus* and *P. strictus* after irrigating with a nutrient solution [electrical conductivity (EC) = 1.0 dS·m^{-1}] or saline solution (EC = 2.5, 5.0, 7.5, or 10.0 dS·m^{-1}) for a period of 2, 4, 6, and 8 weeks, as well as on the increase in plant height (Ht), leaf area (LA), shoot dry weight (DW), root DW, chlorophyll content [Soil Plant Analysis Development (SPAD)], chlorophyll fluorescence parameters (F_v/F_m and PI_{abs}), net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (E), and proline content after irrigating for a period of 8 weeks in a greenhouse.

	Analysis of variance														
Source	VS (2)	VS (4)	VS (6)	VS (8)	Ht	LA	Shoot DW	Root DW	SPAD	F_v/F_m	PI_{abs}	P_n	g_s	E	Proline
Species (S)	**[1]	***	***	*	NS	****	****	****	****	NS	NS	**	NS	NS	****
Treatment (T)	****	****	****	****	****	****	**	**	****	****	****	****	****	****	NS
S × T	**	**	****	NS	****	**	NS	NS	****	**	**	*	NS	NS	NS

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

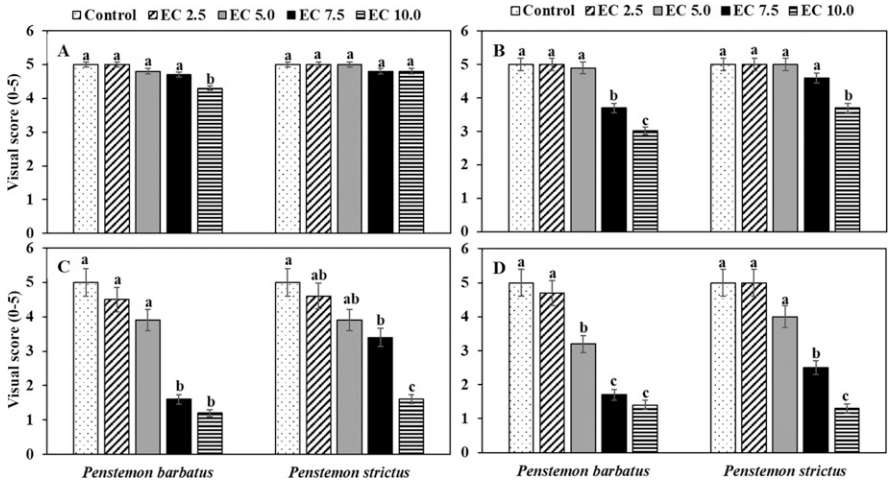

Fig. 2. Visual scores of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} (control) and saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period 2 (**A**), 4 (**B**), 6 (**C**), and 8 (**D**) weeks in a greenhouse. Vertical bars represent *SE*s of 10 plants. The same letters above column bars within species represent no significance among treatments as determined by Tukey's method for multiplicity at $\alpha = 0.05$. Visual scores: 0 = dead plant caused by salinity stress; 1 = severe foliar damage (burnt leaves and necrosis, >90%); 2 = moderate foliar damage (51%–90%); 3 = slight foliar damage (10%–50%); 4 = good quality with minimal foliar damage (<10%); and 5 = excellent without foliar damage (Sun et al. 2015).

average visual score of *P. barbatus* at an EC of 10.0 dS·m^{-1} was 4.3, which was lower than that of other treatments (Fig. 2). After the fourth irrigation event, visual scores were affected by salinity ($P < 0.0001$), and an interaction was observed between species × salinity ($P = 0.002$) (Table 3). *Penstemon barbatus* had an average visual score of 3.7 when irrigated with saline solution at an EC of 7.5 dS·m^{-1} (Fig. 2). However, minimal to no foliar salt damage was observed in *P. strictus* for up to 4 weeks. When irrigated with saline solution at an EC of 10.0 dS·m^{-1}, the visual scores were 3.0 and 3.7 for *P. barbatus* and *P. strictus*, respectively. After the sixth irrigation event, visual scores were affected by salinity ($P < 0.0001$), and an interaction was observed between species × salinity ($P < 0.0001$) (Table 3). *Penstemon barbatus* and *P. strictus* had average visual scores of 1.6 and 3.4, respectively, when irrigated with saline solution at an EC of 7.5 dS·m^{-1} (Fig. 2). Visual scores were 1.2 and 1.6, respectively, when *P. barbatus* and *P. strictus* were irrigated with saline solution at an EC of 10.0 dS·m^{-1}. When irrigated with saline solution at ECs of 7.5 and 10.0 dS·m^{-1}, one *P. barbatus* plant in each treatment died. Finally, after the eighth irrigation event, salinity affected the visual score ($P < 0.0001$), and the interaction between species × salinity was insignificant (Table 3). Visual scores were 3.2 and 4.0 for *P. barbatus* and *P. strictus*, respectively, when irrigated with saline solution at an EC of 5.0 dS·m^{-1} (Fig. 2). *Penstemon barbatus* and *P. strictus* had average visual scores of 1.7 and 2.5, respectively, when irrigated with saline solution at an EC of 7.5 dS·m^{-1}. Similarly, visual scores were 1.4 and 1.3, respectively, when *P. barbatus* and *P. strictus* were irrigated with saline solution at an EC of 10.0 dS·m^{-1}. Furthermore, two *P. barbatus* died when irrigated with saline solution at an EC of 7.5 dS·m^{-1}. At an EC of 10.0 dS·m^{-1}, three *P. barbatus* and five *P. strictus* plants were dead.

