HortScience 59(5):706–715. 2024. https://doi.org/10.21273/HORTSCI17454-23

Morphological and Physiological Responses of Two Penstemon Species to Saline Water Irrigation

Prakriti Nepal, Zirui Wang, McKenna Carnahan, Wes Maughan, Julie Hershkowitz, Youping Sun, Asmita Paudel, Kyle Forsyth, Nick Volesky, Ananta Raj Devkota, and Ji Jhong Chen

Department of Plants, Soils & Climate, Utah State University, 4820 Old Main Hill, Logan, UT 84322, USA

Keywords. canopy temperature, *Penstemon davidsonii* (Davidson's penstemon), *Penstemon heterophyllus* (foothill penstemon), salinity, stomatal conductance, visual quality

Abstract. **Penstemon, with more than 250 species native to North America, holds significant aesthetic and ecological value in Utah, supporting diverse pollinators. Despite their significance, the survival of penstemon is threatened by challenges such as habitat loss, climate change, and Utah's naturally high soil salinity. To address these challenges and understand their adaptability, this study evaluated the salt tolerance of two penstemon species [*Penstemon davidsonii* (Davidson's penstemon) and *Penstemon heterophyllus* (foothill penstemon)] under controlled greenhouse conditions. The aim was to develop baseline information for nursery production and landscape use that utilize reclaimed water for irrigation. Plants were irrigated weekly with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} as control or a saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 dS·m^{-1} for 8 weeks. Half of the plants were harvested after four irrigation events, and the remaining plants were harvested after eight irrigation events. At harvest, visual rating (0 = dead and 5 = excellent without foliage salt damage), plant width, number of shoots, leaf area, shoot dry weight, leaf greenness [Soil Plant Analysis Development (SPAD)], stomatal conductance, and canopy temperature were collected to assess the impact of salinity stress. In both species, salt damage was dependent on the salinity levels and length of exposure. After four irrigation events, both species exhibited foliage damage that increased in severity with rising EC. The most severe damage was observed in plants receiving saline solution at an EC of 10.0 dS·m^{-1}. After eight irrigation events, *P. davidsonii* exposed to a saline solution with an EC of 10.0 dS·m^{-1} received a visual rating of 0, whereas *P. heterophyllus* had a visual rating of 0.4. Both species exhibited salinity-induced effects, with variations observed in the specific parameters and the degree of response. *Penstemon davidsonii* exhibited significant salinity stress, as indicated by reduced leaf area, shoot dry weight, SPAD reading, and stomatal conductance with increasing EC of the saline solution. In addition, in both species, at both harvests, canopy temperatures increased either linearly or quadratically by 8% to 36% as the EC levels of the saline solution increased. These results indicate that *P. davidsonii* was more sensitive to salinity stress than *P. heterophyllus*.**

Soil salinity affects ∼10% of all soils globally and can impact up to 50% of the world's irrigated land (Guo et al. 2022; Negrão et al. 2017). Soils are considered saline when the EC of saturation extract (ECe) reaches or exceeds 4.0 dS·m^{-1}, equivalent to 40 mM sodium chloride (NaCl), resulting in an osmotic pressure of ∼0.2 MPa (Munns and Tester 2008). This significantly hinders plant growth and renders the soil unsuitable for optimal plant cultivation (Chinnusamy et al. 2005). When salt-sensitive plants are exposed to saline water, they experience osmotic stress. This stress can have immediate short-term effects on various aspects of plant physiology, including cell water relations, cell expansion and division, photosynthesis, stomatal conductance, transpiration, and overall growth (Carillo et al. 2022; Munns 2005). In many plants, sodium (Na^+) and chloride (Cl^-) are effectively excluded by roots while water is taken up from the soil (Munns 2005). In the long term, the effects of salt stress can lead to senescence, chlorosis, and necrosis, particularly in mature leaves (Carillo et al. 2022). Soil salinity impedes plant growth through two primary mechanisms. First, it reduces the plant's water uptake capacity, leading to slower growth due to the osmotic or water-deficit effect of salinity. Second, the salt may infiltrate the transpiration stream and ultimately damage cells in the transpiring leaves, further diminishing overall growth. This phenomenon is known as the salt-specific or ion-excess effect of salinity (Munns 2005). Salinity stress decreases stomatal conductance, photosynthesis, and growth; causes nutrient and osmotic imbalances; and reduces tolerance to heat and drought (Liu et al. 2023).

Salinity stress disrupts nutrient and osmotic balance within plants, further impairing their growth and overall health (Carillo et al. 2022). With the rapid growth of global populations and industrialization, the demand for freshwater supply is increasing, while its availability is diminishing (Okello et al. 2015). The increasing use of alternative water sources, including reclaimed water and runoff water, is considered a promising approach to conserving freshwater resources for other critical uses (Niu and Cabrera 2010); however, such water sources often have higher salt concentrations and salt ions can accumulate in the root zone with repeated irrigation, leading to osmotic stress in plants by hindering efficient water uptake (Toor and Lusk 2011). Osmotic stress negatively impacts visual quality and performance. Therefore, it is increasingly important to select ornamental plant species that are tolerant of saline conditions.

Penstemon, a genus of flowering plants belonging to the plantain family, Plantaginaeae, is the largest plant genus endemic to North America, encompassing more than 270 species (Kramer 2009). Utah, at the heart of penstemon's natural diversity, hosts 76 species within its borders, with 22 species found exclusively in the state (Stevens et al. 2020). Thriving in well-drained soils and exhibiting excellent drought tolerance, penstemon adapts to a wide range of temperatures and elevations from mountaintops to sea level. Its durability and aesthetic value have made penstemon popular as a landscape plant throughout the western United States. About $3.75 million worth of potted penstemons are sold annually for landscape and horticultural uses [US Department of Agriculture (USDA) 2020]. However, few studies have examined penstemon's salinity tolerance. Given the increasing prevalence of saline conditions and the use of reclaimed water in landscape settings, it is crucial to screen and cultivate salt-tolerant penstemon varieties.

This study examined the salinity tolerance of two penstemon species, *P. davidsonii* (Davidson's penstemon) and *P. heterophyllus* (foothill penstemon). *Penstemon davidsonii* is a mat-forming perennial, 4 to 10 cm tall, with thick, round, dark green leaves. The flowers are bilaterally symmetrical, ranging in shades of violet to purple. They are present in clusters of 2 to 4 on terminal inflorescences and vary in color from light lavender to purple (Lady Bird Johnson Wildflower Center 2023a; Stevens et al. 2020). In the wild, *Penstemon davidsonii* is found at high-elevation mountains from the north border of British Columbia to the southern tip of California (USDA, Natural Resources Conservation Service 2023). *Penstemon heterophyllus* is an herbaceous perennial, 30 to 150 cm tall, with dark green, blade-like foliage and blue to purple flowers on terminal inflorescence (Lady Bird Johnson Wildflower Center 2023b; Stevens et al. 2020). *Penstemon heterophyllus* is endemic to California, where it is found in coastal areas of the Sierra Nevada foothills. The flowers of this species can be blue, violet, or purple.

Understanding the differential responses of plant species to varying salinity levels is crucial for assessing their adaptability to saline environments. Therefore, we hypothesize that exposing *P. davidsonii* and *P. heterophyllus* to different salinity levels will lead to distinct morphological and physiological responses, reflecting their varying capacities to adapt to saline environments. The objective of this study was to examine the salinity tolerance of two penstemon species, *P. davidsonii* and *P. heterophyllus*, in relation to morphological and physiological responses. By evaluating their relative salinity tolerance, we can assess how these species would respond when planted in a landscape system with higher salt concentrations in the irrigation water and/or soil.

Materials and Methods

Plant materials, treatments, and growing conditions. The experiment was conducted at the Utah State University (USU) Research Greenhouse in Logan, UT, USA (lat. 41°45′28″N, long. 111°48′47″W, elevation 1409 m). On 9 Jan 2023, 50 plants of each of *P. davidsonii* (Davidson's penstemon) and *P. heterophyllus* (foothill penstemon) were purchased from Perennial Favorites (Layton, UT, USA), each potted in 0.712-L containers (12.5 × 8.8 × 8.8 cm^3). The plants were transplanted into 3.9-L injection-molded, polypropylene containers (PC1D-4; Nursery Supplies, Orange, CA, USA) filled with soilless media (Metro-Mix® 820; Canadian sphagnum peatmoss, 35% to 45% composted pine bark, coir, coarse perlite, and dolomitic limestone; SunGro Horticulture, Agawam, MA, USA).

