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WATER CONSERVATION THROUGH DROUGHT-RESILIENT LANDSCAPE
PLANTS AND DEFICIT IRRIGATION

by

Ji-Jhong Chen

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Plant Science

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ABSTRACT

Water Conservation through Drought-Resilient Landscape Plants and Deficit Irrigation

by

Ji-Jhong Chen, Doctor of Philosophy

Utah State University, 2023

Major Professor: Dr. Youping Sun and Dr. Kelly Kopp
Department: Plants, Soils, and Climate

Drought-tolerant plants can modify their morphology and physiology to tolerate water stress and are able to maintain better visual quality and growth with reduced irrigation. *Shepherdia ×utahensis* ‘Torrey’ (‘Torrey’ hybrid buffaloberry) and *Penstemon* spp. (beardtongues) are landscape plants commonly grown in low water-use landscapes. Garden roses (*Rosa ×hybrida* L.) are also used in residential landscapes. However, their drought tolerance and irrigation requirements were still unclear. The objectives of this research were to determine the effects of reduced soil moisture availability or irrigation frequency on the morphological and physiological responses of *S. ×utahensis* and penstemons, including *Penstemon barbatus* (Cav.) Roth ‘Novapenblu’ (Rock Candy Blue[®] penstemon), *P. digitalis* Nutt. ex Sims ‘TNPENDB’ (Dakota[™] Burgundy beardtongue), *P. ×mexicali* Mitch. ‘P007S’ (Pikes Peak Purple[®] penstemon), and *P. strictus* Benth. (Rocky Mountain penstemon), in greenhouse conditions, and five garden rose cultivars, including ‘ChewPatout’ (Oso Easy[®] Urban Legend[®] rose), ‘Meibenbino’ (Petite Knock Out[®] rose), ‘MEIRIFTDAY’ (Oso Easy[®] Double Pink rose), ‘Overedclimb’ (Cherry Frost[™] rose), and ‘Radbeauty’ (Sitting Pretty[™] rose), in field conditions. *Shepherdia ×utahensis* and the four

penstemon species were grown at decreased substrate moisture levels between 0.40 to 0.05 $\text{m}^3 \cdot \text{m}^{-3}$. The five garden rose cultivars were irrigated with three irrigation frequency at 80% reference evapotranspiration (ET_o), 50% ET_o, and 20% ET_o in an open field. *Shepherdia* \times *utahensis* adapted to reduced water availability by modifying morphology and physiology. The leaf trichome density of *S. \times utahensis* increased under water stress to amplify leaf reflectance of visible light. Decreased stomatal conductance resulted in warmer canopy temperatures on water-stressed penstemon plants. Xeric *Penstemon barbatus* and *P. strictus* exhibited lower canopy-air temperature differences and better drought tolerance than mesic *P. digitalis* and *P. \times mexicali*. ‘Meibenbino’ and ‘MEIRIFTDAY’ and roses exhibited growth reduction, unacceptable overall visual quality, and narrow leaves with reduced irrigation. ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses sustained acceptable overall appearance and growth when irrigation frequency was reduced. Landscape plants exhibited different responses to drought stress, and some could maintain acceptable aesthetic quality and plant growth when substrate water availability decreased due to their drought tolerance.

PUBLIC ABSTRACT

Water Conservation through Drought-Resilient Landscape Plants and Deficit Irrigation

Ji-Jhong Chen

Increases in urban population and inadequate rainfall result in imbalanced water budgets in urban and sub-urban regions. Water conservation becomes important in urban landscapes because of increased water demands. Modern landscape designs require drought-resistant plants to maintain urban landscape greenness during water scarcity. Irrigating plants at their irrigation requirements, which is the minimum irrigation rate that can achieve acceptable aesthetic quality, can also conserve water. However, the drought tolerance and irrigation requirements of most landscape plants have not been widely evaluated. *Shepherdia ×utahensis* ‘Torrey’ (‘Torrey’ buffaloberry) and *Penstemon* species (beardtongues) are low-water-use landscape plants, but their drought resistance mechanisms are largely unknown. Despite garden roses (*Rosa ×hybrida* L.) being widely used in residential landscapes, their responses to reduced irrigation frequency and irrigation requirements are unclear. The objectives of this research were to determine the plant growth, morphology, and physiology of ‘Torrey’ buffaloberry, four penstemon species, and five garden rose cultivars under drought stress resulting from reduced substrate water content or irrigation frequency. *Shepherdia ×utahensis* ‘Torrey’ and the four penstemons were grown using an automated irrigation system to precisely control their substrate volumetric water contents at their setpoints between 0.40 to 0.05 m³·m⁻³ in a greenhouse for 50 days, whereas the five rose cultivars were irrigated at three irrigation frequencies

(high, medium, and low) in an open field, where the irrigation frequency at the high, medium, and low levels was controlled using 80%, 50%, and 20% reference evapotranspiration (ET_0), respectively. Under reduced substrate moisture levels, *S. ×utahensis* promoted root growth, closed stomata, and increased leaf trichomes density to regulate canopy temperature. Penstemon species native to arid regions, such as *P. barbatus* (Cav.) Roth ‘Novapenblu’ (Rock Candy Blue[®] penstemon) and *P. strictus* Benth. (Rocky Mountain penstemon), showed greater leaf reflectance, a higher volume of root system, and cooler canopy temperatures than the mesic penstemon species, including *P. digitalis* Nutt. ex Sims ‘TNPENDB’ (Dakota[™] Burgundy beardtongue) and *P. ×mexicali* Mitch. ‘P007S’ (Pikes Peak Purple[®] penstemon). Rose cultivars were able to partially close their stomata to reduce water loss when irrigation frequency decreased or air temperatures increased. ‘MEIRIFTDAY’ and ‘Meibenbino’ roses, which showed reductions in the dry weights of leaves and stems and exhibited unacceptable overall appearance, were less tolerant to reduced irrigation compared with ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses when irrigation events decreased from eight to one time during the growing season. Our research showed that landscape plants might change their morphology and physiology to allow them to tolerate water deficit and leaf overheating under drought conditions. Using plants with drought resilience could maintain acceptable visual quality with reduced irrigation water.

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Ji-Jhong Chen

CONTENTS

	Page
ABSTRACT	iii
PUBLIC ABSTRACT	v
ACKNOWLEDGMENTS	vii
LIST OF TABLES	x
LIST OF FIGURES	xii
CHAPTER	
I. INTRODUCTION, PREVIOUS WORK, AND LITERATURE REVIEW	1
The Effects of Drought or Water Deficit on Landscape Plants	2
The Drought-Tolerant Mechanisms of Landscape Plants.....	4
Landscape Plant Evaluation and Selection Programs	7
Landscape Plant Irrigation Trials.....	9
Evaluating Landscape Plants for Drought Tolerance In Greenhouse Conditions .	11
Hybrid Buffaloberries, Penstemons, and Landscape Roses.....	13
Research Hypotheses and Objectives	15
References Cited	16
II. EFFECTS OF WATER AVAILABILITY ON LEAF TRICHOME DENSITY AND PLANT GROWTH AND DEVELOPMENT OF <i>SHEPHERDIA</i> × <i>UTAHENSIS</i>	29
Abstract	29
Introduction.....	30
Materials and Methods.....	34
Results.....	40
Discussion	44
Conclusions.....	52
References.....	53
III. PHYSIOLOGICAL AND CANOPY TEMPERATURE RESPONSES TO DROUGHT OF FOUR PENSTEMON SPECIES	74
Abstract	74
Introduction.....	75
Materials and Methods.....	79
Results.....	84

Discussion	89
Conclusions	96
References Cited	97
IV. CLIMATE READY LANDSCAPE PLANTS (I): GARDEN ROSES TRIALED IN UTAH	115
Abstract	115
Introduction	116
Materials and Methods	120
Results	126
Discussion	132
Conclusions	141
Literature Cited	142
V. CONCLUSIONS	167
APPENDICES	169
Appendix I: Supplementary Figure S1. Plant mortality of <i>Shepherdia</i> × <i>utahensis</i> at eight substrate volumetric water content treatments at the termination of the experiment	170
Appendix II: Supplementary Figure S2. Correlation between stem water potential, leaf size, and leaf curling index of <i>Shepherdia</i> × <i>utahensis</i> at the termination of the experiment	171
Appendix III: Supplementary Figure S3. Total number of trichomes per leaf and trichome to epidermal cell ratio of <i>Shepherdia</i> × <i>utahensis</i> at different substrate volumetric water contents, correlation between total number of epidermal cells per leaf and leaf size, correlation between trichome density and trichome radius	172
Appendix IV: Supplementary Figure S4. Correlation between near-infrared light reflectance and trichome density of <i>Shepherdia</i> × <i>utahensis</i> on the leaf upper (adaxial) surface	173

LIST OF TABLES

Table	Page
2-1 Substrate matric potential (ψ_m) at eight substrate volumetric water content treatments (θ_t) recorded on 11 Jan 2021	62
2-2 Degree of leaves visually wilted, plant growth index (PGI), relative chlorophyll content [Soil Plant Analysis Development (SPAD) value], water content of leaf and stem, stem water potential (ψ_{stem}) and leaf curling index of <i>Shepherdia ×utahensis</i> at eight substrate volumetric water content treatments (θ_t).....	63
2-3 Number (no.) of leaves and shoots, total leaf area and dry weight (DW), root to shoot ratio (R/S), specific leaf area (SLA), leaf size, and nodule no. of <i>Shepherdia ×utahensis</i> at eight substrate volumetric water content treatments (θ_t) at the termination of the experiment	65
2-4 Leaf-to-air vapor pressure deficit (VPD), stomatal conductance (g_s), transpiration rate (E), and net assimilation rate (P_n) of <i>Shepherdia ×utahensis</i> at eight substrate volumetric water content treatments (θ_t)	66
2-5 Fine-scale morphology and leaf reflectance at the wavelengths of photosynthetically active radiation (PAR), blue, green, and red light of <i>Shepherdia ×utahensis</i> at the substrate volumetric water content treatments (θ_t) of 0.40, 0.30, 0.20, and 0.10 $m^3 \cdot m^{-3}$	67
3-1 Substrate volumetric water content (VWC), number (No.) of shoots and inflorescences of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with volumetric water content treatments of 0.35 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought) during the middle (24 Jan) and at the end (1 Mar) of the experiment.	105
3-2 Number (No.) of leaves, leaf area and size, shoot dry weight (DW) and relative water content (RWC), specific leaf area (SLA), and root-to-shoot ratio (R/S) of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with the volumetric water content treatments of 0.35 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought) at the termination of the experiment	106
3-3 Net assimilation rate (P_n), stomatal conductance (g_s), transpiration rate (E), and leaf reflectance of photosynthetically active radiation (PAR), blue, green, red, and near-infrared (NIR) light of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and	

<i>P. strictus</i> with the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought)	108
3-4 Canopy-air temperature difference of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) at 1400 HR on 2 Feb and 28 Feb 2022	109
4-1 Characteristics of soils at the experimental plot	153
4-2 Cumulative (cum.) reference evapotranspiration rate (ET_0) and precipitation, and maximum (max.) and average (avg.) air temperature, daily light integral (DLI), and avg. vapor pressure during 2022 growing season	154
4-3 Overall relative plant growth indices, leaf width, the dry weights of leaves and stems of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments at the termination of the experiment	155
4-4 Leaf temperature, leaf-air temperature difference, vapor pressure deficit (VPD), and transpiration rate of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments from 1600 HR to 1730 HR on 11 Jul and 23 Aug 2022	156
4-5 Stomatal density of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments on 6 Sep 2022.....	157
4-6 Summary of the drought responses of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses when irrigation frequency decreased from high [80% reference evapotranspiration (ET_0)] to medium (50% ET_0) and low (20% ET_0) treatments.....	158

LIST OF FIGURES

Figure	Page
2-1 Daily average substrate volumetric water content at eight substrate water content volumetric water content treatments (θ_t) recorded using calibrated soil moisture sensors (ECH ₂ O 10HS; Meter Group, Pullman, WA) during the experiment.....	68
2-2 Proportion of visually wilted leaves of the plants grown at eight substrate volumetric water content treatments (θ_t) during the experiment	69
2-3 <i>Shepherdia ×utahensis</i> plants at eight substrate volumetric water content treatments (θ_t) at the end of the experiment.....	70
2-4 Dissected compound microscopy image of the leaf upper (adaxial) surface and scanning electron microscopy image of leaf trichomes and epidermal cells of <i>Shepherdia ×utahensis</i> plants at the substrate volumetric water content treatments (θ_t) of 0.40 and 0.10 m ³ ·m ⁻³	71
2-5 Correlation between leaf size, epidermal cell size, and trichome density, epidermal cell size and density and leaf size, trichome density, trichome coverage fraction, and epidermal cell density, epidermal cell size and stem water potential.	72
2-6 Correlation between the leaf upper (adaxial) surface trichome density and reflectance of photosynthetically active radiation, blue, green, and red light.....	73
3-1 Daily average volumetric water contents of substrates growing <i>P. barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with the volumetric water content treatments of 0.35 m ³ ·m ⁻³ (control) and 0.15 m ³ ·m ⁻³ (drought).	110
3-2 Representative plants of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with the volumetric water content treatments of 0.35 m ³ ·m ⁻³ (control) and 0.15 m ³ ·m ⁻³ (drought) at the end of the experiment.....	111
3-3 Visual quality score, plant growth index, and relative chlorophyll content [soil plant analysis development (SPAD) value] of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with the volumetric water content treatments of 0.35 m ³ ·m ⁻³ (control) and 0.15 m ³ ·m ⁻³ (drought).	112
3-4 Correlation between photosynthetic photon flux density and canopy	

temperature of <i>P. barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> with the volumetric water content treatments of 0.35 m ³ ·m ⁻³ (control) and 0.15 m ³ ·m ⁻³ (drought) on 2 Feb and 28 Feb 2022.....	113
3-5 Canopy temperature of <i>Penstemon barbatus</i> ‘Novapenblu’, <i>P. digitalis</i> ‘TNPENDB’, <i>P. ×mexicali</i> ‘P007S’, and <i>P. strictus</i> at the volumetric water content treatments of 0.35 m ³ ·m ⁻³ (control) and 0.15 m ³ ·m ⁻³ (drought) with high-pressure sodium lights (HPS+) or without (HPS-).	114
4-1 Soil volumetric water contents estimated by soil moisture sensors (TDT [®] ; Acclima, Meridian, ID) installed at the bottom of the targeted root zone (50 cm deep) of a ‘Radbeauty’ rose with high [80% reference evapotranspiration (ET _O)], medium (50% ET _O), and low (20% ET _O) treatments	159
4-2 Leaves visibly wilted (A-E) and foliage appearance (F-J) of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET _O)], medium (50% ET _O), and low (20% ET _O) treatments.	160
4-3 The flower abundance (A-E) and overall appearance (F-J) of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET _O)], medium (50% ET _O), and low (20% ET _O) treatments.	162
4-4 Stomatal conductance of ‘ChewPatout’ (A), ‘Meibenbino’ (B), ‘MEIRIFTDAY’ (C), ‘Overedclimb’ (D), and ‘Radbeauty’ roses (E) with high [80% reference evapotranspiration (ET _O)], medium (50% ET _O), and low (20% ET _O) treatments	164
4-5 Microscopy images of stomatal density on the leaf abaxial surface of ‘Meibenbino’ and ‘Overedclimb’ roses with high [80% reference evapotranspiration (ET _O)] (A and B), medium (50% ET _O) (C and D), and low (20% ET _O) treatments (E and F) on 6 Sep 2022.	166

CHAPTER I

INTRODUCTION, PREVIOUS WORK, AND LITERATURE REVIEW

Approximately 70% of residential water per capita is used for landscape irrigation in the western United States (Hayden et al. 2015). The rapid population growth in urban and suburban regions has led to increased demands for freshwater resources (Hollingshaus and Albers 2020; Perlich et al. 2017). Inadequate precipitation and high air temperature have worsened the water deficit and threatened the water supply in cities (Cook et al. 2018). Water supply in much of the western United States relies on snow in winter, but snowfall across the Rocky Mountain region is unreliable, and for example decreased by 26% in the winter between 2017 and 2018 (Utah Division of Emergency Management 2019). The ambient temperature has been 1.5 °C warmer in the last century (Utah States Environmental Protection Agency 2016). Warm air temperature is related to higher saturation deficit which causes high evapotranspiration, leading to dry soils. More than 60% of land in the western United States experienced severe, extreme, or exceptional drought in 2021 and 2022 (National Integrated Drought Information System 2023). Although the severity of drought decreased in 2023, the western United States still experienced drought that had built up more than six-plus years of water deficit (NOAA National Centers for Environmental Information 2023). This reduction of water resources can result in restrictions on landscape irrigation in water scarcity (St. Hilaire and Graves 2001) and reduce the green spaces in cities (McCammon et al. 2009). For instance, landscape irrigation restrictions during the California drought in 2014 reduced the vegetation coverage by 10% in downtown Santa Barbara, California (Miller et al. 2020).

Traditional landscape plants may require a large volume of irrigation water to

sustain acceptable aesthetic quality in a hot and arid environment (McCammon et al. 2009). Balok and St. Hilaire (2002) reported that limited water supplies and increased water prices promoted cities in the southwestern United States to establish xeriscapes. Using drought-adaptive landscape plants in xeriscapes is a viable method to maintain green spaces in cities when conserving irrigation water (Zollinger et al. 2006). In California, landscape designers are required to include drought-tolerant plants in the modern landscape designs (California Department of Water Resources 2023). In San Diego, California, 75% of the plants in a residential landscape are required to be water-efficient plants, whereas non-residential landscapes are required to grow water-wise plants only (County of San Diego 2020). The State of Nevada pays residents to renovate their landscapes with water-wise plants that can adapt to a desert climate and thrive on very little water (Southern Nevada Water Authority 2023). The Utah Division of Water Resources received \$5 million to promote water-efficient landscaping in residential areas (Utah Division of Water Resources 2023). Despite the importance of drought-tolerant landscape plants for future urban landscaping, most plants have not been investigated for their drought resilience (Zollinger et al. 2006).

The Effects of Drought or Water Deficit on Landscape Plants

Without sufficient irrigation and precipitation, plant available water is depleted quickly in a soil profile because of evaporation and transpiration. Decreased soil water potential makes it harder for plants to maintain water uptake from soil, resulting in reduced turgor and wilting leaves (Ryan 2011). When plants were irrigated once every four weeks, the number of visibly wilted leaves increased on *Echinacea purpurea* (L.)

Moench (purple coneflower), *Gaillardia tristata* Pursh (great blanket flower), *Lavandula angustifolia* P. Mill. (English lavender), *Leucanthemum ×superbum* (J.W. Ingram) Berg. Ex Kent ‘Alaska’ (‘Alaska’ shasta daisy), *Penstemon barbatus* Roth var. *praecox nanus rondo* (‘Rondo Mix’ penstemon), and *Penstemon ×mexicali* Mitch. ‘Red Rocks’ (‘Red Rocks’ penstemon) (Zollinger et al. 2006). Poor visual quality is considered the major effect of water stress on landscape plants (Rafi et al. 2019). Dehydration causes the internal water potential of xylem to become more negative, creating cavitation, which is a air-filled space within xylem that can be detrimental to plant development and health (Tyree and Sperry 1989). Cell expansion is susceptible to water stress because cells lose turgor when water potential gradient between soils and roots decreases (Jones 1992; Raviv and Blom 2001). Cell expansion drives expansive growth, such as leaf expansion and stem elongation, and the leaf size and relative shoot growth rate of water-stressed plants are lower than well-irrigated ones (Hsiao 1990). Oki and Lieth (2004) reported that water stress reduced cell size and stem elongation of *Rosa ×hybrida* L. ‘Kardinal’ (‘Kardinal’ rose). Restrictions in leaf and shoot expansion under drought decrease light interception and whole-plant photosynthesis efficiency, resulting in low dry weights of leaves, stems, and roots (Bañon et al. 2006).

Transpirational cooling, by which energy is consumed through latent heat, sustains leaf temperature close to ambient temperature when plants are well-watered (Nelson and Bugbee 2015). As transpiration rate decreases with declined soil matric potential, the energy previously used by latent heat loss is then stored by leaves, resulting in a warm leaf temperature (Nobel 2020). For instance, when *Brassica oleracea* L. (broccoli), *Capsicum annuum* L. (pepper), *Ocimum basilicum* L. (basil), and *Solanum*

lycopersicum L. (tomato) experienced water stresses, their leaf temperatures were 2 °C higher than ambient temperatures (Nelson and Bugbee 2015). Increased leaf temperatures affect enzyme biochemistry and destabilize membranes and proteins, leading to cell death and impairing photosynthesis systems (Taiz et al. 2015). An increase in leaf temperature may exacerbate drought stress to limit photosynthesis efficiency, which is detrimental to the development of leaves, shoots, and flowers (Bheemanahalli et al. 2021). Light intensity and light sources may worsen water stress. Because of high elevation, solar radiation in the Intermountain West is intense and can enhance canopy overheating (Mee et al. 2003). Although solar radiation reaches its maximum during the midday, ambient temperatures become warmest in the late afternoon in a field, leading to a high saturated vapor pressure deficit (Tuzet et al. 2003). In greenhouse condition, high-pressure sodium lights generate greater heat than light-emitting diodes, and using high-pressure sodium light as a supplemental light can increase leaf temperature to amplify transpirational water loss (Katzin et al. 2021). Previous studies used midday stomatal conductance and photosynthesis rate to evaluate plant drought stress in a field condition (Zollinger et al. 2006), but plant responses during the late afternoon may be more indicative of water stress.

The Drought-Tolerant Mechanisms of Landscape Plants

Plants tolerate drought stress via modifying morphology and physiology to enhance water uptake, restrict water loss from the transpiration, and maintain cooler leaf temperatures (Fang and Xiong 2015). Plants with osmotic adjustment can actively accumulate inorganic ions, amino acids, sugar alcohols, and glycine betaine in cells to

decrease the solute concentration, creating more negative water potential to obtain water from dry soil (Chen and Jiang 2010). Although osmotic adjustment is a commonly found mechanism for landscape plants to tolerate drought stress, little evidence exists to support that osmotic regulation improves the visual quality of ornamental plants (Serraj and Sinclair 2002; Zollinger et al. 2006). Because osmotic adjustment creates a more negative water potential to cope with water stress, plants can experience cavitation damage when drought is prolonged (West et al. 2007). Plants enhance their root-shoot ratio to obtain water from a deep soil profile under droughts (Niu and Rodriguez 2009). The effects of water stress on shoot dry mass are more pronounced than on root dry mass, resulting in an increased root-shoot ratio to uptake water from deeper soil horizons (Álvarez and Sánchez-Blanco 2013). A large root-shoot ratio contributes to a more favorable water status when soil moisture become limited (Henderson et al. 1991), and xeric species thriving in the southern United States exhibits a greater root-shoot ratio with small-sized leaves than mesic species (Stromberg 2013).

Ornamental plants can defoliate to reduce excessive water loss from transpiration (Dosmann et al. 1999). Herbaceous perennial plants die back to the ground to avoid hot and arid environments, and to avoid intense solar radiation during the summer (Zollinger et al. 2006). However, woody plants with summer dormancy senesce leaves when the rainy season ends and survive with a leafless canopy during dry summer (Newell 1991). The reduction in stomatal conductance, which results from the partial closure of stomata, is favorable because ornamental plants can tolerate drought stress while maintaining better visual quality (Kjelgren et al. 2009). Although carbon dioxide is less available for photosynthesis, partial stomatal closure can keep internal water potentials less negative to

avoid cavitation during drought conditions (West et al. 2007). Because of the benefits of partial stomata closure, the capacity of reducing stomatal conductance at decreased soil water availability is an important parameter to estimate drought tolerance (Cai et al. 2012).

As transpirational cooling is becoming limited under water deficit, plants can overcome heat stress by modifying leaf orientation and reducing leaf size (Kjelgren et al. 2009; Mee et al. 2003). Plants change their leaf orientation through leaf curling to reduce light interception to minimize solar radiation absorption, although plants may sacrifice light harvesting efficiency and have a lower photosynthesis efficiency (Lee et al. 1982). Previous studies showed that *Dianella revoluta* 'Breeze' (flax lily) and *Cornus kousa* Hans. (Kousa dogwood) adapted to drought via leaf curling to control solar radiation interception (Augé et al. 2002; Kjelgren et al. 2009). Leaf curling also limits transpirational water loss by modifying the boundary layer resistance to water vapor (Lee et al. 1982). As cell and leaf expansions are limited in drought stress, plants produce smaller leaves, which is beneficial for heat dissipation via sensible heat loss (Nobel 2020). Leigh et al. (2017) reported that small-sized leaves allowed the plants to maintain a leaf temperature close to the ambient temperature. Mee et al. (2003) also found nearly all shrubs, perennial wildflowers, and grasses native to hot and arid Intermountain West regions exhibited a leaf width that was less than 2.5 cm to get rid of the heat more efficiently.

Plants can modify leaf reflectivity to control leaf temperature via enhancing cuticle layer thickness and increasing leaf trichome density. For example, Mee et al. (2003) reported that the leaves of desert species, including *Picea pungens* Engelm. (blue

spruce) and *Pinus monophylla* Torr. & Frém. (singleleaf pinyon), exhibited strong leaf reflectance to solar radiation, especially blue light, to prevent leaves from overheating. Leaf cuticle layer increases when experiencing drought stress because water deficit enhances the biosynthesis of cutin and waxes, both of which are components of cuticle layers (Ma et al. 2015). The thick cuticle layer increases leaf reflectivity to decrease the absorption of shortwave radiation (Leigh et al. 2017). As increased cuticle layer thickness is advantageous for drought tolerance, xeric plants, such as *Reaumuria soongorica* (Pall.) Maxim (reaumuria), show thick cuticle layers and strong leaf reflectivity to regulate leaf temperature (Shi et al. 2013). Drought-tolerant plants may increase trichome density when experiencing water stress (Sriladda et al. 2016). Trichomes are unicellular or multicellular extensions of the epidermis that can increase leaf reflectance and improve abiotic stress tolerance (Bickford 2016). *Shepherdia rotundifolia* Parry (roundleaf buffaloberry), an extreme xeric species, exhibits thicker trichome layers on the adaxial and abaxial surfaces than riparian *Shepherdia argentea* (Pursh) Nutt. (silver buffaloberry) (Sriladda et al. 2016). Apart from regulating leaf temperature, dense trichomes on the leaves of *Eriogonum corymbosum* Benth. (crisp-leaf buckwheat) can help reduce water loss enhancement by wind to maintain leaf water status (Miller 2011).

Landscape Plant Evaluation and Selection Programs

Because of the capacities to modify morphology and physiology in drought stress, some drought-tolerant plants can maintain acceptable aesthetic appearances relying on precipitation only (Kratsch and Skelly 2011). Other traditional landscape plants exhibit abiotic stress because of high solar radiation, warm air temperature, low humidity, and

insufficient precipitation in the growing season in the western United States (Mee et al. 2003). To identify suitable drought-tolerant plants for water-efficient landscaping, plant selection and evaluation programs in the southwestern and western United States were established. The Segoe Supreme™ plant breeding and introduction program at Utah State University develops and promotes drought-tolerant plants exhibiting adaptability to urban landscapes (Rupp et al. 2018). The Segoe Supreme™ program selects drought-tolerant plants for low water-use landscaping to conserve irrigation water via estimating their drought tolerance, adaptability to climate and soils, attractiveness and longevity of blooms, and ease of propagation (Rupp et al. 2018). The Plant Select® program at Colorado State University and Denver Botanic Gardens also selects and promotes drought-tolerant herbaceous and woody plants in the Intermountain West for residential landscape uses (Rupp et al. 2018). Landscape plants are selected by the Plant Select® program based on their excellent performance in garden situations, adaptation to extreme weather conditions, uniqueness of floral color, biotic stress resistance, and noninvasiveness in landscapes. Although plants are selected for low water-use landscaping, the drought tolerance is estimated based on the precipitation rate of their habitats in these plant selection programs (Meyer et al. 2009).

The American Rose Trials for Sustainability® selects garden roses adapting regional climate conditions and showing outstanding aesthetic quality and disease resistance (American Rose Trials for Sustainability® 2023). However, drought tolerance was not investigated in the American Rose Trials for Sustainability®. Texas Superstar® is a marketing assistance program established by Texas A&M University and green industries in Texas (Mackay et al. 2001). The Texas Superstar® program selects

ornamental plants based on their ornamental quality, pest and disease resistance, and tolerance to extreme weather conditions in Texas (i.e., heat and drought stresses) (Pemberton et al. 2011). Within the Texas Superstar[®] program, the drought resilience is determined by evaluating the ornamental quality of candidate plants growing at various climatic zones (Mackay et al. 2001). The Earth-Kind[®] Roses program at Texas AgriLife Extension Service selects rose cultivars with superior pest resistance, adaptation to different soil types, and heat and drought tolerance (George 2009). In the Earth-Kind[®] Roses program, the flower and foliage quantity of roses are evaluated in landscape conditions without supplemental irrigation (Mackay et al. 2008). However, the physiological and morphological mechanisms that allow landscape plants to tolerate drought haven't been investigated within these plant selection programs.

Landscape Plant Irrigation Trials

Watering plants no more than their irrigation requirements can save a significant amount of water while maintaining urban greenness (Hartin et al. 2018). For instance, up to 83% of irrigation water can be conserved when *Ficus nitida* 'Green Gem' (laurel fig) and *Liquidambar styraciflua* (sweet gum) were irrigated according to their irrigation requirements (Hartin et al. 2018). Instead of growing for yield, landscape plants are irrigated to maintain acceptable aesthetic quality (Rafi et al. 2019). The irrigation requirement is the minimum irrigation rate that can achieve acceptable aesthetic quality (Kjelgren et al. 2000). For a foliage plant, the acceptable appearance, by definition of Reid et al. (2019), is the individual with foliage damage less than 25% of the canopy. Flowering plants are considered acceptable if they meet the requirements of foliage

aesthetic quality and sustain their flower number while reducing irrigation (Cameron et al. 2008; Reid et al. 2019). However, the irrigation requirements are largely unknown for a diversity of landscape plants. Homeowners typically irrigate far beyond the irrigation requirements of many landscape plants (Hartin et al. 2018).

Irrigation requirements have been quantified by comparing the growth, foliage quality, and flower abundance of landscape plants irrigated at different deficit levels (Reid and Oki 2016; Schuch and Martin, 2017; Zollinger et al. 2006). Within these deficit irrigation trials, the total amount of water applied to each plant reduces because irrigation frequency decreases (Hartin et al. 2018) or the amount of water reduces at each irrigation (Rafi et al. 2019). Reference evapotranspiration (ET_o) is a hypothetical evapotranspiration value estimated under optimal conditions for a dense, well-watered green canopy, and is a fundamental parameter to schedule deficit irrigation for determining landscape plant irrigation requirements in field trials. Different methods, such as Water Use Classifications of Landscape Species (WUCOLS) method (Costello et al. 2000), plant factor (PF) method (Kjelgren et al. 2000), and Irrigated Public Open Space (IPOS) method (South Australian Water Corporation-IPOS Consulting 2015), have been developed to evaluate landscape plant irrigation requirement. Among the methods, the protocol developed by University of California (UC) Landscape Plant Irrigation Trials™ was the first landscape plant irrigation trial scheduling the irrigation frequency of a fixed volume of water based on ET_o rather than a preset schedule or used ET_o to adjust the amount of irrigation applied. Plants are regularly irrigated during the first year for establishment. Plant quality parameters, including foliage, flower abundance, pest and disease tolerance, vigor, and overall appearance, of each landscape plant at deficit

irrigation treatment are rated at least once per month throughout the deficit season to provide species-specific irrigation recommendations (Reid and Oki 2008). Over eighty taxa of landscape plants have been evaluated in UC Landscape Plant Irrigation Trials™, and plants exhibit different visual quality at reduced irrigation in these trials (Hartin et al. 2018; Reid and Oki 2008; Reid and Oki 2016). However, plant response at the physiological level and mechanisms related to drought tolerance were not investigated. For instance, the visual quality of *Penstemon heterophyllus* Lindl. 'Margarita BOP' (margarita bop bunch leaf penstemon) was not impaired when irrigation frequency reduced from 80% to 20% ETo (Reid and Oki 2013), but the drought-resistant mechanisms were still unknown.

Evaluating Landscape Plants for Drought Tolerance in Greenhouse Conditions

Because the results of field trials may be affected by other abiotic and biotic factors, such as weather and animal damage, plant drought responses are evaluated in greenhouse condition to obtain consolidated data (Augé et al. 1986; Cai et al. 2012; Niu and Rodriguez 2009; Niu et al. 2012). When irrigation frequency declined from twice per week to once every two weeks in a greenhouse condition, *Rosa ×hybrida* L. 'Dr. Huey' ('Dr. Huey' roses), *Rosa multiflora* (multiflora rose), and *Rosa odorata* (tea rose) reduced their dry weights by 22%, 33%, and 38%, whereas the dry weight of 'Fortuniana' rose did not change (Niu and Rodriguez 2009). Cai et al. (2012) reported that 'RADrazz' rose was more drought-tolerant compared with 'Belinda's Dream', 'Old Blush', and 'Marie Pavie' roses in a greenhouse, because the shoot and root growth of 'RADrazz' rose was not affected by reduced irrigation frequency from 3 times per week to once every other

week.

Sensor-based automated irrigation systems, which can control substrate volumetric water contents at their set points, have been successfully used to study plant drought responses in greenhouse conditions (Montesano et al. 2018; Nemali and van Iersel 2006; Nemali and van Iersel 2008; Zhen et al. 2014). Nemali and van Iersel (2006) developed automated irrigation systems that utilized capacitance soil moisture sensors to control the volumetric water contents of soilless substrates. Using a capacitance sensor-based automated irrigation system, Zhen et al. (2014) found *Aquilegia canadensis* L. ‘Pink Lanterns’ (‘Pink Lanterns’ Canadian columbine) increased plant height and net photosynthesis rates when substrate volumetric water contents increased from 0.05 to 0.45 m³·m⁻³. Montesano et al. (2018) grew basil using a capacitance sensor-based automated irrigation system to control their volumetric water contents at 0.20, 0.30, 0.40 m³·m⁻³ for 23 days, and found no significant difference in the growth of basil plants at the three soil moisture levels. Linear curvilinear relationships were observed between their stomatal conductance and substrate water contents when *Salvia splendens* Sellow ex Roem. & Schult. ‘Bonfire Red’ (‘Bonfire Red’ salvia), *Catharanthus roseus* (L.) G. Don ‘Cooler Peppermint’ (‘Cooler Peppermint’ vinca), *Petunia ×hybrida* Vilm. ‘Lavender White’ (‘Lavender White’ petunia), and *Impatiens walleriana* Hook. f. ‘Cherry’ (‘Cherry’ impatiens) were grown at four volumetric water contents of 0.09, 0.15, 0.22, and 0.32 m³·m⁻³ using a sensor-based automated irrigation system (Nemali and van Iersel 2008). *Cymbidium* species (orchid) irrigated using a soil moisture sensor-based automated irrigation system did not reduce their net photosynthetic rate and fresh weights of shoots and roots when substrate volumetric water contents decreased from 0.40 to 0.30

$\text{m}^3 \cdot \text{m}^{-3}$ (An et al. 2021a). However, at the substrate volumetric water content of $0.25 \text{ m}^3 \cdot \text{m}^{-3}$, *Cymbidium* species showed smaller biomass and less leaves compared with the plants grown at the substrate volumetric water content of $0.55 \text{ m}^3 \cdot \text{m}^{-3}$, but the number of leaves and chlorophyll content did not differ (An et al. 2021b). The results of An et al. (2021b) suggest that the morphology and physiology of ornamental plants respond differently to reduced substrate moisture level.