After 8 weeks of growing under different saline solutions, the two penstemon species exhibited differences in terms of growth measurements. Saline solution irrigation significantly impacted the height of penstemon plants ($P < 0.0001$) (Table 3), leading to an 84% to 94% reduction in the height of *P. barbatus* at ECs of 7.5 and 10.0 dS·m^{-1} compared with the control (Table 4). However, there was no notable difference in the plant height of *P. strictus* among treatments. Furthermore, leaf area varied significantly with species and salinity ($P < 0.0001$) (Table 3). The leaf area of *P. barbatus* and *P. strictus* decreased linearly with increasing EC levels in the saline solution ($P < 0.0001$) (Table 4). In addition, the leaf area of *P. strictus* decreased quadratically ($P < 0.0001$). Compared with the control, there was an 87% reduction in the leaf area of *P. barbatus* when irrigated with saline solutions at ECs of 7.5 and 10.0 dS·m^{-1}. Similarly, a 69% to 92% reduction in the leaf area of *P. strictus* was observed when irrigated with saline solutions at ECs of 7.5 and 10.0 dS·m^{-1}. Furthermore, although it is not statistically significant, there was a 12% to 39% reduction in the leaf area of *P. barbatus* and *P. strictus* when irrigated with saline solutions at ECs of 2.5 and 5.0 dS·m^{-1}.

Shoot dry weight was impacted by salinity ($P = 0.003$) (Table 3). The shoot dry weight of *P. strictus* decreased linearly with increasing EC levels in the saline solution

Table 4. Increase in the plant height (ht) and leaf area of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} or saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse.

	Plant ht (cm)		Leaf area (cm^2)	
EC (dS·m^{-1})	*P. barbatus*	*P. strictus*	*P. barbatus*	*P. strictus*
1.0	12.6 a[1]	4.2 a	991 a	1832 a
2.5	9.8 a	5.2 a	775 a	1614 a
5.0	10.6 a	5.9 a	610 a	1361 a
7.5	0.7 b	4.0 a	132 b	576 b
10.0	2.0 b	2.1 a	128 b	145 c
Linear	NS[ii]	NS	<0.0001	<0.0001
Quadratic	NS	NS	NS	<0.0001

[1] The mean values within a column for each species followed by the same letters are not significantly different at $\alpha = 0.05$ according to Tukey's method for multiplicity.
[ii] NS, not significant at $P < 0.05$.

Table 5. Dry weights (DWs) of shoots and roots of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} or saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse.

	Shoot DW (g)		Root DW (g)	
EC (dS·m^{-1})	*P. barbatus*	*P. strictus*	*P. barbatus*	*P. strictus*
1.0	23.2 a[i]	31.4 a	21.0 ab	54.2 ab
2.5	21.6 a	27.2 ab	25.5 a	47.8 ab
5.0	19.1 a	27.2 ab	11.6 b	55.2 a
7.5	21.6 a	21.9 b	10.6 b	41.2 ab
10.0	20.4 a	21.6 b	11.6 b	26.9 b
Linear	NS[ii]	0.02	NS	0.01
Quadratic	NS	NS	NS	0.047

[i] The mean values within a column for each species followed by the same letters are not significantly different at $\alpha = 0.05$ according to Tukey's method for multiplicity.
[ii] NS, not significant at $P < 0.05$.

($P = 0.02$) (Table 5). Compared with the control, although not significant, there were 7%, 18%, 7%, and 12% decreases in shoot DW of *P. barbatus* when irrigated with saline solutions at ECs of 2.5, 5.0, 7.5, and 10.0 dS·m^{-1}, respectively. Similarly, shoot DW of *P. strictus* decreased by 13%, 13%, 30%, and 31%, respectively, when irrigated with saline solutions at ECs of 2.5, 5.0, 7.5, and 10.0 dS·m^{-1}. Furthermore, root DW was significantly impacted by salinity ($P = 0.004$) (Table 3). Root DW of *P. strictus* decreased linearly ($P = 0.01$) and quadratically ($P = 0.047$) with increasing EC levels in the saline solution (Table 5). There were 45% to 50% decreases in root DW of *P. barbatus* when irrigated with saline solution at ECs of 5.0 to 10.0 dS·m^{-1} compared with the control. Similarly, when irrigated with saline solution at an EC of 10.0 dS·m^{-1}, there was a 50% reduction in root DW of *P. strictus*.

The visual quality and growth data suggest that the penstemons underwent salinity stresses, which can be attributed to the accumulation of salts in the substrate. The EC of the leachate solution remained consistent throughout the experiment (Fig. 3). In addition, the pH of the leachate solution during the experiment was 6.6 ± 0.4. However, the EC of the substrate increased with increasing EC level of saline solution (Fig. 4). The average ECs of the substrate were 11.5, 13.4, and 15.2 dS·m^{-1} when irrigated with saline solution at ECs of 5.0, 7.5, and 10.0 dS·m^{-1}, respectively.

Relative chlorophyll content, chlorophyll fluorescence, and gas exchange. The relative chlorophyll content (SPAD reading) of two penstemon species varied with species and salinity ($P < 0.0001$) (Table 3). There were 28% and 26% reductions in the SPAD readings of *P. barbatus* and *P. strictus*, respectively, at an EC of 5.0 dS·m^{-1} compared with those of the control (Fig. 5). Likewise, 71% and 40% reductions in the SPAD readings were observed in *P. barbatus* and *P. strictus*, respectively, when irrigated with saline solution at an EC of 7.5 dS·m^{-1}. In addition, F_v/F_m and PI_{abs} readings varied with salinity levels ($P < 0.0001$) (Table 3). *Penstemon barbatus* had significant reductions in both F_v/F_m and PI_{abs} when irrigated with saline solution at an EC of 7.5 dS·m^{-1}, but readings were similar for *P. strictus* among treatments.

The net photosynthetic rate (P_n) of two penstemon species decreased with increasing salinity levels of the solution ($P < 0.0001$) (Table 3). In addition, P_n varied with species ($P = 0.0024$) and showed interactive effects between species and salinity levels ($P = 0.0477$). *Penstemon barbatus* had a P_n of 13.1 μmol·m^{-2}·s^{-1} when irrigated with saline solution at an EC of 2.5 dS·m^{-1} (Fig. 6). The net photosynthetic rate of *P. barbatus* decreased from 18.6 μmol·m^{-2}·s^{-1} to 7.9 μmol·m^{-2}·s^{-1} when irrigated with saline solution at an EC of 5.0 dS·m^{-1}. Similarly, P_n of *P. strictus* decreased from 20.1 μmol·m^{-2}·s^{-1} to 12.6 and 9.5 μmol·m^{-2}·s^{-1} when irrigated with saline solutions at ECs of 5.0 and 7.5 μmol·m^{-2}·s^{-1}, respectively.

