

Effects of Reduced Substrate Volumetric Water Contents on the Morphology and Physiology of Three Landscape Shrubs Grown in a Greenhouse

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Abstract. Reduced precipitation and increasing temperatures caused by climate change have escalated the irrigation requirements for maintaining the aesthetic quality of urban landscape plants. Many cities in the western United States now mandate the incorporation of drought-tolerant plants in new landscapes because of concerns regarding water scarcity. However, a knowledge gap persists regarding the drought tolerance of ornamental plant species commonly used in urban landscapes. The objectives of this study were to determine the effects of decreased volumetric water contents on the morphology, physiology, and plant growth of *Rosa ×hybrida* ‘Meibenhino’ (Petite Knock Out® rose), *Salvia rosmarinus* ‘Arp’ (‘Arp’ rosemary), and *Vitex agnus-castus* ‘SMVACBD’ (Blue Diddley® chaste tree). Twenty-four plants of each species were randomly assigned to an automated irrigation system, and the substrate volumetric water content was maintained at 0.40 or 0.20 m³·m⁻³ for 50 days. As the substrate volumetric water content declined, plants exhibited an increase in the proportion of visibly wilted and damaged leaves as well as chlorosis. Rose, rosemary, and vitex experienced up to a 30% decrease in the plant growth index [(height + width 1 + width 2)/3], whereas leaf dry weights (DWs) decreased by 84%, 66%, and 58%, respectively. Landscape plants in this study acclimated to drought stress by reducing the total leaf area, developing small leaves, increasing the root-to-shoot ratio, and decreasing stomatal conductance. However, stomatal closure also led to increases in leaf temperatures because of limited transpirational cooling efficiency. For the rosemary, trichome density on the adaxial surface increased as the substrate volumetric water content decreased. The trichome density might be regulated by turgor-pressure-driven cell expansion because the trichome density decreased with the increased leaf width. Rose was sensitive to decreased substrate water availability, resulting in severe growth reduction with a high leaf–air temperature difference. Rosemary maintained better visual quality than that of rose, but the low root-to-shoot ratio resulted in a high leaf–air temperature difference. Vitex, which had the highest root-to-shoot ratio, exhibited the lowest canopy–air temperature and lower growth reduction. Overall, under the experimental conditions, *S. rosmarinus* ‘Arp’ and *V. agnus-castus* ‘SMVACBD’ showed better tolerance to drought stress compared with that of *R. ×hybrida* ‘SMVACBD’.

Urban and suburban areas in the western United States have experienced rapid population growth, leading to increased demands for potable water (Mini et al. 2014). Hayden et al. (2015) reported that 70% of residential water usage per capita in the region is attributed to landscape irrigation. The drier and hotter climates prevalent in these areas have necessitated large quantities of irrigation water to sustain the visual quality, growth, and development of landscape plants (Sun et al. 2012). In addition, states from the Rocky Mountains to the Pacific Coast have experienced a prolonged drought characterized by low rainfall and consistently high temperatures

since 2003, with nine of the top 10 warmest years occurring in this region between 2003 and 2022 (National Centers for Environmental Information 2023). Communities that encounter water shortages have often imposed restrictions on water usage for landscape irrigation (Evans et al. 2022). Such restrictions could significantly compromise the aesthetic quality and growth of landscape plants (Miller et al. 2020). For example, urban green vegetation coverage declined from 29.3% to 24.6% after landscape irrigation restrictions imposed by the County of Los Angeles, CA, USA, during the drought from 2012 to 2016 (Allen et al. 2021). To sustain urban greenery amid water scarcity, new

landscapes are mandated to incorporate drought-tolerant plants capable of maintaining growth and aesthetic quality with reduced irrigation (California Department of Water Resources 2023). In the County of San Diego, CA, USA, new residential landscapes are required to include drought-tolerant plants in 75% of the total plant area (County of San Diego 2020). Similarly, the city of Moab, UT, USA, required that 50% of living plant materials in residential landscapes to be low-water-use plants (WaterNow Alliance 2022). Unfortunately, responses of landscape plants to drought and their tolerance levels have not been widely investigated, and assessments have largely relied on local precipitation rates (Chen et al. 2023b).