Hybrid Buffaloberries, Penstemons, and Landscape roses

Shepherdia ×utahensis 'Torrey' ('Torrey' hybrid buffaloberry) is an interspecific hybrid of two native plants in the Intermountain West, *S. argentea* (silver buffaloberry) and *S. rotundifolia* (roundleaf buffaloberry) (Sriladda et al. 2016). *Shepherdia* species, such as *S. argentea* and *S. rotundifolia*, have extreme resistance to drought and heat stress (Krishnan and Hughes 1991), and *S. ×utahensis* is a water-wise landscape plant developed by the Utah State University for water-efficient landscaping (Sriladda et al. 2016). Dense trichomes on the leaf surface of *S. ×utahensis* may increase leaf reflectivity to avoid excessive solar radiation absorption under water stress (Sriladda et al. 2016). *Shepherdia ×utahensis* can also reduce stomatal conductance when air temperature and saturation deficit increase to regulate transpirational water loss (Sriladda et al. 2016). Nevertheless, no research investigated the drought-tolerant mechanisms of *S. ×utahensis*.

More than 250 penstemons (*Penstemon* spp.) are native to north United States, with diverse forms, sizes, and levels of drought tolerance (Mee et al. 2003). Many penstemons native to the Intermountain West are recommended for water-wise landscaping (Rupp et al. 2018). *Penstemon barbatus* (golden-beard penstemon) is a

water-wise landscape plant native to southern Colorado to northern Mexico (Way and James 1998; Zollinger et al. 2006). *Penstemon ×mexicali* is also a water-wise landscape plant tolerating decreased soil water availability (Henson and Langelo 2021). *Penstemon strictus* (Rocky Mountain beard tongue) is native to grasslands in the Intermountain West and has been widely used in water-wise landscaping (Mee et al. 2003). *Penstemon strictus* performs well on well-drained soil and exhibits excellent tolerance to cold winter and dry summer (Henson and Langelo 2021). *Penstemon digitalis* (foxglove beardtongue) is native to mesic prairies throughout eastern to central North America (Mitchell and Ankeny 2001) and is also recommended for water-wise landscaping (North Carolina Cooperative Extension 2023). However, the drought tolerance of native penstemons is not widely investigated.

Roses are commonly used flowering plants in residential landscapes with diverse drought tolerance (Cai et al. 2012; Sagers 2012). Previous studies showed that roses had various irrigation requirements (Reid et al. 2019), but the physiological characteristics for roses to have low irrigation requirements were not investigated. *Rosa ×hybrida* L. ‘ChewPatout’ (Oso Easy® Urban Legend® rose), ‘MEIRIFTDAY’ (Oso Easy® Double Pink rose), ‘Meibenbino’ (Petite Knock Out® rose), ‘Overedclimb’ (Cherry Frost™ rose), ‘Radbeauty’ (Sitting Pretty™ rose) are disease- and pest-resistant cultivars (Proven Winners 2022; Star Roses and Plants 2022). However, the drought tolerance of these five rose cultivars has not been studied, and determining their physiology and morphology at deficit irrigation trials using the WUCOLS method may provide useful information to understand their drought resilience.

Research Hypotheses and Objectives

Transpirational cooling is limited under drought stress, and *Shepherdia ×utahensis* might modify leaf trichome density to regulate leaf temperature. Penstemon plants, which do not have pubescent leaves, might increase leaf temperature when plants were under drought stress. Due to the relationship between plant water status and canopy temperature, drought-tolerant rose cultivars, which required low amounts of irrigation to maintain acceptable visual quality, might have cooler canopy temperature compare with drought-sensitive cultivars at the same irrigation treatment. The general goal of this objective is to study the plant growth, morphological and physiological responses, and canopy temperature of *Shepherdia ×utahensis*, penstemon species, and garden rose at different water availability.

In this research, we hypothesize that (1) decreases in volumetric water content of a peat-based substrate from 0.40 to 0.10 $\text{m}^3 \cdot \text{m}^{-3}$ reduces substrate matric potential and plant growth and increases canopy temperature and the proportion of visually wilted leaves of container-grown *Shepherdia ×utahensis* (hybrid buffaloberry) and *Penstemon* spp. (penstemon) in a greenhouse condition, (2) *Shepherdia ×utahensis* and *Penstemon* spp. alters the optical properties and morphology of leaf, root to shoot ratio, and stomatal conductance when the volumetric water content of a peat-based substrate decreases from 0.40 to 0.10 $\text{m}^3 \cdot \text{m}^{-3}$ (3) decreases in irrigation frequency from eight to one time within the growing season (with same application volume at each irrigation) affect plant growth, visual quality, flower abundance, and canopy temperature of rose cultivars in field conditions, (4) rose cultivars have different percentage of wilting and burned leaves, plant growth rate, and canopy temperature when irrigation frequency decreases.

Three experiments were conducted to test the hypotheses. The first experiment was conducted to investigate the effects of decreased substrate moisture contents from 0.40 to 0.05 m³·m⁻³ on plant growth and development and trichome density of *S. ×utahensis* in a greenhouse condition. The second experiment was conducted to determine the effects of reduced soil moisture availability from 0.35 m³·m⁻³ to 0.15 m³·m⁻³ on the physiology and canopy temperature of four penstemon species, including *Penstemon barbatus* (Cav.) Roth ‘Novapenblu’ (Rock Candy Blue[®] penstemon), *P. digitalis* Nutt. ex Sims' TNPENDB' (Dakota[™] Burgundy beardtongue), *P. ×mexicali* Mitch. ‘P007S’ (Pikes Peak Purple[®] penstemon), and *P. strictus*. Lastly, an experiment was conducted to study the impacts of reduced irrigation frequency on visual quality, plant growth, and physiology of five garden rose cultivars, including ‘ChewPatout’, ‘MEIRIFTDAY’, ‘Meibenbino’, ‘Overedclimb’, and ‘Radbeauty’.

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CHAPTER II

EFFECTS OF WATER AVAILABILITY ON LEAF TRICHOME DENSITY AND
PLANT GROWTH AND DEVELOPMENT OF *SHEPHERDIA* × *UTAHENSIS*¹**Abstract**

Many arid lands across the globe are experiencing more frequent and extreme droughts because of warmer temperatures resulting from climate change, less predictable precipitation patterns, and decreased soil moisture. Approximately 60-90% of household water is used for urban landscape irrigation in the western United States, necessitating the establishment of landscapes using drought-tolerant plants that conserve water.

Shepherdia × *utahensis* (hybrid buffaloberry) is a drought-tolerant plant with dense leaf trichomes (epidermal appendages) that may limit excessive water loss by transpiration. However, little is known about how *S.* × *utahensis* regulates leaf heat balance when transpirational cooling is limited. The objective of this research was to investigate the effects of substrate water availability on plant growth and development and trichome density of *S.* × *utahensis*. Ninety-six clonally propagated plants were grown using an automated irrigation system, and their substrate volumetric water contents were controlled at 0.05 to 0.40 m³·m⁻³ for two months. Results showed that water stress impaired plant growth and increased the proportion of visually wilted leaves. *Shepherdia* × *utahensis* acclimates to drought by reducing cell dehydration and canopy overheating, which may be accomplished through decreased stomatal conductance, smaller leaf

¹ Author: Chen, J., Y. Sun, K. Kopp, L. Oki, S.B. Jones, and L. Hipps. 2022. Effects of water availability on leaf trichome density and plant growth and development of *Shepherdia* × *utahensis*. *Frontiers in Plant Science*. 13:855858. doi.org/10.3389/fpls.2022.855858

development, leaf curling, increased leaf thickness, and greater root to shoot ratio. Leaf trichome density increased when stem water potential decreased, resulting in greater leaf reflectance of visible light. Cell and leaf expansion were restricted under water stress, and negative correlations were exhibited between epidermal cell size and trichome density. According to our results, plasticity in leaves and roots aids plants in tolerating abiotic stresses associated with drought. Acclimation of *S. ×utahensis* to water stress was associated with increased trichome density due to plasticity in cell size. Dense trichomes on leaves reflected more lights which appeared to facilitate leaf temperature regulation.

Introduction

Hotter and drier climates globally, coupled with periodic drought, often necessitate large quantities of irrigation water to maintain visual quality, growth, and development of landscape plants (Mee et al., 2003). Approximately 60-90% of household water is used for urban landscape irrigation in the western U.S. (Arizona Department of Water Resources, 2022; Center for Water-Efficient Landscaping, 2020; Sovocool et al., 2006). However, due to the increasing water demand of a growing population, designing landscapes with drought-tolerant adaptive plants or plants native to arid and semi-arid areas is important for long-term water conservation in the western U.S. In addition, landscape plants are threatened by increasingly common droughts and heatwaves in the western U.S. because they are largely reliant on irrigation (Miller et al., 2020). A recent drought caused urban vegetation coverage in downtown Santa Barbara, California, to decline from 45% to 35% (Miller et al., 2020). Hence, landscape plants characterized by morphological and physiological plasticity, which can better acclimate to water and heat

stresses, are desirable for future landscapes. Unfortunately, drought responses of landscape plants are seldom investigated, and drought tolerance studies have largely been conducted based on local precipitation rates, rather than well-controlled inputs (Meyer et al., 2009).

Reduction in soil water availability causes cell dehydration, resulting leaf wilting and degrading aesthetic appearance (Zollinger et al., 2006). Cell dehydration then prevents chlorophyll production and photosynthesis, which reduces leaf greenness and plant growth (Ahluwalia et al., 2021). For instance, *Orthosiphon aristatus* (cat's whiskers) exhibited wilted leaves and reduced leaf and root biomass when no irrigation was applied (Kjelgren et al., 2009). Water stress also inhibits leaf expansion, reducing light-capture area (Dale, 1988) and may indirectly induce heat stress in plants because of reduced transpirational cooling to counter absorbed radiation (Nobel, 2009). *Gaillardia aristata* (blanketflower) and *Penstemon barbatus* (golden beard penstemon), for example, showed over 50% of the leaves burned when water was limited (Zollinger et al., 2006). High temperatures may disrupt plant metabolism and protein stability, leading to leaf burn and necrosis (Taiz et al., 2015).

Plant acclimation involves changes in morphology and physiology without genetic modification (Taiz et al., 2015). Under drought conditions, plants may acclimate to drought by decreasing water loss and reducing heat load and leaf temperature (Mee et al., 2003). Root growth may be promoted to increase water uptake, leading to a greater root to shoot ratio (Ahluwalia et al., 2021). Water loss may be minimized via stomatal closure, leaf senescence, and reduced leaf size (Zollinger et al., 2006). For instance, Stromberg (2013) found that xeric species growing in the southern U.S. have greater root

to shoot ratios, but smaller leaves, than mesic species. In hot and arid environments, plants gradually reduced their stomatal conductance and transpiration along with increasing leaf temperatures and higher leaf-to-air VPD to prevent excessive water loss (Roessler and Monson, 1985). Minimizing stomatal conductance when solar radiation and air temperature are greatest at midday can protect plants from xylem dysfunction and maintain water status (Zhang et al., 2013).

Plant leaf temperature may be regulated by adjusted leaf size, orientation, and trichome density (Ehleringer et al., 1976; Nilsen, 1987; Nobel, 2009). For example, small leaves are advantageous for increasing sensible heat loss. The leaves of native plants in the western U.S., such as *Artemisia tridentata* (big sagebrush) and *Cercocarpus montanus* (alder leaf mountain mahogany) are less than 2.5 cm wide, helping to reduce plant heat load more efficiently (Mee et al., 2003). Leigh et al. (2017) reported that plants in hot and dry environments of Australia, such as *Banksia grandis* (bull banksia), *Grevillea agrifolia* (blue grevillea), and *Telopea speciosissima* (waratah) have leaves covered by dense trichomes and vertical leaf orientation, which reduces the interception of solar radiation.

Trichome density has been found to be affected by soil water content, air temperature, and vapor pressure deficit (Banon et al., 2004; Bickford, 2016; Ehleringer, 1982; Shibuya et al., 2016). For instance, trichome density of *Lotus creticus* (cretan trefoil) increased when the amount of irrigation water decreased by 70% (Banon et al., 2004). Shibuya et al. (2009) discovered that *Cucumis sativus* (cucumber) had 255 trichomes per cm² of leaf area at a vapor pressure deficit of 0.4 kPa which increased to 463 trichomes per cm² at 3.8 kPa. Ehleringer (1982) observed that trichome density of

Encelia farinosa (brittlebush) grown in California positively correlated to mean maximum air temperature of the growing habitat. However, the effect of water stress on plant trichome development has not been widely studied. Early research suggested leaf trichome production was promoted under water deficit (Quarrie and Jones, 1977). However, this finding contradicts the fact that plant cell division is inhibited under drought stress conditions (Dale, 1988). Brodribb et al. (2013) reported that changes in cell size provided a substantial means to modify leaf function without disturbing other tissue/organ functions. Carins Murphy et al. (2014) found that epidermal cell expansion facilitated the decrease of stomatal density under shade, where large leaves had low stomatal density. Stomata and trichomes are both epidermal appendages and their development occurs prior to cell expansion. Hence, change in cell size may modify trichome density under water stress.

Shepherdia ×utahensis ‘Torrey’ (hybrid buffaloberry) is an interspecific hybrid between *S. argentea* (silver buffaloberry) and *S. roundifolia* (roundleaf buffaloberry). *Shepherdia argentea* tolerates a wide range of growing conditions from wet to dry soil (Mee et al., 2003), while *S. roundifolia* is extremely resistant to hot and arid conditions (Sriladda et al., 2016). Xeric *S. roundifolia* has denser leaf trichomes as compared to riparian *S. argentea* (Sriladda et al., 2016), which indicates trichome density of *Shepherdia* species may be influenced by water availability. *Shepherdia ×utahensis* has leaf trichomes (Sriladda et al., 2016) and grows well in a variety of substrates (Chen et al., 2021). However, the effects of soil moisture level on trichome density have rarely been investigated. The hypotheses of this research are 1) the morphology and physiology of *S. ×utahensis* change at different substrate water contents, and 2) leaf trichome density

is affected by cell size under drought. To test these hypotheses, the objectives of this research were 1) to evaluate the morphological and physiological responses of *S. ×utahensis* under various substrate volumetric water contents in a greenhouse, and 2) to quantify the relationship between trichome density and water deficit.

Materials and Methods

Plant Materials. Cuttings were collected from *S. ×utahensis* ‘Torrey’ clone plants at the Utah Agricultural Experiment Station’s (UAES) Greenville Research Farm (North Logan, UT) on 16 July 2019 and propagated using the method of Chen et al. (2020). On 1 Oct. 2019, rooted cuttings were transplanted to cone-tainers (D40H; Stuewe and Sons, Tangent, OR) and filled with perlite (Hess Perlite, Malad City, ID). All plants were kept in a UAES’s hoop house (Logan, UT) and irrigated with tap water (electrical conductivity = $0.36 \text{ dS}\cdot\text{m}^{-1}$, pH = 7.73).

On 8 Oct. 2020, ninety-six plants of uniform height and shoot number were transplanted to 7.6-L injection-molded polypropylene containers (No. 2B; Nursery Supplies, Orange, CA) using a soilless substrate (Metro-Mix[®] 820; Sun Gro Horticulture, Agawam, MA). Plants were manually irrigated to container capacity and subsequently irrigated using a capacitance-sensor-based automated system (Nemali and van Iersel, 2006) in a UAES’s research greenhouse (Logan, UT). The experiment had three blocks (replicates) and eight volumetric water content treatments at 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, and $0.40 \text{ m}^3\cdot\text{m}^{-3}$ with four replications in each treatment. Within each block, 32 plants were randomly assigned to the eight treatments and a capacitance sensor (ECH₂O 10HS; Meter Group, Pullman, WA) was vertically inserted into the substrate (15

cm deep) of one randomly selected container in each treatment to measure substrate water content. Twenty-four soil moisture sensors were connected to a multiplexer (AM 16/32B; Campbell Scientific, Logan, UT) connected to a datalogger (CR1000X; Campbell Scientific). The datalogger was programmed to measure sensor output voltage every 15 seconds, and the output voltage was converted to substrate volumetric water content (θ_v) using a substrate-specific calibration equation [$\theta_v = \text{voltage} \times 0.0009 - 0.3688$ ($r^2 = 0.97$, $P < 0.0001$)]. Two relay controllers (SDM-CD16AC; Campbell Scientific) were connected to 24 normally-closed, 24-volt-AC solenoid valves (CPF100; Rainbird, Azusa, CA) to control the irrigation of the four plants in each treatment. The datalogger was programmed to open the solenoid valves for 5 seconds when the substrate volumetric water content measured by capacitance sensor fell below the set point. Each plant in the capacitance-sensor automated irrigation system was irrigated using a pressure-compensated drip emitter with a flow rate at 1.3 ± 0.2 (mean \pm SD) $\text{mL} \cdot \text{s}^{-1}$. For establishment, plants in each treatment were irrigated at the threshold of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ for 26 days following the protocol of Cai et al. (2012). On 15 Oct. 2020, plants were topdressed with a controlled-release fertilizer (Osmocote Plus 15-9-12; Israel Chemicals, Tel Aviv-Yafo, Israel) at a rate of $0.02 \text{ g} \cdot \text{cm}^{-2}$. On 5 Nov. 2020, plants were inoculated with 50 mL soil collected from the rhizosphere of a *S. ×utahensis* ‘Torrey’ plant (lat. $41^\circ 45' \text{ N}$, long. $111^\circ 48' \text{ W}$) growing at the UAES’s Greenville Research Farm. On 13 Nov. 2020, the experiment was initiated, and each sensor was randomly assigned to one of eight irrigation set points ranging from 0.05 to $0.40 \text{ m}^3 \cdot \text{m}^{-3}$. The substrate gradually dried down and maintained at each set point until the experiment was terminated on 12 Jan. 2021.

A substrate-specific water retention curve was established using the van Genuchten model (van Genuchten, 1980) with measurements using Tempe cells (ICT international, Armidale, Australia) and a soil water potentiometer (WP4C; Meter Group) in the Utah State University (USU) Environmental Soil Physics Laboratory (Logan, UT). Our water retention curve was similar to the results of van Iersel et al. (2013), where substrate volumetric water content at 0.40, 0.35, 0.30, 0.25, 0.20, 0.15, 0.10, and 0.05 $\text{m}^3 \cdot \text{m}^{-3}$ were equivalent to corresponding substrate matric potentials of -0.008 , -0.012 , -0.019 , -0.034 , -0.067 , -0.159 , -0.540 , and -4.358 MPa, respectively. On 11 Jan. 2021, substrate volumetric water content in each container (θ_p) was estimated using a handheld soil moisture sensor (Hydro Sense; Campbell Scientific). The sensor output was converted to θ_p using a substrate-specific calibration [$\theta_p = 0.2923 \times \text{output} + 0.3855$ ($P < 0.0001$; $r^2 = 0.99$)]. The θ_p was converted to soil matric potential using the substrate-specific water retention curves.

Greenhouse Environment. The average air temperature within the greenhouse was 24.7 ± 0.4 °C (mean \pm SD) during the day and 21.5 ± 0.3 °C at night. Supplemental light was provided using 1000-W high-pressure sodium lamps (Hydrofarm, Petaluma, CA) at a light intensity of 287.1 ± 1.4 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at plant canopy level. Lamps were turned on from 0600 to 2200 HR when greenhouse light intensity fell below 500 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The daily light integral and photosynthetic photon flux density at the plant canopy level was 27.2 ± 2.4 $\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and 316.2 ± 30.4 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively, recorded using a full-spectrum quantum sensor (SQ-500-SS; Apogee Instruments, Logan, UT).

Data Collection

Data collection of this study followed the protocol of van Iersel et al. (2010) and

Zhen et al. (2014) to compare plant responses to different substrate water content.

Proportion of visually wilted leaves, leaf greenness, and gas exchange responses. Proportion of visually wilted leaves was graded weekly based on the percentage of wilting leaves of the canopy (Zollinger et al., 2006). Plants were rated on a scale of 1-5, where 1 = over 65% of leaves wilted; 2 = 35% to 65% of leaves wilted; 3 = up to 35% of leaves wilted; 4 = less than 10% of leaves wilted; and 5 = plant fully turgid (Zollinger et al., 2006). A chlorophyll meter [Soil Plant Analysis Development (SPAD)-502; Minolta Camera, Osaka, Japan] was used to record relative chlorophyll content on 6 Jan. 2021. Five mature leaves were randomly selected from each plant for measurement, and the average value was recorded.

On 6 Jan. 2021, midday leaf-to-air vapor pressure deficit (VPD), stomatal conductance, transpiration rate, and net assimilation rate were recorded using a portable photosynthesis system (CIRAS-3; PP Systems, Amesbury, MA) with a PLC3 universal leaf cuvette in a sunny day from 1000 and 1400 HR. A fully expanded, mature leaf was randomly selected from each plant. Steady-state gas exchange rates were recorded after the leaf was enclosed in the cuvette for approximately one minute, in which stomatal conductance did not change in response to cuvette ambient conditions (Bunce, 2016). Within the cuvette, photosynthetic photon flux density was set at $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with 38% red, 37% green, and 25% blue light provided from light-emitting diodes, whereas CO_2 level and leaf temperature were controlled at $400 \mu\text{mol}\cdot\text{mol}^{-1}$ and 25°C , respectively.

Plant growth and water potential. On 7 Jan. 2021, plant height was recorded from the substrate surface to the highest shoot tip. Canopy width and length were

measured at perpendicular directions. Number of shoots longer than 5 cm was recorded. Plant growth index [(height + length + width)/3] was calculated. On 11 Jan. 2021, four mature leaves were sampled from the second to the fifth node counting downward from the tip of the main shoot to determine leaf curling index (Nilsen, 1987). Distance between leaf margins was recorded when the leaf was flattened (D_{\max}) and curled (D_i), and leaf curling index was calculated using the equation: $(D_{\max}-D_i)/D_{\max}$.

Stem water potential was measured at noon using a pressure chamber (PMS Instrument Company, Albany, OR) on 11 Jan 2021. Five plants were randomly chosen from each treatment, except for plants at substrate volumetric water content of $0.05 \text{ m}^3 \cdot \text{m}^{-3}$, from which only two plants were selected due to high mortality. Stems from the outer canopy were collected, wrapped with wet paper towels, stored in zip lock bags, and placed in an insulated cooler with ice. Measurements were taken immediately after the stems were collected.

On 12 Jan. 2021, plants were destructively harvested. Leaf number and the fresh weight (FW) of leaves and stems were recorded. Total leaf area was measured using a leaf area meter (LI-3100; LI-COR Biosciences, Lincoln, NE) and the average leaf size of each plant was calculated as the ratio of total leaf area to the number of leaves. Roots were harvested and washed with deionized water. The number of nodules was recorded. Leaves, stems, and roots were dried in an oven at $80 \text{ }^\circ\text{C}$ for 7 d, and the dry weight (DW) was recorded. The specific leaf area was calculated as the ratio of leaf area to leaf dry weight, and the root to shoot ratio was calculated using the dry weight of roots and shoots (leaves and stems). The water content of leaves and stems was calculated using the equation: $[(\text{DW}-\text{FW}) / \text{FW}] \times 100\%$ (Zhou et al., 2021).

Leaf reflectance and environmental scanning electron microscope imagery. On 12 Jan. 2021, images of the upper surface of leaves of plants at substrate volumetric water content of 0.10 and 0.40 $\text{m}^3 \cdot \text{m}^{-3}$ were recorded using a dissecting microscope (BX52; Olympus, Tokyo, Japan) before plants were destructively harvested. Three plants at substrate volumetric water content of 0.10, 0.20, 0.30, or 0.40 $\text{m}^3 \cdot \text{m}^{-3}$ were randomly chosen and three mature leaves were sampled from the third to fifth nodes counting downward from the tip of the main shoot of each plant. Leaf size was also recorded. Leaves were stored in petri dishes containing wet germination paper. The petri dishes were sealed using parafilm and stored in a cooler with ice. A disk from each leaf was sampled using a #12 cork borer (diameter = 3 cm) with an area of 7 cm^2 to study the leaf reflectance using a spectroradiometer (Apogee Instruments). The mean reflectance of photosynthetically active radiation (PAR) was calculated using the wavelengths from 400 nm to 700 nm. The reflectance of blue, green, and red light was calculated using the wavelengths of 450 nm, 530 nm, and 660 nm, respectively (Kusuma et al., 2020).

Following leaf reflectance measurements, leaf disks were immediately sent to the USU Microscopy Core Facility (Logan, UT). A sample (diameter = 0.3 cm) was collected from each leaf disk using a hole punch (McGill, Marengo, IL). Nine fields of view (0.32 mm^2) at $\times 300$ magnification were photographed from the upper (adaxial) surface of each leaf punch using an environmental scanning electron microscope (ESEM) (Quanta FEG 650; FEI Company, Hillsboro, OR). Fine-scale morphological traits were determined following the methods of Carins Murphy et al. (2016). Trichome density (trichome number $\cdot \text{mm}^{-2}$), uncovered stomata (visible stomata $\cdot \text{mm}^{-2}$), trichome radius (μm), trichome coverage fraction [(area covered by trichomes)/ (total image area)], epidermal

cell size (μm^2), and epidermal cell density (epidermal cells $\cdot\text{mm}^{-2}$) were quantified in each field of view using ImageJ (Schneider et al., 2012). The values of fine-scale morphological traits from the nine fields of view were averaged for each leaf, and the mean value of three leaves was recorded for each plant. Total number of epidermal cells and trichomes per leaf were calculated using the density and leaf size, and ratio between trichomes and epidermal cells of each leaf was determined.

Data analysis

The experiment was arranged in a randomized complete block design with eight treatments and three blocks. A mixed model analysis was performed to test the effects of substrate volumetric water contents on all measured parameters. Trend analyses were conducted for all data to test the nature of the relationship between plant responses and substrate volumetric water contents. Correlation analyses were performed to study the relationships between trichome density and leaf size, epidermal cell size, epidermal cell density, or light reflectance; between leaf size and epidermal cell size or epidermal cell density; between stem water potential and epidermal cell size. All statistical analyses were performed using PROC MIXED or PROC REG procedure in SAS Studio 3.8 (SAS Institute, Cary, NC) with significance level specified at 0.05.

Results

Substrate matric potential. Substrate volumetric water contents were maintained well above their irrigation set points 30 days after treatment (Fig. 2-1), and a cubic curvilinear relationship was observed between substrate matric potential and substrate volumetric water contents at the end of the experiment and ranged from -0.89 to -0.03

MPa when substrate volumetric water content increased from 0.05 to 0.40 $\text{m}^3 \cdot \text{m}^{-3}$ (Table 2-1).

Proportion of visually wilted leaves, mortality, and plant growth. The proportion of visually wilted leaves increased at the substrate volumetric water content of 0.25 $\text{m}^3 \cdot \text{m}^{-3}$ or lower during the experiment (Fig. 2-2). At the termination of the experiment, over 35% of leaves wilted on the plants grown at the substrate volumetric water contents of 0.15, 0.10 and 0.05 $\text{m}^3 \cdot \text{m}^{-3}$, and proportion of visually wilted leaves increased as substrate volumetric water content decreased (Table 2-2; Fig. 2-2). Plants grown at the substrate volumetric water content of 0.20 $\text{m}^3 \cdot \text{m}^{-3}$ or higher had acceptable visual quality as their ratings were greater than 3 (Table 2-2; Fig. 2-3). Plant mortality decreased from 58% to 8% when the substrate volumetric water content increased from 0.05 $\text{m}^3 \cdot \text{m}^{-3}$ to 0.25 $\text{m}^3 \cdot \text{m}^{-3}$, and no plants died when substrate volumetric water content was higher than 0.25 $\text{m}^3 \cdot \text{m}^{-3}$ (Supplementary Figure S1). Greater plant growth indices were observed in *S. ×utahensis* plants at higher substrate volumetric water content (Table 2-2; Fig. 2-3). Substrate volumetric water content also had effects on relative chlorophyll content, as SPAD values increased with increasing substrate volumetric water content (Table 2-2). The leaf and stem water contents increased when the substrate volumetric water content increased from 0.05 to 0.40 $\text{m}^3 \cdot \text{m}^{-3}$. Stem water potential reduced from -0.82 to -1.97 MPa when substrate volumetric water content declined from 0.40 $\text{m}^3 \cdot \text{m}^{-3}$ to 0.10 $\text{m}^3 \cdot \text{m}^{-3}$. However, leaf curling indices decreased along with increasing substrate volumetric water content. Cubic curvilinear relationships were found between substrate volumetric water content and proportion of visually wilted leaves, plant growth indices, SPAD, leaf and stem water contents, stem water potential, or leaf curling indices (Table 2-2).

Shepherdia ×utahensis grown at lower substrate volumetric water contents had fewer leaves and shoots (Table 2-3). Plants also had less total leaf area and dry weight when substrate volumetric water contents decreased from 0.40 to 0.05 $\text{m}^3 \cdot \text{m}^{-3}$. However, decreasing substrate volumetric water content increased the root to shoot ratios. As substrate dried down from 0.40 to 0.05 $\text{m}^3 \cdot \text{m}^{-3}$, specific leaf area and leaf size declined from 72.1 to 59.7 $\text{cm}^2 \cdot \text{g}^{-1}$ and 1.97 to 0.97 $\text{cm}^2 \cdot \text{g}^{-1}$, respectively. In addition, nodule number decreased with decreasing substrate volumetric water content, and nodules were not found on the plants at the substrate volumetric water content of 0.05 $\text{m}^3 \cdot \text{m}^{-3}$. Cubic curvilinear relationships were observed between substrate volumetric water content and the number of leaves and shoots, leaf area, total DW, root to shoot ratio, specific leaf area, leaf size, or the number of nodules (Table 2-3). In addition, a positive or negative correlation was found between stem water potential, leaf curling index, and leaf size (all $r^2 \geq 0.17$, all $P \leq 0.02$) (Supplementary Figure S2).

Gas exchange. Decreased substrate volumetric water contents resulted in an increase in leaf-to-air VPD (Table 2-4), which was 2.12 kPa at 0.40 $\text{m}^3 \cdot \text{m}^{-3}$ but became 3.16 kPa at 0.05 $\text{m}^3 \cdot \text{m}^{-3}$. When substrate volumetric water contents increased from 0.05 to 0.40 $\text{m}^3 \cdot \text{m}^{-3}$, stomatal conductance increased from 0.03 to 0.66 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Similarly, transpiration rate increased from 0.9 to 9.4 $\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ when substrate volumetric water contents increased from 0.05 to 0.40 $\text{m}^3 \cdot \text{m}^{-3}$. The net assimilation rate of *S. ×utahensis* ranged from 0.1 to 11.7 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ as the substrate volumetric water content increased from 0.05 to 0.40 $\text{m}^3 \cdot \text{m}^{-3}$. Cubic curvilinear relationships were observed between substrate volumetric water content and VPD, stomatal conductance, transpiration rate, or net assimilation rate (Table 2-4).

Leaf trichomes and fine-scale morphology. *Shepherdia ×utahensis* became silvery when grown in drier substrates toward the end of the experiment (Fig. 2-4A and B). Higher trichome density and smaller epidermal cells were observed on the leaves of plants grown at the substrate volumetric water content of $0.10 \text{ m}^3 \cdot \text{m}^{-3}$ than those at $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ (Fig. 2-4 C-F). Decreasing water content in substrate linearly increased leaf trichome density, trichome coverage fraction, and epidermal cell density (Table 2-5). Nonetheless, uncovered stomata, trichome radius, and epidermal cell size decreased linearly as substrate volumetric water contents decreased. Trichome density was negatively influenced by epidermal cell size and leaf size (Fig. 2-5A), and total number of trichomes per leaf was similar among plants at different substrate volumetric water contents ($P = 0.97$) (Supplementary Figure S3). Leaf size also increased with increasing epidermal cell size or decreasing epidermal cell density (Fig. 2-5B) but was not affected by total number of epidermal cells ($P = 0.19$) (Supplementary Figure S3). Positive correlation showed between the density of trichomes and epidermal cells and trichome coverage fraction (Fig. 2-5C), and plants had a similar trichome to epidermal cell ratio at various substrate volumetric water contents ($P = 0.34$) (Supplementary Figure S3). Epidermal cell size was positively correlated with stem water potential (Fig. 2-5D). In addition, a negative correlation was observed between trichome density and trichome radius ($r^2 = 0.79$, $P < 0.0001$) (Supplementary Figure S3).

Leaf reflectance of PAR, blue, green, and red light increased linearly with decreasing substrate volumetric water content (Table 2-5). Leaves reflected 46% more PAR when plants were grown at the substrate volumetric water content of $0.10 \text{ m}^3 \cdot \text{m}^{-3}$ than those at $0.40 \text{ m}^3 \cdot \text{m}^{-3}$. In addition, blue-, green-, and red-light reflectance increased

by 51%, 29%, and 60%, respectively, when plants were grown at the substrate volumetric water content of $0.10 \text{ m}^3 \cdot \text{m}^{-3}$ than those at $0.40 \text{ m}^3 \cdot \text{m}^{-3}$. The reflectance of PAR, blue-, green-, and red-light correlated positively with trichome density (all $r^2 \geq 0.46$, all $P \leq 0.02$) (Fig. 2-6)

Discussion

Plant morphology and physiology in this study changed along with decreasing substrate matric potential that resulted from reduced substrate volumetric water contents (Table 2-1). As substrate volumetric water content decreased, *S. ×utahensis* leaves and stems dehydrated, and the proportion of visually wilted leaves increased (Table 2-2). In addition, plant growth indices, relative chlorophyll content (SPAD reading), numbers of shoots and leaves, total leaf area and dry weight, and photosynthesis were impaired (Table 2-2, 2-3, and 2-4). These results are in line with previous studies that reported negative effects of water stress on aesthetic appearance, plant growth, and net assimilation rate of ornamental plants (Cai et al., 2012; Niu et al., 2006; Zhou et al., 2021). In this case, decreased stem water potential is best interpreted as a passive response resulting from the effects of decreased soil water potential and higher leaf evaporative demand (Table 2-2). Similarly, *Rosa ×hybrid* (rose) and *Nerium oleander* (oleander) decreased stem water potential in response to low substrate or soil water potential under drought conditions (Cai et al., 2012; Molz, 1981; Niu et al., 2006). Decreased substrate volumetric water contents also inhibited nodule formation in *S. ×utahensis* (Table 2-3), which suggested that infection of symbiotic actinobacteria was affected by water availability. Actinobacteria move with water in the soil, and the process

of reaching and infecting the roots of host plants slows down when soil water content decreases (Huss-Danell, 1997).

Plant morphological and physiological acclimations were observed in this study. In response to drought, *S. ×utahensis* reduced midday stomatal conductance to a value close to 0 when substrate volumetric water content decreased (Table 2-4). Midday stomatal conductance is positively correlated to stomatal opening and plant water status (Zhang et al., 2013). When *S. ×utahensis* plants dehydrated as a result of decreasing substrate volumetric water contents, plants closed their stomata to reduce transpiration and stomatal conductance as a drought acclimation to maintain plant water status and prevent water losses and further dehydration (Martinez-Vilalta and Garcia-Forner, 2017). Although CO₂ uptake is limited when stomata are closed and stomatal conductance reduced (Aroca, 2012), plants had lower proportion of visually wilted leaves in this study or better aesthetic quality under drought conditions in other reports. These plants were considered drought tolerant in ornamental plant evaluations in semi-arid regions in Australia and U.S. (Kjelgren et al., 2009; Reid et al., 2017; Zollinger et al., 2006). *Shepherdia ×utahensis* reduced its midday stomatal conductance at lower water availability and can be considered as a low water-use landscape plant. Plants have the capacity of regulating stomatal conductance that is related to their habitat aridity. Kjelgren et al. (2009) reported that plants native to arid regions, such as *Dianella revoluta* ‘Breeze’ (‘Breeze’ blueberry lily) and *Ptilotus nobilis* (yellow tails), showed greater reduction of stomatal conductance compared with those from humid areas.