The stomatal conductance (g_s) also decreased with increasing salinity levels ($P < 0.0001$) (Table 3). The g_s of *P. barbatus* decreased from 731.3 to 252.3 mmol·m^{-2}·s^{-1} when irrigated with saline solution at an EC of 5.0 dS·m^{-1} (Fig. 6). Similarly, g_s decreased from 783.7 to 174.9 mmol·m^{-2}·s^{-1} for *P. strictus* when irrigated with saline solution at an EC of 7.5 dS·m^{-1}. The transpiration rate (E) decreased as salinity levels in the solution increased for two penstemon species ($P < 0.0001$) (Table 3). The E of *P. barbatus* decreased from 10.3 to 5.4 mmol·m^{-2}·s^{-1} when irrigated with saline solution at an EC of 5.0 dS·m^{-1} compared with the control (Fig. 6). Similarly, E decreased from 10.4 to 4.8 mmol·m^{-2}·s^{-1} for *P. strictus* when irrigated with saline solution at an EC of 7.5 dS·m^{-1}.

Mineral nutrients. Leaves accumulated significant number of anions and cations, particularly Na^+ and Cl^- ($P < 0.0001$) (Table 6). There was a significant effect of species on Na^+ accumulation in leaves ($P < 0.0001$), but not on Cl^-. After 8 weeks of irrigation, the Na^+ content of control plants was 0.05 mg·g^{-1} for *P. barbatus* and 0.03 mg·g^{-1} for *P. strictus*. However, the Na^+ content increased to 5.02 mg·g^{-1} for *P. barbatus* and 2.80 mg·g^{-1} for *P. strictus* when irrigated with saline solution at an EC of 10.0 dS·m^{-1}, which were 99-times and 92-times greater than that of their respective controls. Similarly, control plants had Cl^- contents of 2.3 and 3.0 mg·g^{-1} for *P. barbatus* and *P. strictus*, respectively. However, the Cl^- content increased to 51.1 and 53.5 mg·g^{-1} for *P. barbatus* and *P. strictus*, respectively, when irrigated with saline solution at an EC of 10.0 dS·m^{-1}; these were 21-times and 17-times greater than that of their respective controls.

A low increment was observed in the Ca^{2+} content with increasing salinity levels in the solution, but the content varied with both species and salinity ($P < 0.0001$) (Table 6). After 8 weeks of irrigation, the Ca^{2+} content increased from 20.6 to 32.5 mg·g^{-1} for *P. barbatus* and from 11.7 to 25.5 mg·g^{-1} for *P. strictus* when irrigated with saline solution at an EC of 10.0 dS·m^{-1} compared with control plants.

The reduction in the K^+ content was observed in leaves with increasing salinity levels in the solution ($P = 0.04$) (Table 6). *Penstemon strictus* had 10.9%, 18.4%, 8.8%, and 23.4% reductions in the K^+ content when irrigated with saline solutions at ECs of 2.5, 5.0, 7.5, and 10.0 dS·m^{-1}, respectively, compared with the control. Similarly, there were 15.3%, 9.7%, 2.7%, and 10.8% reductions in the K^+ content of *P. barbatus* leaves when

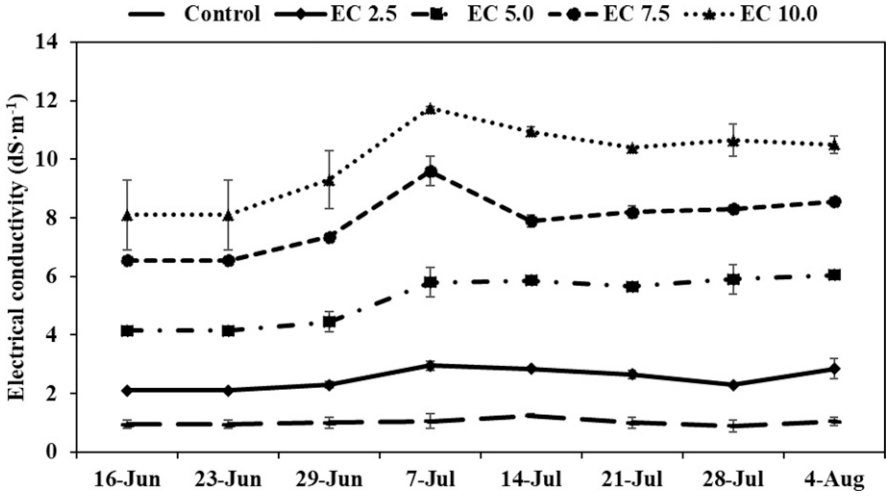

Fig. 3. Electrical conductivity (EC) of leachate solution over the course of the experiment collected after *Penstemon barbatus* and *P. strictus* were irrigated with a nutrient solution at an EC of 1.0 dS·m^{-1} (control) and saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse. Vertical bars represent *SE*s of two measurements.

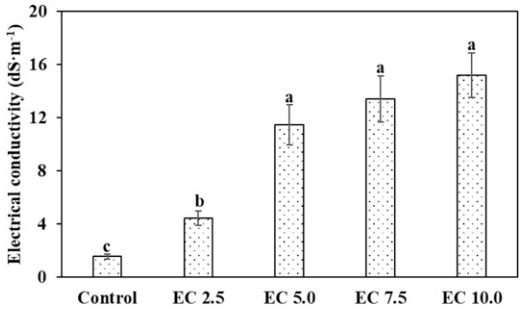

Fig. 4. Electrical conductivity (EC) of soil extraction from *Penstemon barbatus* and *P. strictus* irrigated with a nutrient solution at an EC of 1.0 dS·m^{-1} (control) and saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse. Vertical bars represent *SE*s of five measurements.

irrigated with saline solutions at ECs of 2.5, 5.0, 7.5, and 10.0 dS·m^{-1}, respectively, compared with the control. However, these reductions were not statistically significant. Furthermore, the K^+/Na^+ and Ca^{2+}/Na^+ ratios in penstemon leaves also varied with species and salinity ($P < 0.0001$) (Table 6). As salinity levels increased in the solutions, a decrease in both ratios was observed. The K^+/Na^+ ratio was 112-times and 138-times greater in control for *P. barbatus* and *P. strictus*, respectively, than that in those irrigated with saline solution at an EC of 10.0 dS·m^{-1}. Similarly, the Ca^{2+}/Na^+ ratio was 63-times and 48-times greater in control for *P. barbatus* and *P. strictus* than that in those irrigated with saline solution at an EC of 10.0 dS·m^{-1}, respectively.