Received for publication 5 Sep 2023. Accepted for publication 4 Jan 2024.
Published online 22 Apr 2024.
This research was conducted as a special project in the Plant Stress Physiology (PSC 5280/6280) course in Spring 2023. This project was supported in part by the US Department of Agriculture (USDA) National Institute of Food and Agriculture Hatch project UTA01666, USDA Agricultural Marketing Service Specialty Crop Block Grant program, American Penstemon Society (APS) Graduate Student Scholarship Grant, Utah State University's Center for Water-Efficient Landscaping, and Utah Agricultural Experiment Station (UAES). This is approved as UAES journal paper number 9754. We are grateful for the Open Access Funding at Utah State University Libraries, technical assistance from Abby McKee, Alyssa Fenstermaker, and Macie Booth, and valuable comments from anonymous reviewers. The content is solely the responsibility of the authors and does not necessarily represent the official views of the funding agencies. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA, APS or the American Society for Horticultural Science and does not imply its approval to the exclusion of other products or vendors that also may be suitable.
P.N., Z.W., M.C., W.M., J.H., K.F., N.V., and A.R.D. are Graduate Students in the Plant Stress Physiology (PSC 5280/6280) course.
A.P. and J.J.C. are Teaching Assistants for the Plant Stress Physiology (PSC 5280/6280) course.
Current address for W.M.: Washington State University, Pullman, WA, USA.
Current address for J.J.C.: Department of Plant Science, University of Wyoming, Laramie, WY, USA.
Y.S. is the corresponding author. E-mail: youping.sun@usu.edu.

The plants were kept in the USU Research Greenhouse and sorted into 10 groups (five uniform plants per species within each group) based on their height and canopy size before the experiment. From 2 Feb to 23 Mar 2023, plants were irrigated weekly (eight irrigation events) with a nutrient solution at an EC of 1.0 $dS{\cdot}m^{-1}$ (control) or a saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS{\cdot}m^{-1}$ (Paudel and Sun 2024). At each irrigation event, 800 mL of the treatment solutions were applied, resulting in an average leachate fraction of 30%. The nutrient solution was prepared by adding 80 $g{\cdot}L^{-1}$ 15N–2.2P–12.5K water-soluble fertilizer (Peters Excel 15–5–15 Cal-Mag Special; ICL Specialty Fertilizers, Dublin, OH, USA) in reverse osmosis (RO) water and used as the control. Sodium chloride (NaCl, Fisher Chemical, Waltham, MA, USA) at 0.31, 0.92, 1.45, or 2.27 $g{\cdot}L^{-1}$ plus dihydrate calcium chloride ($CaCl_2{\cdot}2H_2O$, Hi Valley Chemical, Centerville, UT, USA) at 0.40, 1.17, 1.83, or 2.80 $g{\cdot}L^{-1}$ were added to the nutrient solution to prepare a saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS{\cdot}m^{-1}$, respectively. Sufficient calcium (Ca^{2+}) within the irrigation solution is crucial for effectively mitigating the detrimental effects of NaCl-induced Ca^{2+} deficiency (Qadir et al. 2001). The pH of all solutions was adjusted to 6.00–6.5 using 1 $mol{\cdot}L^{-1}$ nitric acid (HNO_3, Fisher Chemical, Fair Lawn, NJ, USA) or 88% potassium hydroxide pellets (Sigma-Aldrich, St. Louis, MO, USA). All solutions were prepared in 100-L tanks, and their ECs were confirmed using an EC meter (LAQUA Twin; Horiba, Kyoto, Japan). The EC of the solutions was recorded before applying. For saline solutions with target EC values of 1.0, 2.5, 5.0, 7.5, and 10.0 $dS{\cdot}m^{-1}$, the measured ECs were 0.93 ± 0.01, 2.64 ± 0.05, 5.33 ± 0.06, 7.90 ± 0.09, and 10.84 ± 0.17 $dS{\cdot}m^{-1}$ (mean ± SE), respectively. All plants were irrigated with the RO water between treatments to prevent the confounding effect of drought. The pots were regularly checked and irrigated with 100–300 mL of RO water.

Throughout the experimental period, the greenhouse temperatures were maintained at 24.69 ± 0.78 °C (mean ± *SD*) during the day and 21.40 ± 0.73 °C (mean ± *SD*) at night. The daily light integral inside the greenhouse was 17.6 ± 6.0 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ (mean ± *SD*) recorded using a full-spectrum quantum sensor (SQ-500-SS; Apogee Instruments, Logan, UT, USA). Supplemental light was provided using light-emitting diodes (Luxx Lighting, Jurupa Valley, CA, USA) at an average light intensity of 514.50 ± 72.88 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ (mean ± *SD*) at the plant's canopy level from 0600 to 2200 HR when light intensity inside the greenhouse was less than 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$.

Leachate and substrate EC. The leachate EC was determined using the pour-through method described by Cavins et al. (2008). Plants were irrigated with respective salinity treatments and nutrient solution onto the substrate, and the resulting leachate was measured with the EC meter. The leachate EC was averaged across each treatment group. One plant per treatment per species was selected for this measurement. The substrate's EC was measured using a modified version of the saturated paste extraction method described by Gavlak et al. (2005). The containers of media were dried in the greenhouse for 2 weeks. Then a 10-g sample was collected from the top 5-cm surface of the substrate. Each sample was placed in a flask with 60 mL of RO water, then covered with parafilm (American National Can, Menasha, WI, USA), and stored at room temperature for 24 h to form a paste. The EC of the saturated paste extract was measured using the EC meter.

Visual quality. Visual ratings of the penstemon plants were recorded weekly using a reference scale of 0 to 5 [0 = dead, 1 = severe foliage damage (>90% leaves with burn, necrosis, and discolor), 2 = moderate foliage damage (50% to 90%), 3 = slight foliage damage (10% to 50%), 4 = acceptable quality with a little foliage damage (<10%), 5 = good quality without any damage] (Sun et al. 2015). The visual quality assessment solely considered plant foliage.

Growth parameter and harvest. Half of the plants in each treatment were destructively harvested ~2 weeks after the fourth irrigation event (7 Mar 2023), and the remaining plants were harvested 1 week after the eighth irrigation event (31 Mar 2023). The first harvest aimed to assess the initial morphological and physiological responses of the two penstemon species to saline water irrigation, whereas the second harvest was to understand the prolonged effects of salinity stress on the two penstemon species. At each harvest, plant width and the number of shoots longer than 5 cm were recorded. Plant width was measured from the major axis (maximum width) and minor axis (perpendicular width) to obtain an accurate representation of the overall width. These measurements were essential for assessing the growth and development of the plants throughout the experiment.

Plants were cut down from the basal part of the stems at the substrate level, and the leaves were separated from the stems. Leaf area (square centimeter) was measured using a leaf area meter (LI-3100; LI-COR Bioscience, Lincoln, NE, USA). Plants were dried in an oven at 60 °C for 7 d, and the shoot dry weight was recorded.

Relative chlorophyll content and stomatal conductance. Relative chlorophyll content and stomatal conductance (g_s) were measured at each harvest. The leaf chlorophyll content was recorded as the average of eight mature leaves on each plant measured with a hand-held chlorophyll meter [Soil Plant Analysis Development (SPAD)-502; Minolta Camera, Osaka, Japan]. At the first harvest, 10 plants were selected from each treatment, and g_s was measured with a Porometer/Fluorometer (LI-600; LI-COR Biosciences, Lincoln, NE, USA). Due to plant mortality, g_s measurement was collected from five, four, or two plants in each treatment at the second harvest. A fully extended and healthy leaf was chosen for measuring g_s. All plants were watered with RO water 1 d before measurement to avoid drought stress, and all these data were recorded between 1300 and 1600 HR.

Canopy temperature. At each harvest, top-view thermal infrared images of plant canopies were taken with a thermal camera (FLIR E5-XT; Teledyne FLIR, Wilsonville, OR, USA). Data were recorded at 1200 HR. The average canopy temperature of each plant was calculated using FLIR Thermal Studio Suite (Teledyne FLIR).

