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Physiological and Canopy Temperature Responses to Drought of Four Penstemon Species

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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 $m^3{\cdot}m^{-3}$ for 50 days. The decreased substrate volumetric water content resulted in a decreased 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 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, the 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*.**

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, CA (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 $m^3{\cdot}m^{-3}$ (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_o) to 25% ET_o 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 polyethylene greenhouse (Logan, UT) and irrigated with Logan City potable water (electrical conductivity = 0.381 $dS\cdot m^{-1}$; 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 Utah Agricultural Experiment Station 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 $m^3\cdot m^{-3}$ (control) and 0.15 $m^3\cdot m^{-3}$ (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 (ECH$_2$O 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 (θ_v = 10HS voltage × 0.0009–0.3688) (Chen et al. 2022). Twenty-four normally closed 24-V-AC solenoid valves (CPF100; Rain Bird, Azusa, CA) were connected to relay controllers (SDM-CD16AC, Campbell Scientific) 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 ± *SD*) $mL\cdot min^{-1}$ 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 min 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 $g\cdot cm^{-2}$ on 4 Jan 2022. The substrate in each container was irrigated to the volumetric water content of 0.40 $m^3\cdot m^{-3}$ 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 $m^3\cdot m^{-3}$, which are equivalent to the matric potentials 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 θ_p = (0.2923 × HydroSense output) − 0.3855.

Greenhouse environment

The ambient temperature within the greenhouse was maintained at 24.1 ± 0.7 °C (mean ± *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 to provide supplemental light at an intensity of 285.9 $\mu mol\cdot m^{-2}\cdot s^{-1}$ at the plant canopy level from 0600 to 2200 HR whenever light intensity inside the greenhouse was less than 500 $\mu mol\cdot m^{-2}\cdot s^{-1}$. The daily light integral and photosynthesis photon flux density at plant canopy level were 29.4 ± 3.9 (mean ± *SD*) $mol\cdot m^{-2}\cdot d^{-1}$ and 343.4 ± 41.0 $\mu mol\cdot m^{-2}\cdot s^{-1}$, 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, with 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

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growth index {[height+(width 1 + 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). The 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 d 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 the fresh weight and dry weight of shoots and the following equation: [(fresh weight − dry weight)/fresh weight] × 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with 90% red light and 10% blue light provided by light-emitting diodes (Small Light Source, LI-COR Biosciences), and the carbon dioxide concentration was set at 420 $\mu mol \cdot mol^{-1}$. 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 and 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 h 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 plants were exposed to supplemental light for 2 h. 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 $m^3 \cdot m^{-3}$. Therefore, substrate volumetric water contents were maintained at levels more than 0.35 $m^3 \cdot m^{-3}$ 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 $m^3 \cdot m^{-3}$; 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 average 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 (Fig. 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 $m^3 \cdot m^{-3}$ 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. 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 ratios of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* experiencing drought stress increased 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,