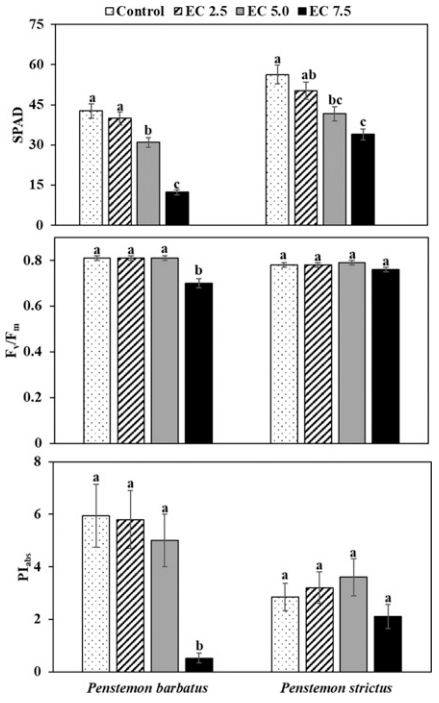

Fig. 5. Chlorophyll content [Soil Plant Analysis Development (SPAD)], chlorophyll fluorescence parameters (F_v/F_m, and PI_{abs}) of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} (control) and saline solutions with varying EC levels ranging from 2.5 to 7.5 dS·m^{-1} for a period of 8 weeks in a greenhouse. Vertical bars represent standard errors of 10 measurements for SPAD and six measurements for F_v/F_m, and PI_{abs}. The same letters above column bars within species represent no significance among treatments as determined by Tukey's method for multiplicity at $\alpha = 0.05$. Penstemons were dead or had severe foliar salt damage when treated with saline solution at an EC of 10.0 dS·m^{-1}; therefore, the chlorophyll content and fluorescence data were not taken.

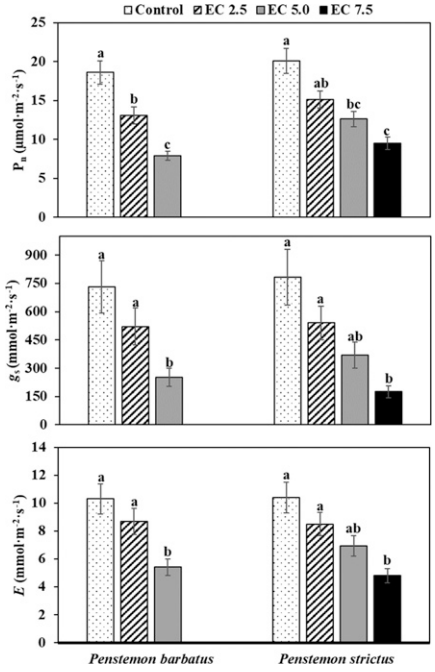

Fig. 6. Net photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration rate (E) of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} (control) and saline solutions with varying EC levels ranging from 2.5 to 7.5 dS·m^{-1} for a period of 8 weeks in a greenhouse. Vertical bars represent *SE*s 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 $\alpha = 0.05$. Gas exchange data of *P. barbatus* at ECs of 7.5 and 10.0 dS·m^{-1} and *P. strictus* at an EC of 10.0 dS·m^{-1} were not measured as plants had severe foliar salt damage or were dead.

In addition, the B content decreased with increasing salinity levels in the solutions for *P. barbatus* and *P. strictus* ($P < 0.0001$) (Table 7). The Mg^{2+} content remained similar among treatments but varied with species. Furthermore, saline solutions had a significant impact on the P, Zn^{2+}, and Mn^{2+} contents of penstemons.

Proline content. The leaf proline content observed in the experiment was mostly species-dependent ($P < 0.0001$) (Table 3). There was no difference among salinity levels in the proline content of *P. barbatus* and *P. strictus* (Table 8). However, a greater proline content was observed in *P. strictus* when compared with that in *P. barbatus*. *Penstemon strictus* had the highest proline content of 1.2 μmol·g^{-1} when irrigated with saline solution at an EC of 7.5 dS·m^{-1}.

Discussion

Salinity stress can severely impact the overall appearance of plants, making visual quality assessments crucial when evaluating the aesthetic appeal and market value of ornamental plants in landscaping projects and horticultural industries. Visual quality considers factors such as flowers, foliage color, texture, shape, and form. The present data revealed the detrimental effects of salinity on the visual quality of *P. barbatus* and *P. strictus* caused by leaf burn and necrosis. The results indicated that *P. barbatus* experienced more foliar salt damage and was more susceptible to saline water irrigation than *P. strictus*. Similarly, *P. eatonii*, *P. pseudospectabilis*, and *P. strictus* had salt injury with leaf necrosis and browning when they were irrigated with saline solutions prepared using NaCl, magnesium sulfate ($MgSO_4$), and $CaCl_2$ for 12 weeks (Niu and Rodriguez 2006). In addition, *P. ×mexicali* exhibited sharp declines in visual quality as salinity levels increased from 3000 to 5000 mg·L^{-1} (~4.7 to 6.3 dS·m^{-1}) (Zollinger et al. 2007). Likewise, severe leaf burns and wilting were observed in *P. palmeri* when exposed to saline solution greater than 3000 mg·L^{-1} (~4.7 dS·m^{-1}) (Zollinger et al. 2007). In this study, Zollinger et al. (2007) irrigated *P. ×mexicali* and *P. palmeri* with a saline solution containing $CaCl_2$ and NaCl at a molar ratio of 2:1.