Mineral analyses. At the first harvest, four plants of each penstemon species per treatment were randomly chosen and subsequently ground with a stainless Wiley mill to a fine powder (Thomas Scientific, Swedesboro, NJ, USA). Samples were sent to the USU Analytical Laboratories (Logan, UT, USA) for mineral analyses. In brief, the concentration of sodium (Na^+), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), manganese (Mn^{2+}), sulfur (S), zinc (Zn^{2+}), and iron (Fe^{3+}) were determined using nitric/hydrogen peroxide according to the protocol by Gavlak et al. (2005). The concentration of Cl^- was determined using a flow injection analysis and ion chromatography system (QuikChem 8000; Lachat Instrument, Loveland, CO, USA) and reported on a dry plant basis ($mg \cdot g^{-1}$). For Na^+, Ca^{2+}, K^+, Mg^{2+}, Mn^{2+}, S, and Zn^{2+}, 0.5 g of powder samples were added with 6 mL of nitric acid (HNO_3) in a digestion tube, which was then subjected to digestion at 80 °C for 10 min, followed by cooling for 2 min. Subsequently, 2 mL of 30% hydrogen peroxide (H_2O_2) were added to the digestion tube, which underwent an additional digestion step at 130 °C for 1 h or until the total digest volume was reduced to ~2.0 to 3.0 mL. The digestion tubes were then mixed using a vortex stirrer and cooled at room temperature. The contents of the digestion tubes were transferred into a 25 mL volumetric flask. The resulting digest was analyzed using an inductively coupled plasma-optical emission spectrometry (iCAP 6300 ICP-AES; Thermo Fisher Scientific, Waltham, MA, USA) and reported on a dry plant basis ($mg \cdot g^{-1}$).

Experimental design and data analyses. The experiment was a randomized complete block design with two species, five treatments, and 10 replicates per species per treatment. An experimental unit consisted of one pot containing one plant. A mixed model analysis was performed to test the effects of the saline water irrigation on all measured parameters. To normalize the data, logarithmic transformation was applied for all response variables, except mineral contents, to improve model performance. Trend analyses were conducted for all data to test the relationship between plant responses and saline levels. All statistical analyses were performed using the PROC MIXED procedure in a SAS Studio (version 3.8; SAS Institute, Cary, NC, USA). Mean separation was done using the Tukey-Kramer method adjusting for multiplicity with a significance level specified at 0.05.

Results and Discussion

Visual quality. There was no notable difference in visual rating after the first irrigation event for both species as they exhibited good quality without any foliage damage (data not shown). After two irrigation events, *P. davidsonii* started showing foliage damage when irrigated with saline solution at an EC of 7.5 and 10.0 $dS \cdot m^{-1}$, whereas *P. heterophyllus* had a visual rating greater than 4.5 (data not shown). This damage observed in *P. davidsonii* likely represents the effects of salt shock as the plants were suddenly exposed to a significantly higher salinity level. One week after the third application of saline solution, *P. davidsonii* showed slight foliage damage with an average visual rating of 3.4 and 3.0 when irrigated with saline solutions at an EC of 7.5 and 10.0 $dS \cdot m^{-1}$, respectively (data not shown). However, minimal to no foliage damage was observed for *P. heterophyllus* in all treatments. One week after the fourth irrigation event (the first harvest), saline solution irrigation had significant effects on the visual ratings of both species ($P < 0.0001$) (Table 1). Both species had minimal to no foliage damage up to an EC of 5.0 $dS \cdot m^{-1}$ with visual ratings equal to or greater than 4.2 (Fig. 1, Table 2). At an EC of 7.5 and 10.0 $dS \cdot m^{-1}$, both species presented slight foliage damage with an average visual rating of 3.2 and 2.8 for *P. davidsonii* and 3.7 and 3.3 for *P. heterophyllus*, respectively (Table 2).

Following the fifth application of saline solution, *P. davidsonii* and *P. heterophyllus* exhibited slight foliage damage with an average visual rating of 2.9 and 3.4 at an EC of 7.5 $dS \cdot m^{-1}$, respectively. In contrast, *P. davidsonii* and *P. heterophyllus* displayed moderate-to-severe foliage damage with an average visual rating of 1.6 and 1.8 when receiving saline solution at an EC level 10.0 $dS \cdot m^{-1}$, respectively (data not shown). Similar results were observed for *P. davidsonii* after the sixth application of saline solution. However, *P. heterophyllus* had an average visual rating of 1.0 when receiving saline solution at an EC of 10.0 $dS \cdot m^{-1}$ (data not shown). Unfortunately, *Penstemon davidsonii* did not survive when exposed to saline solution at an EC 10.0 $dS \cdot m^{-1}$ for 7 weeks, whereas severe foliage damage with an average visual rating of 1.1 was observed at an EC 7.5 $dS \cdot m^{-1}$ (data not shown). Meanwhile, *P. heterophyllus* plants had severe foliage damage with an average visual rating of 0.7 when irrigated with saline solution at an EC 10.0 $dS \cdot m^{-1}$ (data not shown). One week after the eighth irrigation event (second harvest), saline solution irrigation significantly affected the visual ratings of both species ($P < 0.0001$)

Table 1. A summary of analysis of variance for the effect of salinity treatments and their interactions with species on visual rating, plant width, number of shoots (No. of shoots), leaf area (LA), shoot dry weight (DW), leaf greenness [Soil Plant Analysis Development (SPAD) reading], stomatal conductance (g_s), and canopy temperature (CT) of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution [electrical conductivity (EC) = 1.0 $dS \cdot m^{-1}$] or saline solution (EC = 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$) in a greenhouse.[i]

Source	Visual rating	Width	No. of shoots	LA	Shoot DW	SPAD	g_s	CT
				First harvest				
Salinity	****[ii]	**	**	****	**	****	****	****
Species	****	****	****	***	*	****	****	**
Salinity × Species	*	NS	**	*	*	****	NS	*
				Second harvest				
Salinity	****	****	*	**	*	*	***	****
Species	*	NS	****	**	NS	**	***	NS
Salinity × Species	NS	NS	NS	NS	NS	NS	NS	NS

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$) to the nutrient solution.
[ii] NS, *, **, ***, ****: nonsignificant or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

Fig. 1. Two penstemon species, *Penstemon davidsonii* and *Penstemon heterophyllus*, irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or a saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$ after the fourth irrigation event. The photo was taken on 28 Feb 2023.

Table 2. The visual ratings of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$ for 4 weeks (first harvest) and 8 weeks (second harvest) in a greenhouse.[i]

	Visual rating[ii]	
EC ($dS \cdot m^{-1}$)	First harvest	Second harvest
	P. davidsonii	
1.0	4.6 ab[iii]	4.5 a
2.5	4.7 a	4.3 a
5.0	4.2 b	3.4 a
7.5	3.2 c	0.7 b
10.0	2.8 d	0.0 b
Trend[iv]	L****, Q*	L****, Q*
	P. heterophyllus	
1.0	4.7 a	4.8 a
2.5	4.7 a	4.6 a
5.0	4.5 a	4.0 ab
7.5	3.7 b	2.1 b
10.0	3.3 c	0.4 c
Trend[iv]	L****, Q**	L***, Q***

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$) to the nutrient solution. Data were collected 7 d after the fourth (n = 10) and eighth (n = 5) irrigation events for first harvest and second harvest, respectively.

[ii] Visual rating reference scale from 0 to 5, where 0 = dead, 1 = severe foliage damage (>90% leaves with burn, necrosis, and discolor), 2 = moderate foliage damage (50% to 90%), 3 = slight foliage damage (10% to 50%), 4 = acceptable quality with a little foliage damage (<10%), 5 = excellent quality without any damage.

[iii] Means with same lowercase letters within a species and column are not different among treatments by Tukey-Kramer method of multiplicity at $\alpha = 0.05$.

[iv] L: linear; Q: quadratic; *, **, ***, ****: significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

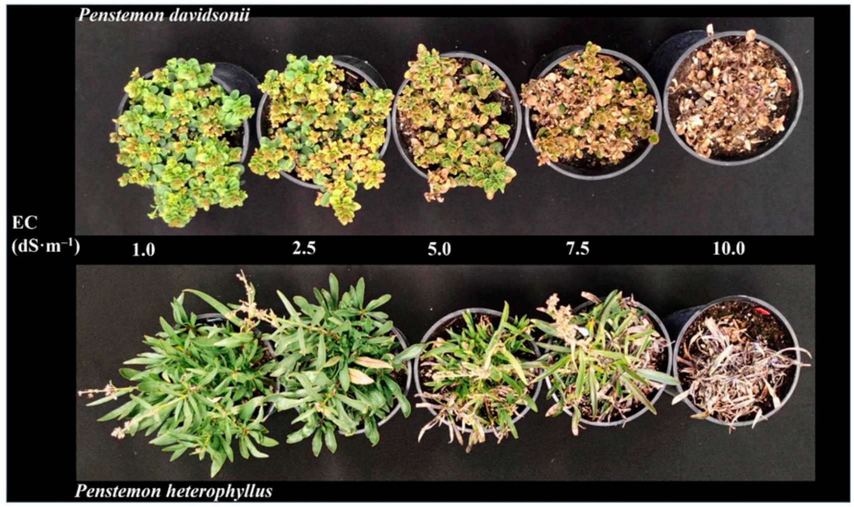

Fig. 2. Two penstemon species, *Penstemon davidsonii* and *Penstemon heterophyllus*, irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or a saline solution at an EC of 2.5, 5.0, 7.5 or 10.0 $dS \cdot m^{-1}$ after the eighth irrigation event. The photo was taken on 29 Mar 2023.