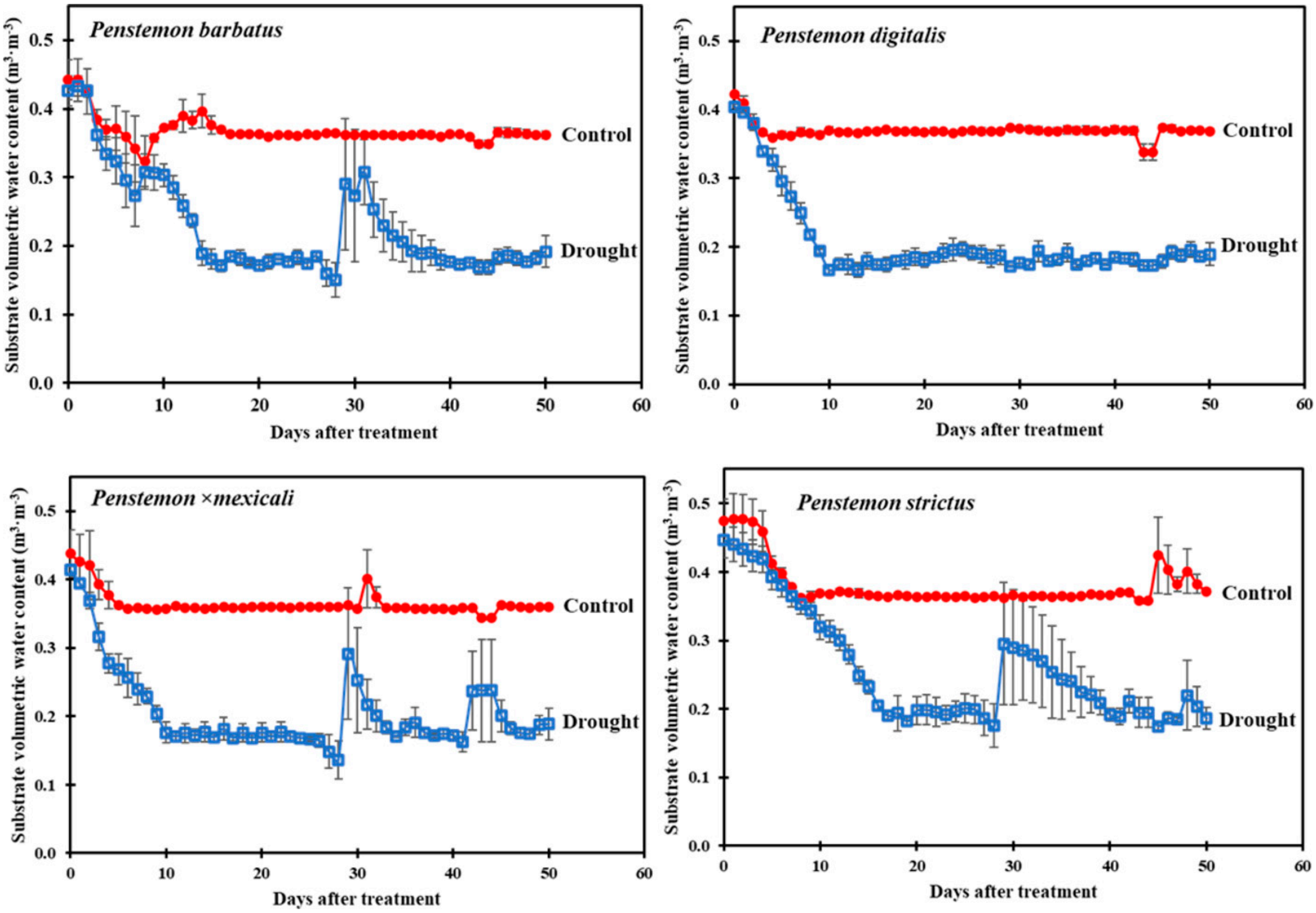

Fig. 1. Daily average volumetric water contents of substrates growing *P. barbatus* 'Novapenblu', *P. digitalis* 'TNPENDB', *P. ×mexicali* 'P007S', and *P. strictus* with the volumetric water content treatments of 0.35 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought). Measurements were recorded using calibrated soil moisture sensors (ECH$_2$O 10HS; Meter Group, Pullman, WA) during the experiment. Error bars represent the *SE* of three sensors.

at the termination of the experiment (Fig. 3I and 3J). 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·$m^{-2} \cdot s^{-1}$, respectively. Although not statistically significant, stomatal conductance of *P. strictus* was

Table 1. Substrate volumetric water content (VWC) and 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 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought) during the middle (24 Jan) and at the end (1 Mar) of the experiment. 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 was counted.

	24 Jan						1 Mar					
	VWC		Shoot no.		Inflorescence no.		VWC		Shoot no.		Inflorescence no.	
Species	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
P. barbatus	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
P. digitalis	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
P. ×mexicali	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
P. strictus	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 the same lowercase letters within a penstemon species and dependent variable are not significantly different among 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, *, ***, and **** represent nonsignificant and significant at $P \leq 0.05$, 0.001, and 0.0001, respectively.