Because of restricted transpiration, plants with acclimation capability may reduce leaf size to enhance convective heat loss to mitigate heat stress that causes high leaf-to-air

VPD and leaf wilting (Table 2-3 and 4; Devi et al., 2015; Nobel, 2009). The fact that leaf-to-air VPD increased when substrate volumetric water content decreased (Table 2-4) is likely a direct consequence of increased leaf temperature, because leaf vapor pressure is estimated by leaf temperature. To avoid heat stress, leaf energy is balanced primarily using sensible heat loss under drought (Bowen, 1926). The efficacy of sensible heat loss relates to boundary layer resistance, which is positively correlated to leaf width (Nobel, 2009). Under drought conditions, cell division and leaf expansion are limited (Dale, 1988), and smaller leaves are beneficial for dissipating heat through convection and conduction to maintain leaf temperature close to air temperature (Nobel, 2009). In this study, *S. ×utahensis* produced smaller leaves under water stress (Table 2-3) and leaf size of plants grown at the substrate volumetric water content of $0.05 \text{ m}^3 \cdot \text{m}^{-3}$ was 51% smaller than those at $0.40 \text{ m}^3 \cdot \text{m}^{-3}$. This result is in line with previous studies that consistently reported reductions in leaf size under water stress for drought-tolerant ornamental plants (Mee et al., 2013; Zollinger et al., 2006). For instance, Zollinger et al. (2006) suggested that small leaves allow *Lavandula angustifolia* (English lavender) and *Penstemon ×mexicali* ‘Red Rocks’ (‘Red Rocks’ penstemon) to reduce water loss when irrigation intervals were increased from one week to four weeks. Toscano et al. (2014) also found that leaf size of *Viburnum tinus* ‘Lucidum’ (‘Lucidum’ viburnum) decreased by 19% to acclimate to drought stress.

Shepherdia ×utahensis decreased total leaf area under water stress as a result of reductions in leaf number and size (Table 2-3). However, plants with decreased total leaf area have fewer stomata and less light interception, which controls transpiration and leaf temperature, respectively (Toscano et al., 2014; Zollinger et al., 2006). Reduced total leaf

area has been reported as a means of avoiding drought stress in ornamental plants such as *Lavandula angustifolia*, *Pittosporum tobira* (pittosporum), and *Viburnum tinus* ‘Lucidum’ (Toscano et al., 2014; Zollinger et al., 2006). The root growth of *S. ×utahensis* was enhanced at low substrate volumetric water content, while shoot growth was inhibited, resulting in a higher root-to-shoot ratio (Table 2-3), which helps plants to obtain water more efficiently. *Rosa hybrida* ‘Ferdy’ (‘Ferdy’ rose) and *Populus cathayana* (poplar) have been observed to increase root growth to maintain water status under water stress (Henderson et al., 1991; Yin et al., 2004). Drought-tolerant plants native to the western U.S. also produce small leaves and deep roots to reduce water demand and loss and increase water uptake (Mee et al., 2003).

In this study, as substrate volumetric water content decreased, leaves of *S. ×utahensis* curled as stem water potential became more negative. At the substrate volumetric water content of $0.05 \text{ m}^3 \cdot \text{m}^{-3}$, the leaf curling index was 0.17, suggesting that the light interception area was 83% that of flattened leaves. Similarly, *Dianella revoluta* ‘Breeze’ and *Ctenanthe setosa* (prayer plant) have been shown to minimize sunlight exposure through leaf curling under water deficit (Kjelgren et al., 2009; Nar et al., 2009). Although light harvesting efficiency is reduced, leaf curling limits water loss from transpiration and protects plants from overheating to sustain photosystem functions and other biochemical/physiological processes (Fitter and Hay, 2002; Hook and Hanna, 1994). In addition, as the rooting substrate became drier in this study, specific leaf area decreased, indicating that leaves became thicker (Table 2-3), which prevented leaves from overheating. Plants may decrease specific leaf area to acclimate to water stress as reported on *Ptilotus nobilis* (Kjelgren et al., 2009).

The trichome density of *S. ×utahensis* in this study was affected by substrate water availability and plant water status (Table 2-5). Water-stressed *S. ×utahensis* produced densely packed trichomes, resulting in a silvery appearance, while well-watered plants had fewer trichomes to cover epidermal cells and exhibited a greener color (Table 2-5; Fig. 2-4). Trichomes promote leaf reflectance (Fig. 2-6), which helps balance energy and reduce heat stress (Ehleringer et al., 1976). Positive effects of trichomes on leaf reflectance of visible light have been reported on *Verbascum thapsus* (common mullein) and *Salix commutata* (undergreen willow) (Mershon et al., 2015; Wuenschel, 1970). However, because trichomes are broad-spectrum reflectors (Bickford, 2016), the reflectance of PAR, blue, green, and red light are proportional to the trichome density (Fig. 2-6). When substrate volumetric water content decreased, the reflectance of green light (530 nm) did not increase as much as blue light (450 nm) and red light (660 nm) due to the chlorophyll in the epidermal cells (Table 2-5). Increased leaf reflectance has been shown to sacrifice the efficacy of light-harvesting pigments (Bickford et al., 2016) and reduce net assimilation rate when plants are grown in drier conditions. Previous research also suggested that trichomes improved the reflectance of near-infrared light (Ehleringer, 1988). However, in this study, denser trichomes produced in drier substrate did not affect near-infrared light reflectance of *S. ×utahensis* (Supplementary Figure S4). Slaton et al. (2001) reported similar results that near-infrared light reflectance was not affected by increased trichome density in 48 species. More studies are needed to evaluate the effects of trichomes on near-infrared reflectance.

Increased trichome density has smaller effects on decreasing gas exchange compared with the effects on leaf reflectance (Jordan et al., 2005; Moles et al., 2020).

However, densely packed trichomes covering the stomata of *S. ×utahensis* may increase resistance to transpiration and reduce water loss (Table 2-5; Fig. 2-4D). Leaf trichomes also increase leaf roughness and increase the laminar boundary layer to restrict air movement across leaf surfaces to reduce transpiration (Grammatikopoulos and Manetas, 1994). *Eriogonum corymbosum* (crisp-leaf buckwheat) and *S. rotundifolia* produce leaf trichomes for better protection from wind and to maintain water status (Miller, 2011). Densely packed trichomes add an atmospheric boundary layer that imposes additional resistance to water vapor diffusion (Nobel, 2009). However, CO₂ influx is also limited by the boundary layer resistance, decreasing net assimilation rate (Ehleringer et al., 1976). Although trichome-induced boundary layer resistance has a smaller effect on transpiration than stomatal conductance (Parkhurst, 1976), it still provides an advantage for desert plants to survive in dry and hot conditions.

Trichome density changes genetically (adaptation) and environmentally (acclimation). The genetic regulation of trichome density of *Caragana korshinskii* (Korshinsk pea shrub) has been reported by Ning et al. (2016). However, it is unclear how xeric plants change their trichome density to acclimate to drought conditions. A negative correlation between leaf trichome density and leaf size or epidermal cell size occurred in this study (Fig. 2-5A), which suggests that cell expansion may control trichome density. Low trichome coverage fraction, which was related to greater space between trichomes, showed when epidermal cell density decreased, indicating cell expansion may coordinate trichome density. Ascensão and Pais (1987) reported the number of trichomes is determined during leaf lifespan, and leaf cell differentiation does not affect trichome number. Similar results showed in our research that plants had a

similar total number of trichomes per leaf at different substrate volumetric water contents. This may indicate that *S. ×utahensis* develops trichomes independent of leaf development. In fact, trichomes develop at the early stage of leaf development and often earlier than stomatal development (Werker, 2000). For instance, trichomes of *Inula viscosa* (false yellowhead) are fully developed and reach mature size when leaves are 2 mm long, however, a mature leaf is 6-8 cm long (Werker and Fahn, 1981). *Ocimum basilicum* (basil) forms trichomes at an early stage of leaf development and trichomes then grow independently (Werker et al., 1993). In the same study, trichomes covered young leaves but became more widely spaced when leaf cells started to expand (Werker et al., 1993). In our study, total number of epidermal cells per leaf was similar on plants at different substrate volumetric water contents, which indicates cell differentiation might have minor effects on regulating trichome density. In contrast, cell expansion might be the main factor for regulating trichome density because leaf size, epidermal cell size, and the space among trichomes changed along with substrate volumetric water contents and correlated significantly with trichome density of *S. ×utahensis* (Fig. 2-5A and B). Ehleringer (1982) found a negative correlation between leaf size and trichome density of *Encelia farinosa*, but cell size was not determined. Cell enlargement at high soil moisture levels amplified leaf size and the space among trichomes, reducing the trichome density on the *S. ×utahensis* leaves in this study. The relationships between trichome density, epidermal cell size and density, and leaf reflectance might indicate changes in cell size predominantly controls trichome density to modify leaf reflectance.

Modifying leaf reflectance via the change in cell size help rapidly acclimate to environmental change without compromising whole leaf function (Brodribb et al., 2013).

Cell-expansion-driven leaf anatomic change has been widely reported on adjusting stomatal density (Carins Murphy et al., 2016; Xu and Zhou, 2008). For instance, Carins Murphy et al. (2016) observed that cell expansion was the predominant factor for coordinating vein and stomata density of eight angiosperm species under sun and shade. Stomatal density decreases and the size of guard cells increases when leaf water potential increases (Xu and Zhou, 2008), suggesting cell expansion not only enlarges the distance between epidermal appendages, but also increases their size.

Environmental factors also promote leaf trichome density. Such factors include increased leaf-to-air VPD (Ehleringer, 1982; Shibuya et al., 2009, 2016) and drought (Banon et al., 2004; Quarrie and Jones, 1977), all of which negatively affect plant water status. For instance, high leaf-to-air VPD may increase water loss via transpiration, leading to plant dehydration. Leaf trichome density of *Cucumis sativus* increased when air humidity decreased from 90% to 20% at 28 °C, causing leaf-to-air VPD to increase from 0.4 to 3.0 kPa (Shibuya et al., 2016). Shibuya et al. (2016) did not investigate cell or leaf expansion of *C. sativus*, but increased leaf-to-air VPD may promote trichome density because rising leaf-to-air VPDs reduces cell size (Carins Murphy et al., 2014), making space between trichomes smaller. In this study, higher leaf-to-air VPD and smaller leaves were observed when *S. ×utahensis* plants grown at the lower θ_t and the smaller epidermal cell size resulted in greater trichome density. Therefore, because increased leaf-to-air VPD and drought led to a reduction in cell enlargement and denser trichomes in *S. ×utahensis*, leaf trichome density was regulated using turgor-pressure-driven cell expansion to acclimate to drought conditions.

Conclusions

As the soilless substrate became drier, *S. ×utahensis* exhibited poorer visual quality due to wilted foliage. Water stress also imposed negative effects on plant growth and gas exchange. When substrate water levels decreased, *S. ×utahensis* increased root growth to increase the ability to uptake water. Stressed plants also lowered total leaf area and stomatal conductance to reduce water loss via transpiration. Leaf temperature was regulated through smaller leaves, curled leaves, and densely-packed trichomes. Substrate volumetric water content and stem water potential negatively affected trichome density, which helped reflect a broad spectrum of visible light under drought. Increase in cell size and leaf expansion may have regulated the trichome density. Under water stress, dense trichomes resulted from the limited cell expansion and small space between trichomes. In contrast, greater water availability increased cell size which promoted cell/leaf expansion and enlarged trichome size and the space between trichomes, leading to lower trichome density and improve light-harvesting efficiency.

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Table 2-1. Substrate matric potential (ψ_m) at eight substrate volumetric water content treatments (θ_t) recorded on 11 Jan. 2021.

θ_t ($\text{m}^3 \cdot \text{m}^{-3}$)	ψ_m^z (MPa)
0.40	-0.08 a ^y
0.35	-0.03 a
0.30	-0.04 a
0.25	-0.23 ab
0.20	-0.26 ab
0.15	-0.56 bc
0.10	-0.51 b
0.05	-0.89 c
Linear	NS ^x
Quadratic	*
Cubic	****

^z ψ_m was calculated from measurements of a handheld soil moisture sensor (Hydro Sense; Campbell Scientific) using a substrate-specific water retention curve estimated using the van Genuchten equation (van Genuchten, 1980), of which the residual water content is 0, the saturated water content is $0.74 \text{ m}^3 \cdot \text{m}^{-3}$, the inverse of the air entry suction is 771.43 MPa^{-1} , and the dimensionless pore-size distribution is 1.33.

^y Means with same lowercase letters are not significantly different among treatments by Tukey-Kramer method with significance level specified at 0.05.

^xNS, *, **** Nonsignificant, significant at $P \leq 0.05$ or 0.0001, respectively.

Table 2-2. Degree of leaves visually wilted, plant growth index (PGI), relative chlorophyll content [Soil Plant Analysis Development (SPAD) value], water content of leaf and stem, stem water potential (ψ_{stem}) and leaf curling index of *Shepherdia ×utahensis* at eight substrate volumetric water content treatments (θ_t).

θ_t ($\text{m}^3 \cdot \text{m}^{-3}$)	Leaves wilted (1-5 scale) ^z	PGI ^y	SPAD	Water content ^y		ψ_{stem} (MPa)	Leaf curling index ^x
				Leaf (%)	Stem (%)		
0.40	4.7 ab ^v	33.4 a	58.9 a	59.2 a	62.7 a	-0.82 ab	0.04 bc
0.35	4.8 a	33.2 a	58.2 a	62.6 a	63.6 a	-0.65 a	0.05 bc
0.30	4.7 ab	36.7 a	58.3 a	59.7 a	60.4 a	-0.90 ab	0.02 c
0.25	3.7 bc	23.1 b	56.1 ab	58.1 a	58.5 ab	-1.95 bc	0.06 bc
0.20	3.4 cd	22.6 b	52.1 ab	57.1 a	58.7 ab	-1.45 b	0.03 bc
0.15	2.2 de	17.2 b	49.0 abc	51.1 a	49.9 b	-1.98 c	0.10 abc
0.10	1.9 e	18.3 b	43.4 bc	51.2 a	52.4 b	-1.97 bc	0.11 ab
0.05	1.0 e	17.6 b	34.9 c	23.3 b	36.8 c	-5.76 ^w	0.17 a
Linear	**u	NS	NS	NS	NS	NS	NS
Quadratic	NS	NS	NS	***	***	NS	NS
Cubic	****	****	****	****	****	*	****

^z1 = over 65% of the leaves wilted; 2 = 35% to 65% of the leaves wilted; 3 = up to 35% of the leaves wilted; 4 = less than 10% of the leaves wilted; 5 = plant was fully turgid (Zollinger et al., 2006).

^y Plant growth index = [(height + length + width)/3], while water content of leaf and stem was calculated using the equation: [dry weight (DW)-fresh weight (FW)]/FW×100% (Zhou et al., 2021).

^x Leaf curling index was determined using the equation: [(distance between the margins of flattened leaf (D_{max})- distance between the margins of curling leaf (D_i)]/ D_{max} (Nilsen, 1987).

^w Only two data were recorded due to high plant mortality.

^v Means with same lowercase letters within a column are not significantly different among treatments by Tukey-Kramer method with significance level specified at 0.05.

^uNS, *, **, ***, **** Nonsignificant, significant at $P \leq 0.05, 0.01, 0.001, \text{ or } 0.0001$, respectively.

Table 2-3. Number (no.) of leaves and shoots, total leaf area and dry weight (DW), root to shoot ratio (R/S), specific leaf area (SLA), leaf size, and nodule no. of *Shepherdia × utahensis* at eight substrate volumetric water content treatments (θ_t) at the termination of the experiment.

θ_t ($\text{m}^3 \cdot \text{m}^{-3}$)	Leaf no.	Shoot no.	Leaf area (cm^2)	DW (g) ^z	R/S ($\text{g} \cdot \text{g}^{-1}$) ^y	SLA ($\text{cm}^2 \cdot \text{g}^{-1}$) ^x	Leaf size (cm^2) ^w	Nodule no.
0.40	390.5 ab ^v	13.1 abc	776.1 ab	25.8 ab	0.48 c	72.1 a	1.97 ab	65.6 ab
0.35	438.5 a	15.7 ab	882.5 a	26.4 a	0.47 c	83.6 a	2.06 a	72.4 a
0.30	434.4 a	20.7 a	987.8 a	30.1 a	0.44 c	76.8 a	2.18 a	35.3 bc
0.25	259.2 bc	9.8 bc	414.3 c	17.8 bc	0.90 ab	68.2 a	1.54 abc	37.0 abc
0.20	274.6 bc	9.1 bc	477.7 bc	17.8 bc	0.74 bc	72.2 a	1.71 abc	18.5 c
0.15	126.6 d	6.0 bc	205.8 c	10.2 c	1.04 ab	66.8 a	1.47 bc	1.4 c
0.10	156.1 cd	7.6 bc	208.3 c	12.0 c	1.15 a	67.7 a	1.37 bc	6.3 c
0.05	115.3 d	5.4 c	109.3 c	8.0 c	1.15 ab	59.7 b	0.97 c	0.0 c
Linear	NS ^u	NS	NS	NS	NS	NS	NS	***
Quadratic	NS	NS	NS	NS	NS	NS	NS	NS
Cubic	****	****	****	****	****	**	****	****

^z Total DW was the sum of the DW of stems, leaves, and roots.

^y Root to shoot ratio was calculated using the DW of roots and shoots (leaves and stems).

^x SLA was calculated as the ratio of leaf area to leaf DW.

^w Leaf size of each plant was calculated as the ratio of total leaf area to the leaf no.

^v Means with same lowercase letters within a column are not significantly different among treatments by Tukey-Kramer method with significance level specified at 0.05.

^uNS, **, **** Nonsignificant, significant at $P \leq 0.01$ or 0.0001, respectively.

Table 2-4. Leaf-to-air vapor pressure deficit (VPD), stomatal conductance (g_s), transpiration rate (E), and net assimilation rate (P_n) of *Shepherdia × utahensis* at eight substrate volumetric water content treatments (θ_t).

θ_t ($\text{m}^3 \cdot \text{m}^{-3}$)	VPD (kPa)	g_s ($\text{mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	E ($\text{mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	P_n ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
0.40	2.12 b ^z	0.66 ab	9.4 ab	11.7 ab
0.35	1.87 b	0.80 a	11.0 a	13.4 a
0.30	1.79 b	0.83 a	10.8 a	14.6 a
0.25	2.39 ab	0.38 bc	7.1 bc	8.9 bc
0.20	2.05 b	0.61 ab	8.9 ab	11.6 ab
0.15	2.96 a	0.17 c	4.3 cd	5.2 bcd
0.10	2.93 a	0.10 c	3.0 d	4.0 cd
0.05	3.16 a	0.03 c	0.9 d	0.1 d
Linear	NS ^y	NS	NS	NS
Quadratic	NS	NS	NS	NS
Cubic	****	****	****	****

^z Means with same lowercase letters within a column are not significantly different among treatments by Tukey-Kramer method with significance level specified at 0.05.

^yNS, **, **** Nonsignificant, significant at $P \leq 0.01$ or 0.0001, respectively.

Table 2-5. Fine-scale morphology and leaf reflectance at the wavelengths of photosynthetically active radiation (PAR), blue, green, and red light of *Shepherdia ×utahensis* at the substrate volumetric water content treatments (θ_t) of 0.40, 0.30, 0.20, and 0.10 $\text{m}^3 \cdot \text{m}^{-3}$.

θ_t ($\text{m}^3 \cdot \text{m}^{-3}$)	Fine-scale morphology						Leaf reflectance ^x			
	Trichome density (mm^{-2})	Trichome coverage fraction ^z	Uncovered stomata (mm^{-2})	Trichome radius (μm)	Epidermal cell size ^y (μm^2)	Epidermal cell density (mm^{-2})	PAR	Blue	Green	Red
0.40	23.9 b ^w	0.54 b	29.1 ab	195 a	666 a	1544 b	12.9 b	11.6 b	17.5 b	10.9 a
0.30	24.3 b	0.61 ab	34.0 a	193 a	668 a	1539 b	14.0 b	11.7 ab	18.8 a	11.9 ab
0.20	34.7 ab	0.81 a	12.9 bc	164 b	402 b	2583 a	16.1 b	15.0 a	19.3 a	14.6 ab
0.10	44.6 a	0.82 a	10.0 c	137 b	386 b	2662 a	18.8 a	17.5 a	22.5 a	17.4 a
Linear	*** ^v	**	**	****	****	****	**	**	*	**
Quadratic	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Cubic	NS	NS	*	NS	**	**	NS	NS	NS	NS

^z Trichome coverage fraction = (area covered by trichomes)/(total image area).

^y Epidermal cell size was estimated by measuring the area of eight randomly selected epidermal cells in each image.

^x Reflectance of PAR was determined using the wavelengths from 400 nm to 700 nm, while the reflectance of blue, green, and red light was recorded at the wavelengths of 450 nm, 530 nm, and 660 nm, respectively (Kusuma et al., 2020).

^w Means with same lowercase letters within a column are not significantly different among treatments by Tukey-Kramer method with significance level specified at 0.05.

^v NS, *, **, ***, **** Nonsignificant, significant at $P \leq 0.05, 0.01, 0.001, \text{ or } 0.0001$, respectively.

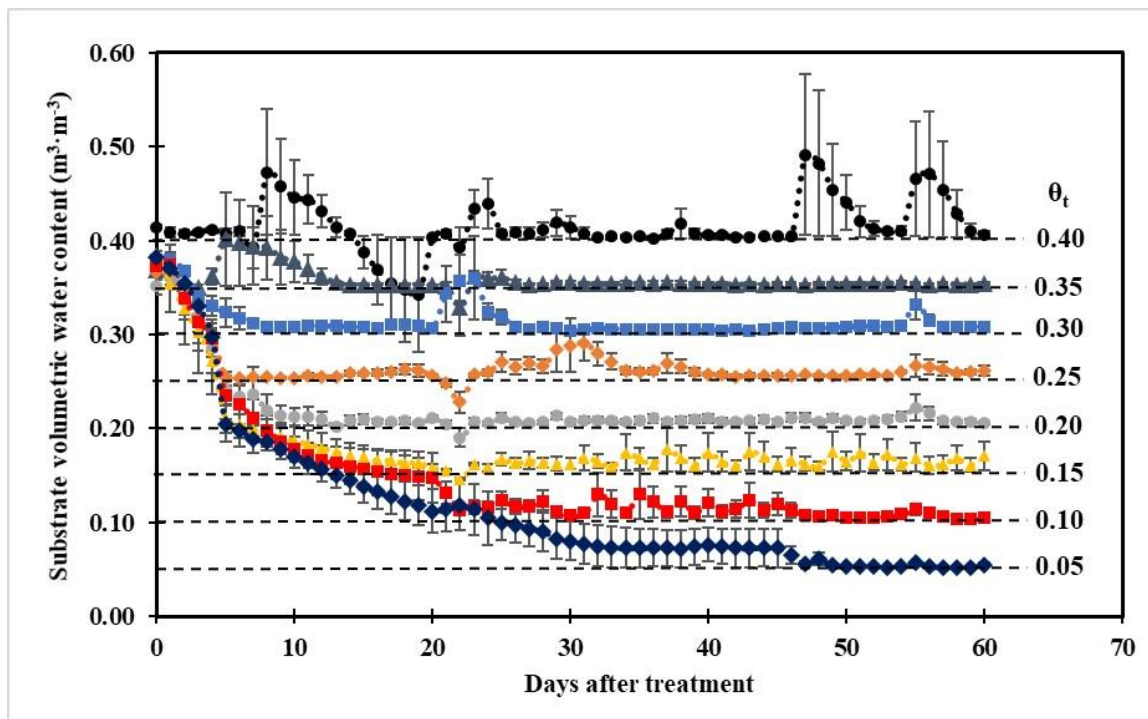


Figure 2-1. Daily average substrate volumetric water content at eight substrate water content volumetric water content treatments (θ_t) recorded using calibrated soil moisture sensors (ECH₂O 10HS; Meter Group, Pullman, WA) during the experiment. Error bars represent standard errors of three sensors.

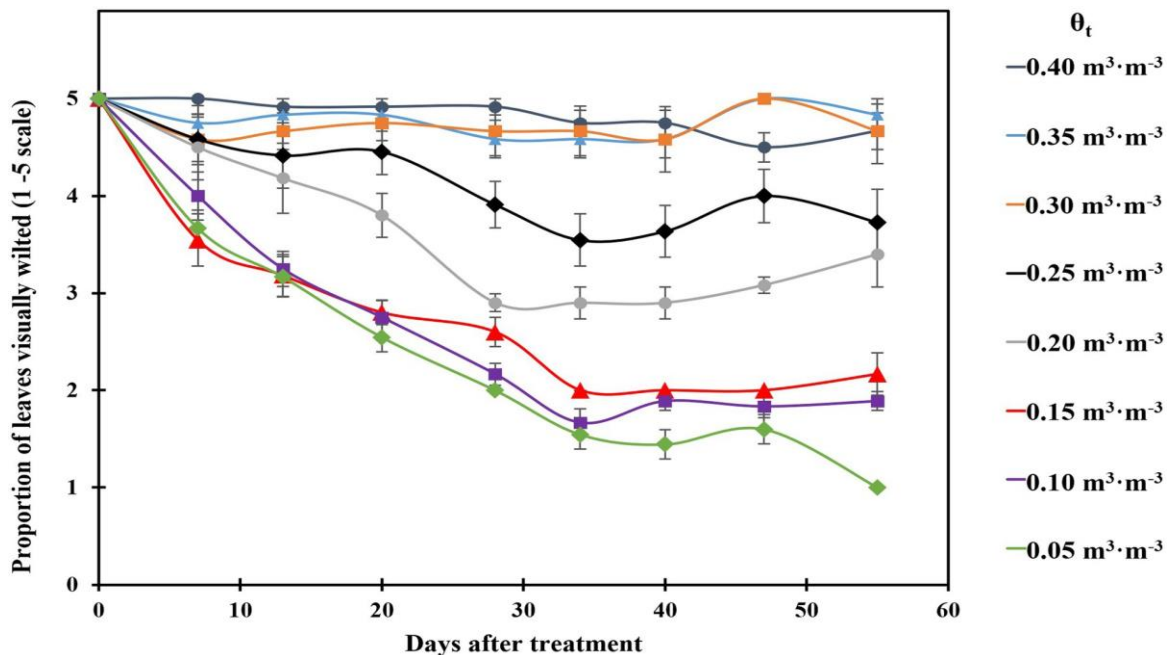


Figure 2-2. Proportion of visually wilted leaves of the plants grown at eight substrate volumetric water content treatments (θ_t) during the experiment. Plants were rated on a scale of 1-5, where 1 = over 65% of the leaves wilted; 2 = 35% to 65% of the leaves wilted; 3 = up to 35% of the leaves wilted; 4 = less than 10% of the leaves wilted; 5 = plant was fully turgid (Zollinger et al., 2006). Error bars represent standard errors of 12 plants.

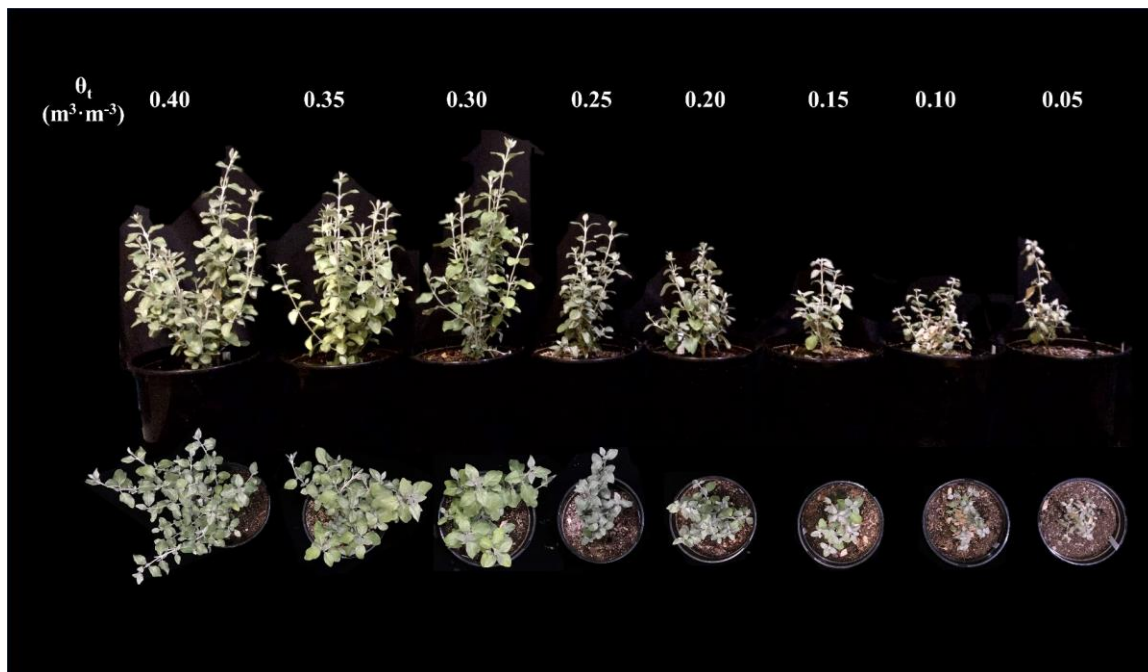


Figure 2-3. *Shepherdia ×utahensis* plants at eight substrate volumetric water content treatments (θ_t) at the end of the experiment (photo taken on 10 Jan. 2021).

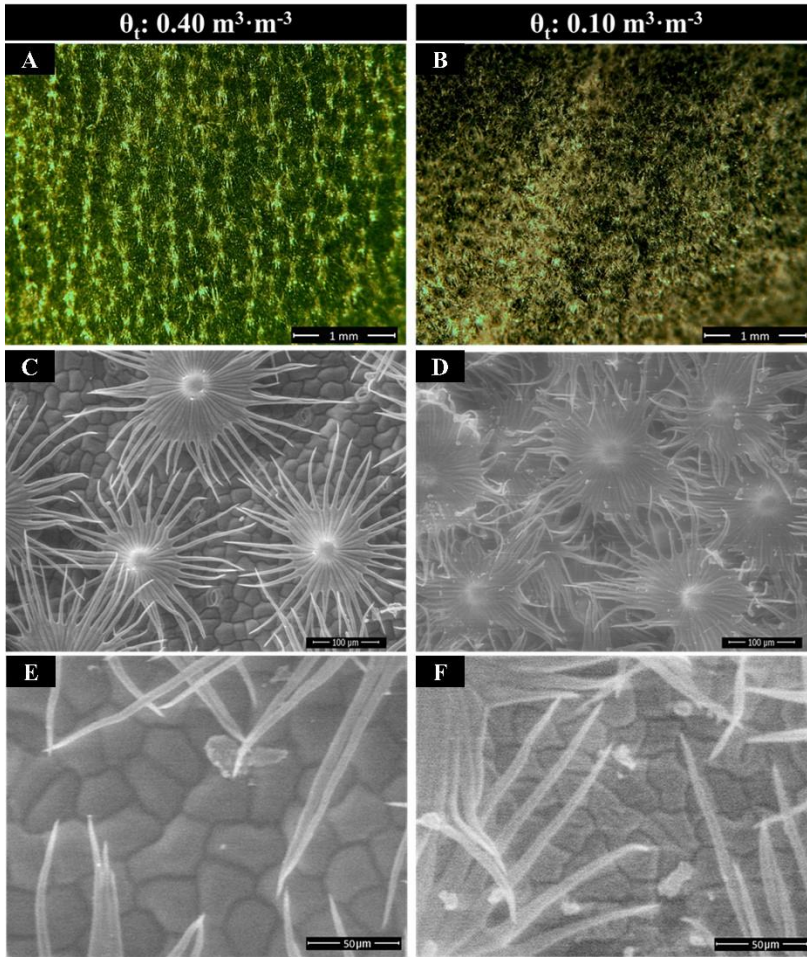


Figure 2-4. Dissected compound microscopy image of the leaf upper (adaxial) surface (**A and B**) and scanning electron microscopy image of leaf trichomes (**C and D**) and epidermal cells (**E and F**) of *Shepherdia ×utahensis* plants at the substrate volumetric water content treatments (θ_t) of 0.40 and 0.10 $\text{m}^3 \cdot \text{m}^{-3}$.

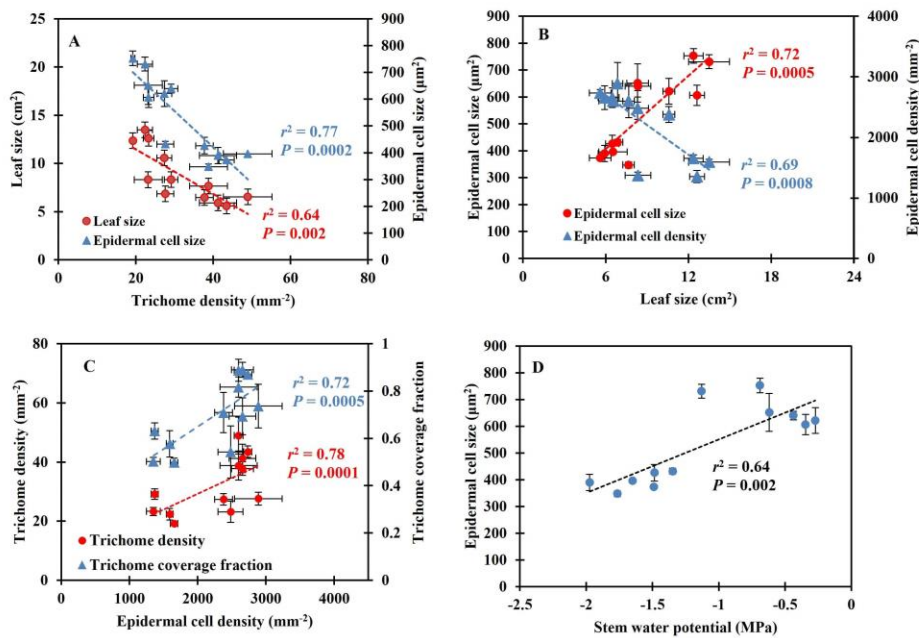


Figure 2-5. Correlation between leaf size, epidermal cell size, and trichome density (**A**), epidermal cell size and density and leaf size (**B**), trichome density, trichome coverage fraction, and epidermal cell density (**C**), epidermal cell size and stem water potential (**D**). The error bars represent the standard errors of three leaves sampled from each plant.

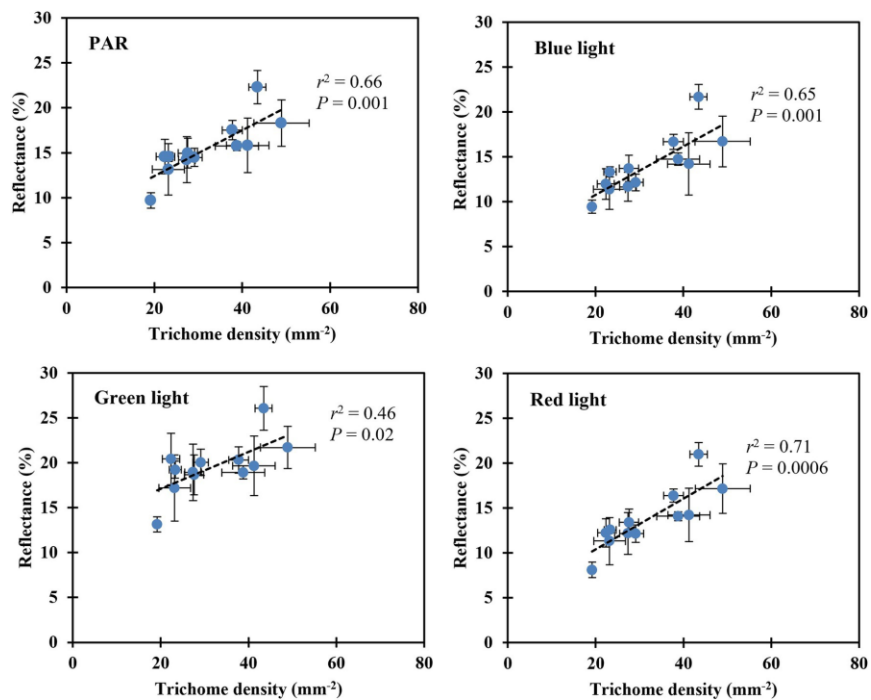


Figure 2-6. Correlation between the leaf upper (adaxial) surface trichome density and reflectance of photosynthetically active radiation (PAR), blue, green, and red light. The reflectance of PAR was determined using the mean reflectance between the wavelengths (λ) ranging from 400 to 700 nm. The reflectance of blue, green, and red light was determined using the λ at 450 nm, 530 nm, and 660 nm, respectively (Kusuma et al., 2020). The error bars represent the standard errors of three leaves sampled from each plant.