Evapotranspiration gradually depletes the amount of plant available water in the soil profile, thus causing plant dehydration and compromising the aesthetic quality of landscape plants by increasing wilted and damaged leaves and reducing floral abundance (Chen et al. 2023b). For example, when irrigation water decreased from 80% to 20% of the reference evapotranspiration (ET₀), the overall visual quality score of *Abelia ×grandiflora* ‘Bailbeliaone’ (‘Bailbeliaone’ glossy abelia) decreased from 3.2 to 2.8, thereby reaching unacceptable aesthetic quality (Reid et al. 2021). Furthermore, Zollinger et al. (2006) found that *Echinacea purpurea* (purple coneflower) exhibited an increase in the number of visibly wilted and burned leaves when irrigation intervals increased from once each week to once every 4 weeks. Drought stress reduces the net photosynthetic rate and plant growth, thereby significantly decreasing the ornamental value of landscape plants (Cai et al. 2012). *Phillyrea angustifolia* (narrow-leaved mock privet) showed decreased stomatal conductance, a decreased net photosynthetic rate, and decreased leaf dry weight (DW) when irrigation water was decreased by 40% (Álvarez et al. 2019). Moreover, drought-induced leaf senescence and chlorosis can impair the aesthetic quality of *Petunia ×hybrida* (petunia) (Clark et al. 2004). However, drought-tolerant landscape plants often maintain visual quality and growth under drought stress. For example, Caser et al. (2012) reported that *Salvia dolomitica* (dolo-mite sage) and *Salvia sinaloensis* (sinaloan blue sage) are low-water-use landscape plants because their relative leaf chlorophyll contents were unaffected by decreases in substrate volumetric water contents from 100% to 60% of the container capacity.

Aside from plant dehydration, heat stress and canopy overheating can negatively affect the visual quality and growth of landscape plants when water availability decreases. When plants are adequately irrigated, a large proportion of solar radiation absorbed by a leaf is balanced through transpirational cooling (Bowen 1926). However, under drought stress, stomatal closure reduces the efficiency of transpirational cooling, leading to an increase in leaf temperature (Nelson and Bugbee 2015). The leaf temperature of a water-stressed plant can exceed the ambient temperature, resulting in a positive

leaf–air temperature difference (Jagadish et al. 2021). An elevation in the leaf–air temperature difference can have adverse effects on the visual quality and physiology of landscape plants (Chen et al. 2023a). Zhang et al. (2019) found that leaf–air temperature differences were negatively correlated with transpiration rates and net photosynthetic rates. For landscape plants, a high leaf–air temperature difference diminishes the overall aesthetic quality by increasing the proportion of visibly wilted leaves and decreasing the floral abundance (Rafi et al. 2019). When the irrigation rate decreased from 100% to 25% ET_O, drought-sensitive *Begonia* × *semperflorens* ‘Vodka’ (‘Vodka’ wax begonias) exhibited an increase in leaf–air temperature differences from 4.2 to 10.2 °C, resulting in severe leaf damage (Henson et al. 2006). In contrast, the leaf–air temperature difference of drought-tolerant *Zinnia angustifolia* ‘Crystal Orange’ (‘Crystal Orange’ narrowleaf zinnia) was 2.1 °C at an irrigation rate of 25% ET_O, thus demonstrating good ornamental quality with minimal signs of water stress (Henson et al. 2006).