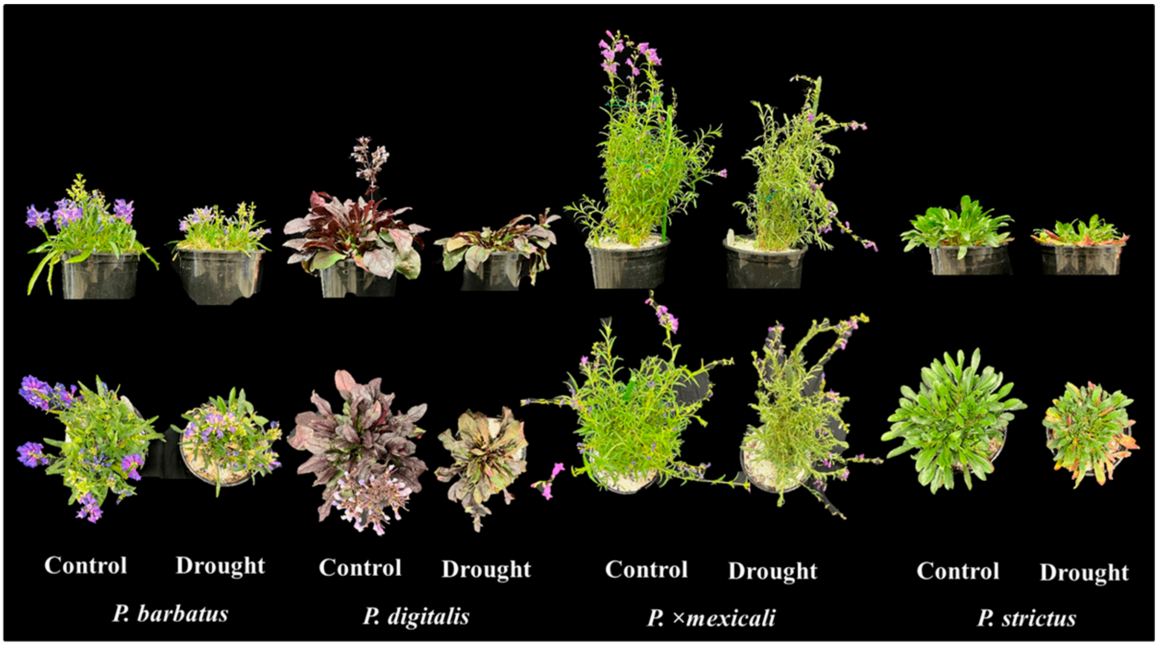

Fig. 2. Representative plants of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of 0.35 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought) at the end of the experiment (photo taken on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

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 differences 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 differences of *P. barbatus*, *P. digitalis*, and *P. ×mexicali* were 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