CHAPTER III

PHYSIOLOGICAL AND CANOPY TEMPERATURE RESPONSES TO DROUGHT
OF FOUR PENSTEMON SPECIES²**Abstract**

Available water for urban landscape irrigation is likely to become more limited because of inadequate precipitation and the ever-increasing water demand of a growing population. Recent droughts in the western United States have also increased the demand for low water-use landscapes in urban areas. Penstemon species (beardtongues) are ornamental perennials commonly grown in low-water-use landscapes, but their drought tolerance has not been widely investigated. The objectives of this study were to determine the effects of water availability on the morphology, physiology, and canopy temperature of *Penstemon barbatus* (Cav.) Roth ‘Novapenblu’ (Rock Candy Blue[®] penstemon), *P. digitalis* Nutt. ex Sims ‘TNPENDB’ (Dakota[™] Burgundy beardtongue), *P. ×mexicali* Mitch. ‘P007S’ (Pikes Peak Purple[®] penstemon), and *P. strictus* Benth. (Rocky Mountain penstemon). Twenty-four plants of each penstemon species were randomly assigned to blocks in an automated irrigation system, and the substrate volumetric water content was maintained at 0.15 or 0.35 m³·m⁻³ for 50 days. The decreased substrate volumetric water content resulted in a decline in aesthetic appearance of the four penstemon species because of the increased numbers of visibly wilted leaves and chlorosis. Plant growth index: [(height+(width 1+width 2)/2)/2], shoot number, shoot dry weight, leaf size, and

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total leaf area also decreased as the substrate volumetric water content decreased, but the root-to-shoot ratio and leaf thickness increased. Photosynthesis decreased, stomatal resistance increased, and warmer canopy temperatures were observed when plants were dehydrated. Additionally, as substrate volumetric water content decreased, leaf reflectance of *P. barbatus* and *P. strictus* increased. *Penstemon digitalis*, which had the highest canopy-air temperature difference, was sensitive to drought stress, exhibiting a large proportion of visibly wilted leaves. *Penstemon ×mexicali*, which had the lowest root-to-shoot ratio, had the lowest shoot water content of the species studied and more than 65% of leaves visibly wilted when experiencing drought stress. *Penstemon barbatus* and *P. strictus*, native to arid regions, exhibited lower canopy-air temperature differences and better aesthetic quality than the other two species. Under the conditions of this study, *Penstemon barbatus* and *P. strictus* exhibited better drought tolerance than *P. digitalis* and *P. ×mexicali*.

Introduction

Approximately 60 to 90% of per capita residential water use is applied as landscape irrigation in the western United States (Hayden et al., 2015). Additionally, an increase in warmer and drier periods of weather has threatened water supplies in many urban areas in this region. On 7 Oct. 2022, 37 of the 47 reservoirs in Utah were below 55% of available capacity, and 94% of the state was experiencing severe drought (Utah Division of Water Resources 2022). In the western United States, 73% of the state was still experiencing moderate drought or worse conditions on 1 Nov 2022 (United States Drought Monitor 2022). Concurrently, the rapid growth of urban and suburban

populations has created a higher water demand, forcing restrictions on irrigating landscape plants where drought has occurred (Mini et al. 2014). For example, during the California drought between 2012 and 2016, landscape irrigation was prohibited, which caused reductions in urban vegetation coverage from 45% to 35% in downtown Santa Barbara, California (Miller et al. 2020). As water became increasingly scarce, homeowners replaced traditional ornamental plants with drought-tolerant landscape plants to conserve water and maintain urban greenness (Myjer 2022).

When available water in the soil is depleted frequently or over a long period, the visual aesthetic of ornamental plants may be impaired because of wilted leaves, chlorosis, and reductions in floral formation. Zollinger et al. (2006) found that the quality of *Echinacea purpurea* (L.) Moench (purple coneflower), *Gaillardia aristata* Pursh (blanketflower), and *Lavandula angustifolia* Mill. (English lavender) declined because of visibly wilted leaves as the intervals between irrigations increased. *Orthosiphon aristatus* (Blume) Miq. (cat's whiskers), a tropical rainforest species, exhibited severe leaf wilting when substrate volumetric water content decreased from 0.30 to 0.10 m³·m⁻³ (Kjelgren et al. 2009). Drought often decreases shoot dry weight, leaf number, and total leaf area (Niu and Rodriguez 2009; Taiz et al. 2015). Moreover, traditional/commercial landscape plants are often more sensitive to water stress than plants native to arid regions. For instance, McCammon et al. (2006) found that landscape designs containing traditional ornamental plants, such as *Spiraea japonica* L. f. 'Bumalda' ('Bumalda' Japanese spirea) and *Paeonia lactiflora* Pall. (Chinese peony), had greater losses in visual quality than those containing well-adapted native plants, such as *Penstemon strictus* (Rocky Mountain penstemon), when a 5-week dry-down period was imposed.

Stomata close when experiencing water stress, not only reducing carbon assimilation but also limiting transpiration rates and latent heat consumption of available energy, causing an increase in leaf temperature (Chapman and Augé 1994; Taiz et al. 2015). For instance, decreasing irrigation from 100% reference evapotranspiration (ET_0) to 25% ET_0 increased the temperature difference between the canopy and air by 7 °C of *Alcea rosea* L. (hollyhock), *Callistephus chinensis* (L.) Nees (China aster), *Rudbeckia hirta* L. (black-eyed susan), and *Malva sylvestris* L. (common mallow) (Rafi et al. 2019). Increased canopy temperature under drought conditions also directly affected the aesthetic appearance of landscape plants because of leaf burn and necrosis (Zollinger et al. 2006). Additionally, high canopy temperatures disturb the biochemical functions of plant enzymes and destabilize membranes and proteins, which can lead to cell death and inhibition of photosynthesis (Taiz et al. 2015). The canopy-air temperature difference, which is the deviation of canopy temperature from ambient air temperature, is a better measure of potential stress than canopy temperature alone. This difference was also affected by plant water status and correlated with the degree of plant drought stress (Gajanayake et al. 2011).

Drought acclimations are modifications in plant morphology and physiology, without genetic changes, to adapt to water stress (Taiz et al. 2015). However, the capacity to adapt to drought stress is highly variable among plant species. Most drought-tolerant plants can change their leaf morphology (size, shape, and orientation) to avoid water and heat stress under drought conditions (Álvarez et al. 2009). For example, Mee et al. (2003) reported that native plants in the arid western United States, such as *Artemisia tridentata* Nutt. (big sagebrush) and *Cercocarpus montanus* Raf. (alderleaf mountain mahogany),

have small leaves to reduce light interception to maintain leaf temperature close to ambient air temperature. Additionally, leaves may develop protective structures, such as dense leaf hairs and thick cuticle layers, to increase leaf reflectivity and impede boundary layer air movement to avoid excessive absorption of solar radiation (Leigh et al. 2017). For example, a significant reduction in light absorption was reported for leaves of *Acer rubrum* L. (red maple) and *Acer ×freemanii* A.E. Murray (freeman maple) when experiencing drought stress (Bauerle et al. 2003). Root growth increases to explore deeper soil horizons, thereby resulting in greater root-to-shoot ratios (Ahluwalia et al. 2021). Not surprisingly, xeric plants native to the southern United States have been characterized by small leaves with high root-to-shoot ratios (Stromberg 2013).

Penstemon spp. (beardtongues) are popular for use in low-water-use landscapes because many of the species thrive in arid and semi-arid regions (Mee et al. 2003). Approximately 250 species of penstemons are native to North America, with diverse forms, sizes, and levels of drought tolerance (Mee et al. 2003). Unfortunately, the drought tolerance of penstemon species has not been widely investigated, and their relative drought resistance has been estimated based on local precipitation rates rather than in precisely controlled experiments (Meyer 2009). For example, although *P. digitalis* ‘Husker Red’ (‘Husker Red’ penstemon) was considered more drought-sensitive than *P. strictus*, they had similar visual quality scores after a 5-week drought treatment (McCammon et al. 2006). This indicates the importance of drought studies that properly account for the key factors that govern plant responses to water stress.

The goals of this research were to investigate the effects of drought on the growth, morphological, physiological, and canopy temperature responses of four penstemon

species. We hypothesized that significant decreases in volumetric water content of a peat-based substrate reduce plant growth of penstemon species while increasing canopy temperature and the proportion of visibly wilted leaves, and that penstemon species significantly alter morphological and physiological characteristics such as leaf size, root-to-shoot ratio, leaf reflectance, and stomatal conductance when water availability decreases. To test these hypotheses, the objectives of this research were to determine plant growth, morphological, and physiological differences of four penstemon species under two substrate volumetric water contents in a greenhouse, and to investigate the effects of a precise level of water stress on canopy temperature of penstemon species.

Materials and Methods

Plant Materials

Penstemon barbatus ‘Novapenblu’ (Rock Candy Blue[®] penstemon), *P. digitalis* ‘TNPENDB’ (Dakota[™] Burgundy beardtongue), *P. ×mexicali* ‘P007S’ (Pikes Peak Purple[®] penstemon), and *P. strictus* purchased from Perennial Favorites (Layton, UT) on 1 Nov 2021, were maintained in a Utah Agricultural Experiment Station (UAES) polyethylene greenhouse (Logan, UT) and irrigated with Logan City potable water (electrical conductivity = 0.381 dS·m⁻¹, pH = 7.73). Plants were transplanted to 7.6-L injection-molded polypropylene containers (No. 2B; Nursery Supplies, Orange, CA) filled with a soilless substrate (Metro-Mix[®] 820; Sun Gro Horticulture, Agawam, MA) and manually irrigated to container capacity on 3 Nov 2021. Then, plants were moved to a UAES research greenhouse (Logan, UT) and irrigated using an automated irrigation system (Nemali and van Iersel 2006).

The automated irrigation system contained three blocks and imposed two volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) with 16 replications of each treatment within each block. These two substrate volumetric water contents were chosen following the protocol of Cai et al. (2012). Four plants were randomly selected from each species and were assigned to each treatment of each block. A capacitance sensor (ECH₂O 10HS; Meter Group, Pullman, WA) was vertically inserted into the substrate (15 cm deep) of one randomly chosen container in each treatment per species within each block to measure substrate volumetric water content. Twenty-four capacitance sensors were connected to a multiplexer (AM 16/32B; Campbell Scientific, Logan, UT) that was connected to a datalogger (CR1000X; Campbell Scientific). The datalogger was programmed to scan the voltage output (mV) of each sensor every 5 minutes to calculate substrate volumetric water content (θ_v) using a substrate-specific calibration equation ($\theta_v = 10\text{HS voltage} \times 0.0009 - 0.3688$) (Chen et al. 2022). Twenty-four normally closed, 24-volt-AC solenoid valves (CPF100; Rain Bird, Azusa, CA) were connected to relay controllers (SDM-CD16AC; Campbell Scientific, Logan, UT) to control the irrigation of four plants in each treatment of each block. The datalogger was programmed to open solenoid valves for 1 minute to irrigate plants using pressure-compensated drip emitters with a flow rate at 165.6 ± 7.4 (mean \pm SD) $\text{mL} \cdot \text{min}^{-1}$ when measured substrate volumetric water contents were less than the corresponding setpoints.

From 5 Nov 2021 to 9 Jan 2022, the irrigation system was set to irrigate all plants for 5 mins every other day for establishment. A 15N–3.9P–10K slow-release fertilizer (Osmocote Plus 15-9-12; Israel Chemicals, Tel Aviv-Yafo, Israel) was applied as top-dressing to each plant at a rate of $0.04 \text{ g} \cdot \text{cm}^{-2}$ on 4 Jan 2022. The substrate in each

container was irrigated to the volumetric water content of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ at the initiation of the experiment on 10 Jan 2022. Then, each sensor was randomly assigned to an irrigation setpoint at either 0.35 or $0.15 \text{ m}^3 \cdot \text{m}^{-3}$, which are equivalent to the matric potential of -0.012 and -0.159 MPa, respectively (Chen et al. 2022). The substrate was gradually dried and maintained at the appropriate setpoints until the experiment was ended on 1 Mar 2022. In addition to the capacitance sensor measurements throughout the experiment, a handheld soil moisture sensor (HydroSense; Campbell Scientific) was inserted into the substrate of each container to determine the volumetric water content (θ_p) on 24 Jan and 1 Mar 2022. The sensor-specific calibration for this substrate was used to obtain water content as $\theta_p = (0.2923 \times \text{HydroSense output}) - 0.3855$.

Greenhouse Environment

The ambient temperature within the greenhouse was maintained at 24.1 ± 0.7 °C (mean \pm SD) during the day and 21.1 ± 0.3 °C at night. Furthermore, 1000-watt, high-pressure sodium lamps (Hydrofarm, Petaluma, CA) were installed 1.5 m above the growing bench and provided supplemental light at an intensity of $285.9 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at the plant canopy level from 0600 to 2200 HR whenever light intensity inside the greenhouse was less than $500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The daily light integral and photosynthesis photon flux density at plant canopy level were 29.4 ± 3.9 (mean \pm SD) $\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and $343.4 \pm 41.0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively, and recorded using a full-spectrum quantum sensor (SQ-500-SS; Apogee Instruments, Logan, UT).

Data Collection

Visual quality score, morphology, and plant growth. Visual quality was evaluated weekly for each plant, and plants were graded using a scale of 1 to 5 (1 = plant

close to death with > 65% of leaves wilted; 2 = unacceptable visual quality 35%-65% of leaves wilted; 3 = acceptable visual quality, up to 35% of leaves wilted; 4 = good visual quality, less than 10% of leaves wilted; 5 = excellent visual quality, plant was fully turgid) (Zollinger et al. 2006). Plant height was recorded every 2 weeks from the surface of the substrate to the tallest shoot tip. Plant width was measured in perpendicular directions every 2 weeks. Plant growth index: $[(\text{height} + (\text{width } 1 + \text{width } 2)/2)/2]$ was also calculated (Reid and Oki 2013). For *P. barbatus* and *P. ×mexicali*, the number of shoots longer than 5 cm was recorded. The number of inflorescences and the number of stems with three mature and expanded leaves were recorded on 24 Jan and 1 Mar 2022.

On 1 Mar 2022, plants were harvested to quantify the number of leaves and fresh weight of shoots (leaves and stems). Total leaf area was measured using a leaf area meter (LI-3100; LI-COR Biosciences, Lincoln, NE), and leaf size was calculated as the ratio of the total leaf area to the number of leaves. Roots within each container were washed with potable water, and stems, leaves, and roots were oven-dried at 80 °C for 16 days to obtain dry weights. The root-to-shoot ratio was calculated as the ratio of dry weight of roots to shoots (leaves and stems), and the specific leaf area was calculated using the total leaf area and leaf dry weight. The relative water content of shoots was determined using fresh weight and dry weight of shoots and the equation: $[(\text{fresh weight} - \text{dry weight}) / \text{fresh weight}] \times 100\%$ (Zhou et al. 2021).

Physiological responses. The relative chlorophyll content [soil plant analysis development (SPAD)] was recorded every 2 weeks using a chlorophyll meter (SPAD-502; Minolta Camera, Osaka, Japan), and the average SPAD value of five randomly selected leaves of each plant was recorded. Gas exchange responses of individuals,

including net assimilation rate, stomatal conductance, and transpiration rate, were recorded using a portable photosynthesis system (LI-6800; LI-COR Biosciences) with a multiphase flash fluorometer chamber on a sunny day between 1000 to 1400 HR. Within the chamber, photosynthetic photon flux density was controlled at $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with 90% red light and 10% blue light provided by light-emitting diodes (Small Light Source; LI-COR Biosciences), and carbon dioxide concentration was set at $420 \mu\text{mol}\cdot\text{mol}^{-1}$. A healthy, fully expanded leaf was randomly selected from the outer canopy of each plant. The steady-state gas exchange rates were recorded when a leaf was enclosed in the cuvette for ~ 1 min (Bunce 2016).

Leaf reflectance and canopy temperature. On 23 Feb, three plants were randomly selected from each species within each treatment to record leaf reflectance, except for *P. ×mexicali* because of the small leaf size. Three healthy and fully expanded leaves were randomly sampled from each plant, and their reflectance spectrum of the adaxial surface was recorded using a spectroradiometer (PS-300; Apogee Instruments). The mean reflectance of photosynthetically active radiation was calculated using wavelengths between 400 to 700 nm, whereas blue, green, red, and near-infrared light reflectance was calculated using wavelengths of 450, 530, 660, and 730 nm, respectively (Kusuma et al. 2020).

On 2 Feb and 28 Feb top-view, thermal infrared images of plant canopies were recorded every 2 hours from 0800 to 1800 HR using a thermal image camera (FLIR E5-XT; Teledyne FLIR, Wilsonville, OR). Supplemental lights were turned off during canopy temperature measurements. On 1 Mar thermal canopy images of each plant were collected at 0800 HR after each plant was exposed to supplemental light for 2 hours. The

average canopy temperature of each plant was calculated using FLIR Thermal Studio Suite (Teledyne FLIR). The canopy-air temperature difference was calculated as the difference between ambient air and leaf temperature at 1400 HR using brightness temperature and assuming leaves emissivity equal to 1.0.

Data analysis

The experiment was designed as a randomized complete block design with two treatments and three blocks. A mixed model was used to analyze the effects of substrate volumetric water content on all measured parameters. Correlation analyses were performed to evaluate the relationship between leaf relative water content and canopy temperature. Regression analyses were performed to evaluate relationships between canopy temperature and time of day. All statistical analyses were conducted using PROC MIXED or PROC REG procedures in SAS Studio 3.8 (SAS Institute, Cary, NC) with a significance level specified at 0.05.

Results

Substrate volumetric water content, visual quality, and plant growth. The volumetric water content of substrates for growing *P. barbatus*, *P. digitalis*, *P. ×mexicali*, and *P. strictus* reached their irrigation setpoints 2 weeks after experiment initiation and were maintained at levels more than the corresponding setpoints thereafter (Fig. 1). For the control plants, irrigation was triggered when the measurements of the capacitance soil moisture sensors were less than $0.35 \text{ m}^3 \cdot \text{m}^{-3}$. Therefore, substrate volumetric water contents were maintained at levels more than $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ throughout this study, and this volumetric water content was reported adequate for container-grown ornamental plants (Cai et al. 2012). In contrast, plants that received drought treatment

were irrigated when their volumetric water contents of substrates were less than $0.15 \text{ m}^3 \cdot \text{m}^{-3}$, at that point, plants exhibited symptoms of drought stress (Chen et al. 2022). Substrate volumetric water contents in containers under drought treatment were less than that of the control on 24 Jan and 1 Mar 2022 (Table 1). Reduced substrate volumetric water contents also led to canopy wilting and decreased visual quality scores of the four penstemon species evaluated (Figs. 2 and 3). *Penstemon barbatus* maintained acceptable visual quality when experiencing drought stress for 2 weeks after experiment initiation, when the proportion of visibly wilted leaves was less than 35% (Fig. 3A). At the termination of the experiment, *Penstemon barbatus* had an average visual quality score of 2.0. The visual quality score of *P. digitalis* experiencing drought stress was 2.9 at 2 weeks after experiment initiation (Fig. 3B). At the termination of the experiment, *P. digitalis* under the drought treatment exhibited the poorest aesthetic quality, with an average visual quality score of 1.3. *Penstemon ×mexicali* maintained good aesthetic quality, with 10% of leaves visibly wilted until 3 weeks after experiment initiation (Fig. 3C). However, the proportion of visibly wilted leaves of *P. ×mexicali* increased rapidly, and the visual quality score was 1.7 at the end of the experiment. For *P. strictus*, the visual quality scores were 3.8 at 4 weeks after experiment initiation and 2.3 at the termination of the experiment, with less than 65% of leaves visibly wilted (Fig. 3D).

Plant growth indices of *P. digitalis* and *P. barbatus* under the drought treatment were reduced at 2 and 4 weeks, respectively, after experiment initiation (Figs. 3E and 3F). When experiencing drought stress, plant growth indices of *P. barbatus* and *P. digitalis* were 31% and 46% smaller, respectively, compared with the control at the termination of the experiment. The plant growth index of *P. ×mexicali* did not change

until 6 weeks after experiment initiation (Fig. 3G). At the end of the experiment, the plant growth index of *P. ×mexicali* under drought treatment was 27% smaller compared with the control. Under drought treatment, the plant growth index of *P. strictus* decreased 4 weeks after experiment initiation and was 34% smaller than the control at the end of the experiment (Fig. 3H). Similarly, the number of shoots of *P. barbatus* and *P. ×mexicali* at the substrate volumetric water content of $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ exhibited fewer shoots compared with well-irrigated plants, whereas the number of inflorescences of *P. ×mexicali* decreased under the drought treatment at the end of the experiment (Table 1).

Under the drought treatment, *P. barbatus*, *P. digitalis*, and *P. ×mexicali* had fewer leaves compared with the control (Table 2), and the total leaf areas of *P. barbatus*, *P. digitalis*, *P. ×mexicali*, and *P. strictus* were 69%, 58%, 57%, and 39% lower than the control, respectively. Drought stress also reduced the leaf size of *P. digitalis*, *P. ×mexicali*, and *P. strictus* by 21%, 32%, and 23%, respectively. The dry weights of all penstemon species and shoot relative water contents of *P. digitalis* and *P. ×mexicali* declined under the drought treatment (Table 2). Drought treatment also decreased the specific leaf area of *P. digitalis*, *P. ×mexicali*, and *P. strictus* (Table 2). Conversely, the root-to-shoot ratio of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* experiencing drought stress increased as compared with that of the control (Table 2).

Leaf relative chlorophyll content, leaf reflectance, and gas exchange responses.

Drought stress caused leaf chlorosis in *P. barbatus* and *P. digitalis* 4 weeks after experiment initiation (Fig. 3). SPAD values also decreased from 58.8 and 63.0 for the control to 42.6 and 51.4 under the drought treatment for *P. barbatus* and *P. digitalis*, respectively, at the termination of the experiment (Figs. 3I and 3J). The leaf chlorophyll

content of *P. ×mexicali* was sensitive to drought stress and leaf chlorosis was observed 2 weeks after experiment initiation (Fig. 3K). At harvest, SPAD values of *P. ×mexicali* were 35.7 and 24.2 for the control and under the drought treatment, respectively. The leaf chlorophyll content of *P. strictus* was affected by drought stress 4 weeks after experiment initiation and SPAD values decreased from 65.7 for the control to 56.7 under the drought treatment at the termination of the experiment (Fig. 3L).

The net assimilation rates of *P. barbatus*, *P. digitalis*, *P. ×mexicali*, and *P. strictus* under the drought treatment decreased by 74%, 64%, 70%, and 60%, respectively, compared with the control (Table 3). Similarly, when substrate volumetric water content decreased, the stomatal conductance of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* decreased from 0.21 to 0.03, 0.12 to 0.02, and 0.08 to 0.03 mol·m⁻²·s⁻¹, respectively. Although not statistically significant, stomatal conductance of *P. strictus* was also found to decrease ($P = 0.06$) (data not shown). Under the drought treatment, transpiration rates of *P. barbatus*, *P. digitalis*, *P. ×mexicali*, and *P. strictus* were 70%, 68%, 51%, and 43% less than that of the control, respectively. The leaf reflectance of photosynthetically active radiation of *P. barbatus* and *P. strictus* became greater when substrate volumetric water content was reduced (Table 3). The leaves of *P. barbatus* and *P. strictus* experiencing drought stress reflected greater blue, green, and red light, whereas *P. digitalis* only had increased leaf reflectance of green light. Reduced substrate volumetric water content also increased leaf reflectance of near-infrared light from *P. barbatus* and *P. strictus*.

Canopy temperature. Linear relationships were observed between photosynthetic photon flux density and canopy temperature on 2 Feb and 28 Feb, and the

warmest canopy temperature occurred when solar radiation was strongest (Fig. 4). On 2 Feb, *P. barbatus*, *P. digitalis*, and *P. strictus* experiencing drought stress had warmer canopy temperatures compared with the control (all $P < 0.0001$) and their canopy-air temperature difference became 5.6, 3.2, and 5.2 °C higher, respectively (Table 4). However, the canopy-air temperature difference of *P. ×mexicali* was unaffected by decreased substrate volumetric water content. On 28 Feb, reduced substrate volumetric water content increased the canopy temperature of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* (all $P \leq 0.0006$). The canopy-air temperature difference of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* was 6.3, 6.4, and 4.4 °C higher when substrate volumetric water content decreased, but drought stress did not affect the canopy-air temperature difference of *P. strictus* at the termination of the experiment (Table 4).

High-pressure sodium lights heated the canopy of the four penstemon species that were evaluated, and plants received high-pressure sodium light and grown in substrate at a volumetric water content of $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ had the warmest canopy temperatures (Fig. 5). For instance, high-pressure sodium lights increased the canopy temperatures of *P. barbatus* from 15.2 to 21.1 °C and from 16.9 to 24.6 °C when the substrate volumetric water content was decreased from 0.35 and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$, respectively. Without high-pressure sodium light, the canopy temperature of *P. digitalis* and *P. ×mexicali* with the two substrate volumetric water contents were between 16.5 and 18.8 °C, but high-pressure sodium lights warmed their canopies to temperatures ranging from 22.5 and 24.7 °C. Without high-pressure sodium light, the canopy temperature of *P. strictus* was 14.8 °C for plants under both the control and drought treatments. However, increases of 6.4 and 8.2 °C in canopy temperature occurred in *P. strictus* with substrate volumetric water

contents of 0.35 and 0.15 m³·m⁻³, respectively, when high-pressure sodium lights were on. Therefore, the effects of water stress on canopy temperature were enhanced with increases in incident radiation. This is logical because larger available energy values are associated with larger differences in energy dissipation by latent heat between well-watered and stressed plants.

Discussion

Decreased substrate water availability caused plant dehydration and visibly wilted leaves (Table 2), which negatively affected visual quality (Fig. 3). Additionally, water stress decreased the shoot and flower numbers, total leaf area, shoot dry weights, leaf greenness, plant sizes, and photosynthesis rates (Tables 1 and 2; Fig. 3). The effects of water stress on plant growth and ornamental quality of penstemon species have been reported by Reid and Oki (2013) and Zollinger et al. (2006), with different responses. *Penstemon heterophyllus* Lindl. ‘Margarita BOP’ (margarita bop bunchleaf penstemon), a species native to California, showed the highest relative plant growth rate and visual quality score at 20% ET_o, which was the lowest level of deficit irrigation in one study (Reid and Oki, 2013). However, all penstemon species in this study had decreased visual quality scores when substrate water availability decreased, and *P. digitalis* and *P. ×mexicali* had the highest percentage of visibly wilted leaves and the lowest visual scores at the end of the experiment (Figs. 2 and 3). *Penstemon digitalis* also had the largest reduction in plant growth index as compared with other species. In contrast, *P. barbatus* and *P. strictus* exhibited a lower percentage of wilting leaves, resulting in better aesthetic quality at the termination of the experiment. Zollinger et al. (2006) reported a similar

result after finding that *P. barbatus* ‘Rondo’ (Rondo beardtongue) was more drought-tolerant than *P. ×mexicali* ‘Red Rocks’ (Red Rocks penstemon). Our findings were similar to those of Zollinger et al. (2006) because *P. ×mexicali* ‘Red Rocks’ could withstand moderate drought stress, but prolonged drought stress severely reduced its visual quality. The differences in drought tolerance among penstemon species may be related to the environment of their native habitats. *Penstemon barbatus* is indigenous to arid habitats in the southwestern United States and Mexico and is drought-resilient (Way and James 1998). One of the parents of *P. ×mexicali* is a mesic species, which could cause *P. ×mexicali* to be sensitive to drought stress (Zollinger et al. 2006). *Penstemon digitalis* naturally occurs in moist to mesic prairies throughout eastern to central North America (Mitchell and Ankeny 2001), which could make it more susceptible to drought stress. Conversely, *P. strictus*, a plant native to the western United States and northern Mexico, has been found to be very drought-tolerant (Mee et al. 2003).

In this study, four penstemon species reduced total leaf area by producing smaller leaves and restricting leaf formation when substrate water availability decreased (Table 2). Plants experiencing water stress limited leaf size by restricting leaf cell expansion (Chen et al. 2022). A reduction in total leaf area is considered an avoidance mechanism to minimize canopy surface area for transpiration. Additionally, small leaves can reduce light interception and have more efficient convective heat exchange, resulting in leaf temperatures remaining closer to those of the air (Taiz et al. 2015). Therefore, plants with higher total leaf area, such as *P. digitalis*, were more sensitive to drought stress. Through defoliation and the restriction of leaf expansion, *Pittosporum tobira* (Thunb.) W.T. Aiton (Japanese cheesewood) and *Viburnum tinus* L. (laurustinus) decreased total leaf areas

experiencing water stress to limit water loss (Toscano et al. 2014). *Polygala myrtifolia* L. (myrtle-leaf milkwort), a Mediterranean ornamental shrub, also defoliated when substrate volumetric water content declined from 40% to 10% (Tribulato et al. 2019). Álvarez et al. (2009) found that defoliation was a drought acclimation of *Dianthus caryophyllus* L. (carnation) when the amount of irrigation water was decreased by 65% as compared with a control. Summer dormancy was also a strategy that plants used to avoid drought stress (Newell 1991). For instance, leaves of *Aesculus californica* (Spach) Nutt. (California buckeye) senesced when rains ceased, resulting in a leafless canopy during summer (Newell 1991). However, defoliation can result in unfavorable ornamental quality and impaired whole-plant photosynthesis efficiency (Bañon et al. 2006).

Reduced substrate water availability also decreased the specific leaf area of the four penstemon species evaluated in this study (Table 2). The effect of water stress on leaf thickness has been reported on *Ptilotus nobilis* (Lindl.) F. Muell. (yellow tails) and *Acer ×freemanii* (Kjelgren et al. 2009; Zwack et al. 1998). Thick leaves have been found to have dense and compact laminar cells that sustained photosynthesis efficiency without increases in leaf area (Nash and Graves 1993). Toscano et al. (2018) also found that water-stressed *Lantana camara* L. (common lantana) and *Ligustrum lucidum* W.T. Aiton (glossy privet) exhibited a higher leaf biomass per unit of leaf area that helped limit evaporative surface area but still maintained a consistent photosynthesis rate. With the exception of *P. strictus*, the allocation of biomass to roots and shoots changed under the drought treatment, resulting in a higher root-to-shoot ratio. Previous studies have confirmed that root growth was promoted when experiencing drought stress to improve water uptake (Álvarez et al. 2009; Balok and St. Hilaire 2002). However, reductions in

leaf and stem growth may restrict water consumption, leading to an increased root-to-shoot ratio when experiencing drought stress. In previous research, *Acer* L. species (hard maple) that received deficit amounts of irrigation (based on ET) had double the root-to-shoot ratio of plants that were well-irrigated (St. Hilaire and Graves 2001). In our study, *P. ×mexicali* had the lowest root-to-shoot ratio at the end of the experiment, and this may have led to a low relative water content of shoots and a high proportion of visibly wilted leaves.

The stomatal conductance of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* was reduced to very low values close to zero when the substrate volumetric water content decreased from 0.35 to 0.15 m³·m⁻³. As stomatal conductance declined, transpiration rates were constrained, suggesting that penstemon species coped with tissue dehydration via stomatal closure. Stomata close to prevent water loss via transpiration, thus protecting plant tissue from further dehydration and vascular vessels from cavitation (Martínez-Vilalta and Garcia-Forner 2017), and stomatal conductance is correlated to the plant water status (Zhang et al. 2013). Chapman and Augé (1994) reported a positive correlation between stomatal conductance and leaf water potential for *Helianthus angustifolius* L. (swamp sunflower), *Monarda didyma* L. (scarlet beebalm), and *Rudbeckia fulgida* Aiton var. *sullivantii* (orange coneflower), indicating that ornamental plants close stomata to restrict water loss when their tissues are dehydrated. Similarly, stomata may close when the stem water potential and relative plant water content decrease (Chen et al. 2022). For native ornamental plants such as *E. purpurea* and *P. barbatus* ‘Rondo’, a positive correlation was found between stomatal conductance and leaf water potential when the interval between irrigations increased from 1 to 4 weeks

(Zollinger et al. 2006). Plants that adjust stomatal conductance to tolerate water stress were found to be more desirable for low-water-use landscapes because they often exhibited better resistance to prolonged drought (Kjelgren et al. 2009; West et al. 2007). However, net photosynthesis efficiency may be impaired as the intake of carbon dioxide is inhibited when stomata close, and this could decrease the photosynthesis rate.

The growth and aesthetic quality of penstemon plants could also be affected by heat stress (Fig. 4). According to Nelson and Bugbee (2015), leaf temperatures of *Brassica oleracea* L. (broccoli), *Capsicum annuum* L. (pepper), *Ocimum basilicum* L. (basil), and *Solanum lycopersicum* L. (tomato) were directly affected by plant water status and light intensity. In this study, solar radiation also positively affected leaf temperature of penstemons. When solar radiation became stronger, plants experiencing drought stress showed greater increases in canopy temperature compared with the control. Under drought conditions, plants dehydrated, and stomata closed, thus limiting transpiration rates (Table 3). Therefore, Transpirational cooling effects were limited, causing the leaf temperature to increase under drought conditions (Nobel 2020). Hence, decreased substrate volumetric water content increased the canopy temperature of penstemon species. Nelson and Bugbee (2015) also observed that well-watered plants with a stomatal conductance of $0.50 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ had cooler leaf temperatures as compared with water-stressed plants with a stomatal conductance of $0.1 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Apart from sunlight and stomatal conductance, high-pressure sodium lights in a greenhouse could exacerbate drought stress as canopy temperature increased when these lights were on (Table 4). In addition to radiation, high-pressure sodium lights produce more heat than other light sources, such as light-emitting diodes, and that heat is another

source of energy that amplifies transpiration rates (Katzin et al. 2021). *Penstemon strictus* had similar canopy temperatures under the two substrate volumetric water contents at the end of the experiment, which may have resulted from the fact that *P. strictus* modified both morphology and physiology to acclimate to reduced substrate water content. Therefore, solar radiation alone may not have been sufficient to induce a difference in canopy temperature for *P. strictus* under the control and drought treatments. However, under high-pressure sodium lights, which delivered heat vertically to the canopy, the canopy temperature of *P. strictus* experiencing drought stress was higher than that of the control, suggesting that drought stress affected its plant water status.

Greater canopy-air temperature differences were observed in plants experiencing drought stress during the middle and the end of this experiment (Table 4). Because of continuous drought stress, the canopy-air temperature differences of plants at the substrate volumetric water content of $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ became greater at the termination of the experiment. Plants grown without water stress often have canopy-air temperature differences within $2 \text{ }^\circ\text{C}$ of ambient temperature in a glass greenhouse (Nelson and Bugbee 2015). In our study, however, *P. digitalis* and *P. ×mexicali* had canopy-air temperature differences greater than $2 \text{ }^\circ\text{C}$, the lowest visual quality scores, and reduced water content of shoots when experiencing drought stress. In contrast, the canopy-air temperature difference was less than $2 \text{ }^\circ\text{C}$ for *P. Barbatus* and *P. strictus*, and these plants did not decrease the shoot relative water content when the substrate volumetric water content was decreased. When receiving the same amount of irrigation water, high-water-use ornamental plants had higher canopy-air temperature differences at midday compared with low-water-use plants, and ornamental plants that performed well in arid and semi-

arid regions often had lower canopy-air temperature differences (Bheemanahalli et al. 2021). For instance, Rafi et al. (2019) found that *M. sylvestris*, which requires large amounts of irrigation water to maintain acceptable visual quality, had a canopy-air temperature difference of 3.52 °C, whereas drought-tolerant *A. rosea* had a canopy-air temperature difference of -3.08 °C. Therefore, *P. barbatus* and *P. strictus* may have better drought tolerance than *P. digitalis* and *P. ×mexicali*.