(Table 1). Both species maintained good visual quality when receiving saline solution at an EC of 2.5 or 5.0 $dS \cdot m^{-1}$, with visual ratings equal to or greater than 3.4 (Fig. 2, Table 2). However, at EC levels of 7.5 and 10.0 $dS \cdot m^{-1}$, visual ratings were lower for both species compared with the first harvest. When irrigated with saline solution at an EC level of 7.5 $dS \cdot m^{-1}$ *P. davidsonii* and *P. heterophyllus* exhibited moderate-to-severe foliage damage with an average visual rating of 0.7 and 2.1, respectively. At an EC of 10.0 $dS \cdot m^{-1}$, *P. davidsonii* did not survive; however, *P. heterophyllus* exhibited severe foliage damage with an average visual rating of 0.4. This observation aligns with the findings in the study by Andrenko et al. (2020), who observed that higher salinity levels had varying effects on the aesthetic appeal of different plant species.

These results indicate that foliage damage was influenced by both the salinity level of the solution and the duration of saline solution irrigation. Similar results were found by Niu and Rodriguez (2006), who observed that *Penstemon eatonii* (firecracker penstemon), *Penstemon pseudospectabilis* (desert beardtongue), and *Penstemon strictus* (rocky mountain beardtongue) did not survive when irrigated with a saline solution containing NaCl, magnesium sulfate ($MgSO_4$), and $CaCl_2$ at an EC of 3.2 $dS \cdot m^{-1}$ or higher. The differences seen in visual quality between the first and second harvests are likely a result of salt accumulation in the substrate.

In this study, the leachate EC, used as an indirect method for assessing salinity levels in soil or growing substrates, demonstrated a decline from 1.50 to 0.98 $dS \cdot m^{-1}$ in the control (EC 1.0 $dS \cdot m^{-1}$) throughout the study (Fig. 3). However, the leachate EC increased progressively from 3.45 to 4.27 $dS \cdot m^{-1}$, 4.10 to 8.25 $dS \cdot m^{-1}$, 6.15 to 13.36 $dS \cdot m^{-1}$, and 6.30 to 16.67 $dS \cdot m^{-1}$ when collected from plants exposed to saline solutions at ECs of 2.5, 5.0, 7.5, and 10.0 $dS \cdot m^{-1}$, respectively. The substrate EC, a direct measure of salinity levels in soil or growing substrates, was 3.56, 5.86, 12.14, and 14.89 $dS \cdot m^{-1}$ at the first harvest when treated with saline solutions at ECs of 2.5, 5.0, 7.5 and 10.0 $dS \cdot m^{-1}$, respectively (Fig. 4). By the second harvest, the substrate EC increased to 5.11, 9.66, 15.77, and 31.10 $dS \cdot m^{-1}$ for the corresponding salinity treatments. Consistent with findings in various studies (Paudel et al. 2019; Sun and Palmer 2018; Sun et al. 2018, 2020; Xing et al. 2021) using peat-based soilless growing substrate, both leachate and substrate EC increased over time with saline solution irrigation. This rise in leachate and substrate EC reflects the accumulation of salts in the substrate, directly correlating with the observed damage to the plant foliage.

Plant growth. Saline solution irrigation significantly influenced the width of both species at the first ($P = 0.002$) and second harvest ($P < 0.0001$) (Table 1). At the first harvest, a linear reduction in the width of *P. davidsonii* occurred with increasing saline solution EC (Table 3). Specifically, the width of *P. davidsonii* decreased from 19.4 to 15.6 cm. In contrast, no significant difference in width was observed for *P. heterophyllus* in response to the saline solution irrigation. At the second

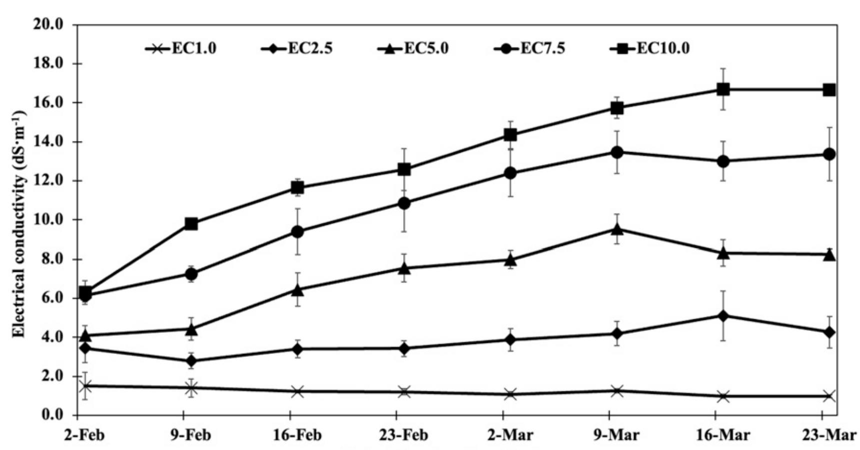

Fig. 3. Leachate electrical conductivity (EC) recorded after irrigating *Penstemon davidsonii* and *Penstemon heterophyllus* with a nutrient solution at an EC of 1.0 $dS \cdot m^{-1}$ (EC1.0) or a saline solution at an EC of 2.5 $dS \cdot m^{-1}$ (EC2.5), 5.0 $dS \cdot m^{-1}$ (EC5.0), 7.5 $dS \cdot m^{-1}$ (EC7.5), or 10.0 $dS \cdot m^{-1}$ (EC10.0). Vertical bars indicate standard error of four samples.

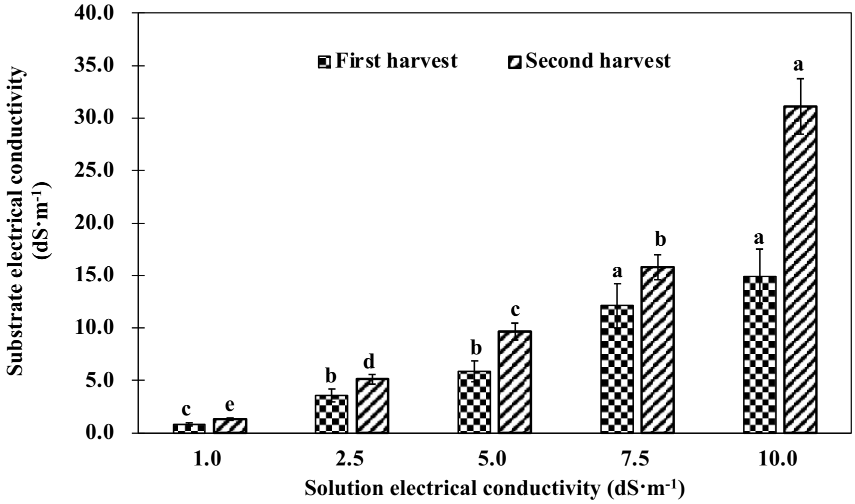

Fig. 4. Electrical conductivity (EC) of the soil extraction recorded for *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an EC of 1.0 dS·m^{-1} or a saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 dS·m^{-1}. Plants were harvested on 7 Mar (first harvest) and 31 Mar 2023 (second harvest). Vertical bars indicate standard errors of eight samples. Same lowercase letters above columns within the harvest date represent no significance among treatments by Tukey-Kramer method of multiplicity at α = 0.05.

harvest, there was no significant change in the width of *P. davidsonii* (Table 3). However, a quadratic decrease in the width of *P. heterophyllus* was evident, declining from 19.4 to 10.3 cm with increasing EC of the saline solution. Salinity stress, as elucidated by Munns and Tester (2008), exerts adverse effects on plant development by reducing cell expansion and causing nutrient imbalance, ultimately suppressing growth. Our study aligns with these observations, as plants exposed to higher concentrations of NaCl and $CaCl_2$ in the saline solution exhibited a pronounced reduction in width. The accumulation of salts contributed to leaf necrosis and senescence, limiting the availability of carbohydrates and/or growth hormones to meristematic parts, thereby inhibiting plant growth, as reported by Acosta-Motos et al. (2017).