During this study, we observed salt injury on the leaves of *P. barbatus* and *P. strictus* as the salinity levels in the solution increased, but no mortality was observed at less than 7.5 dS·m^{-1}. However, Niu and Rodriguez (2006) reported that *P. strictus* did not survive when irrigated with saline solution at an EC of 3.2 dS·m^{-1} or greater. This difference in observations could be attributed to variations in climate, saline solutions, growing substrates, and irrigation procedures. Saline solutions with various compositions can lead to different responses in plants, influencing nutrient uptake, osmotic regulation, and plant health (Nebauer et al. 2013). Niu and Rodriguez (2006) used saline solutions prepared with NaCl, $MgSO_4$, and $CaCl_2$, whereas the present study only used NaCl and $CaCl_2$. Moreover, local climate conditions and growing

Table 6. Contents of sodium (Na^+), chloride (Cl^-), calcium (Ca^{2+}), potassium (K^+), K^+/Na^+ ratio, and Ca^{2+}/Na^+ ratio in leaves of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} or saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse.

		Ion content (mg·g^{-1})					
Species	EC (dS·m^{-1})	Na^+	Cl^-	Ca^{2+}	K^+	K^+/Na^+	Ca^{2+}/Na^+
P. barbatus	1.0	0.05 d[i]	2.30 c	20.61 b	22.48 a	452.85 a	415.04 a
	2.5	0.41 c	12.03 b	23.61 b	19.05 a	45.97 b	56.97 b
	5.0	1.79 b	34.64 a	28.20 a	20.29 a	11.32 c	15.73 c
	7.5	4.48 a	47.58 a	31.45 a	21.87 a	4.88 d	7.02 d
	10.0	5.02 a	51.08 a	32.51 a	20.04 a	3.99 d	6.47 d
P. strictus	1.0	0.03 e	3.00 c	11.72 d	24.63 a	938.43 a	446.46 a
	2.5	0.14 d	11.57 b	13.97 c	21.95 ab	154.19 b	98.15 b
	5.0	0.50 c	32.50 a	17.93 b	20.11 ab	40.2 c	35.82 c
	7.5	1.34 b	47.36 a	23.10 a	22.46 ab	16.75 d	17.22 cd
	10.0	2.80 a	53.49 a	25.45 a	18.87 b	6.74 e	9.1 d
Species (S)		****[ii]	NS	****	NS	****	****
Treatment (T)		****	****	****	*	****	****
S × T		NS	NS	**	NS	NS	NS

[i] The mean values within a column for each species followed by the same letters are not significantly different at $\alpha = 0.05$ according to Tukey's method for multiplicity.
[ii] NS, *, **, ****: not significant or significant at $P < 0.05$, 0.01, or 0.0001, respectively.

substrate properties have been found to influence the response to salinity stress in previous studies (Costello et al. 2003; Fox et al. 2005). Microclimate conditions like temperature and humidity in a greenhouse play an important role in plant physiology and growth patterns.

In addition to its visual effects, salinity stress can significantly impede plant growth. In this study, the plant heights of both *P. barbatus* and *P. strictus* were affected by salinity stress. Exposure of ornamental plants to saline conditions can lead to decreased plant growth, which may have the benefit of achieving more compact plant sizes. However, it is essential to consider that maintaining compact plant size may require continued irrigation with saline water, potentially posing harm to other plants in the landscape. Additionally, salinity stress impacts the expansion of cells in young leaves, resulting in a decrease in leaf area (Munns and Tester 2008). Reduced leaf growth is the earliest response of glycophytes when exposed to salinity stress (Munns and Termaat 1986). Plants reduce leaf size to minimize water loss by transpiration, which allows conservation of soil moisture and prevents an increase in salt concentration in the soil (Munns and Tester 2008). In the case of *P. barbatus* and *P. strictus*, an increase in EC levels in the saline solution corresponded to a reduction in leaf area. Likewise, the decrease in leaf area was noted in numerous plants as the concentration of saline water increased (Paudel et al. 2019; Sun et al. 2020; Wu et al. 2016).

Plant biomass is one of the most direct indicators of salinity tolerance. Acosta-Motos et al. (2017) reported that the decrease in shoot DW of plants exposed to salinity stress is primarily attributed to the development of smaller and fewer leaves and stunted plant growth. In this study, there was a significant reduction in shoot DW of *P. strictus*. Similarly, shoot DW of *P.* ×*mexicali* and *P. palmeri* decreased with increasing salinity levels in the solution (Zollinger et al. 2007). Additionally, Niu et al. (2010) found that *Angelonia angustifolia* (angelonia) cultivars in the Plantaginaceae family exhibited 25% and 50% reductions in shoot DW when irrigated with saline solution at ECs of 5.1 and 7.4 dS·m^{-1}, respectively, compared with those at an EC of 2.8 dS·m^{-1}. Plant roots are highly susceptible to salinity because they are in direct contact with salts, impacting their ability to absorb water, their water use efficiency, and other physiological processes (Sanchez-Blanco et al. 2014). In this study, there was a decreasing trend in the root DW of penstemons, reflecting the inhibition of root growth caused by osmotic and toxic effects of high salinity (Banon et al. 2012). Inhibition of root growth may have been caused by the reduced capacity of the shoot to deliver nutrients to the roots, which can affect plant development and survival (Munns and Termaat 1986).

The negative effects on the visual quality and stunted growth of *P. barbatus* and *P. strictus* may be attributed to the salts accumulated in the growing substrate, which can directly affect plant health. This accumulation of salts in the substrate can be evaluated through the pour-through method as described by Cavins et al. (2008) or the saturated paste extraction method described by Gavlak et al. (2005). During the experiment, although leachate ECs from the substrate remained similar throughout the duration of each treatment, there was a significant difference

Table 7. Contents of boron (B), magnesium (Mg^{2+}), phosphorus (P), zinc (Zn^{2+}), and manganese (Mn^{2+}) in leaves of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} or saline solutions with varying EC levels ranging from 2.5 to 10.0 dS·m^{-1} for a period of 8 weeks in a greenhouse.