Penstemon ×mexicali grown at the two substrate water contents had similar canopy temperatures during the middle of our experiment. This could be attributed to the fact that the small leaves of *P. ×mexicali* promote heat dissipation via sensible heat loss (Nobel 2020). However, *P. ×mexicali* also had higher canopy-air temperature differences as water stress continued and a smaller root-to-shoot ratio at the end of the experiment. In contrast, *P. digitalis*, which has larger leaves, was disadvantaged in dissipating heat through sensible heat loss, resulting in the highest canopy temperature at the end of the experiment. Apart from leaf size differences, *P. barbatus* and *P. strictus* exhibited greater leaf reflectance that helped reduce excessive heat load and avoided heat stress. This may have resulted from a thicker leaf cuticle that developed when experiencing drought stress. Drought stress has been shown to enhance cuticle biosynthesis, which increases leaf reflectance under both visible and infrared light to reduce photoinhibition of photosynthesis as well as transpirational water loss (Micco and Aronne 2012; Tafolla-Arellano et al. 2018). For example, when *Cynanchum komarovii* Al. Iljinski (dog-strangling vine) experienced drought stress, the biosynthesis of cuticle components, including cutin and waxes, was enhanced to increase drought resistance (Ma et al. 2015). Xeric species *Reaumuria soongorica* (Pall.) Maxim (reaumuria) often has thick cuticle

layers that help it acclimate to drought stress as well (Shi et al. 2013). Slaton et al. (2001) also found that near-infrared reflectance of leaves was positively correlated with cuticle thickness. Hence, the fact that near-infrared reflectance of *P. barbatus* and *P. strictus* increased (Table 3) may suggest that their cuticle layers became thicker as substrate water availability decreased, which helped reduce excessive heat and led to a lower canopy-air temperature difference and better visual quality.

Conclusions

Decreased substrate volumetric water content impaired the visual quality of four penstemon species as the proportion of visibly wilted leaves increased. The net photosynthesis rate was also restricted when plants were dehydrated, and plant growth was limited. However, penstemon species can modify their morphology and physiology by limiting stomatal conductance and increasing root-to-shoot ratios to acclimate to decreased substrate water levels. As the stomatal conductance decreased to restrict the transpiration rate over the course of this study, the canopy temperature of penstemon species increased, leading to greater canopy-air temperature differences. Nonetheless, *P. barbatus* and *P. strictus* were able to modify leaf reflectance to avoid excessive solar radiation through the increased thickness of cuticle layers when experiencing water stress. *Penstemon mexicali* and *P. digitalis*, which have larger leaves, greater total leaf area, and lower root-to-shoot ratios, were more sensitive to water stress and had greater canopy-air temperature differences than *P. barbatus* and *P. strictus*. Our findings document the morphological and physiological acclimations of drought-tolerant plants responding to water stress and their effects on plant canopy temperature.

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Table 3-1. Substrate volumetric water content (VWC), number (No.) of shoots and inflorescences of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with volumetric water content treatments of 0.35 m³·m⁻³ (control) and 0.15 m³·m⁻³ (drought) during the middle (24 Jan) and at the end (1 Mar) of the experiment. Substrate volumetric water content was measured using a handheld soil moisture sensor (Hydro Sense; Campbell Scientific, Logan, UT), and the number of shoots with three mature leaves were counted.

Species	24 Jan						1 Mar					
	VWC		Shoot no.		Inflorescence no.		VWC		Shoot no.		Inflorescence no.	
	Contro l	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
<i>P. barbatus</i>	19.5 a ⁱ	11.1 b	20.9 a	16.4 b	1.4 a	1.1 a	33.8 a	14.5 b	36.6 a	21.7 b	3.9 a	3.2 a
<i>P. digitalis</i>	30.3 a	9.4 b	10.3 a	6.9 a	0.9 a	0.2 a	21.8 a	8.1 b	15.0 a	8.3 a	1.5 a	0.1 a
<i>P. ×mexicali</i>	23.4 a	9.3 b	60.8 a	44.4 b	5.3 a	5.8 a	31.0 a	8.7 b	97.1 a	69.6 b	29.8 a	16.3 b
<i>P. strictus</i>	25.4 a	12.5 b	16.5 a	14.2 a	ii		27.6 a	15.3 b	24.0 a	24.0 a		
Species (S)	NS ⁱⁱⁱ		****		****		****		****		****	
Treatment (T)	****		****		NS		****		****		***	
S×T	*		****		NS		*		***		****	

ⁱ Means with same lowercase letters within a penstemon species, date, and dependent variable are not significantly different between treatments according to the Tukey–Kramer method with a significance level specified at 0.05.

ⁱⁱ No inflorescence was observed on *P. strictus* during the experiment.

ⁱⁱⁱ NS, *, ***, **** represents nonsignificant and significant at $P \leq 0.05$, 0.001, or 0.0001, respectively.

Table 3-2. Number (No.) of leaves, leaf area and size, shoot dry weight (DW) and relative water content (RWC), specific leaf area (SLA), and root-to-shoot ratio (R/S) of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of 0.35 m³·m⁻³ (control) and 0.15 m³·m⁻³ (drought) at the termination of the experiment.

Species	Leaves no.		Leaf area (cm ²)		Leaf size (cm ²) ⁱ		Shoot DW (g)		Shoot RWC (g·g ⁻¹) ⁱⁱ		SLA (cm ² ·g ⁻¹) ⁱⁱ		R/S (g·g ⁻¹) ⁱⁱⁱ	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
<i>P. barbatus</i>	257.2 a ^{iv}	95.3 b	1566.8 a	479.2 b	6.1 a	5.0 a	29.5 a	12.6 b	0.75 a	0.69 a	71.5 a	72.8 a	3.3 b	5.5 a
<i>P. digitalis</i>	193.5 a	103.7 b	3564.2 a	1513.2 b	18.4 a	14.6 b	52.3 a	25.0 b	0.74 a	0.65 b	73.2 a	60.8 b	2.7 b	4.4 a
<i>P. ×mexicali</i>	2413.2 a	1513.2 b	1931.4 a	827.2 b	0.8 a	0.5 b	55.1 a	30.5 b	0.71 a	0.55 b	61.4 a	48.8 b	0.6 b	0.9 a
<i>P. strictus</i>	203.3 a	161.5 a	1170.9 a	717.3 b	5.8 a	4.4 b	20.4 a	14.1 b	0.72 a	0.68 a	64.0 a	56.8 b	4.8 a	4.9 a
Species (S)	****v		****		****		****		****		****		****	
Treatment (T)	****		****		****		****		****		****		****	
S×T	**		NS		NS		NS		*		*		NS	

ⁱ The leaf size of each plant was calculated as the ratio of total leaf area to the leaf number.

ⁱⁱ The relative water content of shoots was calculated using the equation: [fresh weight (FW) – dry weight (DW)]/FW × 100%, whereas SLA was calculated as the ratio of leaf area to leaf DW.

ⁱⁱⁱ The root-to-shoot ratio was calculated using the DW of roots and shoots.

^{iv} Means with same lowercase letters within a penstemon species and dependent variable are not significantly different between treatments according to the Tukey–Kramer method with a significance level specified at 0.05.

^v NS, *, **, ***, **** represents nonsignificant and significant at $P \leq 0.05$, 0.01, 0.001, or 0.0001, respectively.

Table 3-3. Net assimilation rate (P_n), stomatal conductance (g_s), transpiration rate (E), and leaf reflectance of photosynthetically active radiation (PAR), blue, green, red, and near-infrared (NIR) light of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought).

ⁱThe reflectance of PAR was determined using the wavelengths from 400 to 700 nm, and the reflectance of blue, green, red, and near-infrared light was recorded using wavelengths of 450, 530, 660, and 730 nm, respectively (Kusuma et al. 2020).

Species	Gas exchange responses						Leaf reflectance ⁱ									
	P_n		g_s		E		PAR		Blue		Green		Red		NIR	
	$(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$		$(\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$		$(\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$						(%)					
	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
<i>P. barbatus</i>	14.31 a ⁱⁱ	3.68 b	0.21 a	0.03 b	3.63 a	1.07 b	4.7 b	9.9 a	2.9 b	5.5 a	7.0 b	14.7 a	3.4 b	7.9 a	36.8 b	44.0 a
<i>P. digitalis</i>	8.09 a	2.94 b	0.12 a	0.02 b	3.05 a	0.99 b	3.0 a	4.3 a	2.6 a	3.2 a	1.2 b	3.7 a	4.1 a	5.0 a	37.9 a	40.8 a
<i>P. ×mexicali</i>	7.86 a	2.33 b	0.08 a	0.03 b	2.40 a	1.18 b	iii									
<i>P. strictus</i>	16.35 a	6.53 b	0.15 a	0.06 a	3.11 a	1.78 b	4.0 b	7.9 a	2.5 b	4.7 a	6.7 b	10.1 a	2.8 b	7.0 a	35.0 b	42.9 a
Species (S)	****iv		NS		NS		****		*		****		NS		NS	
Treatment (T)	****		****		****		****		****		****		****		****	
S×T	*		NS		NS		**		NS		**		**		NS	

ⁱⁱ Means with same lowercase letters within a penstemon species and dependent variable are not significantly different between treatments according to the Tukey–Kramer method with a significance level specified at 0.05.

ⁱⁱⁱ Leaf reflectance of *P. ×mexicali* was not recorded because of small leaves.

^{iv} NS, *, **, **** represents nonsignificant and significant at $P \leq 0.05$, 0.01, or 0.0001, respectively.

Table 3-4. Canopy-air temperature difference of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of 0.35 m³·m⁻³ (control) and 0.15 m³·m⁻³ (drought) at 1400 HR on 2 Feb and 28 Feb 2022.

Species	Canopy-air temperature difference (°C)			
	2 Feb		28 Feb	
	Control	Drought	Control	Drought
<i>P. barbatus</i>	-4.4 b ⁱ	1.2 a	-4.6 b	1.7 a
<i>P. digitalis</i>	-3.5 b	-0.3 a	-0.4 b	6.0 a
<i>P. ×mexicali</i>	-1.4 a	-0.2 a	-1.1 b	3.3 a
<i>P. strictus</i>	-5.3 b	-0.1 a	-3.2 a	-2.5 a
Species (S)	NS ⁱⁱ		****	
Treatment (T)	****		****	
S×T	*		**	

ⁱ Means with same lowercase letters within a penstemon species and date are not significantly different between treatments according to the Tukey–Kramer method with a significance level specified at 0.05.

ⁱⁱ NS, *, **, **** represents nonsignificant and significant at $P \leq 0.05$, 0.01, or 0.0001, respectively.

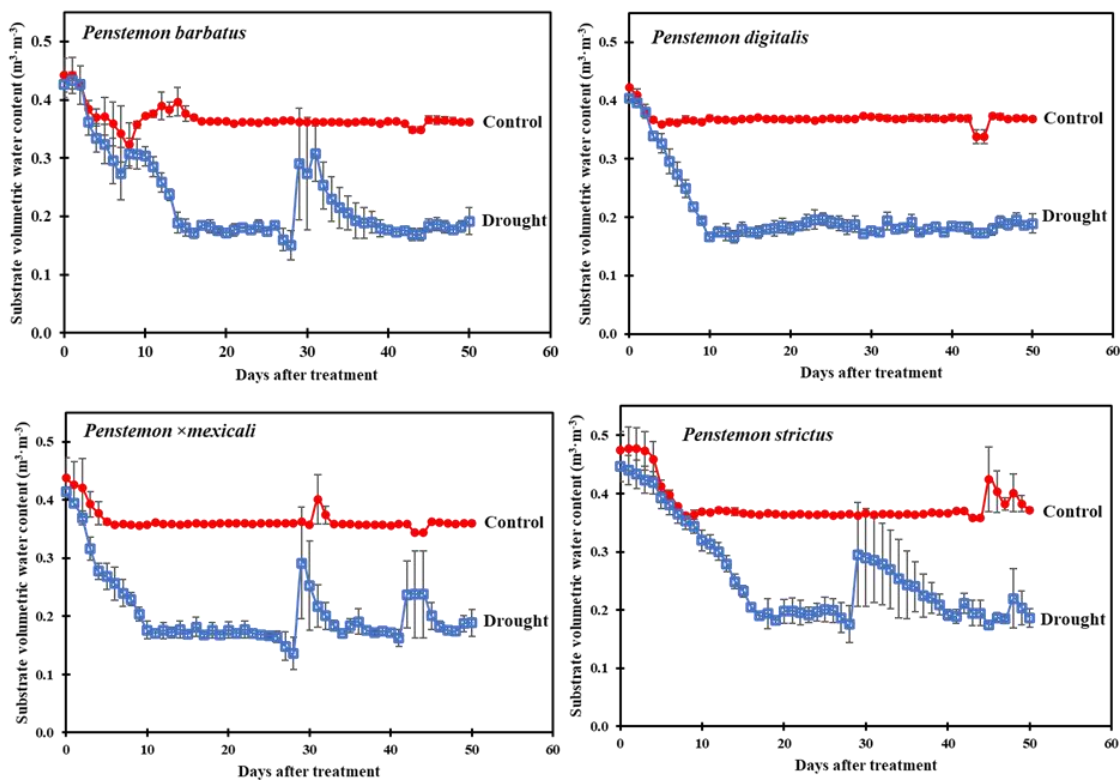


Figure 3-1. Daily average volumetric water contents of substrates growing *P. barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought). Measurements were recorded using calibrated soil moisture sensors (ECH₂O 10HS; Meter Group, Pullman, WA) during the experiment. Error bars represent the *SE* of three sensors.

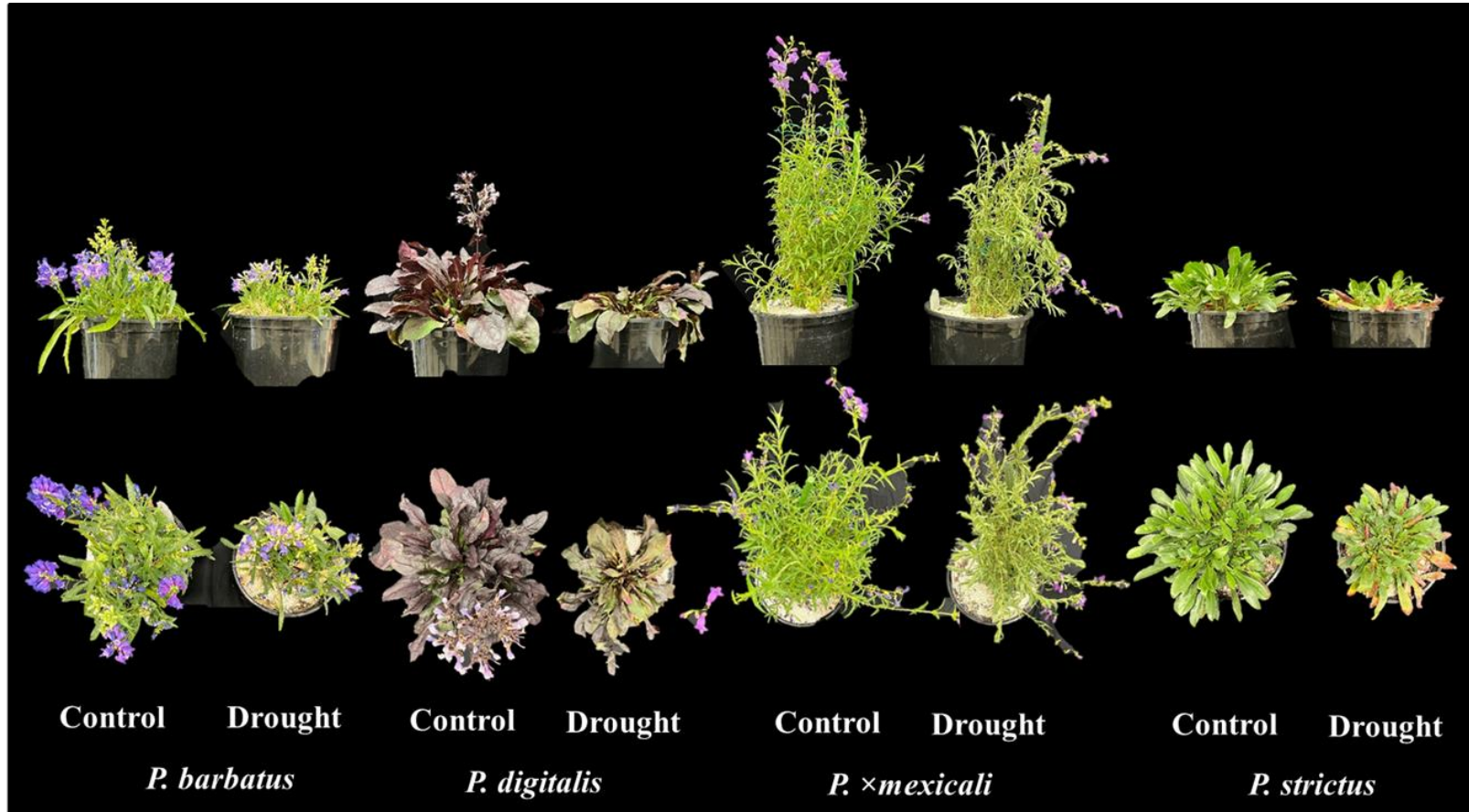


Figure 3-2. Representative plants of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) at the end of the experiment (photo taken on 28 Feb 2022).

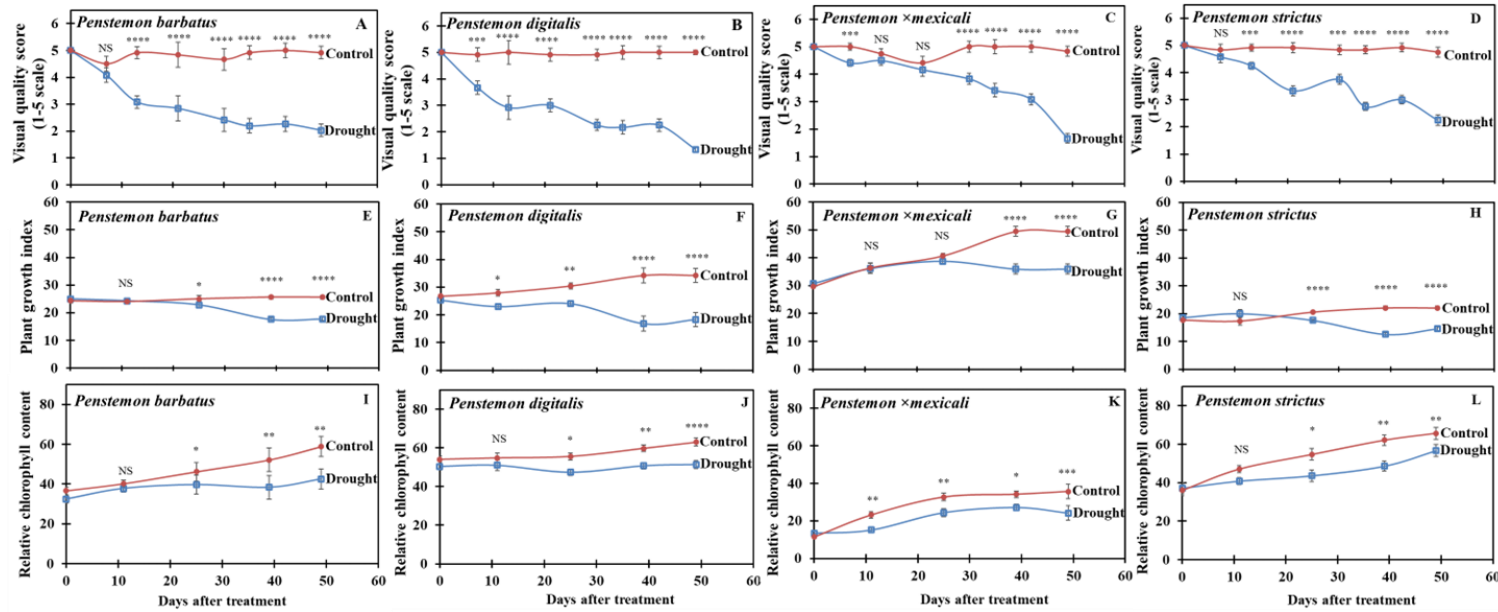


Figure 3-3. Visual quality score (A-D), plant growth index (E-H), and relative chlorophyll content [soil plant analysis development (SPAD) value] (I-L) of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought). The visual quality score was rated weekly using a scale of 1 to 5 based on the proportion of visibly wilted leaves (1 = > 65% of the leaves wilted; 2 = 35%–65% of the leaves wilted; 3 = up to 35% of the leaves wilted; 4 = < 10% of the leaves wilted; 5 = plant was fully turgid) (Zollinger et al. 2006). Plant height, width, and SPAD were recorded every 2 weeks. Error bars represent the *SE* of 12 plants. NS, *, **, ***, **** represents nonsignificant and significant at $P \leq 0.05$, 0.01, 0.001, or 0.0001, respectively.

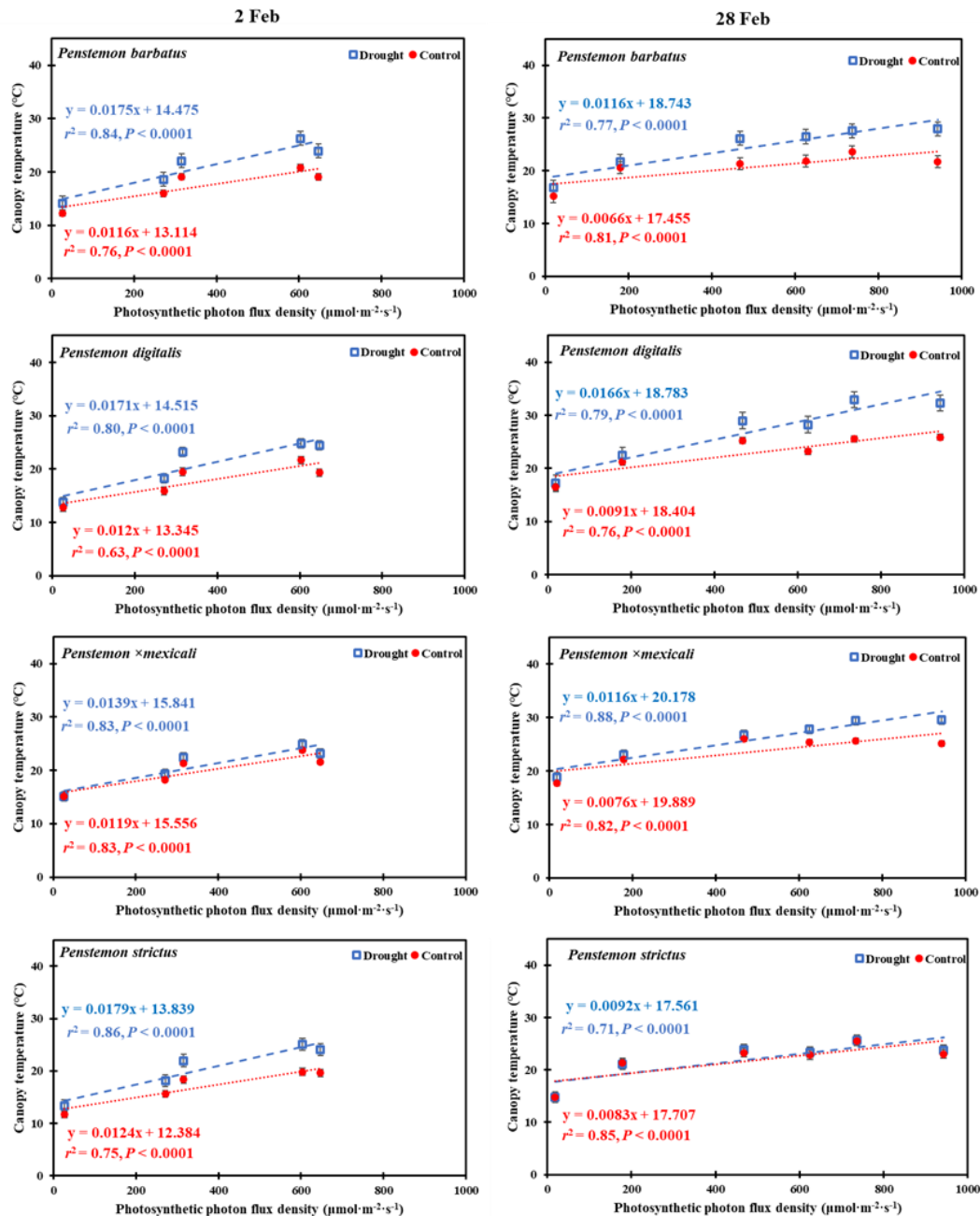


Figure 3-4. Correlation between photosynthetic photon flux density and canopy temperature of *P. barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of $0.35 \text{ m}^3\cdot\text{m}^{-3}$ (control) and $0.15 \text{ m}^3\cdot\text{m}^{-3}$ (drought) on 2 Feb and 28 Feb 2022. Error bars represent the *SE* of 12 plants.

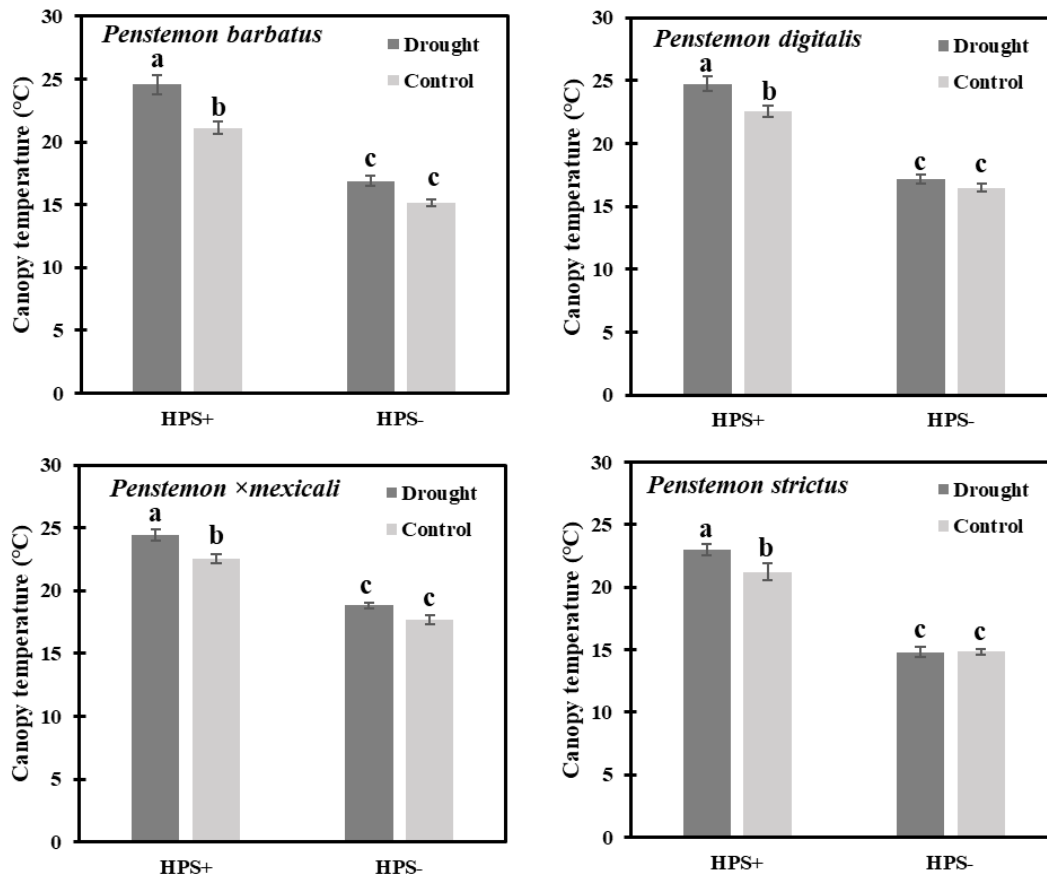


Figure 3-5. Canopy temperature of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. mexicali* ‘P007S’, and *P. strictus* at the volumetric water content treatments of $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.15 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) with high-pressure sodium lights (HPS+) or without (HPS-). Error bars represent standard errors of 12 plants. Treatments with same lowercase letters within each species are not significantly different among treatments by Tukey–Kramer method with a significance level specified at 0.05.

CHAPTER IV

CLIMATE READY LANDSCAPE PLANTS (I): GARDEN ROSES TRIALED IN
UTAH³**Abstract**

Increased urban and suburban populations in the arid western United States have resulted in higher water demand, whereas water availability in the region has become limited because of inadequate precipitation. Recent droughts have led to restrictions on irrigating landscape plants. Garden roses (*Rosa ×hybrida* L.) are commonly used as flowering plants in residential landscapes, but their drought tolerance has not been widely studied. The objective of this study was to determine the impact of reduced irrigation frequency on visual quality, plant growth, and physiology of five garden rose cultivars, including ‘ChewPatout’ (Oso Easy[®] Urban Legend[®] rose), ‘Meibenbino’ (Petite Knock Out[®] rose), ‘MEIRIFTDAY’ (Oso Easy[®] Double Pink rose), ‘Overedclimb’ (Cherry Frost[™] rose), and ‘Radbeauty’ (Sitting Pretty[™] rose). Twenty-four plants of each rose cultivar were established in a trial plot in the summer of 2021. Plants were randomly assigned to one of three deficit irrigation treatments, for which irrigation frequencies were calculated using 80% reference evapotranspiration (ET_O) (high), 50% ET_O (medium), and 20% ET_O (low). The total volume of irrigation water applied to each plant was 345.6, 172.8, and 43.2 liters at the high, medium, and low treatment, respectively, during the deficit irrigation trial. Root zones were wetted more frequently as irrigation

³ Author: Chen J, Sun Y, Oki LR, Sisneroz J, Reid K, Nackley LL, Kim S-H, Schuch UK, Haver DL, Stuke M, Fron A, Kopp K, Jones SB, and Hipps L. 2023. Climate Ready Landscape Plants (I): Garden Roses Trialed in Utah. HortTechnology. (Submitted to HortTechnology on 30 Apr 2023).

frequency was increased from low to high irrigation treatments. Decreased irrigation frequency increased the number of visibly wilted and damaged leaves on all rose cultivars. However, only 'Meibenbino' and 'MEIRIFTDAY' roses exhibited a reduction in overall appearance under decreased irrigation frequency. The relative growth indices and dry weights of stems and leaves of 'Meibenbino' and 'MEIRIFTDAY' roses also decreased as irrigation frequency decreased. Roses in this study appeared to decrease stomatal conductance when irrigation frequency declined, or when air temperature increased. 'Meibenbino' and 'MEIRIFTDAY' roses exhibited unacceptable overall appearance, growth reduction, higher leaf-air temperature difference, and were less tolerant to reduced irrigation. Although the 'Radbeauty' rose maintained plant growth under the reduced irrigation treatment, the large leaf size led to a more visibly wilted appearance and the potential for heat stress, impairing visual quality. 'ChewPatout' and 'Overedclimb' roses were the most tolerant cultivars to deficit irrigation at 20% ET_0 and maintained plant growth with acceptable visual quality and lower leaf temperatures when receiving one irrigation during the growing season.

Introduction

Landscape irrigation accounts for 70% of residential water use per capita in the western United States (Hayden et al. 2015). However, as extreme weather events challenge water supplies, water demands in the urban and suburban sector have grown rapidly because of increased population (Mini et al. 2014). Water scarcity has forced restrictions on irrigating landscape plants when drought occurs. For example, residents of North Logan, Utah, were limited to two irrigation days per week for trees, shrubs or

bushes, flowers, and gardens to conserve water during drought in June 2022 (North Logan City 2022). Also, in the summer of 2022, landscape water restrictions in California allowed local homeowners to irrigate their landscape plants no more than three times per week because of insufficient precipitation (California Water Boards 2022). However, these restrictions have the potential to negatively affect the growth and greenness of urban vegetation. For example, landscape irrigation was prohibited during the California droughts between 2012 and 2016, reducing urban vegetation coverage from 45% to 35% in downtown Santa Barbara, CA (Miller et al. 2020). Subsequently, new landscapes were required to be designed using drought-tolerant plants that require less irrigation (California Department of Water Resources 2022). For instance, the County of San Diego in California requires that landscape designs for residential areas contain water-efficient plants for 75% of the plant area, whereas non-residential areas must install water-efficient landscape plants in 100% of the plant area (County of San Diego, 2020).

Reference evapotranspiration (ET_0) calculated from local weather station data may be used to schedule irrigation frequency or the amounts of irrigation water applied to residential landscapes (Evans et al. 2022). However, when irrigation frequency and amounts of irrigation water decrease, the visual quality of landscape plants may be impaired because of an increase in the number of necrotic leaves and a reduction in floral abundance (Hartin et al. 2018; Zollinger et al. 2006). Growth reduction under water stress can also impair visual quality by limiting leaf density and shoot uniformity (Cameron et al. 2006). When experiencing water stress, partial closure of stomata not only reduces carbon assimilation but also limits the effects of transpirational cooling, resulting in an increase in leaf temperature (Nobel 2020). Increases in leaf canopy temperatures, if large

enough, can disturb the biochemical functions of enzymes and destabilize membranes and proteins, which can lead to the inhibition of photosynthesis and cell death (Taiz et al. 2015). Heat stress often becomes most severe in the late afternoon because of large saturation deficit at the time, resulting in plants having the highest leaf temperatures and lowest stomatal conductance (Tuzet et al. 2003).

Plants can acclimate to water stresses by modifying their morphology and physiology. However, the capacity to adapt to drought stress is highly variable among plant species (Taiz et al. 2015). Plants may respond to drought stress by reducing leaf area to restrict transpirational water loss. For instance, carnation (*Dianthus caryophyllus* L.) defoliated to limit leaf surface area for transpiration when irrigation was decreased by 65% (Álvarez et al. 2009). Dormancy also allows plants to avoid drought and heat during summer months through leaf senescence and abscission (Newell 1991). The leaves of California buckeye [*Aesculus californica* (Spach) Nutt.] senesced and abscised before the dry season, allowing the plants to have leafless canopies during summer to avoid water stress (Newell 1991). Drought-resistant plants can also adjust stomatal conductance to limit water loss from the transpiration pathway (Chen et al. 2022). McCammon et al. (2006) reported that landscape designs containing drought-tolerant ornamental plants could maintain better visual quality as compared with those with high water-use plants when a five-week-long dry-down period was imposed. Reid and Oki (2008) reported that drought-tolerant landscape plants, including Van Houtte's columbine (*Aquilegia eximia* Van Houtte ex Planch.) and blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], maintained acceptable appearances when the interval between irrigations increased from 13 to 58 days.

Roses (*Rosa ×hybrida* L.) are flowering plants often used in residential landscapes (Sagers 2012). In the United States, more than 24 million roses are sold annually with an estimated sales value of 168 million, accounting for 24.9% of the total value of deciduous shrubs sold in the U.S. market (US Department of Agriculture 2020). The drought tolerance of roses, however, is highly diverse among cultivars (Cai et al. 2012). Cai et al. (2012) reported that container-grown roses could utilize partial closure of stomata to acclimate to drought stress in a greenhouse. A deficit irrigation treatment of 20% ET_0 resulted in a marginally acceptable visual quality of ‘Aushouse’ rose, but good aesthetic quality for ‘Meijocos’ rose grown in an open field in Davis, CA (Reid et al. 2019). The drought tolerance of roses has not been widely studied, and morphological and physiological mechanisms that allow roses to maintain aesthetic appearance under drought have rarely been investigated.

‘ChewPatout’ (Oso Easy[®] Urban Legend[®] rose) and ‘MEIRIFTDAY’ roses (Oso Easy[®] Double Pink rose) are disease- and heat-tolerant landscape roses that have compact and mounding canopies (Proven Winners 2023). The rose cultivar ‘Meibenbino’ (Petite Knock Out[®] rose) is a miniature rose with pest tolerance, and ‘Overedclimb’ (Cherry Frost[™] rose) is a climbing rose exhibiting excellent disease resistance (Star Roses and Plants 2022). ‘Radbeauty’ rose (Sitting Pretty[™] rose) has good disease resistance and is highly attractive to pollinators (Star Roses and Plants 2023). These cultivars are commercially available, however, their performance under deficit irrigation had not been investigated. This study aimed to investigate the effects of reduced irrigation frequency on the growth, morphological, physiological, and canopy temperature changes of the five rose cultivars. We hypothesized that (1) decreased irrigation frequency (with the same

application volume at each irrigation) would reduce floral abundance and dry weights of stems and leaves of rose cultivars and would increase canopy temperatures and the proportion of leaves visibly wilted, and (2) rose cultivars will reduce stomatal conductance and leaf area when irrigation frequency decreases.