A statistically significant difference was observed in the number of shoots at the first harvest when considering the interaction between saline solution and plant species ($P = 0.007$) (Table 1). Specifically, for *P. davidsonii*, the number of shoots was significantly greater when irrigated with saline solution at an EC of 2.5 dS·m^{-1} compared with plants at an EC of 7.5 and 10.0 dS·m^{-1} (Table 3). In contrast, a marginal quadratic trend ($P = 0.054$) was observed for *P. heterophyllus*. At the second harvest, the number of shoots for *P. davidsonii* ranged from 14 to 21, but no significant trend was observed (Table 3). For *P. heterophyllus*, the number of shoots was significantly greater when irrigated with saline solution at an EC of 2.5 and 5.0 dS·m^{-1} compared with plants at an EC of 10.0 dS·m^{-1}. These results suggest that salinity-induced water stress impacted shoot production for both *P. davidsonii* and *P. heterophyllus*. Salinity stress is recognized as a critical factor influencing plant development and physiology, particularly during the osmotic phase. This phase begins immediately after the salt concentration around the roots increases to a threshold level (4.0 dS·m^{-1}), leading to a significant reduction in the rate of shoot growth (Munns and Tester 2008). During this period, emerging leaves expand at a slower rate, resulting in delayed emergence of new leaves and a reduction in lateral bud development. The overall effect is seen in fewer branches or lateral shoots (Munns and Tester 2008).

Table 3. Width and number of shoots of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 dS·m^{-1} or saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 dS·m^{-1} for 4 weeks (first harvest) and 8 weeks (second harvest) in a greenhouse.[i]

EC (dS·m^{-1})	Width (cm)		No. of shoots	
	First harvest	Second harvest	First harvest	Second harvest
		P. davidsonii		
1.0	19.4 a[ii]	19.2 a	23 a	21 a
2.5	18.7 ab	20.8 a	26 a	21 a
5.0	18.5 ab	17.7 a	18 ab	18 a
7.5	17.1 ab	16.6 a	15 b	14 a
10.0	15.6 b	ND[iii]	13 b	ND[iii]
Trend[iv]	L*, Q^{NS}	L^{NS}, Q^{NS}	L^{NS}, Q^{NS}	L^{NS}, Q^{NS}
		P. heterophyllus		
1.0	26.5 a	19.4 a	12 a	9 a
2.5	25.9 a	20.8 a	10 a	10 a
5.0	25.0 a	19.3 a	10 a	9 a
7.5	23.6 a	16.7 a	11 a	5 ab
10.0	23.2 a	10.3 b	10 a	3 b
Trend[iv]	L^{NS}, Q^{NS}	L^{NS}, Q*	L^{NS}, Q^{NS}	L^{NS}, Q^{NS}

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2·2H_2O$) to the nutrient solution. Data were collected 7 d after the fourth (n = 10) and eighth (n = 5) irrigation events for first harvest and second harvest, respectively, except *P. davidsonii* that did not survive when irrigated with saline solution at an EC of 10.0 dS·m^{-1} for 8 weeks.

[ii] Means with same lowercase letters within a species and column are not different among treatments by Tukey-Kramer method of multiplicity at α = 0.05.

[iii] Data were not collected due to plant death.

[iv] L: linear; Q: quadratic; NS, *: nonsignificant or significant at $P < 0.05$.

Saline solution irrigation significantly affected leaf area at both the first ($P < 0.0001$) and second harvests ($P = 0.009$) (Table 1). At the first harvest, *P. davidsonii* exhibited a linear decrease in leaf area with increasing EC of the saline solution (Table 4). Compared with the control, the leaf area of *P. davidsonii* decreased by 49% and 48% when irrigated with saline solution at an EC of 7.5 and 10.0 dS·m^{-1}, respectively. *Penstemon heterophyllus* also showed a linear trend, with the leaf area decreasing by 31% at an EC of 10.0 dS·m^{-1} compared with the control. At the second harvest, the leaf area of *P. davidsonii* decreased by 24% when the EC was increased to 7.5 dS·m^{-1} (Table 4). Similarly, *P. heterophyllus* exhibited a substantial decrease in leaf area, with a reduction of 72% when treated with saline solution at an EC of 10.0 dS·m^{-1}, compared with the control. The reduction in leaf expansion observed in response to salinity is primarily attributed to the osmotic effect of salts around the roots, leading to decreased water availability to leaf cells (Carillo et al. 2011). This diminished water availability results in decreased cell growth and division in leaves, ultimately leading to smaller leaf size and a reduction in overall leaf area (Munns and Tester 2008). In addition, salinity-induced leaf senescence also resulted in a smaller number of leaves, ultimately reducing overall leaf area. Our study aligns with these findings, demonstrating a consistent pattern of reduced leaf area with higher salt concentrations in the saline solution.

At the first harvest, *P. davidsonii* exhibited a linear reduction in shoot dry weight with increasing EC of the saline solution (Table 4). The shoot dry weight decreased by 43% when the EC of the saline solution was increased from 1.0 dS·m^{-1} to 10.0 dS·m^{-1}. However, *P. heterophyllus* did not show a significant difference in the shoot dry weight. At the second harvest, the shoot dry weight of *P. davidsonii* remained unchanged when the EC of the saline solution was increased to 7.5 dS·m^{-1} (Table 4). In contrast, *P. heterophyllus* displayed a quadratic trend in shoot dry weight, with a 53% decrease observed when the EC of the saline solution was raised from 1.0 $dS \cdot m^{-1}$ to 10.0 $dS \cdot m^{-1}$. The results highlight the significant effects of saline solution irrigation on shoot dry weight in both species. These findings align with a study by Zollinger et al. (2007), reporting a decrease in shoot dry weight for both *Penstemon ×mexicali* 'Red Rocks' (red rocks penstemon) and *Penstemon palmeri* (palmer penstemon) when exposed to saline solution, composed of a 1:2 M ratio of NaCl to $CaCl_2$. Cassaniti et al. (2009) also found variations in the effects of saline solution irrigation on plant growth and leaf necrosis across different plant species and salinity levels.

The results highlight a robust growth rate (measured through leaf area and shoot dry weight) in *P. davidsonii* plants under saline stress, particularly those irrigated with a saline solution at an EC of 2.5 and 7.5 $dS \cdot m^{-1}$, between the first and second harvests (Table 4). In contrast, control plants exhibited comparatively less growth, a trend possibly related to abiotic factors, such as nutrient availability or soil moisture (Carillo et al. 2011). Notably, control plants showed quicker drying compared with other treatments. The lack of significant effects in the second harvest, despite prolonged exposure to stress, can be attributed to the plant's adaptation to prevailing stress conditions (Carillo et al. 2011). Plants can exhibit adaptive responses that mitigate the negative effects of stress on growth parameters. However, the lack of convergence between visual quality and growth responses, especially for the species *P. davidsonii*, is evident in this study. The decline in visual ratings does not align consistently with growth parameters such as leaf area and shoot dry weight (Tables 2 and 4). This observation highlights the complex and multifaceted impact of salinity stress on plant species, where visual appearance and growth parameters may respond differently to the same stressor. These findings emphasize the need for comprehensive assessment methods to accurately evaluate salt tolerance in ornamental species. It is crucial to consider both quantitative and qualitative aspects to capture the complex and multifaceted impact of salinity stress on ornamental plants, as proposed in the study by de Oliveira et al. (2018).

Leaf greenness, stomatal conductance, and canopy temperature. Saline solution irrigation had significant effects on SPAD readings at both the first ($P < 0.0001$) and second harvests ($P = 0.01$) (Table 1). In *P. davidsonii*, SPAD readings ranged from 41.2 to 61.7 at the first harvest, showing a decreasing linear and quadratic trend as the EC level of the saline solution increased from 1.0 to 10.0 $dS \cdot m^{-1}$ (Table 5). Similarly, for *P. heterophyllus*, SPAD readings ranged from 57.8 to 62.8, displaying no significant trend. At the second harvest, SPAD readings for *P. davidsonii* exhibited a linear decline with the increasing EC of the saline solution (Table 5). The decline was notable, ranging from 57.6 to 33.6 as the EC increased from 1.0 to 7.5 $dS \cdot m^{-1}$. In *P. heterophyllus*, a slight decrease in SPAD readings from 64.0 to 51.2 was observed as EC levels increased from 1.0 to 10.0 $dS \cdot m^{-1}$. Salinity stress induces chlorophyll degradation and reduces chlorophyll content (Santos 2004). Our findings align with studies by Chen et al. (2019), Paudel and Sun (2022), and Sun et al. (2015), where SPAD readings of ornamental plants decreased with an increase in the EC of the saline solution. Identifying early indicators of salinity stress, such as reductions in SPAD readings, is critical for ensuring the health and visual quality of ornamental plants.