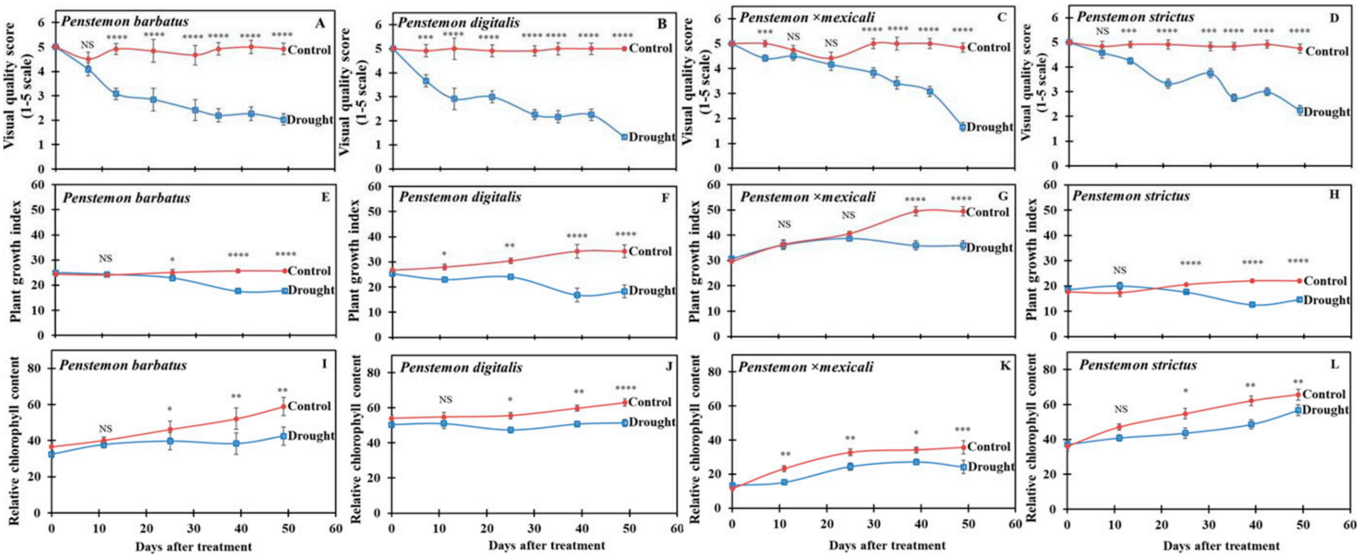

Fig. 3. Visual quality score (**A–D**), plant growth index {[height+(width 1 + width 2)/2]/2} (**E–H**), and relative chlorophyll content [Soil Plant Analysis Development (SPAD) value] (**I–L**) of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* with the volumetric water content treatments of 0.35 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (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, *, **, ***, and **** represent nonsignificant and significant at $P \leq 0.05$, 0.01, 0.001, and 0.0001, respectively.

Table 2. Number 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 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought) at the termination of the experiment.

	Leaves no.		Leaf area (cm^2)		Leaf size (cm^2)[i]		Shoot DW (g)		Shoot RWC ($g \cdot g^{-1}$)[ii]		SLA ($cm^2 \cdot g^{-1}$)[ii]		R/S ($g \cdot g^{-1}$)[iii]	
Species	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
P. barbatus	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
P. digitalis	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
P. ×*mexicali*	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
P. strictus	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 following equation: [fresh weight (FW) − dry weight (DW)]/FW × 100%, whereas the 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, *, **, ***, and **** represent nonsignificant and significant at $P \leq 0.05$, 0.01, 0.001, and 0.0001, respectively.

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 $m^3 \cdot m^{-3}$ 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 $m^3 \cdot m^{-3}$, respectively. Without high-pressure sodium light, the canopy temperature of *P. digitalis* and *P.* ×*mexicali* with the two substrate volumetric water contents was 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 $m^3 \cdot m^{-3}$, 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

Table 3. Net assimilation rate (P_n), stomatal conductance (g_s), transpiration rate (*E*), and leaf reflectance of photosynthetically active radiation (PAR) and 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 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought).

	Gas exchange responses						Leaf reflectance[i]									
	P_n		g_s		*E*		PAR		Blue		Green		Red		NIR	
	($\mu mol \cdot m^{-2} \cdot s^{-1}$)		($mol \cdot m^{-2} \cdot s^{-1}$)		($mmol \cdot m^{-2} \cdot s^{-1}$)		(%)									
Species	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
P. barbatus	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
P. digitalis	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
P. ×*mexicali*	7.86 a	2.33 b	0.08 a	0.03 b	2.40 a	1.18 b	[iii]									
P. strictus	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	

[i] Reflectance of PAR was determined using the wavelengths from 400 to 700 nm, while 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).

[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 the small leaves.

[iv] NS, *, **, and **** represent nonsignificant and significant at $P \leq 0.05$, 0.01, and 0.0001, respectively.