To test these hypotheses, the objectives of this research were (1) to determine plant growth, morphological, and physiological differences of five rose cultivars at three decreased irrigation frequencies in a field setting, (2) to investigate the relationship between the overall aesthetic of rose cultivars and their morphological and physiological modifications in responses to reductions in irrigation.

Materials and Methods

Plant materials and field layout. ‘ChewPatout’ and ‘MEIRIFTDAY’ roses donated by the Spring Meadow Nursery (Grand Haven, MI) were received on 23 Mar 2021, and ‘Meibenbino’, ‘Overedclimb’, and ‘Radbeauty’ roses donated by the Star[®] Roses and Plants Nursery (West Grove, PA) were received on 9 Apr 2021. The roses were transplanted to 2-gal injection-molded polypropylene containers (No. 2B; Nursery Supplies, Orange, CA) filled with a soilless substrate (Metro-Mix[®] 820; Sun Gro Horticulture, Agawam, MA) once received. Plants were irrigated with Logan City potable water (electrical conductivity = $0.403 \text{ dS} \cdot \text{m}^{-1}$, pH = 7.88) until substrates reached the container capacity and kept in a Utah Agricultural Experiment Station’s (UAES) research greenhouse (Logan, UT).

On 19 May 2021, plants were transplanted to an experimental plot at UAES’s Greenville Research Farm (North Logan, UT) (lat. $41^{\circ} 45' 56.66''$ N, long. $111^{\circ} 48'$

37.00" W, elevation 1400 m) with 2.0 m between rows and 2.0 m between plants in full sun conditions. All plants were irrigated by pressure-compensating emitters (PCR4-36, Damm Corporation, Manitowoc, WI) connected to dribble rings at a flow rate of 2.35 ± 0.03 (mean \pm SD) $\text{mL}\cdot\text{s}^{-1}$ using secondary water (untreated, unfiltered water) (electrical conductivity = $0.373 \text{ dS}\cdot\text{m}^{-1}$, pH = 8.38). The soil in the experimental plot is a Millville silt loam, of which the values of field capacity and permanent wilting point were estimated to be 0.24 and $0.06 \text{ m}^3\cdot\text{m}^{-3}$ (Or 1990), resulting in plant available water value at $0.18 \text{ m}^3\cdot\text{m}^{-3}$ (O'Geen et al. 2017). The experimental plot was covered with large-size, chunk bark mulch (Mountain West Products, Rexburg, ID) to control weeds. Soil samples collected from the plot were submitted to the Utah State University Analytical Laboratory (Logan, UT) for analysis, and the soil pH, salinity, and mineral contents are presented in Table 1. Weather data, including cumulative ET_0 and precipitation, maximum and average air temperatures, daily light integral, and average vapor pressure, were recorded by a Utah Climate Center weather station (lat. $41^\circ 45' 59.32''$ N, long. $111^\circ 48' 37.8''$ W, elevation 1400 m), approximately 250 m away from the experimental plot.

Deficit irrigation and soil moisture contents. Plants were evaluated for their growth, visual quality, and physiological responses following the method developed by the University of California Landscape Plant Irrigation Trial (2023). In 2021, roses were irrigated approximately once every 3 days by setting the adjusted irrigation at 90% ET_0 for establishment. The experiment was initiated on 12 May 2022, and plants were randomly assigned to one of the three treatments after receiving 43.2 liters of irrigation water. Cumulative ET_0 and precipitation were used to calculate the irrigation thresholds

for controlling the three irrigation treatments (high, medium, and low) following the method described by Costello et al. (2000). In brief, the adjusted irrigation of the high, medium, and low treatments was calculated based on 80%, 50%, and 20% of ET_0 , respectively. For instance, if the ET_0 for the day was 0.8 cm, the adjusted daily irrigation for high, medium, and low treatments were 0.64, 0.40, and 0.16 cm, respectively. A targeted root zone for each plant was defined as a cylinder 100 cm in diameter and 50 cm deep. Irrigation was applied when the cumulative adjusted irrigation minus cumulative precipitation for each treatment was equal to or greater than 50% of plant available water in the target root zone, which was 4.6 cm within the top 50 cm of the Millville silt loam at the UAES's Greenville Research Farm. We assumed runoff and deep percolation were zero, and the amount of water equal to 50% of plant available water within the target root zone (43.2 liters of water) was applied to refill the depleted plant available water in the target root zone with each irrigation. The plants were maintained under the deficit irrigation treatments until the experiment ended on 30 Sep 2022. A soil moisture sensor (TDT[®]; Acclima, Meridian, ID) was installed at the bottom of the targeted root zone (50 cm deep) of a 'Radbeauty' rose randomly selected from each treatment to monitor and record volumetric water contents and wetting fronts.

Data Collection

Visual quality score. Leaf wilting was graded using a scale of 1 to 5 (1 = complete wilting with > 65% of leaves wilted; 2 = severe wilting with 35% to 65% of leaves wilted; 3 = moderate wilting, up to 35% of leaves wilted; 4 = minor wilting, less than 10% of leaves wilted; 5 = plant was fully turgid) (Zollinger et al. 2006). Foliage appearance, flower abundance, and overall appearance were recorded monthly using a

scale of 1 to 5, following the methods of Reid et al. (2019). Foliage appearance was determined by the percentage of leaves that were visibly damaged (i.e., leaf edge burn, curling, necrosis, etc.), where 1 = poor quality with 50% of leaves showing visible damage; 2 = unacceptable quality with 25% to 50% of leaves showing visible damage; 3 = acceptable quality with 10% to 25% of leaves showing visible damage; 4 = good quality with less than 10% of leaves showing visible damage; and 5 = excellent quality with less than 1% of leaves showing visible damage. Flower abundance was rated based on the percentage of the canopy covered in open blooms, where 1 = up to 20% of plant in bloom; 2 = 21% to 40% of plant in bloom; 3 = 41% to 60% of plant in bloom; 4 = 61% to 80% of plant in bloom; and 5 = 81% to 100% of plant in bloom. Overall appearance was rated based on how the plant performed in the landscape, where 1 = plant close to death; 2 = unacceptable performance; 3 = acceptable performance; 4 = good performance but not quite optimal; 5 = excellent performance with eye-catching, uniform, and healthy appearance.

Plant growth and leaf width. Plant height was measured monthly from the ground to the tallest leaf, and two widths were measured monthly in perpendicular angles along the row (in a north-south direction) and across the row (in an east-west direction), respectively, using the outermost leaves in each direction. Plant growth indices were calculated as $[(\text{height} + (\text{length} + \text{width})/2)/2]$ (Irmak et al. 2004). The relative plant growth index of each month was calculated using the ratio of the monthly plant growth index to the initial plant growth index (Reid et al. 2019), and the overall relative plant growth index was calculated by averaging the monthly relative plant growth index. To determine leaf width at the termination of the experiment, three mature leaves were

sampled from the second to the fifth node counting downward from the tip of the main shoot of four randomly selected plants of each cultivar within each treatment. Plant leaves and stems were then harvested and oven-dried at 80 °C for one month to obtain the dry weights of leaves and stems.

Physiological responses. Gas exchange parameters, including leaf temperature, leaf-to-air vapor pressure deficit (VPD), stomatal conductance, and transpiration rate, were recorded using a LI-600 porometer (LI-COR Biosciences, Lincoln, NE) using the auto mode setup on 6 Jun, 11 Jul, 23 Aug, and 20 Sep 2022. The parameters were recorded on the terminal leaflet of one healthy, fully expanded, full sun compound leaf at the outer canopy of 8 replications in each treatment at midday between 1100 HR to 1230 HR. In addition to the midday measurements, the parameters were recorded on roses at the high and low irrigation treatment in the late afternoon from 1600 HR to 1730 HR, when air temperature reached the maximum on 11 Jul. Gas exchange parameters were recorded on roses in the three treatments in the late afternoon during the same period on 23 Aug and 20 Sep 2022. Air temperature recorded by the onsite weather station was used to calculate leaf-air temperature difference via the deviation between ambient air and leaf temperature.

Stomatal density. Four plants were randomly selected from each cultivar per treatment and a mature and fully expanded leaf at the outer canopy was randomly selected on each plant on 6 Sep 2022. Wet dental putty (Affinis light body; Coltene, Cuyahoga Falls, OH) was applied to the abaxial surface of each leaf and allowed to air dry for 1 hour. Clear nail polish (Sally Hansen, New York, NY) was applied over the putty to obtain a surface impression of the leaf abaxial. Ten fields of view (0.12 mm²) at

×400 magnification were photographed from each impression using a transmitted/reflected light microscope (BX51 BF/DF; Olympus Corporation, Tokyo, Japan) with a digital camera (DP 74; Olympus Corporation) and a differential interference contrast prism condenser (U-DPA40; Olympus Corporation) for the UPlanFL N 40× microscope objective (Olympus Corporation). The image of each field of view was acquired and processed using cellSens Dimension (Olympus Corporation).

Prior to the analyses, each image was resized to 1831×1144 pixel, and 80 images were randomly selected and uploaded to the Stomata Counter (Fetter et al. 2019) to obtain the value of threshold probability (0.881 in our research) with the lowest error count, at which the Pearson correlation coefficient between human and automatic stomata counts was 0.81 ($P < 0.0001$) (data not shown). Thereafter, stomata on all images were automatically counted using the Stomatal Counter with a threshold probability at 0.881.

Data analysis. The experiment was designed in a completely randomized design with three deficit irrigation treatments and 8 replications in each treatment of each cultivar. An analysis of variance (ANOVA) procedure was used to test the effects of the irrigation treatment on all measured parameters and the effects of ambient temperature on the stomatal conductance of rose cultivars. Means separation among treatments was adjusted using Tukey–Kramer method or Student’s t test at $\alpha = 0.05$. Means separation was not conducted among cultivars due to difference in growth habit of plants. All statistical analyses were conducted using the PROC MIXED procedure in SAS Studio 3.8 (SAS Institute, Cary, NC) with a significance level specified at 0.05.

Results

Weather and soil water content data. The cumulative ET_0 in June, July, and August were higher than in May and September (Table 2). Monthly cumulative precipitation decreased from May to July, and July was the driest month in this trial with a cumulative rainfall of 0.1 cm (Table 2). Because of heavy rains, August had the highest cumulative precipitation at 7.3 cm. Average air temperature increased from May to July, and the air temperatures in July and August were higher than those in other months. The highest ambient temperature during the experiment was recorded at 37.1°C in July, whereas daily light integrals in June and July were greater than 50 mol·m⁻²·d⁻¹. Average vapor pressure, which is related to air humidity, increased from May to August, and August had the highest average vapor pressure at 1.4 kPa. During the trial (Fig. 1), the deficit irrigation treatments resulted in eight-, four-, and one-irrigation events at the high, medium, and low treatment, respectively. The total volume of irrigation water applied to each rose was 345.6, 172.8, and 43.2 liters at the high, medium, and low treatment, respectively. A rapid increase in soil moisture content was observed after irrigation was triggered, indicating the wetting front had passed the 50 cm depth in the soil profile (Fig. 1).

Visual quality

The proportion of leaves visibly wilted. For all three treatments, ‘ChewPatout’ rose had minor wilting with less than 10% of leaves wilted, and plants at the high and medium treatments had a lower proportion of wilted leaves than those at the low treatment in July (Fig. 2A). The proportion of wilted leaves was less than 10% in ‘Meibenbino’ rose at the high and medium treatments, except for those recorded in June

when 35% of the leaves were wilted (Fig. 2B). ‘Meibenbino’ rose at the low treatment exhibited a higher number of wilted leaves from August to September than those at the high and medium treatments. Minor foliage wilting was discovered in ‘MEIRIFTDAY’ rose at all deficit irrigation treatments from May to July but decreased irrigation frequency from the high to low treatment resulted in an increased number of wilted leaves in August, with 35% of leaves wilted at the low treatment (Fig. 2C). The proportion of wilted leaves was less than 10% in ‘Overedclimb’ rose in the high treatment, but the medium and low treatments resulted in 35% of wilted leaves in July (Fig. 2D). Irrigation treatments did not affect the proportion of wilted leaves in ‘Radbeauty’ rose in May and June (Fig. 2E). However, the proportion of visibly wilted leaves in ‘Radbeauty’ rose increased in July, August, and September when the irrigation frequency declined.

Foliage appearance. Reduced irrigation frequency did not increase the proportion of damaged leaves in ‘ChewPatout’ rose, resulting in foliage appearances equal to or higher than acceptable quality (Fig. 2F). ‘Meibenbino’ roses at the high and medium treatments had a lower proportion of damaged leaves than those at the low treatment in July ($P = 0.09$), August, and late September (Fig. 2G). More than 25% of leaves in ‘Meibenbino’ rose under the low treatment were impaired by drought in August, leading to unacceptable foliage appearance. Additionally, Increased irrigation frequency decreased the percentage of damaged leaves in ‘MEIRIFTDAY’ rose, and plants irrigated at the high treatment had better foliage appearance than those at the medium and low treatments in July, August, and late September (Fig. 2H). The low treatment also impaired the foliage appearance of ‘Overedclimb’ rose in August and late September,

with leaf damage occurring in 25% of the canopy (Fig. 2I). Under the three irrigation treatments, ‘Radbeauty’ roses were able to maintain acceptable foliage appearance throughout the trial, but increased irrigation frequency enhanced foliage appearance in September (Fig. 2J).

Flower abundance and overall appearance. Rose cultivars in this study had two bloom peaks (Fig. 3). Bloom peaks of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, and ‘Overedclimb’ roses occurred in July and September (Figs. 3A-D), whereas ‘Radbeauty’ roses had bloom peaks in July and August (Fig. 3E). Deficit irrigation treatments did not affect the flower abundance of all cultivars, except ‘Meibenbino’ rose, which had a higher percentage of canopy covered in blooms under the high and medium treatments than plants under the low treatment in August and September (Fig. 3B). The overall appearance of ‘ChewPatout’ rose did not decline at reduced irrigation frequency and exhibited acceptable or higher overall quality during the trial with average scores equal to or greater than 3 (Fig. 3F). ‘Meibenbino’ plants receiving the high and medium treatments had better overall appearances than those at the low treatment from August to September (Fig. 3G). Increased irrigation frequency improved the overall appearance of ‘MEIRIFTDAY’ rose in early August and late September (Fig. 3H). ‘MEIRIFTDAY’ roses at medium and low treatments had unacceptable overall appearances with average scores at 1.9 and 1.8, respectively, in early August. ‘Overedclimb’ and ‘Radbeauty’ roses showed acceptable or higher overall appearance throughout the trial regardless of irrigation treatment (Figs. 3I and 3J).

Plant growth responses

Relative plant growth index and leaf width. The relative plant growth indices of ‘Meibenbino’ roses ($P = 0.02$) and ‘MEIRIFTDAY’ ($P = 0.09$) decreased as irrigation frequency declined, indicating that these plants will have smaller sizes under reduced irrigation (Table 3). However, the relative plant growth indices of ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses were not affected by reduced irrigation frequency. ‘Meibenbino’ rose at the high and medium treatments had significantly higher relative plant growth indices compared with those at the low treatment (Table 3). Similarly, the relative plant growth index of ‘MEIRIFTDAY’ rose significantly decreased from 1.65 to 1.55 when irrigation frequency was reduced from the high to low treatment (Table 3). ‘Meibenbino’, ‘MEIRIFTDAY’, and ‘Radbeauty’ roses had narrower leaf widths as irrigation frequency decreased from the high to low treatment (Table 3). ‘Meibenbino’ rose had a leaf width reduction of 0.45 cm, ‘MEIRIFTDAY’ rose had a 0.69 cm reduction, and ‘Radbeauty’ rose had a 0.33 cm reduction under the low treatment compared with the high treatment (Table 3).

Dry weights of leaves and stems. Leaf dry weights were affected by reduced irrigation frequency in ‘Meibenbino’ and ‘MEIRIFTDAY’ roses, whereas ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses were not affected (Table 3). ‘Meibenbino’ and ‘MEIRIFTDAY’ roses responded similarly to reduced irrigation by decreasing their leaf dry weights by 36% to 37% at the low treatment than at the high treatment. ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses maintained stem dry weights under reduced irrigation frequency, whereas ‘Meibenbino’ and ‘MEIRIFTDAY’ roses reduced stem dry weights as irrigation frequency declined. ‘Meibenbino’ rose had a 10% decrease in stem dry weight as irrigation frequency decreased from the high to low treatment,

whereas ‘MEIRIFTDAY’ rose had 6% less stem dry weight at the low treatment than at the high treatment.

Physiological responses.

Stomatal conductance. Overall, stomatal conductance generally decreased as irrigation frequency decreased (Fig. 4). In June, increased irrigation frequency did not increase stomatal conductance for all cultivars, except for ‘Radbeauty’ rose. In July, although trends of decreased stomatal conductance were observed at midday when irrigation frequency was reduced, they were not significantly different except for ‘ChewPatout’ rose. However, all roses showed decreased stomatal conductance under reduced irrigation frequency in the late afternoon. In August, reduced irrigation frequency did not affect stomatal conductance of all cultivars at midday but reduce in the afternoon for all cultivars, except for ‘Overedclimb’. In September, reduced irrigation frequency did not affect midday or afternoon stomatal conductance for any cultivar. Additionally, a lower stomatal conductance was observed when air temperature became higher from midday to late afternoon in July and August (all $P < 0.05$; data not shown). This decreased trend was most significant for the roses under the low treatment, except for ‘Meibenbino’, which exhibited similar stomatal conductance at midday and late afternoon in August and September (both $P > 0.05$; data not shown).

Leaf temperature, gas exchange parameters, and stomatal density. The impact of reducing irrigation frequency on leaf temperature, leaf-air temperature difference, VPD, and transpiration rates was most pronounced in the afternoon in July and August (Table 4). In July, when the irrigation frequency was decreased from the high to low treatment, the leaf temperature of ‘ChewPatout’ and ‘Radbeauty’ roses increased by 2.2

and 2.7 °C, respectively, in the afternoon, resulting in greater leaf-air temperature differences and VPD. However, the leaf temperature, leaf-air temperature difference, and VPD of ‘Meibenbino’, ‘MEIRIFTDAY’, and ‘Overedclimb’ roses did not increase in response to decreased irrigation frequency in July. All cultivars showed reduced transpiration rates from the high to low treatment, except for ‘Meibenbino’ rose in the afternoon in July. In August, ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, and ‘Radbeauty’ roses increased their leaf temperature by 2.9, 3.0, 2.0, and 2.4 °C, respectively, under decreased irrigation frequency. Additionally, the leaf-air temperature difference and VPD of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, and ‘Radbeauty’ roses increased from the high to low treatment. Reduced irrigation frequency led to decreased transpiration rates in ‘ChewPatout’, ‘Meibenbino’, and ‘Overedclimb’ roses. In August, decreased irrigation frequency decreased the transpiration rates of ‘MEIRIFTDAY’ and ‘Radbeauty’ roses, although the changes were not statistically significant.

The stomatal density of ‘Meibenbino’ ($P = 0.07$) and ‘Overedclimb’ roses ($P = 0.09$) increased as the irrigation frequency increased from the low to high treatment (Table 5). However, ‘ChewPatout’, ‘MEIRIFTDAY’, and ‘Radbeauty’ did not show an increase in stomatal density as irrigation frequency increased. At the high and medium treatments, the abaxial leaf surface of ‘Meibenbino’ had 94 and 106 stomata per mm², respectively, whereas those at the low treatment had 92 stomata per mm² (Fig. 5). ‘Overedclimb’ rose at the low treatment had 67 stomata per mm², but those plants under the high and medium treatments had 77 and 82 stomata per mm², respectively, on their abaxial surfaces (Fig. 5). Compared with other cultivars, ‘Overedclimb’ rose had a

significantly lower stomatal density, whereas ‘MEIRIFTDAY’ and ‘Radbeauty’ had the highest stomatal densities ($P < 0.05$; data not shown).

Discussion

Low vapor pressure and high air temperature during the summer in Utah resulted in higher ET_O rates than other months (Table 2) (Mee et al. 2003). Solar radiation in the summer in Utah can exacerbate water loss through the transpiration pathway. Rainfall amounts are typically very low in the area during the growing season (Table 2). For instance, Zollinger et al. (2006) reported that heavy precipitation was very uncommon at the Greenville Research Farm during the summer months. Historic cumulative precipitation (1960 - 2022) at the experiment site from June through September is 10.9 cm, but the cumulative ET_O is 62.2 cm (Utah Climate Center, 2023). In order to maintain growth and visual aesthetic quality of landscape plants, the gap between ET_O and precipitation is supplied by irrigation water in residential landscapes (Mee et al. 2003).

As irrigation became more frequent from the low to high treatment in this study, plant available water in the root zone was replenished more often with more wetting fronts passing the soil moisture sensors in the high treatment than the low treatment (Fig.1A). A wetting front is an interface between the soil in the initial condition and the soil wetted by irrigation or infiltration (Stirzaker 2003). Wetting fronts form after irrigation is triggered, leading to an increase in soil moisture content after passing through a soil profile (Stirzaker 2003). If wetting fronts were not identified by our soil moisture sensors, which were at the bottom of the targeted root zone, the targeted root zone may have only been partially wetted (Blonquist et al. 2006). Except for the monsoon

rainfalls in August and September, wetting fronts were not detected after the rain events in this study, indicating that the precipitation was inadequate to wet the entire soil profile of the target root zone. On the other hand, soil water depleted by transpiration from June through July could be replenished by the heavy rainfalls of the monsoon season.

More frequent irrigation improved foliage quality by reducing the number of wilted leaves and leaf damage in this study (Fig. 2). However, the proportion of visibly wilted and damaged leaves varied among rose cultivars when irrigation frequency was reduced, indicating roses tested in this research may have differing drought tolerance (Fig. 2). The effects of reduced irrigation frequency on increased leaf wilting and impaired foliage appearance were most significant in July and August. This may result from insufficient plant available water and a hot and dry environment that caused the roses to lose turgor and damage to leaves. Therefore, some roses may require more irrigation water to sustain acceptable foliage visual quality (Table 2). Zollinger et al. (2006) found that the hot and dry weather in summer and reduced irrigation could exacerbate canopy wilting and leaf burn of eastern purple coneflower [*Echinacea purpurea* (L.) Moench] and blanketflower (*Gaillardia aristata* Pursh). After increasing irrigation frequency, visual quality, especially for drought-sensitive species, was significantly improved (Zollinger et al. 2006). For instance, the foliage quality of mat rush (*Lomandra confertifolia* subsp. *rubiginosa* ‘Seascape’), a drought-sensitive species, could be improved by increasing irrigation frequency, but tangerine stalked bulbine (*Bulbine frutescens* ‘Tiny Tangerine’), a xeric species, maintained acceptable quality regardless of irrigation frequency (Reid and Oki 2016). This may relate to the fact that drought-sensitive species lack mechanisms to limit water loss or promote water uptake.

Therefore, they rely on irrigation to maintain plant growth and acceptable aesthetic quality in highly evaporative environments (Kjelgren et al. 2009).

In addition to foliage quality, a reduction in flower formation was one of the main contributors impairing the overall visual appearance of flowering plants (Toscano et al. 2019). Reduced flower abundance on ‘Meibenbino’ roses, for example, negatively affected its overall appearance in this study (Fig. 3B). The quality of four landscape roses, including ‘RADrazz’, ‘Belinda’s Dream’, ‘Old Blush’, and ‘Marie Pavie’ also declined when flower numbers decreased by 37% to 60% after irrigation frequency was reduced from three times per week to once per week (Cai et al. 2012). The flower abundance in a variety of taxa was also shown to decrease when the amount of irrigation water declined from 100% ET_0 to 25% ET_0 (Rafi et al. 2019). Drought-resilient ornamental plants, such as ivy leaf geranium [*Pelargonium peltatum* (L.) L'Hér. ex Aiton], sustained their flower numbers under deficit irrigation, but drought-sensitive species such as treasure-flower [*Gazania rigens* (L.) Gaertn.] had a reduction in the size and number of flowers (Rydlová and Püschel 2020). In contrast, reducing irrigation from 80% ET_0 to 20% ET_0 did not reduce the number of flowers in a study of ten different roses (Reid et al. 2019), indicating that the roses in this study may tolerate reduced irrigation rates. However, ‘Meibenbino’ roses showed decreased flower numbers under deficit irrigation in this study, indicating that ‘Meibenbino’ rose may not be able to tolerate water stresses (Fig. 3B).

Overall appearance is also an important parameter that has been used to assess the impact of drought stress on the aesthetic quality of landscape plants (Rafi et al. 2019; Reid and Oki 2008). For instance, under deficit irrigation of 25% ET_0 , ‘Imagination’

South American mock vervain [*Glandularia tenuisecta* (Briq.) Small ‘Imagination’], a low water-use landscape plant, maintained an acceptable and better overall aesthetic quality than ‘Tempo White’ busy lizzy (*Impatiens walleriana* Hook. f. ‘Tempo White’), a high water-use plant (Henson et al. 2006). Because ‘Meibebino’ and ‘MEIRIFTDAY’ roses exhibited unacceptable overall appearances when irrigation frequency was decreased from high to low in this study, these cultivars may be considered drought-sensitive and require higher amounts of irrigation to maintain acceptable overall quality during the growing season.

Leaf expansion and stem elongation are the most sensitive types of expansive growth to water stress (Hsiao 1990). The expansive growth of new stems and leaves in roses have been the most susceptible to water stress because reductions in cell turgor under drought stress limited shoot elongation and leaf expansion (Jones 1992; Raviv and Blom 2001). Decreases in the water potential gradient between growing substrate and roots limited the stem elongation rate of ‘Kardinal’ roses (Oki and Lieth 2004). Small-sized plants under water stress have also been reported on numerous ornamental plants (Cameron et al. 2008; Jafari et al. 2019). The relative plant growth index (calculated the same way as in this study) of ‘Korbin’ rose was reduced from 3.1 to 2.4 when the irrigation rates were reduced from 80% ET_0 to 20% ET_0 (Reid and Oki 2016). Decreased relative plant growth indices were also observed on rose ‘KORfloci01’ and ‘KORsixkono’ under reduced irrigation rates (Reid et al. 2019). Because drought-sensitive plants can’t maintain turgor under water stress, they may exhibit more plant growth reduction than drought-tolerant plants (Cameron et al. 2006). For instance, a decrease in soil water content of 50% reduced the plant height of ‘Deep Rose’ busy lizzy

(*Impatiens walleriana* ‘Deep Rose’) by 7%, but the plant height of drought-tolerant ivy leaf geranium was not affected by the decreased soil moisture content (Chyliński et al. 2007). In this study, ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses were able to maintain their growth under reduced irrigation frequency, indicating that they may be more drought-tolerant than ‘Meibenbino’ and ‘MEIRIFTDAY’ roses.

Decreased leaf and stem dry weights of ‘Meibenbino’ and ‘MEIRIFTDAY’ roses under deficit irrigation may result from limited photosynthesis rates because partial stomatal closure can limit the amount of carbon dioxide available to the chloroplast (Taiz et al. 2015). The leaf dry weights reduced from the high to low treatment in this study, which may also result from the defoliation of ‘Meibenbino’ and ‘MEIRIFTDAY’ roses, leading to the reduced leaf surface area, transpiration and light interception rates under drought stress (Kjelgren et al. 2009). Zollinger et al. (2006) reported similar results for purple coneflower and ‘Alaska’ shasta daisy [*Leucanthemum ×superbum* (J.W. Ingram) Berg. ex Kent, ‘Alaska’], which adapted to deficit irrigation conditions by drastically eliminating leaf area. Although ‘Meibenbino’ and ‘MEIRIFTDAY’ roses can defoliate to avoid drought stress, defoliation is not a favorable drought-tolerant trait because of the negative effects on visual quality and whole-plant photosynthesis efficiency (Bañon et al. 2006). In contrast, ‘ChewPatout’, ‘Overedclimb’, and ‘Radbeauty’ roses sustained their leaves under reduced irrigation frequencies and, therefore, may be more suitable for low water-use landscapes.

According to our plant growth and visual quality data, rose cultivars with larger canopy size and leaf area, such as ‘ChewPatout’ and ‘Overedclimb’ roses, were more tolerant of reduced irrigation frequencies than those with smaller canopies, including

'Meibebino' and 'MEIRIFTDAY' roses. However, previous studies considered a species with a larger leaf area to be less drought-tolerant because they often require higher amounts of supplemental water to sustain transpiration (Bheemanahalli et al. 2021). For instance, Sun et al. (2012) found that the irrigation requirements of landscape vegetation to maintain turgor were positively correlated with leaf area. Despite the smaller canopy size, 'Meibebino' and 'MEIRIFTDAY' roses exhibited reduced plant growth and unacceptable aesthetic qualities. The size of their root system may also contribute to their drought sensitivity as Schenk and Jackson (2002) found that a woody plant's root system volume is positively correlated with its above-ground size under drought conditions. The small aboveground size of 'Meibebino' and 'MEIRIFTDAY' roses may suggest that these roses might have smaller root system that were disadvantageous for tolerating prolonged drought.

Partial stomatal closure may conserve transpirational water loss and protect plant tissues from further dehydration (Martínez-Vilalta and Garcia-Forner 2017) since stomatal conductance is correlated to plant water status (Zhang et al. 2013). Chapman and Augé (1994) reported a positive correlation between stomatal conductance and leaf water potential in swamp sunflower (*Helianthus angustifolius* L.), beebalm (*Monarda didyma*), and orange coneflower (*Rudbeckia fulgida* Aiton var. *sullivantii*). Our observation of roses modifying stomatal conductance under deficit irrigation and high ambient temperature suggest that partial stomatal closure may be one of the strategies that roses utilize to cope with drought (Table 4; Fig. 4). Modifying stomatal conductance to regulate transpiration water loss is a favorable drought-resistance mechanism compared with defoliation, which significantly impairs visual aesthetics by eliminating

leaf area (Zollinger et al. 2006). Additionally, partial stomatal closure may allow plants to have less negative internal water potential in the xylem, helping avoid cavitation and maintain plant growth under prolonged drought (West et al. 2007). Although roses may close their stomata when experiencing water stress, the stomata of drought-tolerant roses have been shown to be more sensitive to environmental changes, resulting in a greater reduction in stomatal conductance when water availability became limited (Cai et al. 2012). Increased air temperature from midday to late afternoon also created a greater water vapor flux in transpiration, exacerbating water stress (Mrad et al. 2019). All rose cultivars in this study modified their stomatal conductance in response to increased air temperatures, except for 'Meibenbino' rose which did not exhibit significant reductions in stomatal conductance that may have led to a reduction in growth and unacceptable visual quality (Fig. 4).

Partial stomatal closure under reduced irrigation limited the transpirational cooling, leaf temperatures increased as transpiration rates declined in this study (Table 4) (Nobel 2020; Tuzet et al. 2003). Heat stress resulting from increased leaf temperature also led to increasing differences in leaf-air temperatures and VPD, which could exacerbate leaf wilting (Table 4; Devi et al. 2015). A similar relationship was reported by Nelson and Bugbee (2015) in which drought-stressed plants, with stomatal conductance of $0.10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, had higher leaf temperatures than well-irrigated plants that had a stomatal conductance of $0.50 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In this study, the narrower leaf widths of 'Meibenbino', 'MEIRIFTDAY', and 'Radbeauty' roses under reduced irrigation may indicate that leaf size was reduced to acclimate to drought conditions. Reduced cell expansion also limits leaf expansion, resulting in small leaves under water stress (Taiz et

al. 2015). When water is insufficient, leaf energy is primarily balanced using sensible heat loss (Bowen 1926). Smaller leaves that have a lower boundary layer resistance to sensible heat loss may also promote heat convection and conduction to sustain leaf temperature close to air temperature (Leigh et al. 2017). Previous research showed that ‘Torrey’ hybrid buffaloberry (*Shepherdia ×utahensis* ‘Torrey’) leaves were 51% smaller when substrate volumetric water content decreased by $0.35 \text{ m}^3 \cdot \text{m}^{-3}$ (Chen et al. 2022). In this study, ‘Meibenbino’, ‘MEIRIFTDAY’, and ‘Radbeauty’ roses were the cultivars with the highest leaf-air temperature differences at the low treatment (Table 4). Reduced leaf size may have helped these plants acclimate to heat stress when transpirational cooling was limited. The large leaf size of ‘Radbeauty’ rose may have resulted in less effective heat dissipation through sensible heat loss (Table 4). However, under the hot and arid conditions of this experiment, ‘Radbeauty’ rose was still able to maintain plant growth (Table 3) but lost aesthetic quality because of an increased number of visibly wilted and damaged leaves (Fig. 2E).

Nelson and Bugbee (2015) concluded that leaf-air temperature differences were within $2 \text{ }^\circ\text{C}$ of ambient temperature if plants did not experience water stress. Although only ‘MEIRIFTDAY’ and ‘Radbeauty’ roses under the low treatment showed leaf-air temperature differences greater than $2 \text{ }^\circ\text{C}$ in July (Table 4), the leaf-air temperature differences of all rose cultivars were greater than $2 \text{ }^\circ\text{C}$ at the medium and low treatments in August. The increases in leaf-air temperature differences suggest that roses may suffer continuous water stress from July through August that worsen their water status. When experiencing water stress, roses adapted to hot and arid environments may exhibit fewer leaf-air temperature differences (Bheemanahalli et al. 2021). Rafi et al. (2019) reported

that high mallow, a high water-use species, had a leaf-air temperature difference at 3.52 °C, but drought-resilient hollyhock had a leaf-air temperature difference of -3.08 °C. Similar results were found in this study for ‘Meibenbino’ and ‘MEIRIFTDAY’ roses, which had reduced growth, unacceptable overall appearance, and greater leaf-air temperature differences under reduced irrigation than drought-tolerant ‘ChewPatout’ and ‘Overedclimb’ roses. Compared with ‘ChewPatout’ and ‘Overedclimb’ roses, ‘Radbeauty’ rose had a greater leaf-air temperature difference, which may have resulted from its large-sized leaves. The heat stress could lead to an increase in visibly wilted leaves by ‘Radbeauty’ in July and August, even though no reduction in growth was observed.

Apart from the stomatal closure, roses may have the capacity to modify stomatal density on the leaf in response to decreased soil water availability (Table 5; Fig. 5). Because low stomatal density may conserve more water and increase tolerance to drought stress by limiting water loss (Caine et al. 2019), plants may decrease leaf stomatal density when experiencing drought stress (Chen 2022). This study showed that ‘Meibenbino’ and ‘Overedclimb’ roses reduced stomatal density as irrigation frequency was decreased, indicating that their reduction in stomatal conductance under deficit irrigation may have resulted from a reduction in the number of stomata on the leaves. The low stomatal density on ‘Overedclimb’ rose may be an advantageous characteristic for conserving water under drought stress. This may be the reason that ‘Overedclimb’ rose had fewer wilted leaves during the trial compared with ‘Radbeauty’, although both had large-sized leaves (Table 3). The findings of this research indicated that rose cultivars responded

differently when irrigation frequency decreased, but they also were able to modify their morphology and physiology to tolerate drought stress (Table 6).

Conclusions

Reducing irrigation frequency can decrease the visual quality and restrict plant growth rates and photosynthesis efficiency of roses. Five rose cultivars tested in this study defoliated and closed their stomata to reduce the surface area and transpirational water vapor flux under drought stress. Additionally, roses changed their stomatal density to limit stomatal conductance. Although the reduction in leaf size may mitigate heat stress resulting from limited transpirational cooling, decreased irrigation frequency led to higher leaf temperature and increased leaf-air temperature differences. Increased air temperature also exacerbated water stress in roses receiving the lowest irrigation treatment, and stomatal conductance declined under high temperatures.