With an escalating EC in the saline solution, the g_s of both species exhibited a significant decrease at both the first ($P < 0.0001$) and second harvest ($P = 0.0005$) (Table 1). In *P. davidsonii* at the first harvest, g_s demonstrated a linear and quadratic reduction as the EC increased from 1.0 to 10.0 $dS \cdot m^{-1}$, decreasing from 0.25 to 0.02 $mol \cdot m^{-2} \cdot s^{-1}$ (Table 5). *Penstemon heterophyllus* also experienced a quadratic reduction in g_s, dropping from 0.09 to 0.01 $mol \cdot m^{-2} \cdot s^{-1}$ with increasing

Table 4. Leaf area and shoot dry weight of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$ for 4 weeks (first harvest) and 8 weeks (second harvest) in a greenhouse.[i]

	Leaf area (cm^2)		Shoot dry wt (g)	
EC ($dS \cdot m^{-1}$)	First harvest	Second harvest	First harvest	Second harvest
		P. davidsonii		
1.0	354.8 a[ii]	527.9 a	9.1 a	13.2 a
2.5	345.6 a	612.3 a	9.0 a	17.1 a
5.0	320.2 a	430.2 a	8.0 ab	10.5 a
7.5	181.6 b	402.1 a	4.6 c	12.5 a
10.0	184.9 b	ND[iii]	5.2 bc	ND[iii]
Trend[iv]	L***, Q^{NS}	L^{NS}, Q^{NS}	L***, Q^{NS}	L^{NS}, Q^{NS}
		P. heterophyllus		
1.0	421.6 a	360.0 a	9.2 a	11.1 a
2.5	360.8 a	300.4 a	7.8 a	10.6 a
5.0	339.9 a	286.3 a	8.7 a	10.4 a
7.5	318.7 a	235.6 ab	8.7 a	9.8 a
10.0	289.1 a	102.1 b	7.2 a	5.2 a
Trend[iv]	L*, Q^{NS}	L^{NS}, Q*	L^{NS}, Q^{NS}	L^{NS}, Q*

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$) to the nutrient solution. Data were collected 7 d after the fourth (n = 10) and eighth (n = 5) irrigation events for first harvest and second harvest, respectively, except *P. davidsonii* that did not survive when irrigated with a saline solution at an EC of 10.0 $dS \cdot m^{-1}$ for 8 weeks.
[ii] Means with same lowercase letters within a species and column are not different among treatments by Tukey-Kramer method of multiplicity at $\alpha = 0.05$.
[iii] Data were not collected due to plant death.
[iv] L: linear; Q: quadratic; NS, *, ***: nonsignificant or significant at $P < 0.05$ or 0.001, respectively.

Table 5. Leaf greenness [Soil Plant Analysis Development (SPAD) reading] and stomatal conductance (g_s) of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$ for 4 weeks (first harvest) and 8 weeks (second harvest) in a greenhouse.[i]

	SPAD		g_s ($mol \cdot m^{-2} \cdot s^{-1}$)	
EC ($dS \cdot m^{-1}$)	First harvest	Second harvest	First harvest	Second harvest
		P. davidsonii		
1.0	61.7 a[ii]	57.6 a	0.25 a	0.11 a
2.5	60.9 a	57.4 a	0.21 a	0.10 ab
5.0	49.0 b	45.1 ab	0.15 a	0.04 c
7.5	43.0 bc	33.6 b	0.08 b	0.04 bc
10.0	41.2 c	ND[iii]	0.02 c	ND[iii]
Trend[iv]	L***, Q*	L*, Q^{NS}	L****, Q****	L*, Q^{NS}
		P. heterophyllus		
1.0	57.8 a	64.0 a	0.09 a	0.06 a
2.5	58.6 a	60.1 a	0.10 a	0.05 a
5.0	62.8 a	57.4 a	0.07 a	0.03 a
7.5	58.6 a	51.2 a	0.04 b	0.02 a
10.0	58.4 a	56.2 a	0.01 c	0.01 a
Trend[iv]	L^{NS}, Q^{NS}	L^{NS}, Q^{NS}	L^{NS}, Q*	L^{NS}, Q^{NS}

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$) to the nutrient solution. Data were collected 7 d after the fourth (n = 10) and eighth (n = 5) irrigation events for first harvest and second harvest, respectively, except *P. davidsonii* that did not survive when irrigated with a saline solution at an EC of 10.0 $dS \cdot m^{-1}$ for 8 weeks.
[ii] Means with same lowercase letters within a species and column are not different among treatments by Tukey-Kramer method of multiplicity at $\alpha = 0.05$.
[iii] Data were not collected due to plant death.
[iv] L: linear; Q: quadratic; NS, *, ***, ****: nonsignificant or significant at $P < 0.05$, 0.001, or 0.0001, respectively.

Table 6. Canopy temperature of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$ after 4 weeks (first harvest) and 8 weeks (second harvest) in a greenhouse.[i]

	Canopy temp (°C)	
EC ($dS \cdot m^{-1}$)	First harvest	Second harvest
	P. davidsonii	
1.0	22.4 d[ii]	24.1 c
2.5	22.5 d	25.5 bc
5.0	24.4 c	27.4 b
7.5	26.3 b	32.7 a
10.0	28.0 a	ND[iii]
Trend[iv]	L****, Q****	L**, Q^{NS}
	P. heterophyllus	
1.0	23.3 c	22.9 c
2.5	23.9 c	25.6 bc
5.0	25.1 b	28.2 ab
7.5	26.6 a	30.5 a
10.0	27.7 a	30.4 ab
Trend[iv]	L****, Q***	L***, Q*

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$) to the nutrient solution. Data were collected using a thermal camera (FLIR E5-XT; Teledyne FLIR, Wilsonville, OR, USA) at 1200 HR, 7 d after the fourth (n = 10) and eighth (n = 5) irrigation events for first harvest and second harvest, respectively, except *P. davidsonii* that did not survive when irrigated with a saline solution at an EC of 10.0 $dS \cdot m^{-1}$ for 8 weeks.

[ii] Means with same lowercase letters within a species and column are not different among treatments by Tukey-Kramer method of multiplicity at $\alpha = 0.05$.

[iii] Data were not collected due to plant death.

[iv] L: linear; Q: quadratic; NS, *, **, ***, ****: nonsignificant or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

Table 7. Leaf mineral contents of *Penstemon davidsonii* and *Penstemon heterophyllus* irrigated with a nutrient solution at an electrical conductivity (EC) of 1.0 $dS \cdot m^{-1}$ or saline solution at an EC of 2.5, 5.0, 7.5, or 10.0 $dS \cdot m^{-1}$.[i]

	Ion content ($mg \cdot g^{-1}$)[ii]								
EC ($dS \cdot m^{-1}$)	Na^+	Cl^-	Ca^{2+}	K^+	Mg^{2+}	Mn^{2+}	S	Zn^{2+}	Fe^{3+}
				P. davidsonii					
1.0	0.01 b[iii]	1.10 d	4.55 d	15.20 ab	1.65 b	0.04 d	1.49 a	0.03 bc	0.03 a
2.5	0.06 b	5.84 d	6.57 d	14.63 b	1.95 b	0.05 c	1.72 a	0.03 c	0.02 a
5.0	0.23 b	20.31 c	10.71 c	14.98 b	2.52 a	0.08 b	1.56 a	0.04 abc	0.03 a
7.5	0.51 ab	28.89 b	14.07 b	16.15 ab	2.67 a	0.08 ab	1.67 a	0.05 ab	0.03 a
10.0	1.05 a	37.91 a	17.56 a	18.64 a	2.84 a	0.10 a	1.72 a	0.05 a	0.03 a
Trend[iv]	L^{NS}	L**	L***	L^{NS}	L**	L****	L^{NS}	L^{NS}	L^{NS}
	Q**	Q****	Q****	Q*	Q****	Q****	Q^{NS}	Q**	Q^{NS}
				P. heterophyllus					
1.0	0.02 b	0.91 b	7.16 c	15.91 a	2.63 b	0.03 c	1.63 a	0.03 a	0.03 a
2.5	0.05 b	1.10 b	8.88 bc	14.93 a	2.84 ab	0.03 c	1.76 a	0.03 a	0.03 a
5.0	0.25 b	5.13 b	11.15 b	10.06 b	2.97 ab	0.05 b	1.65 a	0.04 a	0.03 a
7.5	1.21 a	20.84 a	15.93 a	14.14 a	3.28 a	0.06 ab	2.12 a	0.04 a	0.03 a
10.0	1.36 a	18.59 a	15.22 a	12.45 ab	2.8 b	0.07 a	1.94 a	0.04 a	0.03 a
Trend[iv]	L^{NS}	L^{NS}	L*	L^{NS}	L^{NS}	L^{NS}	L^{NS}	L^{NS}	L^{NS}
	Q**	Q****	Q****	Q***	Q^{NS}	Q****	Q^{NS}	Q*	Q^{NS}
Salinity	****[iii]	****	****	**	****	****	NS	**	NS
Species	NS	****	*	****	****	****	*	*	NS
Salinity × Species	NS	****	**	***	***	NS	NS	NS	NS

[i] Saline solution was created by adding sodium chloride (NaCl) and dihydrate calcium chloride ($CaCl_2 \cdot 2H_2O$) to the nutrient solution.