		Ion content (mg·g^{-1})				
Species	EC (dS·m^{-1})	B	Mg^{2+}	P	Zn^{2+}	Mn^{2+}
P. barbatus	1.0	0.03 a[i]	4.57 a	3.19 a	0.02 a	0.03 b
	2.5	0.03 ab	4.44 a	3.11 a	0.02 a	0.04 ab
	5.0	0.02 bc	4.57 a	3.24 a	0.02 a	0.04 ab
	7.5	0.02 bc	4.11 a	3.27 a	0.02 a	0.05 a
	10.0	0.02 c	4.10 a	2.79 a	0.02 a	0.05 a
P. strictus	1.0	0.02 a	4.52 a	4.86 a	0.02 b	0.03 bc
	2.5	0.02 a	4.98 a	4.07 ab	0.03 ab	0.02 c
	5.0	0.02 bc	5.10 a	3.96 ab	0.03 a	0.04 ab
	7.5	0.02 b	5.15 a	3.85 b	0.03 ab	0.04 ab
	10.0	0.02 c	5.13 a	3.46 b	0.02 ab	0.06 a
Species (S)		****[ii]	****	****	*	NS
Treatment (T)		****	NS	**	**	***
S × T		NS	NS	NS	NS	NS

[i] The mean values within a column for each species followed by the same letters are not significantly different at $\alpha = 0.05$ according to Tukey's method for multiplicity.
[ii] NS, *, **, ***, ****: not significant or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

Table 8. Proline contents in leaves of *Penstemon barbatus* and *P. strictus* after irrigation with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} (control) or saline solutions with varying EC levels ranging from 2.5 to 7.5 dS·m^{-1} in a greenhouse.[i]

	Proline content (μmol·g^{-1})			
Species	1.0	2.5	5.0	7.5
P. barbatus	0.30 a[ii]A[iii]	0.20 aB	0.21 aB	0.23 aB
P. strictus	0.64 aA	1.02 aA	0.60 aA	1.22 aA

[i] Leaves were harvested after the sixth irrigation event. Because of foliar damage observed in penstemons when irrigated with saline solution at an EC of 10.0 dS·m^{-1}, proline estimation was not performed.

[ii] The mean values within a row followed by the same lowercase letters are not significantly different among treatments at $\alpha = 0.05$ according to Tukey's method for multiplicity.

[iii] The mean values within a column followed by the same uppercase letters are not significantly different between species at $\alpha = 0.05$ according to Tukey's method for multiplicity.

among the treatments. The EC of the substrate was greater than that of the corresponding saline solution, indicating the presence of salt accumulation in the growing substrate.

The results of the study revealed significant variations in the SPAD readings of *P. barbatus* and *P. strictus* under different salinity levels. These findings align with those of previous research that found that increasing levels of salinity in the solution caused reductions in the SPAD readings of several landscape plants (Liu et al. 2017; Niu et al. 2007). Interestingly, the present study also demonstrated species-specific responses to salinity stress. The SPAD readings of *P. barbatus* exhibited greater sensitivity to salinity compared with *P. strictus*. This was evident from the larger reductions in SPAD readings for *P. barbatus* at an EC of 7.5 dS·m^{-1}. Furthermore, the measurements of chlorophyll fluorescence parameters (F_v/F_m and PI_{abs}) provided insights into the photosynthetic efficiency of the penstemon species. The significant reduction in F_v/F_m and PI_{abs} for *P. barbatus* with increasing salinity levels in the solution indicated compromised photosynthetic activity. The F_v/F_m parameter is of crucial importance because it signifies the effectiveness of the light reaction and is extensively used for studying the effects of stress on plants. Salinity stress obstructs the process of electron transfer from the primary acceptor to the secondary acceptor in the PSII, which may have led to a reduction in F_v/F_m (Shu et al. 2012).

Salinity stress can have significant effects on plant growth because it disrupts several essential physiological processes. These processes may encompass interference with photosynthesis, osmoregulation, and mineral supply to the aerial part (Negrao et al. 2017). The photosynthetic apparatus of plants may be harmed, and plant photosynthesis can be inhibited under salinity stress (Taiz et al. 2015). Exposing plants to high levels of soil salinity can disrupt their water balance, resulting in water moving out of plant cells and into the surrounding soil (Munns and Tester 2008). This, in turn, can lead to dehydration and reduction in P_n. Additionally, high levels of salt can also cause damage to chloroplasts, which are responsible for P_n, and interfere with the process of photosynthesis itself. Furthermore, the buildup of excessive amounts of Na^+ and Cl^- ions can impede P_n, as noted by Zhang et al. (2014). Moreover, salinity stress can also impact g_s, which refers to the opening and closing of the stomata. When plants are exposed to high levels of salinity, the stomata may close to conserve water, reducing the uptake of carbon dioxide (CO_2) for P_n and the release of oxygen (O_2). In the present study, P_n and g_s of the penstemons were reduced in response to salinity stress. Similarly, there were decreases in the P_n and g_s rates in *P. palmeri* with increasing salinity levels in the solution (Zollinger et al. 2007). To mitigate the negative impacts of salinity stress on P_n and g_s, several strategies can be used. For instance, the application of silicon (Si) can improve the shoot growth and net photosynthetic rates. Research indicated that Si may play a crucial role in sustaining high photosynthetic rates in plants under salt stress conditions (Coskun et al. 2019; Zargar et al. 2019). Furthermore, applying arbuscular mycorrhizal fungi has been found to help maintain osmotic balance, exhibit a greater g_s, and improve the overall photosynthetic efficiency of plants (Evelin et al. 2009). In addition, saline conditions may create a water deficit in plants, leading to stomatal closure and, ultimately, a decrease in *E* (Wang et al. 2019). Likewise, two penstemon species in this study exhibited reductions in *E* in response to salinity stress.