In the hot and arid conditions of this experiment, ‘ChewPatout’ and ‘Overedclimb’ roses, which had smaller leaf sizes and lower stomatal densities, respectively, were able to maintain lower leaf temperatures and avoid reductions in plant growth and aesthetic quality. ‘ChewPatout’ and ‘Overedclimb’ roses may be recommended for low-water-use landscaping because of their capacity to tolerate water stress. ‘Meibenbino’ and ‘MEIRIFTDAY’ roses may not be suitable for low water-use landscapes since they lacked the capacity to modify stomatal conductance in response to changing environment conditions. Additionally, their small canopy sizes may have resulted in shallow root systems, which are disadvantageous for maintaining plant turgor at deficit irrigation. Under reduced irrigation, ‘Radbeauty’ roses maintained their growth,

but their large leaf size could have resulted in more visibly wilted leaves because of heat stress.

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Table 4-1. Characteristics of soils at the experimental plot.

pH	Electrical Conductivity	P	K	Zn	Fe	Cu	Mn
	dS·m ⁻¹	mg·kg ⁻¹					
7.87	0.75	17.77	149.67	2.39	6.20	0.74	7.96

Table 4-2. Cumulative (cum.) reference evapotranspiration rate (ET_O) and precipitation, and maximum (max.) and average (avg.) air temperature, daily light integral (DLI), and avg. vapor pressure during 2022 growing season.

Time ⁱ	Cum. ET _O (cm)	Cum. precipitation (cm)	Avg. air temperature (°C)	Max. air temperature (°C)	DLI (mol·m ⁻² ·d ⁻¹)	Avg. vapor pressure (kPa)
12 - 31 May	8.4	3.8	12.2	29.8	47.4	0.7
1 - 30 Jun	16.8	1.8	18.2	34.2	55.5	0.9
1 - 31 Jul	20.2	0.1	25.0	37.1	58.7	1.1
1 - 31 Aug	14.4	7.3	22.3	34.2	45.3	1.4
1 - 30 Sep	11.4	4.5	18.4	35.8	40.2	1.0

ⁱExperiment was initiated on 12 May and ended on 30 Sep 2022.

Table 4-3. Overall relative plant growth indices, leaf width, the dry weights of leaves and stems of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET_O)], medium (50% ET_O), and low (20% ET_O) treatments at the termination of the experiment.

Taxa	Treatment	Overall relative plant growth index ⁱ	Leaf width	Leaf dry weight	Stem dry weight
			cm	(g)	(g)
‘ChewPatout’	High	2.09 a ⁱⁱ	1.78 a	596 a	1227 a
	Medium	2.07 a	1.78 a	552 a	1156 a
	Low	2.23 a	1.67 a	549 a	1201 a
‘Meibenbino’	High	1.58 a	2.08 a	286 a	919 a
	Medium	1.58 a	2.38 a	220 ab	852 ab
	Low	1.48 b	1.63 b	181 b	826 b
‘MEIRIFTDAY’	High	1.65 a	1.73 a	205 a	845 a
	Medium	1.61 ab	1.45 a	150 ab	812 ab
	Low	1.55 b	1.04 b	131 b	796 b
‘Overedclimb’	High	2.37 a	2.91 a	619 a	1340 a
	Medium	2.21 a	3.19 a	460 a	1188 a
	Low	2.16 a	2.98 a	453 a	1086 a
‘Radbeauty’	High	2.09 a	3.31 a	678 a	1255 a
	Medium	1.96 a	2.78 b	618 a	1199 a
	Low	2.04 a	2.98 b	623 a	1214 a

ⁱ The overall relative plant growth index was calculated by averaging monthly relative plant growth indices, which were determined by the ratio of the monthly plant growth index to the initial plant growth index (Reid et al. 2019), and the plant growth indices were calculated using the equation: $[(\text{height} + (\text{length} + \text{width})/2)/2]$ (Irmak et al. 2004).

ⁱⁱ Means with same lowercase letters within a rose cultivar and dependent variable are not significantly different among treatments according to the Tukey–Kramer method with a significance level specified at $\alpha \leq 0.05$.

Table 4-4. Leaf temperature, leaf-air temperature difference, vapor pressure deficit (VPD), and transpiration rate of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET_O)], medium (50% ET_O), and low (20% ET_O) treatments from 1600 HR to 1730 HR on 11 Jul and 23 Aug 2022.

Taxa	Treatment	Leaf temperature (°C)		Leaf-air temperature difference (°C)		Leaf-air VPD (kPa)		Transpiration rate (mmole·m ⁻² ·s ⁻¹)	
		July	August	July	August	July	August	July	August
‘ChewPatout’	High	31.2 b ⁱ	31.8 b	-0.2 b	1.0 b	3.2 b	3.1 b	16.5 a	15.7 a
	Medium	ⁱⁱ	33.9 ab		3.1 ab		3.8 a		14.8 a
	Low	33.4 a	34.7 a	2.0 a	3.8 a	4.0 a	4.1 a	11.6 b	11.0 b
‘Meibenbino’	High	31.5 a	32.7 b	0.6 a	1.9 b	3.3 a	3.4 b	13.6 a	13.6 a
	Medium		34.2 ab		3.4 ab		3.9 ab		12.3 ab
	Low	32.0 a	35.7 a	1.0 a	4.8 a	3.4 a	4.5 a	11.8 a	10.1 b
‘MEIRIFTDAY’	High	33.3 a	33.1 b	2.3 a	2.3 b	3.8 a	3.5 b	15.7 a	15.3 a
	Medium		34.2 ab		3.4 ab		3.9 ab		13.7 a
	Low	33.7 a	35.1 a	2.8 a	4.7 a	4.0 a	4.1 a	10.5 b	12.8 a
‘Overedclimb’	High	31.6 a	33.6 a	0.2 a	2.7 a	3.5 a	3.8 a	11.1 a	12.6 a
	Medium		33.8 a		3.0 a		3.9 a		9.4 b
	Low	32.9 a	34.3 a	1.5 a	3.7 a	3.9 a	4.0 a	8.7 b	10.7 ab
‘Radbeauty’	High	32.0 b	33.2 b	0.9 b	2.3 b	3.6 b	3.6 b	12.1 a	13.2 a
	Medium		35.2 ab		4.4 ab		4.2 ab		12.9 a
	Low	34.7 a	35.6 a	3.7 a	4.9 a	4.5 a	4.4 a	7.7 b	10.8 a

ⁱ Means with same lowercase letters within a rose cultivar, dependent variable and month are not significantly different among treatments according to the Tukey–Kramer method with a significance level specified at $\alpha \leq 0.05$.

ⁱⁱ Gas exchange parameters were recorded on plant at the high and low treatments in the afternoon in July.

Table 4-5. Stomatal density of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses with high [80% reference evapotranspiration (ET_O)], medium (50% ET_O), and low (20% ET_O) treatments on 6 Sep 2022.

Taxa	Treatment	Stomatal density (stomata·mm ⁻²)
‘ChewPatout’	High	107 a ⁱ
	Medium	98 a
	Low	108 a
‘Meibenbino’	High	94 ab
	Medium	106 a
	Low	92 b
‘MEIRIFTDAY’	High	110 a
	Medium	121 a
	Low	112 a
‘Overedclimb’	High	77 ab
	Medium	82 a
	Low	67 b
‘Radbeauty’	High	117 a
	Medium	108 a
	Low	121 a

ⁱMeans with same lowercase letters within a rose cultivar are not significantly different among treatments according to the Tukey–Kramer method with a significance level specified at $\alpha \leq 0.05$.

Table 4-6. Summary of the drought responses of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overedclimb’, and ‘Radbeauty’ roses when irrigation frequency decreased from high [80% reference evapotranspiration (ET_O)] to medium (50% ET_O) and low (20% ET_O) treatments.

Taxa	Visual quality score	Plant growth responses	Physiological responses
‘ChewPatout’	Leaves visibly wilted (-) ⁱ	Plant growth responses were not affected by reduced irrigation frequency	Stomatal conductance (-); Leaf temperature (+); Leaf-air temperature difference (+); Vapor pressure deficit (+); Transpiration rate (-)
‘Meibenbino’	Leaves visibly wilted (-); Foliage appearance (-); Flower abundance (-); Overall appearance (-)	Relative plant growth index (-); Leaf width (-); Leaf dry weight (-); Stem dry weight (-)	Stomatal conductance (-); Stomatal density (-); Leaf temperature (+); Leaf-air temperature difference (+); Vapor pressure deficit (+); Transpiration rate (-)
‘MEIRIFTDAY’	Leaves visibly wilted (-); Foliage appearance (-); Overall appearance (-)	Relative plant growth index (-); Leaf width (-); Leaf dry weight (-); Stem dry weight (-)	Stomatal conductance (-); Leaf temperature (+); Leaf-air temperature difference (+); Vapor pressure deficit (+); Transpiration rate (-)
‘Overedclimb’	Leaves visibly wilted (-); Foliage appearance (-)	Plant growth responses were not affected by reduced irrigation frequency	Stomatal conductance (-); Stomatal density (-); Transpiration rate (-)
‘Radbeauty’	Leaves visibly wilted (-); Foliage appearance (-)	Leaf width (-)	Stomatal conductance (-); Leaf temperature (+); Leaf-air temperature difference (+); Vapor pressure deficit (+); Transpiration rate (-)

ⁱ(-) indicated the values of tested parameters reduced due to decreased irrigation frequency, while (+) suggested the values of tested parameters increased because of decreased irrigation frequency.

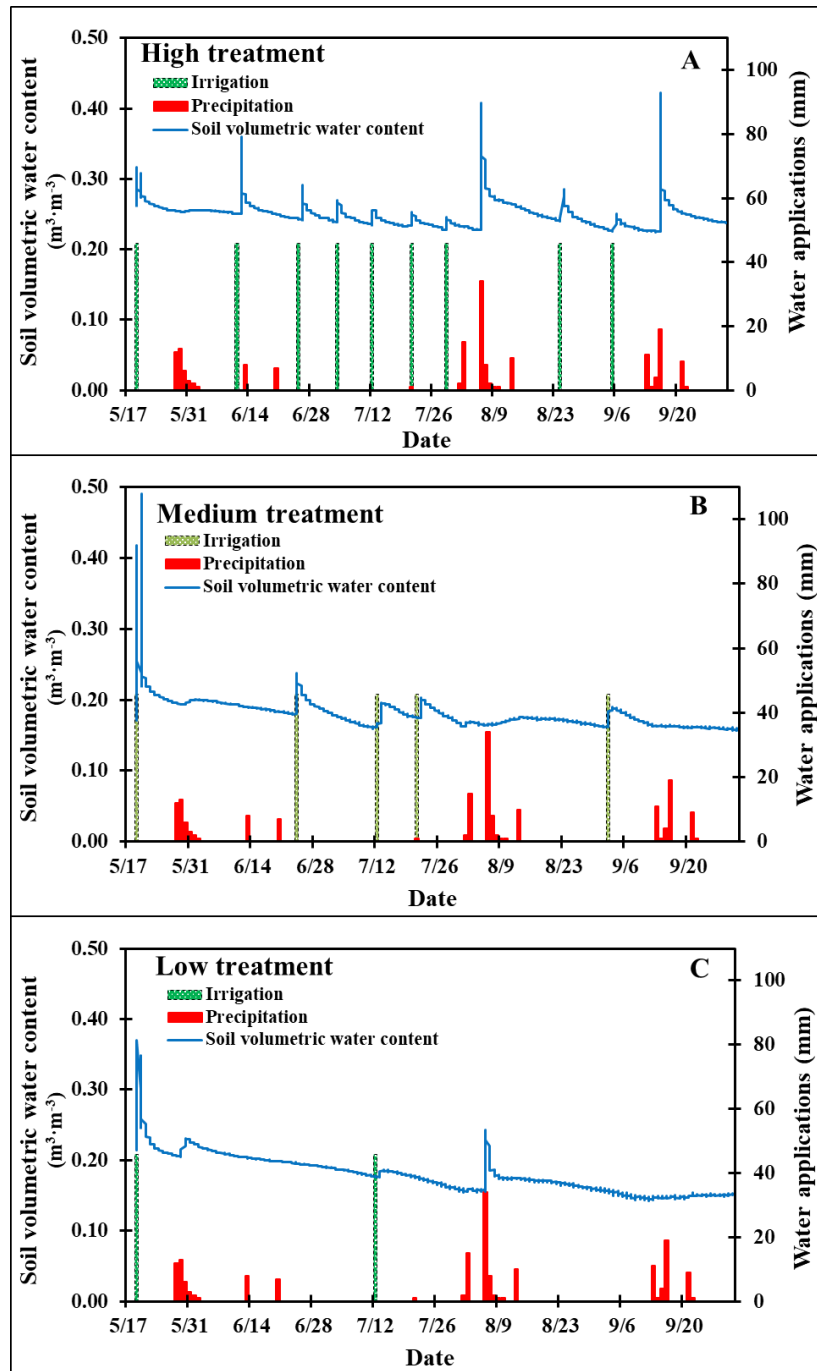


Figure 4-1. Soil volumetric water contents estimated by soil moisture sensors (TDT[®]; Acclima, Meridian, ID) installed at the bottom of the targeted root zone (50 cm deep) of a ‘Radbeauty’ rose with high [80% reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments.

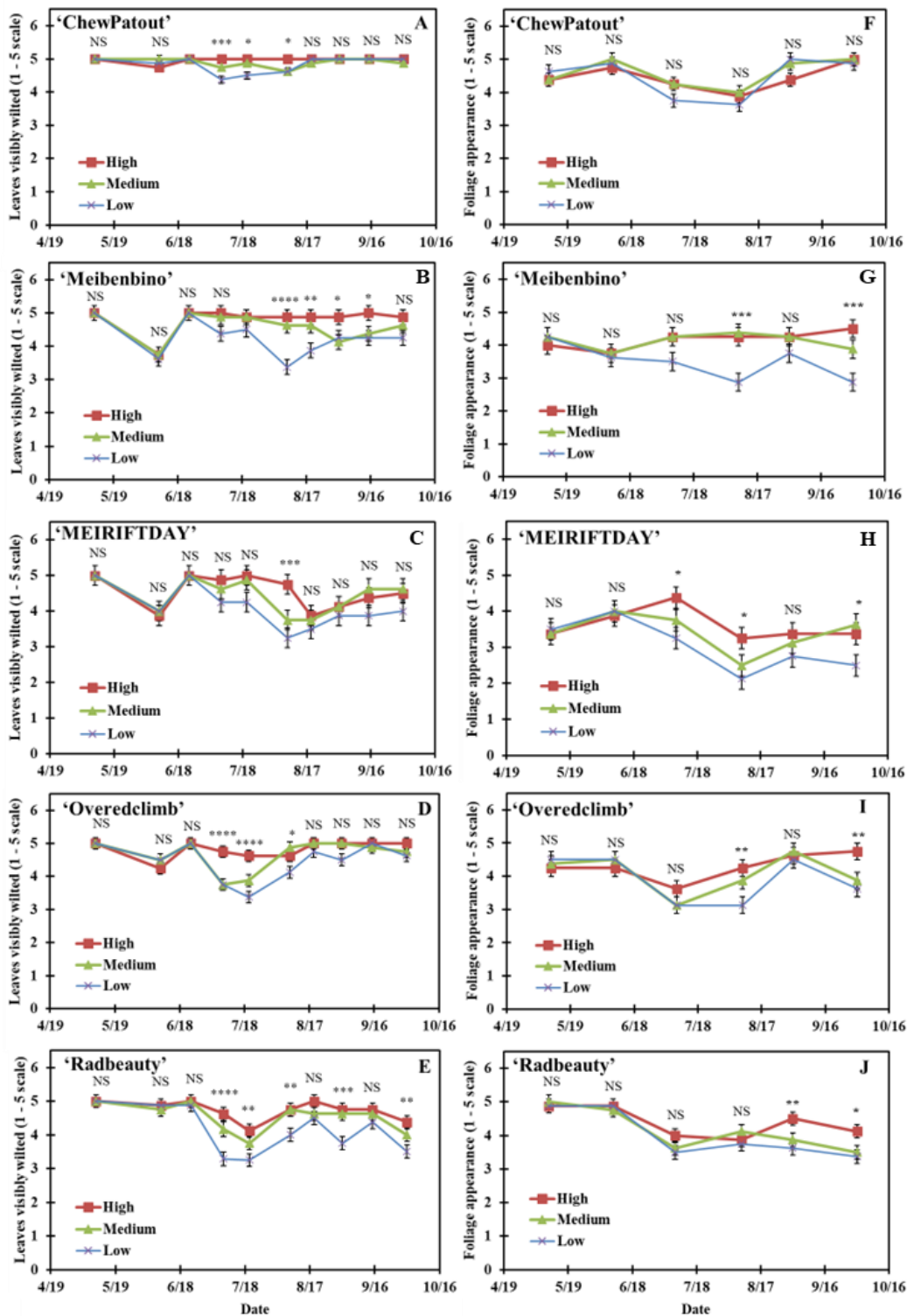


Figure 4-2. Leaves visibly wilted (A-E) and foliage appearance (F-J) of ‘ChewPatout’, ‘Meibenbino’, ‘MEIRIFTDAY’, ‘Overredclimb’, and ‘Radbeauty’ roses with high [80%

reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments. The proportion of leaves visibly wilted was rated using a scale of 1 to 5 (1 = more than 65% of the leaves wilted, and 5 = plant was fully turgid) (Zollinger et al. 2006). Foliage appearance was determined by the proportion of foliage that was visibly damaged (i.e., leaf edge burn, curling, necrosis, etc.) using a scale of 1 to 5 (1 = poor quality and more than 50% of leaves showing visible damage; and 5 = excellent quality with less than 1% of leaves showing visible damage) (Reid et al. 2019). Error bars represent *SE* of 8 plants. NS, *, **, ***, **** represent nonsignificant, and significant at $\alpha \leq 0.05$, 0.01, 0.001, or 0.0001, respectively.

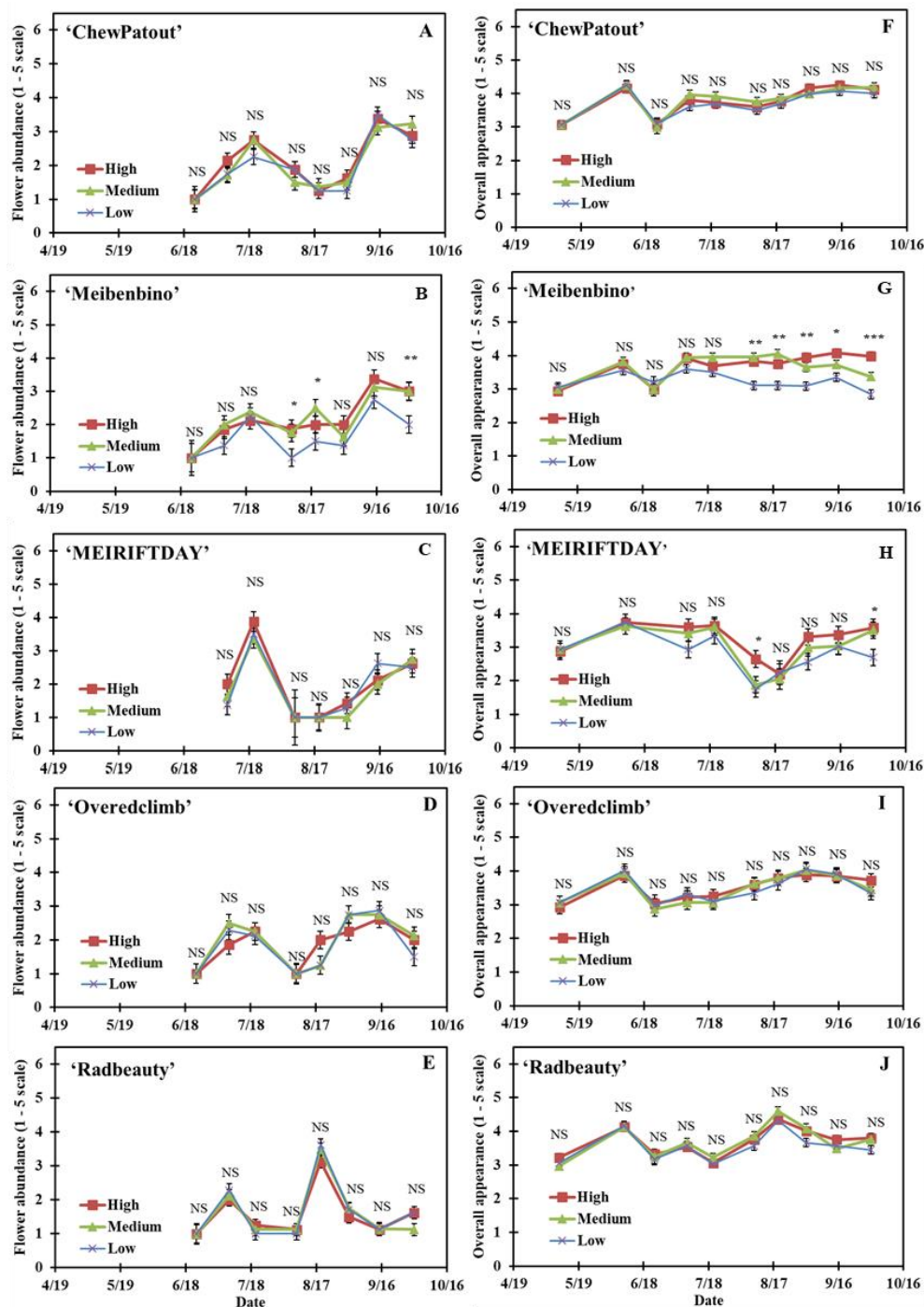


Figure 4-3. The flower abundance (A-E) and overall appearance (F-J) of 'ChewPatout', 'Meibebino', 'MEIRIFTDAY', 'Overedclimb', and 'Radbeauty' roses with high [80% reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments. Flower abundance was determined using the percentage of plants covered in open

blooms, whereas the overall appearance was rated based on how the plant was performing in the landscape (Reid et al. 2019). Error bars represent standard errors of 8 plants. NS, *, **, *** represent nonsignificant, and significant at $\alpha \leq 0.05$, 0.01, or 0.001 respectively.

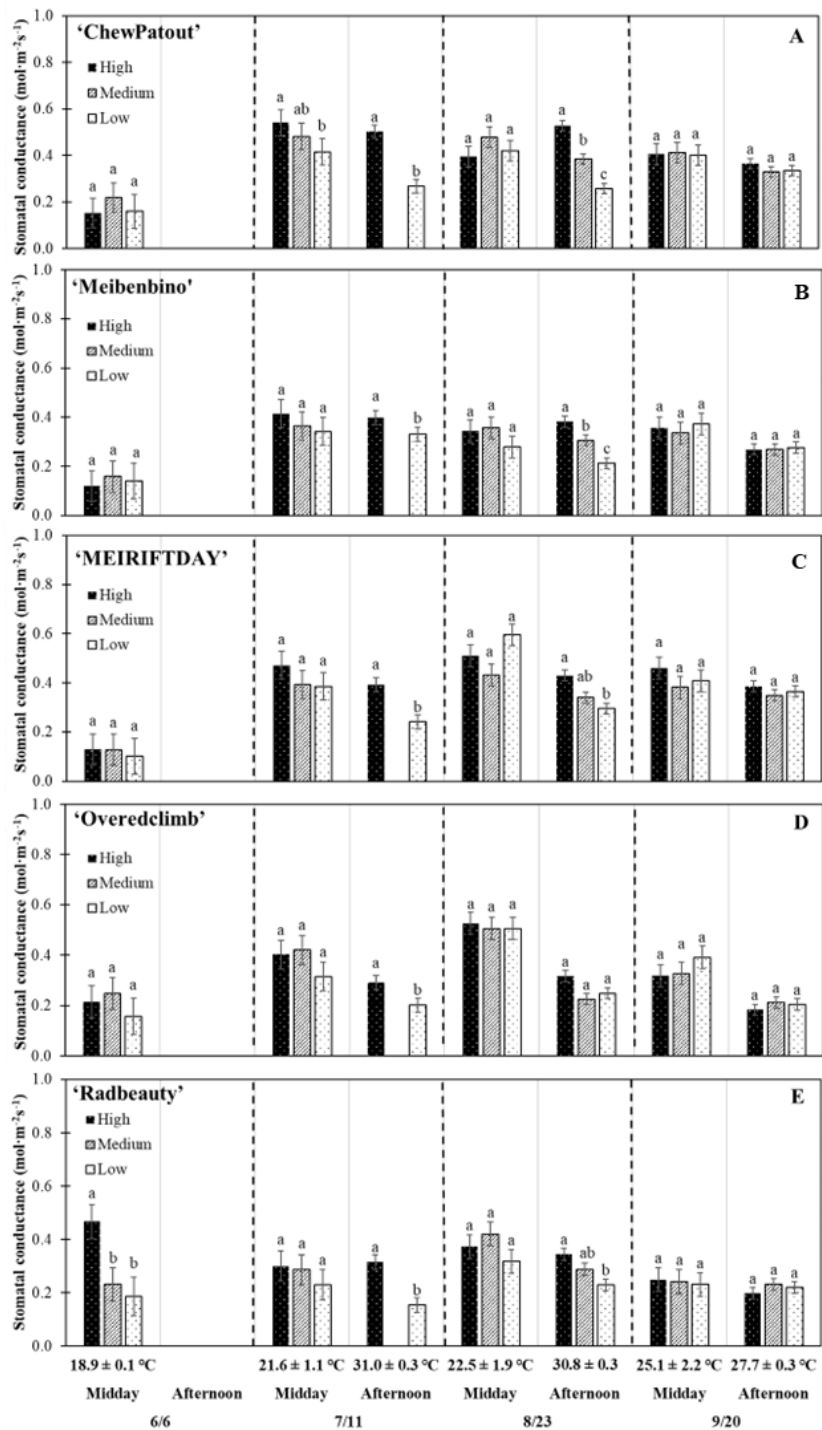


Figure 4-4. Stomatal conductance of 'ChewPatout' (A), 'Meibebino' (B), 'MEIRIFTDAY' (C), 'Overedclimb' (D), and 'Radbeauty' roses (E) with high [80% reference evapotranspiration (ET_0)], medium (50% ET_0), and low (20% ET_0) treatments

during the trial with the mean and *SD* of air temperature during the measurements. The midday conductance was recorded between 1100 HR to 1230 HR, whereas the afternoon conductance was recorded between 1600 HR to 1730 HR. Error bars represent *SE* of 8 plants. Treatments with the same lowercase letters within each species and the time of the day are not significantly different by Tukey–Kramer method with a significance level specified at $\alpha \leq 0.05$. Stomatal conductance was only recorded at midday on 6 Jun, whereas afternoon stomatal conductance was recorded on roses under the high and low treatment on 11 Jul 2022.

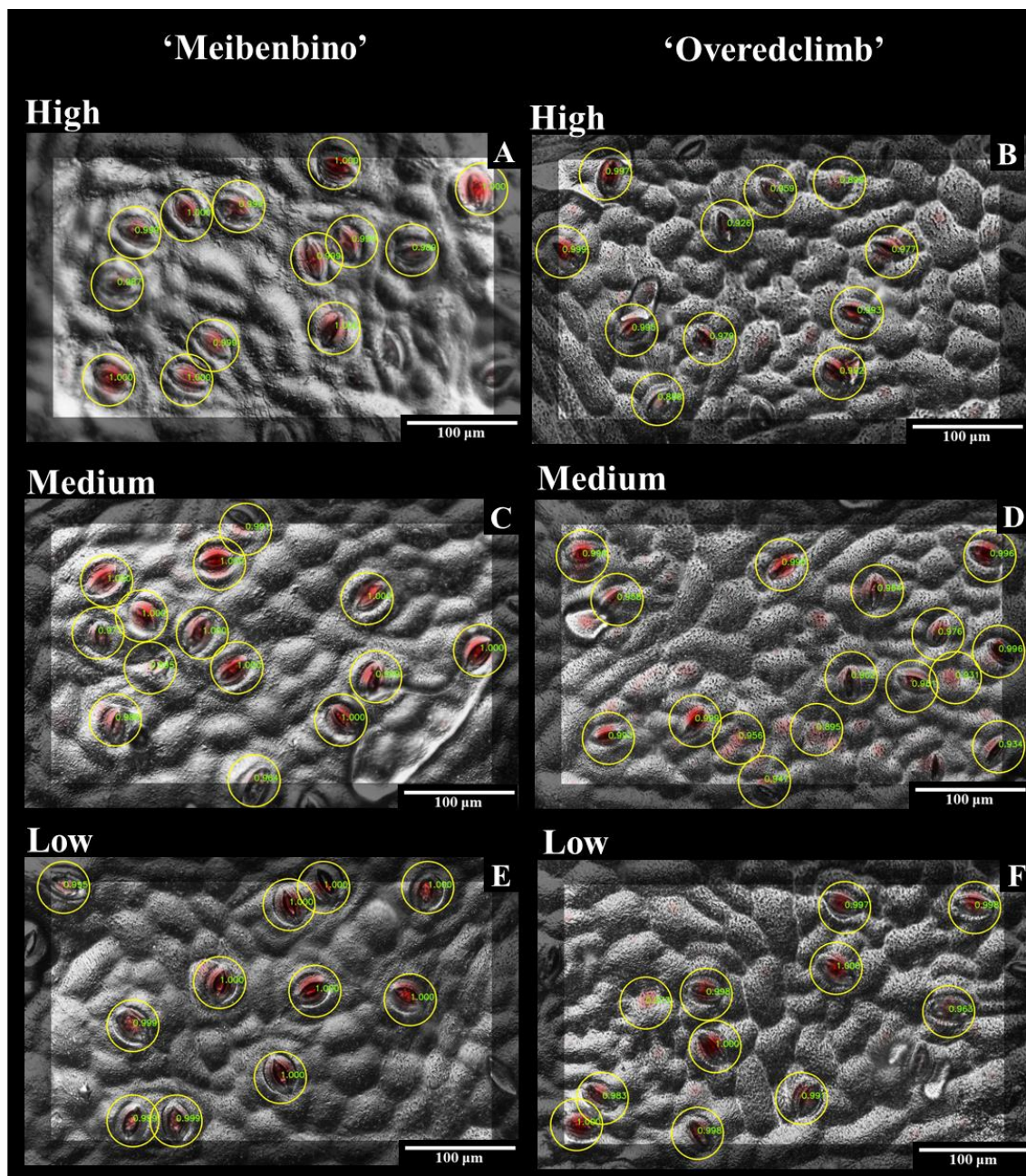


Figure 4-5. Microscopy images of stomatal density on the leaf abaxial surface of 'Meibembino' and 'Overredclimb' roses with high [80% reference evapotranspiration (ET_0)] (A and B), medium (50% ET_0) (C and D), and low (20% ET_0) treatments (E and F) on 6 Sep 2022. The number of stomata on each image was counted using a Stomatal Counter (Fetter et al. 2019) with a threshold probability of 0.881.

CHAPTER V

CONCLUSIONS

Shepherdia ×utahensis ‘Torrey’ (hybrid buffaloberry) and the four penstemon species, including *Penstemon barbatus* (Cav.) Roth ‘Novapenblu’ (Rock Candy Blue[®] penstemon), *P. digitalis* Nutt. ex Sims’ TNPENDB’ (Dakota[™] Burgundy beardtongue), *P. ×mexicali* Mitch. ‘P007S’ (Pikes Peak Purple[®] penstemon), and *P. strictus* Benth. (Rocky Mountain penstemon), responded differently as substrate water content decreased. Nonetheless, reduction in soil moisture availability led to low stem water potential, which caused the landscape plants in this study to dehydrate, decreasing overall visual quality. When drought stress became severe, the plants adjusted their morphology and physiology to acclimate to reduced soil moisture by promoting water uptake.

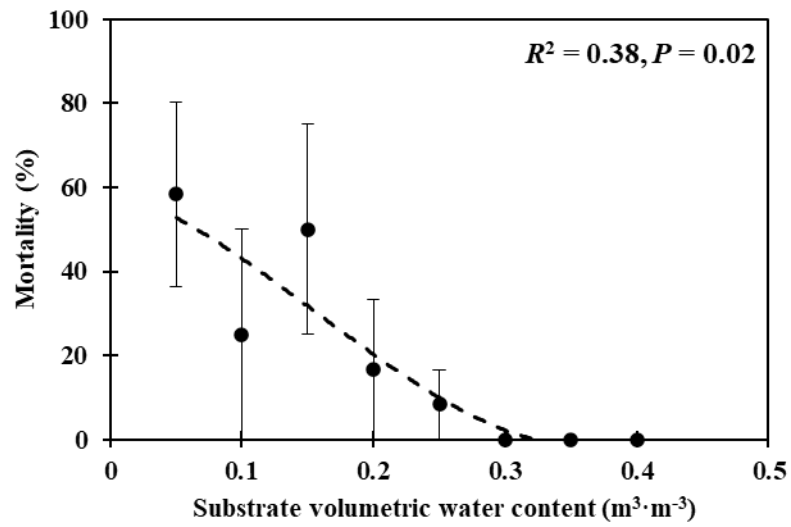
Shepherdia ×utahensis exhibited partial stomatal closure and enhanced root growth to promote water uptake and limit water loss. Small and curling leaves on *S. ×utahensis* under water stress were also advantageous to dissipating heat via sensible heat loss. Reductions in cell and leaf expansion under drought contributed to dense trichomes on the adaxial surface of *S. ×utahensis*, which enhanced leaf reflectance of visible light. Because of its drought-tolerant mechanisms, *S. ×utahensis* may be suitable for low-water-use landscaping in hot and arid regions. The morphological features of mesic penstemon species, such as the large leaves of *P. digitalis* and the low root-to-shoot ratio of *P. ×mexicali*, may have resulted in their sensitivity to water stress. Penstemon species native to arid regions, *P. barbatus* and *P. strictus*, increased leaf reflectance by producing thick cuticle layers and had cooler canopy temperatures than mesic penstemon species. These species maintained acceptable visual quality despite soil moisture levels being

reduced by 57%. Therefore, *P. barbatus* and *P. strictus* are more drought tolerant and suitable for low-water-use landscaping applications as compared with *P. digitalis* and *P. ×mexicali* under the conditions of this research.

Five garden rose cultivars, including 'ChewPatout' (Oso Easy® Urban Legend® rose), 'MEIRIFTDAY' (Oso Easy® Double Pink rose), 'Meibenbino' (Petite Knock Out® rose), 'Overedclimb' (Cherry Frost™ rose), and 'Radbeauty' (Sitting Pretty™ rose), had different irrigation requirements and drought tolerance when irrigation frequency was reduced. The rose cultivars were able to adapt to drought stress by reducing stomatal conductance and stomatal density. In response to water stress, 'MEIRIFTDAY' and 'Meibenbino' roses had unacceptable overall appearances and defoliation. In contrast, drought-tolerant 'ChewPatout', 'Overedclimb', and 'Radbeauty' roses were able to maintain acceptable overall appearances even as the total amount of irrigation applied to each plant was decreased by 87%. Compared with 'MEIRIFTDAY' and 'Meibenbino' roses, 'ChewPatout', 'Overedclimb', and 'Radbeauty' roses are better suited for low-water-use landscape applications in Utah. This research documented the morphological, physiological, and plant growth responses of ten landscape plant taxa under decreased water availability induced by a reduction in substrate moisture levels or irrigation frequency.