[ii] Sodium (Na^+), chloride (Cl^-), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), manganese (Mn^{2+}), sulfur (S), Zinc (Zn^2), and iron (Fe^{3+}) ions. Plants at the first harvest were used for mineral analyses.

[iii] Means with same lowercase letters within a species and column are not different among treatments by Tukey-Kramer method of multiplicity at $\alpha = 0.05$.

[iv] L: linear; Q: quadratic; NS, *, **, ***, ****: nonsignificant or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

EC from 1.0 to 10.0 $dS \cdot m^{-1}$. At the second harvest, a linear decrease in the g_s of *P. davidsonii* was observed with an increase in the EC of the saline solution (Table 5). Significantly, g_s decreased from 0.11 to 0.04 $mol \cdot m^{-2} \cdot s^{-1}$ with increasing EC from 1.0 to 7.5 $dS \cdot m^{-1}$. For *P. heterophyllus*, g_s decreased from 0.06 to 0.01 $mol \cdot m^{-2} \cdot s^{-1}$ as the EC increased from 1.0 to 10.0 $dS \cdot m^{-1}$. These findings underscore the influence of saline solution irrigation on g_s over varying timeframes. Previous studies by Chen et al. (2020) and Paudel and Sun (2022, 2023) reported a decrease in g_s in response to higher EC levels in several ornamental plants. Elevated salinity induces osmotic challenges, leading to a protective reduction in g_s to minimize water loss. However, this adjustment can compromise photosynthesis, impacting not only plant growth but also overall visual appeal (Dourado et al. 2022).

At both harvest dates, significant differences in canopy temperature among treatments were observed (all $P < 0.0001$) (Table 1). At the first harvest, canopy temperature exhibited a linear and quadratic increase for both species as the saline solution EC increased from 1.0 to 10.0 $dS \cdot m^{-1}$. Compared with control, canopy temperature increased by 9%, 17%, and 25% for *P. davidsonii* and 8%, 14%, and 19% for *P. heterophyllus*, respectively, when plants were irrigated with saline solution at ECs of 5.0, 7.5, and 10.0 $dS \cdot m^{-1}$ (Table 6). At the second harvest, canopy temperature linearly increased by 14% and 36% for *P. davidsonii* when the saline solution EC increased to 5.0 and 7.5 $dS \cdot m^{-1}$, respectively. Similarly, canopy temperature linearly and quadratically increased by 23%, 33%, and 32% for *P. heterophyllus* when the saline solution EC increased to 5.0, 7.5, and 10.0 $dS \cdot m^{-1}$, respectively. Infrared thermometry and thermal imaging are now recognized as effective methods for evaluating plant water status (Costa et al. 2013; Jones 2004). Canopy temperature serves as a valuable indicator of osmotic stress due to salt stress (Azevedo-Neto et al. 2004; Kluitenberg and Biggar 1992). Osmotic stress reduces transpiration, leading to an elevation in leaf temperature and resulting in temperature differences between control and salt-stressed plants (Kluitenberg and Biggar 1992). Numerous studies, including those on *Myrtus communis* (myrtle) and *Euonymus japonica* (euonymus), have demonstrated that canopy temperature reliably reflects osmotic effects due to salt stress, with salt-stressed plants exhibiting higher canopy temperature compared with controls (Acosta-Motos et al. 2016; Gómez-Bellot et al. 2015). These findings align with our study, in which the canopy temperature increased with the rising EC of the saline solutions.

Mineral contents. The Na^+ content in the leaf exhibited a significant increase in response to escalating EC levels of the saline solution ($P < 0.0001$) (Table 7). Although *P. davidsonii* showed a slower uptake of Na^+ compared with *P. heterophyllus*, there was no significant difference between the species in the way they reacted to the saline conditions ($P = 0.30$). Both species exhibited a quadratic decrease in the Na^+ content with increasing EC levels of the saline solution. For *P. davidsonii*, the Na^+ content significantly increased from 0.01 to 1.05 $mg \cdot g^{-1}$ as the EC of the saline solution increased from 1.0 to 10.0 $dS \cdot m^{-1}$. Similar results were observed for *P. heterophyllus* where Na^+ content increased from 0.02 to 1.21 and 1.36 $mg \cdot g^{-1}$ as the EC of the saline solution increased from 1.0 to 7.5 and 10.0 $dS \cdot m^{-1}$, respectively. In contrast, Paudel and Sun (2024) reported even higher Na^+ content for *Penstemon barbatus* (rock candy blue® penstemon) (5.02 $mg \cdot g^{-1}$) and *P. strictus* (2.80 $mg \cdot g^{-1}$) when irrigated with saline solution at an EC of 10.0 $dS \cdot m^{-1}$. In another study by Paudel and Sun (2023) on *Arctostaphylos uva-ursi* (kinnikinnick), plants exposed to an EC 10.0 $dS \cdot m^{-1}$ saline solution exhibited Na^+ content as high as 8.3 $mg \cdot g^{-1}$, 35 times greater than the plants receiving nutrient solution (EC 1.2 $dS \cdot m^{-1}$). However, in our study, the highest Na^+ content was only 1.36 $mg \cdot g^{-1}$. Notably, the accepted ideal range for Na^+ content in ornamental plants is relatively low, with concentrations exceeding 0.07 $mg \cdot g^{-1}$ having the potential to negatively impact the growth and quality of many ornamental crops (Farnham et al. 1985).

On the other hand, this study revealed a remarked increase in Cl^- content in both species with rising EC levels ($P < 0.0001$) (Table 7). For *P. davidsonii*, Cl^- content increased linearly and quadratically from 1.10 $mg \cdot g^{-1}$ at an EC of 1.0 $dS \cdot m^{-1}$ to 37.91 $mg \cdot g^{-1}$ at an EC of 10.0 $dS \cdot m^{-1}$. Likewise, for *P. heterophyllus*, Cl^{-} content increased quadratically from 0.91 $mg \cdot g^{-1}$ at an EC of 1.0 $dS \cdot m^{-1}$ to 20.84 $mg \cdot g^{-1}$ at an EC of 7.5 $dS \cdot m^{-1}$ and 18.59 $mg \cdot g^{-1}$ at an EC of 10.0 $dS \cdot m^{-1}$. It is noteworthy that the observed symptoms in our plants strongly indicate Cl^{-} toxicity. The minimum accepted Cl^{-} content for plant growth typically ranges from 0.2 to 0.4 $mg \cdot g^{-1}$, depending on the plant species, with several species capable of tolerating higher levels (Colmenero-Flores et al. 2019). The adverse effects of excessive Cl^{-} within chloroplasts on photosynthesis are well documented. It can impede photosynthesis by affecting enzymes responsible for carbon dioxide fixation, damaging photosystem II (PSII) reaction centers, and inducing reactive oxygen species production, leading to oxidative stress (Geilfus 2018). In addition, excessive Cl^{-} ions can disrupt nitrate uptake, resulting in reduced nitrogen supply that adversely impacts chlorophyll content and photosynthesis (Geilfus 2018).