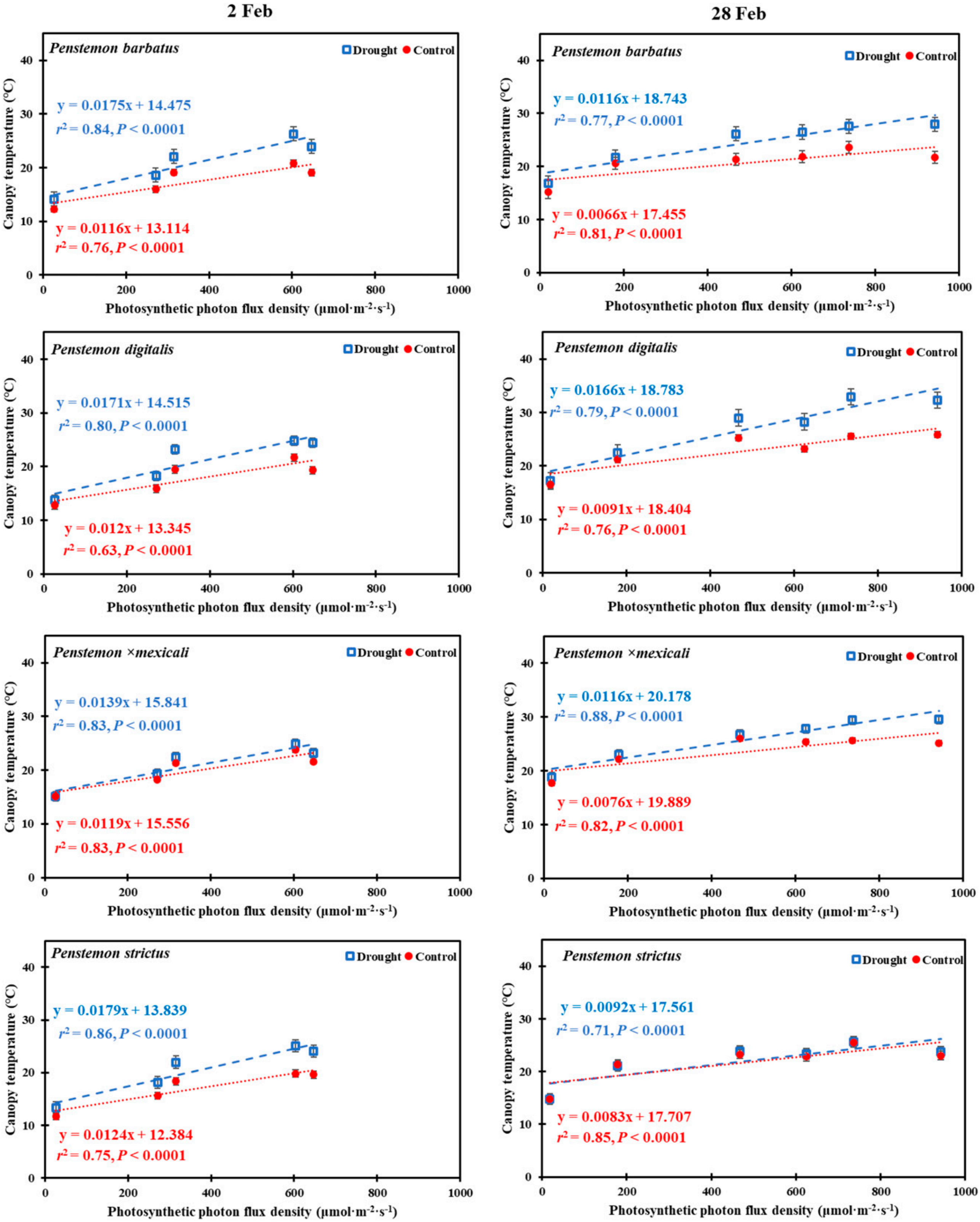

Fig. 4. Correlation between photosynthetic photon flux density and canopy temperature of *P. barbatus* 'Novapenblu', *P. digitalis* 'TNPENDB', *P. ×mexicali* 'P007S', and *P. strictus* with the volumetric water content treatments of 0.35 m^3·m^{-3} (control) and 0.15 m^3·m^{-3} (drought) on 2 Feb and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

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

Table 4. Canopy–air temperature differences of *Penstemon barbatus* ‘Novapenblu’, *P. digitalis* ‘TNPENDB’, *P. ×mexicali* ‘P007S’, and *P. strictus* 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 1400 HR on 2 Feb and 28 Feb 2022.

	Canopy–air temp difference (°C)			
	2 Feb		28 Feb	
Species	Control	Drought	Control	Drought
P. barbatus	−4.4 b[i]	1.2 a	−4.6 b	1.7 a
P. digitalis	−3.5 b	−0.3 a	−0.4 b	6.0 a
P. ×mexicali	−1.4 a	−0.2 a	−1.1 b	3.3 a
P. strictus	−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, *, **, and **** represent nonsignificant and significant at $P \leq 0.05$, 0.01, and 0.0001, respectively.

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 a 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 for *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 $m^3 \cdot m^{-3}$. 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 with 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 the 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 $mol \cdot m^{-2} \cdot s^{-1}$ had cooler leaf temperatures as compared with water-stressed plants with a stomatal conductance of 0.1 $mol \cdot m^{-2} \cdot s^{-1}$. 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 $m^3 \cdot m^{-3}$ became greater at the termination of the experiment. Plants grown without water stress often have canopy–air temperature differences within 2 °C of ambient temperature in a glass greenhouse (Nelson and Bugbee 2015). In