The nutritional status of a plant is influenced by salinity stress through a complicated network of interactions, which may involve a reduction in the uptake and/or transportation of nutrients from roots to shoots (Munns and Tester 2008). Although low Na^+ levels can be beneficial to plants in some situations, moderate and high levels are harmful to most plants (Maathuis 2014). Furthermore, plants take-up Cl^- ions, which are important for stabilizing membrane potential and regulating pH and turgor (Marschner 2012). Although plants generally require only small amounts of Cl^-, deficiencies are rare. However, excessive Na^+ and Cl^- ions in plants can lead to toxicity. Under the salinity treatments in this study, the Na^+ and Cl^- contents of penstemon leaves in both species were dramatically increased. This suggests an accumulation of these ions in the plant tissues caused by salinity stress. Importantly, a negative correlation between the visual score and Na^+ and Cl^- contents was observed ($P < 0.0001$) (Fig. 7). The visual score provides an indication of the foliar salt damage, and the negative correlation suggests that higher Na^+ and Cl^- contents are associated with greater visual damage. In addition to the visual damage, the reduction in P_n observed in the penstemons under salinity stress was also negatively correlated with the Na^+ and Cl^- contents in the leaf tissue ($P \leq 0.009$) (Fig. 8). Similarly, leaf Na^+ and Cl^- concentrations in *A. angustifolia* increased as salinity levels of irrigation water increased (Niu et al. 2010). The increasing ion concentration in the leaves of penstemons could have caused foliar salt damage.

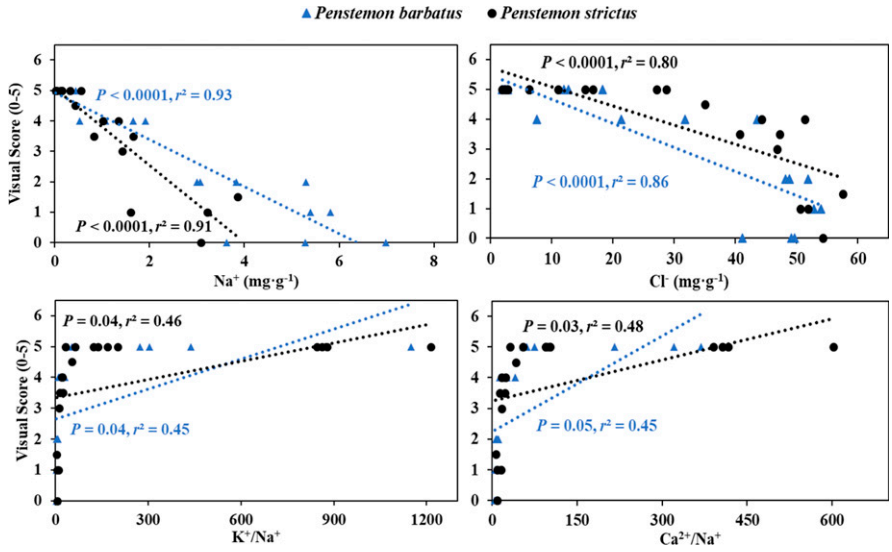

Fig. 7. Correlation analyses between the sodium (Na^+), chloride (Cl^-), potassium-to-sodium ratio (K^+/Na^+), calcium-to-sodium ratio (Ca^{2+}/Na^+), and visual score of *Penstemon barbatus* and *P. strictus*. Visual scores: 0 = dead plant caused by salinity stress; 1 = severe foliar damage (burnt leaves and necrosis, >90%); 2 = moderate foliar damage (51%–90%); 3 = slight foliar damage (10%–50%); 4 = good quality with minimal foliar damage (<10%); and 5 = excellent quality without foliar damage (Sun et al. 2015).

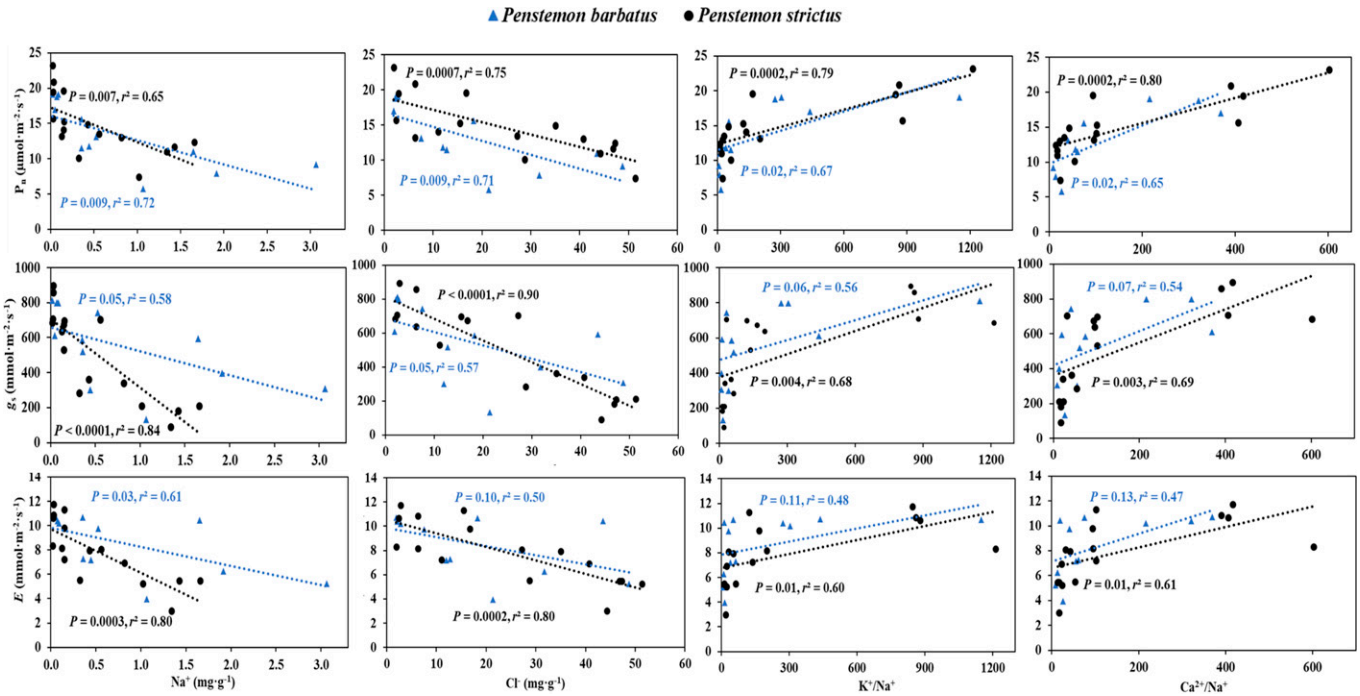

Fig. 8. Correlation analyses between the sodium (Na^+), chloride (Cl^-), potassium-to-sodium ratio (K^+/Na^+), calcium-to-sodium ratio (Ca^{2+}/Na^+), net photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration rate (E) of *Penstemon barbatus* and *P. strictus*.