The accumulation of Na^{+} and Cl^{-} ions under salinity conditions is known to be species specific. Studies conducted by Álvarez et al. (2012) and Sun et al. (2020) have also found that Na^{+} and Cl^{-} contents increased in leaves, stems, and roots of ornamental plants treated with saline solutions, with species displaying differences in ion accumulation, particularly with respect to Na^{+} and Cl^{-}. In this study, while Na^{+} concentration was less than 1.4 $mg \cdot g^{-1}$ in both species, the higher Cl^{-} concentration indicates that the observed effects were primarily due to Cl^{-} ion accumulation in the leaf tissue. The accumulation of Na^{+} and Cl^{-} ions under saline conditions can have detrimental effects on plant physiology and photosynthesis, with chloride interference impacting nitrogen uptake and indirectly affecting chlorophyll and photosynthesis (Carillo and Rouphael 2022).

Nutrients are integral to plant cell structure, metabolism, and osmoregulation. Salinity can disrupt nutrient availability, uptake, translocation, and intercellular partitioning (Munns and Tester 2008). Rapid ion accumulation in the cell walls or cytoplasm, due to the inability of vacuoles to effectively sequester incoming salts, can lead to salt damage (Acosta-Motos et al. 2017). In this study, Ca^{2+} levels were notably higher at the EC levels of 7.5 and 10.0 $dS \cdot m^{-1}$, with values increasing linearly and quadratically from 4.55 to 17.56 $mg \cdot g^{-1}$ in *P. davidsonii* and 7.16 to 15.93 $mg \cdot g^{-1}$ in *P. heterophyllus* ($P < 0.0001$) (Table 7). The observed Ca^{2+} levels fell within the typical healthy range of 3.6 to 20.0 $mg \cdot g^{-1}$ derived from soybean (Vitosh et al. 1995), likely influenced by $CaCl_2$ in the saline solution. Calcium plays a role in preserving membrane integrity and regulating ion transport, mitigating the detrimental impacts of salinity stress on plants (Martinez-Ballesta et al. 2008; Nedjimi and Daoud 2009).

K^{+} content exhibited significant variation for both species as the EC levels increased ($P = 0.006$) (Table 7). A quadratic increase in K^{+} content was observed for both species with values ranging from 14.63 to 18.64 $mg \cdot g^{-1}$ for *P. davidsonii* and 10.06 to 15.91 $mg \cdot g^{-1}$ for *P. heterophyllus*. Notably, the typical healthy range for plants can vary depending on the species, with the ideal range for soybean typically falling between 20.0 and 25.0 $mg \cdot g^{-1}$ (Vitosh et al. 1995). However, the observed values in this study indicate that plants might be experiencing a potassium deficiency. Potassium plays an important role in plant growth and development, and in maintaining cell turgor and membrane potential (Munns and Tester 2008). It stands as the primary cation counteracting the negative charge of anions, activating enzymes vital for metabolism, protein and carbohydrate synthesis, and the regulation of stomatal movement (Rahneshan et al. 2018). The role of K^{+} ions in mitigating the effects of Na^{+} ions is vital. Potassium is used as a cost-effective osmotic regulator to counteract the effects of Na^{+} in the cytosol. Sodium ions can have toxic effects on plants primarily by elevating the osmotic potential within the cell, potentially leading to water loss and cell damage. Potassium serves as an essential countermeasure by preserving the osmotic balance in plant cells, thus helping to prevent water loss and preserve cellular integrity (Geilfus 2018).

Magnesium content in the leaf tissue of penstemons was affected by EC levels ($P < 0.0001$) (Table 7). A typical healthy range for Mg^{2+} is 0.26% to 0.60% (Richards 2017). For *P. davidsonii*, plants at the EC levels of 1.0 and 2.5 $dS \cdot m^{-1}$ suffered from Mg^{2+} deficiencies with 1.65 $mg \cdot g^{-1}$ (0.165%) and 1.95 $mg \cdot g^{-1}$ (0.195%), respectively. On the contrary, none of the *P. heterophyllus* plants recorded an average Mg^{2+} content below 2.63 $mg \cdot g^{-1}$ (0.263%) at an EC of 1.0 $dS \cdot m^{-1}$; however, it should be noted that Mg^{2+} contents at the EC levels of 1.0 and 10.0 $dS \cdot m^{-1}$ were significantly less than 7.5 $dS \cdot m^{-1}$, which had the highest Mg^{2+} content at 3.28 $mg \cdot g^{-1}$ (0.38%). Manganese content increased with the rise in EC levels ($P < 0.0001$) (Table 7) but remained within the sufficiency range of 0.02 to 0.30 $mg \cdot g^{-1}$ (The Fertilizer Institute 2023). *Penstemon davidsonii* and *P. heterophyllus* both exhibited a gradual quadratic increase in Mn^{2+} content as the EC of the saline solution increased, with values ranging from 0.04 to 0.10 $mg \cdot g^{-1}$ for *P. davidsonii* and 0.03 to 0.07 $mg \cdot g^{-1}$ for *P. heterophyllus*. Both Mg^{2+} and Mn^{2+} are important nutrients for plants. They function as a part of chlorophyll structure and play a critical role in preserving the molecular structure in plant cells as well as activation of enzymes, which helps in the growth and development of plants under stress (Farhangi-Abriz and Ghassemi-Golezani 2021).

No significant difference in S content was observed among the plants receiving saline solution at different EC levels for both species (Table 7). Specifically, S concentrations ranged from 1.49 to 1.72 $mg \cdot g^{-1}$ for *P. davidsonii* and 1.63 to 2.12 $mg \cdot g^{-1}$ for *P. heterophyllus*. The S sufficiency for soybean is typically defined as 2.10 to 4.00 $mg \cdot g^{-1}$ (0.21% to 0.40%) (Vitosh et al. 1995). However, only one of the analyzed plants met the minimum S level, indicating S deficiency for majority of the plants examined. S is not only crucial for the growth and development of higher plants but also plays an important role in stress tolerance (Marschner 1995). The lower levels of S observed in this study could potentially account for the salinity stress evident in plants exposed to saline solutions with higher EC levels. The zinc content in penstemon leaf tissue was significantly influenced by EC levels ($P = 0.001$) (Table 7). There was a significant quadratic rise in Zn^{2+} content in *P. davidsonii* and *P. heterophyllus* with increasing EC levels (Table 7). The established sufficiency range for Zn^{2+} in soybean typically ranges from 0.02 to 0.05 $mg \cdot g^{-1}$ (Vitosh et al. 1995). Notably, all analyzed samples were found to fall within this sufficiency range, with Zn^{2+} concentrations measuring between 0.03 and 0.05 $mg \cdot g^{-1}$ for *P. davidsonii* and between 0.03 and 0.04 $mg \cdot g^{-1}$ for *P. heterophyllus*.

This study reported no statistical difference for Fe^{3+} concentration in both species when subjected to saline solution irrigation (Table 7). The observed iron concentrations (either 0.03 or 0.02 $mg \cdot g^{-1}$) were consistently beneath the accepted healthy range for soybeans, which is between 0.05 and 0.35 $mg \cdot g^{-1}$ (Vitosh et al. 1995), denoting a deficiency. Iron, a critical mineral nutrient, ranks as the fourth most abundant element in the earth's crust but has limited solubility. The reduced solubility of micronutrients in saline soils can subsequently lead to nutrient deficiencies in plants. Soil salinity can hinder the absorption of iron, as elevated salt cations compete at the root interface, potentially disrupting the equilibrium of nutrient assimilation (Ashraf et al. 2023).

Conclusions

This study evaluated the tolerance of *P. davidsonii* and *P. heterophyllus* to saline conditions. The extent of salt damage was dependent on the salinity levels of the solution and the duration of exposure to the solution. After eight irrigation events with a saline solution at an EC of 10.0 $dS \cdot m^{-1}$, *P. davidsonii* exhibited a visual rating of 0, while *P. heterophyllus* showed a visual rating of 0.4. However, both species maintained good visual quality up to an EC of 5.0 $dS \cdot m^{-1}$. Although *P. davidsonii* and *P. heterophyllus* shared many similar reactions to the saline solution irrigation, the overall evidence suggests that *P. davidsonii* may be less tolerant to saline conditions than *P. heterophyllus*. However, it is important to note that the response to salinity varied among different parameters and conditions. Saline solution irrigation reduced the growth and biomass of both species, as evidenced by reductions in width, number of shoots, leaf area, and shoot dry weight. In addition, physiological parameters such as leaf greenness and stomatal conductance also declined in the plants receiving saline solutions with higher EC levels. Furthermore, increased canopy temperatures were observed in plants subjected to saline solutions at higher EC levels. In saline conditions, Na^{+} and Cl^{-} are taken up by plants; however, in this study, Cl^- accumulation in leaf tissue was more prominent than Na^+.

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