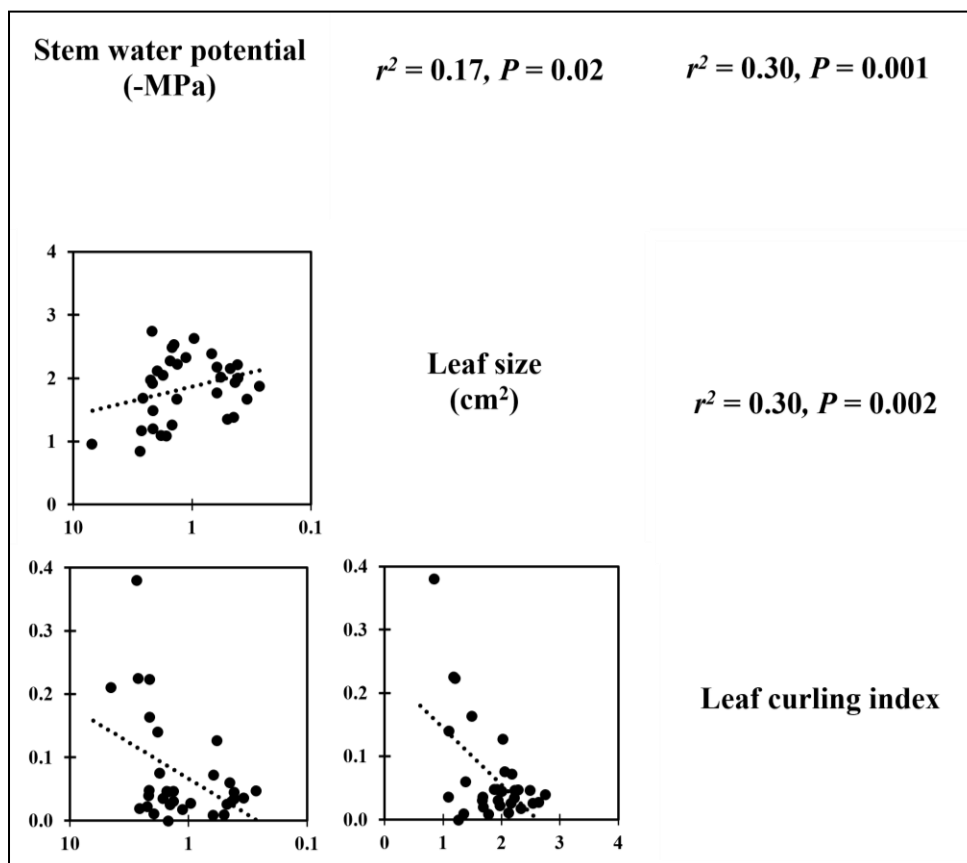
APPENDICES

APPENDIX I



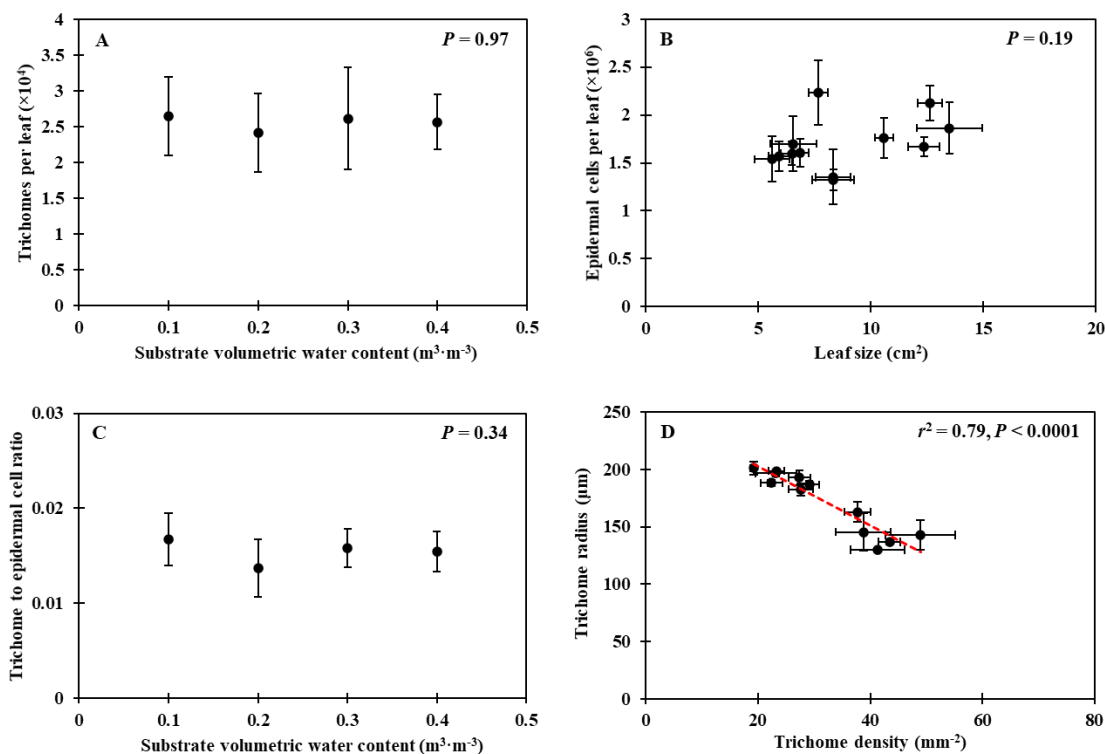
Supplementary Figure S1. Plant mortality of *Shepherdia ×utahensis* at eight substrate volumetric water content treatments (θ_t) at the termination of the experiment. The error bars represent the standard errors of three blocks (replicates), four plants in each block and treatment.

APPENDIX II



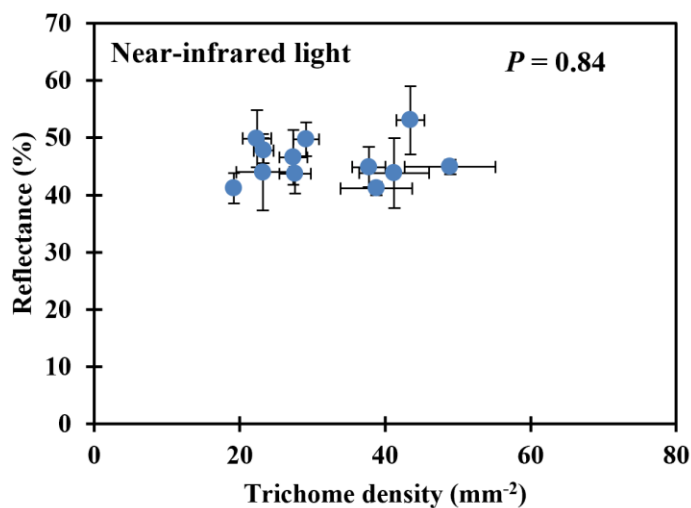
Supplementary Figure S2. Correlation between stem water potential, leaf size, and leaf curling index of *Shepherdia × utahensis* at the termination of the experiment. The leaf size of each plant was calculated as the ratio of total leaf area to the number of leaves. Leaf curling index was determined using the equation: [distance between the margins of flattened leaf (D_{max})-distance between the margins of curling leaf (D_i)]/ D_{max} (Nilsen, 1987).

APPENDIX III



Supplementary Figure S3. Total number of trichomes per leaf (A) and trichome to epidermal cell ratio of *Shepherdia × utahensis* (C) at different substrate volumetric water contents, correlation between total number of epidermal cells per leaf and leaf size (B), correlation between trichome density and trichome radius (D). The error bars represent the standard errors of three plants in (A) and (C), while the error bars represent the standard errors of three leaves sampled from each plant in (B) and (D).

APPENDIX IV



Supplementary Figure S4. Correlation between near-infrared light reflectance and trichome density of *Shepherdia × utahensis* on the leaf upper (adaxial) surface. The reflectance of near-infrared light was determined using the wavelength at 730 nm (Kusuma et al., 2020). The error bars represent the standard errors of three leaves sampled from each plant.

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EDUCATION

- 2020-August 2023 (expected) Ph.D. Candidate in Plant Science
 Utah State University, USA.
 Dissertation title: *Water conservation through drought-resilient plants and deficit irrigation*
 Advisors: Youping Sun and Kelly Kopp
- 2018-2020 M.S. in Plant Science
 Utah State University, USA.
 Thesis title: *Nodulation and Growth of Shepherdia ×utahensis 'Torrey'*
 Advisor: Youping Sun
- 2014-2018 B.S. in Horticultural Science
 National Chung Hsing University, Taiwan.

RESEARCH EXPERIENCE**Plant Drought Responses**

- 2021-Present Climate Ready Landscape Plants
- Established trial plots to determine the effects of deficit irrigation on the aesthetic value of 15 ornamental plant species.
 - Established an automated soil moisture sensing system to continuously monitor soil water contents and wetting fronts passing root zones.
 - Collected data, organized Extension activities, managed plots, conducted statistical analyses, and prepared manuscripts.
- 2021-Present Biojet Fuel Production from Pinyon Juniper and Reed Grass
- Established an automated soil moisture sensing system to continuously monitor soil water contents.
 - Established plots and deficit irrigation systems to evaluate the potential of reed grass for bio-fuel production under five irrigation rates based on evapotranspiration rate.
 - Designed and built sensor systems and plots, collected data, conducted statistical analyses, and prepared a manuscript.
- 2022 Growth and Physiology of Four Container-grown Ornamental Plants Responding to Water Stress
- Built a sensor-based, automated irrigation system to test drought responses of rose of Sharon, rose, rosemary, and chastetree.

- Established a sensor-based irrigation system to induce drought stress precisely.
 - Established an irrigation system, collected data, conducted statistical analysis, and prepared a manuscript.
- 2021-2022 Effects of Substrate Water Contents on Plant Development and Physiology of Four Penstemon Species
 - Applied thermal imagery cameras to determine the water status of four penstemon species.
 - Determined the relationship between canopy temperatures and the drought tolerance of penstemon plants.
 - Established a sensor-based irrigation system to induce drought stress precisely.
 - Designed an experiment, processed thermography and plant growth data, presented a poster, and prepared a manuscript.
- 2020-2021 Leaf Morphology and Reflectivity Changes of *Shepherdia ×utahensis* under Drought Conditions
 - Investigated the effects of water stress on the plant development and trichome density of *S. ×utahensis* growing at eight substrate volumetric water contents.
 - Developed the substrate-specific calibration equations for two soil moisture sensors.
 - Determined hydraulic properties of peat-based substrate in containers.
 - Conducted lab measurements to determine the water retention curves of peat-based substrates.
 - Established a datalogger system containing quantum sensors to automatically and continuously monitor light intensity.
 - Established a sensor-based, automated irrigation system, collected data, processed scanning electron microscope images, presented a poster, and prepared a manuscript.
- 2019-2021 Quantifying Evapotranspiration Rates of Three New Landscapes Using Landscape-scale Drainage Lysimeters
 - Used a landscape-scale drainage lysimeter to determine the water use of ornamental plants.
 - Established plots, installed soil moisture sensors and plants, and calibrated sensors.

Sensor and Irrigation Systems

- 2019-2021 Sustaining Green Industry Production Through Irrigation Management with the SensorWeb™ Irrigation Control System
 - Evaluated the performance of a wireless, sensor-based irrigation system in nursery production.
 - Established the wireless and sensor-based irrigation in a polyethylene house, and programmed the system.
 - Designed an experiment, analyzed data, and prepared a poster.
- 2020-2021 Water Content Sensor Integrity: Is Your Sensor Still Accurate?

- Determined the accuracy of soil moisture sensors in dialectical solutions.
 - Established a datalogger system to calibrate 50 soil moisture sensors in solutions with different dielectric permittivity.
 - Wrote software programs for the calibration system, analyzed data, and prepared a poster.
- 2019 Using a Normalized Difference Vegetation Index Sensor to Determine the Chlorophyll Content of *Shepherdia ×utahensis* ‘Torrey’
- Compared chlorophyll content measurements using commercial meters and normalized difference vegetation index (NDVI) sensors.
 - Built the NDVI sensor system and developed a system-specific datalogger program.
 - Prepared nutrient solutions at different nitrogen levels to induce nitrogen deficiency in *Shepherdia ×utahensis*.
 - Extracted leaf chlorophyll to determine actual chlorophyll content.
 - Designed the experiment, established the sensor system, created sensor programs, recorded measurements in greenhouses and fields, analyzed data, presented a poster, and prepared a manuscript.

Plant Salinity Tolerance and Water Quality

- 2020-2021 Monitoring Groundwater Quality and Developing Best Water Management Practices for Sustainable Green Industry Production
- Collaborated with five Utah nurseries to collect water samples monthly for determining the salinity levels of irrigation water.
- 2019 Salinity Tolerance of 12 *Viburnum* Taxa
- Evaluated morphological and physiological responses of *viburnum* plants irrigated with saline solutions in a greenhouse.
 - Led a research team to set up the experiment, collect and analyze data, presented a poster, and prepare two manuscript.
- 2018-2019 Comparing the Salt Tolerance of Three Landscape Plants Using a Near-Continuous Gradient (NCGD) System
- Built an NCGD in a greenhouse that automatically applied salinity treatments and irrigated plants to screen plant salinity tolerance.
 - Used the NCGD system to evaluate 3 ornamental species for salinity tolerance with eight electrical conductivity levels.
 - Collected and analyzed data, presented a poster, and prepared a manuscript.

Horticultural Crop Evaluations

- 2022 Selecting Pomegranate Cultivars for Fruit Production in Utah
- Assisted Utah State University (USU)’s Washington County Extension agents in designing a field plot and a drip irrigation system.
- 2021-2022 Selecting Pinyon Pine for Nut Production
- Established two field plots to evaluate different pinyon pine varieties for pine nut production.

- Collaborated with Utah State University's Washington County Extension agents to design a drip irrigation system.
- 2019-2021 Field Trials of 26 Ornamental Grass Species in the Intermountain West
 - Evaluated the field performance of 26 ornamental grasses and grass-like species.
 - Established the field trial plot, collected and analyzed data, and prepared a poster for presentations at 2022 annual conference of ASHS.
- 2019-2020 Selecting Utah Native Plant for Sustainable Landscape Uses
 - Helped collect seeds and cuttings of *Ceanothus velutinus* and *Cercocarpus montanus* for propagation studies.
 - Assisted the cutting propagation experiments of *Ceanothus velutinus*.
- 2019-2020 Using Actinobacteria to Improve Native Plant Adaptability and Fertilizer Use Efficiency in Nursery Production
 - Determined the nodulation of *Shepherdia ×utahensis*, a xeric plant.
 - Prepared nitrogen-free nutrient solutions to induce plant nitrogen deficiency stress.
 - Compared different nodulation and plant growth of *Shepherdia ×utahensis* grown in different soilless substrates.
 - Studied the application of actinobacteria to reduce the amounts of controlled-release fertilizers used in nursery production to minimize the pollution of nitrate runoff.
 - Extracted DNA of the symbiotic bacteria and conducted polymerase chain reaction studies to investigate the phylogeny of symbiotic bacterial strains.
 - Designed experiments, managed greenhouse research, collected and analyzed data, performed phylogenetic analysis, presented a poster, and prepared manuscripts for publication.

TEACHING EXPERIENCE

- | | |
|------------------|---|
| 2023 | Guest Lecturer for Plant Stress Physiology (PSC 6900)
Lecture Topic: Plant Drought Stress |
| 2020, 2021, 2023 | Teaching Assistant for Plant Stress Physiology (PSC 6900) |
| 2022 | Guest Lecturer for Plant Propagation (PSC 3700)
Lecture Topic: Propagation Environment |
| 2020 | Teaching Assistant for Applied Statistics in Agricultural Research (PSC 6900) |

EXTENSION EXPERIENCE

Chen J, and Sun Y. The Drought Tolerance of Roses and the Climate Ready Landscape Plant Irrigation Trials at Utah State University. Sugar House Garden Center, Salt Lake City. 16 February 2023. (12 participants, members of Utah Rose Society).

- Chen J**, and Sun Y. Utah State University Climate Ready Landscape Plant Irrigation Trials. Field Day. Utah Agricultural Experiment Station's Greenville Research Farm, North Logan, UT. 21 October 2022. (20 participants, undergraduate students from Brigham Young University-Idaho, Rexburg, ID).
- Chen J**, and Sun Y. Utah State University Climate Ready Landscape Plant Irrigation Trials. Field Day. Utah Agricultural Experiment Station's Greenville Research Farm, North Logan, UT. 18 October 2022. (10 participants, students and teachers from InTech Collegiate Academy, Logan, UT).
- Chen J**, and Sun Y. Utah State University Climate Ready Landscape Plant Irrigation Trials. Center for Water-Efficient Landscaping at USU Virtual Field Day. Virtual. 13 September 2022. (50 participants).
- Chen J**, and Sun Y. Utah State University Climate Ready Landscape Plants Open House. Utah Agricultural Experiment Station's Greenville Research Farm, North Logan, UT. 17 August 2022. (47 participants).
- Chen J**, and Sun Y . Utah State University Climate Ready Landscape Plant Irrigation Trials. Field Day. Utah Agricultural Experiment Station's Greenville Research Farm, North Logan, UT. 22 June 2022. (15 participants, summer citizens).
- Chen J**, and Sun Y . Field trials of newly developed landscape plants under deficit irrigation. Field Day. Utah Agricultural Experiment Station's Greenville Research Farm, North Logan, UT. 18 June 2022. (6 participants, Master Gardeners led by an Extension Educator at the University of Idaho).
- Chen J**, and Sun Y . Field trials of newly developed landscape plants under deficit irrigation. Field Day. Utah Agricultural Experiment Station's Greenville Research Farm, North Logan, UT. 27 October 2021. (10 participants, undergraduate students from Brigham Young University-Idaho, Rexburg, ID).

PUBLICATIONS

Peer-Reviewed Publications

- Chen J**, Sun Y, Oki LR, Sisneroz J, Reid K, Nackley LL, Kim S-H, Schuch UK, Haver DL, Stuke M, Fron A, Kopp K, Jones SB, and Hipps L. 2023. Climate Ready Landscape Plants (I): Garden Roses Trialed in Utah. HortTechnology (Submitted on 30 Apr 2023).
- Chen J**, Sun Y, Kopp K, Oki L, Jones SB, and Hipps L. 2023. Physiological and canopy temperature responses to drought of four penstemon species. HortScience 58:539-549. <https://doi.org/10.21273/HORTSCI16996-22>.
- Chen J**, Sun Y, Kopp K, Oki L, Jones SB, and Hipps L. 2022. Effects of water availability on leaf trichome density and plant growth and development of *Shepherdia ×utahensis*. Frontiers in Plant Science. 13:855858. <https://doi.org/10.3389/fpls.2022.855858>
- Chen J**, Norton J, Kratsch H, Sun Y, and Rupp L. 2021. Nodulation of *Shepherdia ×utahensis* 'Torrey' and the diversity of symbiotic *Frankia* strains. HortScience 56:762-768. <https://doi.org/10.21273/HORTSCI15726-21>
- Chen J**, Zhen S, and Sun Y. 2021. Estimating leaf chlorophyll content of buffaloberry using normalized difference vegetation index sensors. HortTechnology 31:297-

303. <https://doi.org/10.21273/HORTTECH04808-21>
- Xing H, Hershkowitz J, Paudel A, Sun Y, **Chen J**, Dai X, and Chappell M. 2021. Morphological and physiological responses of ornamental grasses to saline water irrigation. *HortScience* 56:678-686. <https://doi.org/10.21273/HORTSCI15700-21>
- Chen J**, Kratsch H, Norton J, Sun Y, and Rupp L. 2020. Growth and nodulation of *Shepherdia ×utahensis* ‘Torrey’ topdressed with controlled-release fertilizer. *HortScience* 55:1956-1962. <https://doi.org/10.21273/HORTSCI15260-20>
- Chen J**, Xing H, Paudel A, Sun Y, and Niu G. 2020. Gas exchange and mineral nutrition of twelve viburnum taxa irrigated with saline water. *HortScience* 55:1242-1250. <https://doi.org/10.21273/HORTSCI14941-20>
- Sun Y, **Chen J**, Xing H, Paudel A., Niu G, and Chappell M. 2020. Growth, visual quality, and morphological responses of twelve viburnum taxa to saline water irrigation. *HortScience* 55:1233-1241. <https://doi.org/10.21273/HORTSCI14940-20>
- Chen J**, Wang Y, Paudel A, and Sun Y. 2019. Comparing the salt tolerance of three landscape plants using a near-continuous gradient dosing system. *HortTechnology* 29:611-619. <https://doi.org/10.21273/HORTTECH04385-19>
- Paudel A, **Chen J**, Sun Y, Wang Y, and Anderson R. 2019. Salt tolerance of Sego Supreme™ plants. *HortScience* 54:2056-2062. <https://doi.org/10.21273/HORTSCI14342-19>

Manuscripts in Preparation

- Chen J**, Sun Y, and Agblevor FA. 2022. The effects of deficit irrigation on the plant growth of feather reed grass. *Industrial Crops and Products*.
- Chen J**, Sun Y, Kopp K, Oki L, Jones SB, and Hippi L. 2022. Comparing the drought tolerance of four landscape plants at two volumetric water contents. *HortScience*.
- Chen J**, Sun Y. and Paudel A. 2022. Evaluation of twenty-six ornamental grasses and grass-like plants for landscape performance in the Intermountain West. *HortTechnology*.
- Chen J**, Sun Y, and Kopp K. 2022. The effects of drought on urban landscape vegetation coverage in Moab, Utah. *HortTechnology*.

Abstracts

- Chen J**, Sun Y, and Kopp K. 2022. Detecting drought stress of penstemons using infrared thermal imaging. *Hortscience*. 57(9): S58.
- Chen J**, Mathews J, Paudel A, and Sun Y. 2022. Field Trials of 26 Ornamental Grasses and Grass-like Plants. *HortScience*. 57(9): S129.
- Chen J**, Jones SB, and Sun Y. 2021. Water content sensor integrity: Is your sensor still accurate? ASA, CSSA, and SSSA International Annual Meetings, Salt Lake City, UT. <https://scisoc.confex.com/scisoc/2021am/meetingapp.cgi/Paper/135718>.
- Jones SB, Naruke C, **Chen J**, and Sheng W. 2021. Standardizing particulate porous media for sensor evaluation, calibration and validation. ASA, CSSA, and SSSA International Annual Meetings. Nov. 7-10, 2021.
- Chen J**, and Sun Y. 2021. Buffaloberry changes its leaf morphology and reflectivity under water stress. *HortScience* 56(9): S214.
- Kratsch HA, **Chen J**, Sun Y, and Rupp LA. 2021. Barriers to production and landscape use of the native hybrid *Shepherdia ×utahensis*. *Hortscience* 56(9): S239.

- Matthews J, **Chen J**, and Sun Y. 2021. Application of Sensorweb™ irrigation control system in plant production. *HortScience* 56(9):S18.
- Chen J**, Zhen S, and Sun Y. 2020. Using NDVI sensors to determine the chlorophyll content of *Shepherdia ×utahensis* ‘Torrey’. *HortScience* 55(9): S340.
- Chen J**, Kratsch HA, Norton J, and Sun Y. 2020. Nodulation of *Shepherdia ×utahensis* ‘Torrey’ topdressed with controlled-release fertilizer. *HortScience* 55(9): S188.
- Chen J**, Xing H, Paudel A, Sun Y, and Niu G. 2020. Salinity tolerance of 12 viburnum taxa. *HortScience* 55(9): S113.
- Hershkowitz J, Xing H, Paudel A, **Chen J**, Sun Y, and Dai X. 2020. Salinity tolerance of six ornamental grass species. *HortScience* 55(9): S113.
- Paudel A, **Chen J**, and Sun Y. 2020. Determining the salt tolerance of two penstemons using a near-continuous gradient dosing system. *HortScience* 55(9): S339.
- Chen J**, Wang Y, Paudel A, and Sun Y. 2019. Comparing the salt tolerance of three landscape plants using a near-continuous gradient dosing system. *HortScience* 54(9): S283.
- Paudel A, Guo S, **Chen J**, Wang Y, Sun Y, Rupp L, and Anderson R. 2019. Salt tolerance of Se-go Supreme™ plants. *HortScience* 54(9): S283.
- Chen J**. 2019. Comparing the salt tolerance of three landscape plants using a near-continuous gradient dosing system. Spring Runoff Conference, Logan, UT. <https://digitalcommons.usu.edu/runoff/2019/all/19/>.

Miscellaneous Writing

- Chen J**, and Sun Y. 2019. Evaluating physiological responses of viburnum species to salinity stress. PP Systems application note. <https://ppsystems.com/application-notes>.

RESEARCH-RELATED AWARDS

- Utah State University Open Access Funding Award**
(\$900 each) **2020, 2021, 2022**
Support publication fees for publications in open access journals.
- Don J. Wang Endowment Scholarship**
(\$2,200 each) **2021, 2022, 2023 (declined due to graduation)**
Present to outstanding graduate students in the College of Agriculture and Applied Sciences, Utah State University.
- Zahedi International Scholarship (\$3,000 each)** **2021, 2022**
Present to outstanding international graduate students in the College of Agriculture and Applied Sciences, Utah State University.
- Daniel M. Teng & Lina C. Teng Endowed Fellowship (\$3,400 each)** **2019, 2020, 2021, 2022**
Present to outstanding graduate students in the Department of Plants, Soils, and Climate.
- 2021–2022 Encompass Scholarship of the Soil Science Society of America (SSA)** **2021**
Present to graduate students with outstanding leadership to support their SSA membership fee.
- 2021 Outstanding Graduate Horticulture Student of the American Society for Horticultural Science** **2021**

Recognize outstanding graduate students in horticulture.

2021 Finalist for Master's Student Researcher of the Year, Robins Award 2021
Present to the highest achieving student.

Third Place Graduate Student Poster at the 2020 Annual Conference of the American Society for Horticultural Science 2020
Poster presentation "Using NDVI sensors to determine the chlorophyll content of *Shepherdia ×utahensis* 'Torrey'."

2019-2020 Utah State University College of Agriculture and Applied Sciences Master's Student Researcher of the Year 2020
Present to one M.S. student each year who "has gone above and beyond the norm to make the college a place of increased quality and merit".

Outstanding Graduates of the Year 2018
Present to outstanding graduates of National Chung Hsing University.

TRAVEL GRANTS

American Society for Horticultural Science Graduate Student Travel Grant (\$500 each) 2020, 2022
Present to graduate students with outstanding academic performance.

Utah State University Student Association Academic Opportunity Fund (\$500 each) 2021, 2022
Provide financial support to outstanding graduate students who wish to present research in an academic competition.

Utah State University College of Agriculture and Applied Sciences Graduate Student Travel Grant (\$300 each) 2019, 2020, 2021, 2022
Present to ten graduate students in the College of Agriculture and Applied Sciences to attend a professional conference.

School of Graduate Studies Graduate Student Travel Award (\$300 each) 2019, 2021, 2022
Promote student involvement in their discipline by partially funding travel costs associated with professional presentations at regional, national, and international conferences.

Graduate Student Travel Scholarship for the American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America International Annual Meeting (\$550) 2021
Present to graduate students with outstanding academic performance.

2019 PP-Systems Innovator's Travel Award (\$1,000) 2019
Present to graduate students involved in leaf gas exchange and chlorophyll fluorescence research.

PROPOSAL WRITING EXPERIENCE

Proposals

Chen J, Paudel A, and Sun Y. 2019. Salinity tolerance of viburnum species. The Center for Applied Nursery Research Grant, University of Georgia, Athens, GA. 3/1/2019-3/1/2020. Total Project Award: \$2,500.

- Chen J**, and Sun Y. 2022. Quantifying Soil Water Availability to Select Low Water Use Plants for Water-Efficient Landscaping. Grant A. Harris Fellowship, Meter Group, Inc., Pullman, WA. (Declined).
- Chen J**, and Sun Y. 2022. Determining Drought Tolerance of Penstemons Using Automatic Irrigation System. Graduate Student Grant Opportunity for Penstemon Research, The American Penstemon Society, Marsing, ID. (Declined).
- Chen J**, and Sun Y. 2019. Studying the Plant-Bacteria Association and Symbiosis of Utah Native Plants. Graduate Research and Creative Opportunities Award, Utah State University, Logan, UT. (Declined).

Proposal Writing Workshop

Sep 2022 Graduate Student Proposal Writing Seminar

PRESENTATIONS AT NATIONAL MEETINGS

Oral Presentations

- Chen J**, and Sun Y. Using thermal imaging to detect plant water status. Scholars Ignite Competition at the 2022 American Society for Horticultural Science Annual Conference, Chicago, IL. 31 July 2022.
- Chen J**, and Sun Y, and Kopp K. Detecting drought stress of penstemons using infrared thermal imaging. 2022 American Society for Horticultural Science Annual Conference, Chicago, IL. 31 July 2022.
- Chen J**, Jones SB, and Sun Y. Is your sensor still accurate? Soil Physics and Hydrology Division at the 2021 Soil Science Society of America Annual Conference, Salt Lake City, UT. 8 Nov. 2021.
- Chen J**, and Sun Y. Natural sunscreen for buffaloberry. Scholars Ignite Competition at the 2021 American Society for Horticultural Science Annual Conference, Denver, CO. 6 Aug. 2021.
- Chen J**. How to be successful in graduate student competitions at the ASHS annual conference. American Society for Horticultural Science Webinar Series, Virtual. 20 May 2021.
- Chen J**, and Sun Y. Nodulation of *Shepherdia ×utahensis* ‘Torrey’ top-dressed with controlled-release fertilizer. 2020 American Society for Horticultural Science Annual Conference, Virtual. 12 Aug. 2020.
- Chen J**. Research and life at Utah State University. National Chung Hsing University, Taiwan. [Sponsored by the International Partnership in Agriculture, Climate and Environment (iPACE) at Utah State University]. 19 Dec. 2019.
- Chen J**, and Sun Y. Comparing the salt tolerance of three landscape plants using a near-continuous gradient dosing system. Scholars Ignite Competition at the 2019 American Society for Horticultural Science Annual Conference, Las Vegas, NV. (Placed 8th of 55 students). 24 July 2019.

Poster Presentations

- Chen J**, Mathews J, Paudel A, and Sun Y. Field trials of 26 ornamental grass and grass-

like plants. 2022 American Society for Horticultural Science Annual Conference, Chicago, IL. 2 Aug. 2022.

Chen J, Jones SB, and Sun Y. Water content sensor integrity: Is your sensor still accurate? Soil Science Society of America Annual Conference, Salt Lake City, UT. 8 Nov. 2021.

Chen J, and Sun Y. Buffaloberry changes its leaf morphology and reflectivity under water stress. 2021 American Society for Horticultural Science Annual Conference, Denver, CO. (Placed 5th of 62 Ph.D. students). 8 Aug. 2021.

Chen J, Zhen S, and Sun Y. Using NDVI sensors to determine the chlorophyll content of *Shepherdia ×utahensis* ‘Torrey’. 2020 American Society for Horticultural Science Annual Conference, Virtual. (**3rd Place in Graduate Student Poster Competition**). 13 Aug. 2020.

Chen J, Xing H, Paudel A, Sun Y, and Niu G. Salinity tolerance of 12 viburnum taxa. 2020 American Society for Horticultural Science Annual Conference, Virtual. 11 Aug. 2020.

Chen J, Wang Y, Paudel A, and Sun Y. Comparing the salt tolerance of three landscape plants using a near-continuous gradient dosing system. 2019 American Society for Horticultural Science Annual Conference, Las Vegas, NV. 23 July 2019.

PRESENTATIONS AT REGIONAL/LOCAL MEETINGS

Oral Presentations

Chen J, and Sun Y. An evaluation of homeowner preference for native landscape plants under deficit irrigation. 2022 Annual Meeting of Western Education/Extension and Research Activity (WERA)-1013 group, Intermountain Regional Evaluation and Introduction of Native Plants, Virtual. 28 Oct. 2022.

Chen J. Using satellite imagery to monitor urban vegetation. Project Presentation of the Remote Sensing of the Environment Class, Logan, UT. 17 Apr. 2022.

Chen J, and Sun Y. Turgor-driven trichome density change of buffaloberry. 2021 Annual Meeting of WERA-1013 group, Intermountain Regional Evaluation and Introduction of Native Plants, Virtual. 29 Oct. 2021.

Chen J, Kratsch H, Norton J, Sun Y, and Rupp L. Nodulation and growth of *Shepherdia ×utahensis* ‘Torrey’ treated with controlled-release fertilizer. 2020 Annual Meeting of WERA-1013 group, Intermountain Regional Evaluation and Introduction of Native Plants, Virtual. 18 Sept. 2020.

Chen J, and Sun Y. Nodulation of *Shepherdia ×utahensis* ‘Torrey’. 2019 Annual Meeting of WERA-1013 group, Intermountain Regional Evaluation and Introduction of Native Plants, Spokane, WA. 4 Oct. 2019.

Poster Presentations

Chen, J. Using Satellite Imagery to Quantify the Impacts of Utah Drought on Urban Vegetation Coverage. Spring Run-Off Conference, Logan, UT. 15 Mar. 2023.

Chen J, and Sun Y. Drought resistant mechanisms of water-wise landscape plants. USU

Research Symposium, Virtual. 15 Apr. 2021.

Chen J, and Sun Y. Mechanisms of water-wise ornamental plants to tolerate water stress. Intermountain Sustainability Summit, Virtual. 18 Mar. 2021.

Chen J, Zhen S, and Sun Y. Using NDVI sensors to determine chlorophyll content of *Shepherdia ×utahensis* ‘Torrey’. USU Research Symposium, Logan, UT. 11 Apr. 2020.

Chen J, and Sun Y. Nodulation of *Shepherdia ×utahensis* ‘Torrey’ topdressed with controlled-release fertilizer. Intermountain Sustainability Summit at Weber State University, Ogden, UT. 19 Mar. 2020.

Chen J, Wang Y, Paudel A, and Sun Y. Comparing the salt tolerance of three landscape plants using a near-continuous gradient dosing system. Spring Run-Off Conference, Logan, UT. 11 Mar. 2020.

SKILLS

1. Chlorophyll Extraction using Dimethyl Sulphoxide Solvent
2. CIRAS-3 Portable Photosynthesis System (PP Systems, Amesbury, MA)
3. CM-100 Chlorophyll Meter (Apogee Instruments, Logan, UT)
4. CR1000X Datalogger (Campbell Scientific, Logan, UT)
5. DNA Extraction and Polymerase Chain Reaction (PCR) Techniques
6. EE08-SS Relative Humidity Probe (E+E Elektronik, Engerwitzdorf, Austria)
7. Li-Cor Portable Area Meter Model Li-3000 (LI-COR Biosciences, Lincoln, NE)
8. NDVI and Quantum Sensors (Apogee Instruments, Logan, UT)
9. Pressure Chamber Instrument (PMS Instrument Company, Albany, OR)
10. SAS Studio (SAS Institute, Cary, NC)
11. SPAD-502 Chlorophyll 210 Meter (Spectrum Technologies, Bridgend, UK)
12. TDR-315H Soil Water Content Sensor (Acclima, Boise, ID)
13. Hydrus-1D Numerical Simulation
14. Programming Skills for Remote Sensing Data Analysis using HydroShare JupyterHub

SERVICE

1. **Moderator, 2022 American Society for Horticultural Science Annual Conference.** Moderated the "Nursery Crops/Technology Applications in Horticulture" and "Growth Chamber and Controlled Environment" sessions in the conference. Chicago, IL. 31 July 2022.
2. **Moderator, 2022 Conference of Applied Statistics in Agriculture and Natural Resources.** Moderated virtual and in-person Q&A sessions at the conference. Logan, UT. 3 May 2022.
3. **Judge, 2022 Utah State University Student Research Symposium.** Judged the undergraduate student poster competition. Logan, UT. 4 Apr. 2022.
4. **Judge, 2021 ASA, CSSA, SSS Undergraduate Student Poster Competition.** Judged the student poster competition of diversity, equity, inclusion (DEI), and justice. Salt Lake City, UT. 7 Nov. 2021.
5. **Organizer, 2021 Annual Meeting of Western Education/Extension and Research**

- Activity 1013 group, Intermountain Regional Evaluation and Introduction of Native Plants.** Organized meeting and moderated the presentations. Virtual. 29 Oct. 2021.
- 6. Moderator, 2021 American Society for Horticultural Science Annual Conference.** Moderated the "Nursery Crops" poster session in the conference. Denver, CO. 1 Aug. 2021.
 - 7. Volunteer Chinese Tutor.** Helped religious missionaries practice Mandarin in preparation of mission trips to Taiwan. Virtual. 1 Dec. 2020 – 30 Apr. 2021.
 - 8. Secretary of the International Horticultural Issues and Networking Group of the American Society for Horticultural Science.** Helped organize business meetings of the international horticultural issues and networking group. Virtual. 1 Oct. 2019 – 30 Sept. 2020.
 - 9. Leadership Role in the Cache Valley Toastmasters Club.** Assisted in the operation of the Toastmasters Club and helped people from the community practice oral presentations and leadership skills. Logan, UT. 1 Apr. 2019 – 31 Dec. 2019.