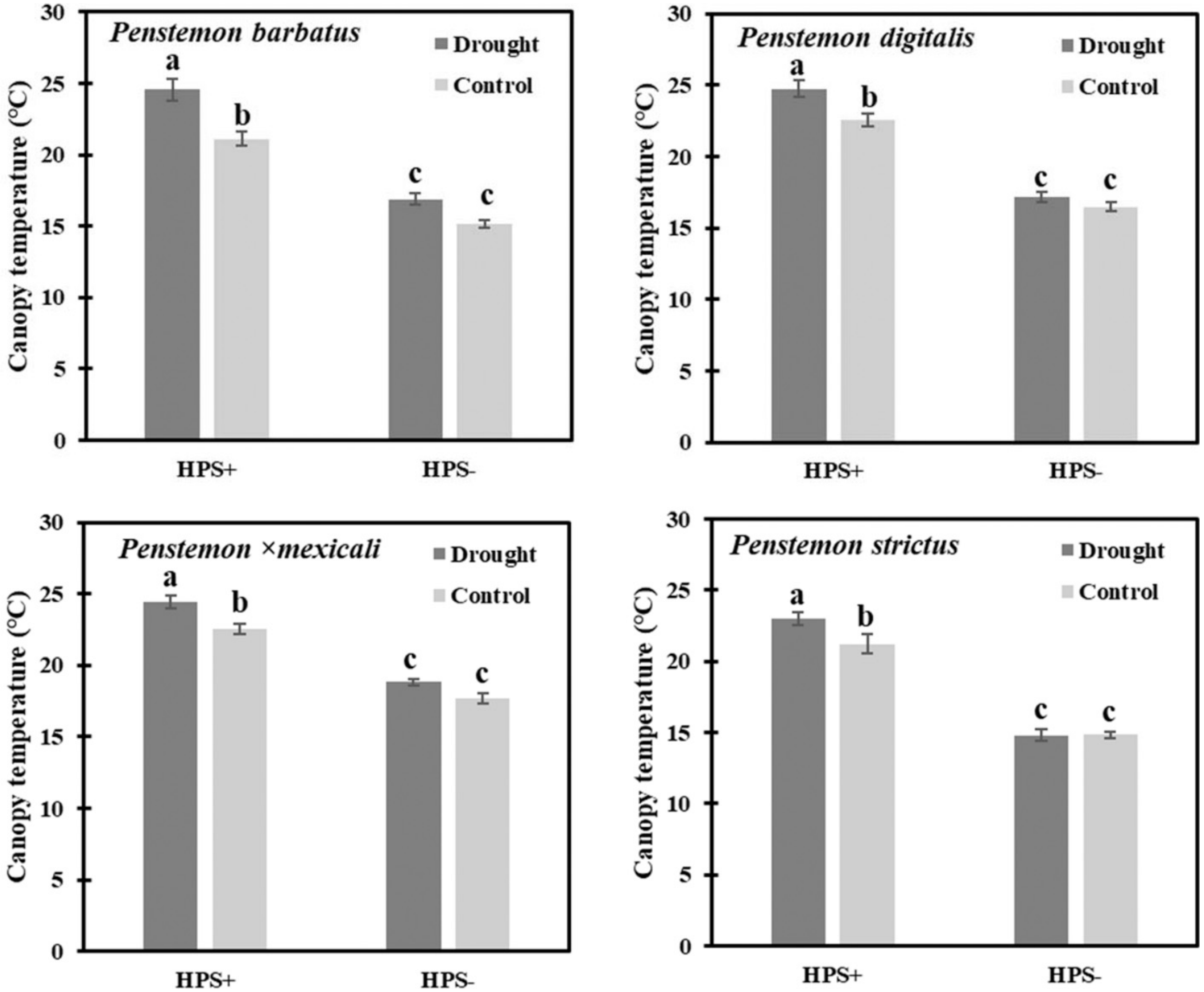

Fig. 5. Canopy temperature of *Penstemon barbatus* 'Novapenblu', *P. digitalis* 'TNPENDB', *P.* ×*mexicali* 'P007S', and *P. strictus* with the volumetric water content treatments of 0.35 $m^3 \cdot m^{-3}$ (control) and 0.15 $m^3 \cdot m^{-3}$ (drought) with high-pressure sodium lights (HPS+) or without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

our study, however, *P. digitalis* and *P.* ×*mexicali* had canopy–air temperature differences greater than 2 °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 °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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