Calcium plays a crucial role in maintaining the integrity of cell plasma membranes in roots and restricting the toxic effect of Na^+ (Gucci and Tattini 1997; Rengel 1992). It also serves as a secondary messenger in regulating signal transduction pathways for abiotic stress response and in promoting K^+/Na^+ selectivity (Rengel 1992). Similarly, the leaf Ca^+ concentration has been reported to increase with increasing salinity in many ornamental plant species (Paudel et al. 2019; Sun et al. 2015; Wu et al. 2016). Consistent with these findings, the present study also observed an increase in leaf Ca^+ concentration, likely caused by the use of $CaCl_2$ in the preparation of the saline solution (Table 1). A positive correlation was observed between visual score and K^+/Na^+ and Ca^{2+}/Na^+ ratios ($P \leq 0.05$) (Fig. 7). The increment in Ca^{2+} content was low in penstemons when compared with the Na^+ and Cl^- increments. These findings highlight the role of Ca^{2+} in mitigating the toxic effects of Na^+ and its involvement in maintaining ion selectivity and osmotic adjustment in response to salinity stress (Rengel 1992). The positive correlation between the visual score and Ca^{2+}/Na^+ ratio further supports the significance of Ca^{2+} in minimizing the harmful effects of salinity. Enhancing Ca^{2+} availability to plants under salinity stress is crucial for maintaining normal physiological processes in plants. In our case, calcium chloride was added to the solution so that plants could presumably access more Ca^{2+}. To increase calcium uptake in plants, boosting water flow to the roots is an option, but it is not ideal because of limited freshwater availability (Yang et al. 2012). Increasing the cation exchange capacity of soil can be another strategy to make more Ca^+ available to plants (Mengel 2023).

In plants, K^+ serves as the primary cation that counterbalances anions and activates enzymes for metabolic processes, protein and carbohydrate synthesis, and the regulation of stomatal movement (Rahneshan et al. 2018). In the present study, the K^+ contents remained similar for *P. barbatus* and slightly reduced for *P. strictus* under salinity stress. However, the K^+/Na^+ and Ca^{2+}/Na^+ ratios decreased with increasing salinity levels for both penstemon species. This suggests that the high concentration of Na^+ present in saline soils may have replaced the essential K^+ and Ca^{2+} ions in the penstemons, which are crucial for proper growth and development. Furthermore, P_n of the penstemons was reduced in response to salinity and positively correlated with K^+/Na^+ and Ca^{2+}/Na^+ ratios ($P \leq 0.02$) (Fig. 8). Similarly, g_s and E of *P. strictus* were also influenced by K^+/Na^+ and Ca^{2+}/Na^+ ratios ($P \leq 0.01$) (Fig. 8). These findings suggest that the imbalance caused by the replacement of K^+ and Ca^{2+} with Na^+ in the penstemons negatively affected their physiological processes.

Boron plays an important role in several physiological processes in plants, including cell wall structure, root elongation, shoot growth, membrane integrity, and reproduction (Broadley et al. 2012). Boron deficiency can lead to the inhibition of root elongation and shoot meristematic growth (Broadley et al. 2012). In this study, it was observed that the B content was reduced in two penstemons species in response to salinity stress, which also may have contributed to the reduction in the growth of shoots and roots.

Magnesium is a component of chlorophyll and is required for photosynthesis and protein synthesis, whereas P is crucial for nucleic acids and carbohydrate transfer in leaf cells (Hawkesford et al. 2012). Zinc contributes to detoxification of superoxide radicals, membrane integrity, protein synthesis, and phytohormone production (Broadley et al. 2012). Manganese activates enzymes involved in detoxification and lignin synthesis (Broadley et al. 2012). In this study, Mg^{2+} content remained consistent in both penstemon species, but the P content decreased in *P. strictus* under higher salinity levels. Plant type and growing conditions play an important role in P accumulation (Grattan and Grieve 1999). Moreover, the Zn^{2+} content increased in *P. strictus* and the Mn^{2+} content increased in both species, suggesting a potential role in detoxification of superoxide radicals (Broadley et al. 2012).

Some plants can tolerate salinity stress through osmotic adjustment, which involves the accumulation of solutes that help reduce cellular solute potential and maintain water uptake (Hasegawa et al. 2000). Proline is one such solute that can assist plants in adjusting the pH in the cytosol, thereby protecting cellular membranes and proteins from damage during salinity stress (Behzadi Rad et al. 2021). However, in this study, the proline content in the leaves varied between the two penstemon species while remaining similar across all treatments. This suggests that proline may not play a significant role in the salinity stress responses for these penstemon species within the context of this study. The variations in proline content observed could be attributed to inherent genetic differences or physiological adaptations between the species.

Conclusions

Two penstemon species tested during this study showed variations in response to salinity stress. Saline solution irrigation reduced the growth and biomass of both penstemon species. The net photosynthetic rate, g_s, and E of penstemons were negatively impacted by salinity stress. Furthermore, the Na^+ and Cl^- uptake increased, and the K^+ and Ca^{2+} uptake was also affected. Based on the findings of this study, *P. barbatus* and *P. strictus* are sensitive to salinity levels at ECs of 7.5 and 10.0 $dS \cdot m^{-1}$. These results have implications for the cultivation and management of these penstemon species in saline environments, thus highlighting the need for appropriate irrigation strategies to mitigate the negative effects of salinity stress on their growth and physiological processes.

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