Drought-tolerant landscape plants have the capacity to modify their morphology and physiology to adapt to heat stress and cell dehydration under drought conditions (Zollinger et al. 2006). These plants can close their stomata and reduce the total leaf area to minimize excessive water loss through canopy transpiration (Zollinger et al. 2006). Although soil water availability decreases, root growth is promoted. However, shoot development is restricted, resulting in an increased root-to-shoot ratio to promote water uptake from soil profiles (Niu and Rodriguez 2009). Under drought conditions, drought-tolerant plants can produce small leaves to dissipate heat through convection and conduction, thus maintaining leaf temperature close to air

temperature (Leigh et al. 2017). For example, the leaf width of herbaceous and woody plants native to the arid Intermountain West regions is often less than 2.5 cm, thus allowing leaves to dissipate heat more efficiently when latent heat loss is restricted (Mee et al. 2003). Some drought-tolerant plants can also develop protective leaf structures, such as dense leaf hairs, to increase leaf reflectance of visible light and avoid excessive solar radiation absorption (Ehleringer et al. 1976). Ehleringer (1982) observed that *Encelia farinosa* (brittlebush) exhibited a higher density of leaf hairs when air temperature increased or the amounts of irrigation water were reduced.

Rosa × *hybrida* ‘Meibenhino’ (Petite Knock Out® rose), which is hereafter referred to as rose, is a miniature rose with outstanding disease resistance (Star Roses and Plants 2022). Although a nursery in the humid Great Lakes region lists it as a drought-tolerant cultivar (McKay Nursery 2023), this cultivar showed unacceptable visual aesthetic quality when the total amount of irrigation water was reduced from 80% to 20% ET_O during a field study conducted in the Intermountain West (Chen et al. 2023b). *Salvia rosmarinus* ‘Arp’ (‘Arp’ rosemary), which is hereafter referred to as rosemary, is a cold-hardy shrub with an upright growth habit (Monrovia Nursery 2023). It performs well in areas with intense solar radiation and hot temperatures (High Country Gardens 2023). *Vitex agnus-castus* ‘SMVACBD’ (Blue Diddle® chaste tree), which is hereafter referred to as vitex, is a deciduous shrub native to arid and semi-arid Mediterranean regions (Daniele et al. 2005). Previous studies have observed that vitex can acclimate to hot and dry environments (Ari et al. 2015). However, further studies are necessary to assess the relative drought responses of these three ornamental plant species in the semi-arid climate of northern Utah.

This research aimed to determine the effects of reduced substrate volumetric water contents on the growth, morphological, and physiological responses of the rose, rosemary, and vitex plants in a greenhouse. We hypothesized that decreasing the substrate volumetric water content from 0.40 to 0.20 m³·m⁻³ would reduce plant growth and stem water potentials while increasing canopy temperatures and the proportion of visibly wilted leaves, and that the three ornamental plant species would modify their morphology and physiology to acclimate to water stress. To test these hypotheses, the objectives of this research were to quantify the growth, morphological, and physiological differences of the three ornamental plant species at the volumetric water contents of 0.40 and 0.20 m³·m⁻³ under greenhouse conditions, and to determine the relationship between the visual quality of each species and their morphological and physiological changes under decreased substrate volumetric content.

Materials and Methods

Plant materials

Rosemary plants purchased from Monrovia Nursery (Azusa, CA, USA) were received

on 20 May 2022, whereas vitex plants purchased from Spring Meadow Nursery (Grand Haven, MI, USA) were received on 7 Jun 2022. Rose plants donated by Star Roses and Plants Nursery (Grove, PA, USA) were received on 21 Jun 2022. Plants were transplanted to 7.6-L injection-molded polypropylene containers (No. 2B; Nursery Supplies, Orange, CA, USA) filled with a soilless substrate (Metro-Mix® 820; SunGro Horticulture, Agawam, MA, USA). Plants were kept in a Utah Agricultural Experiment Station research greenhouse (Logan, UT, USA) and irrigated manually using tap water (electrical conductivity = 0.381 dS·m⁻¹; pH = 7.73). Each plant was top-dressed with 15N–3.9P–10K slow-release fertilizer (Osmocote Plus 15–9–12; Israel Chemicals, Tel Aviv-Yafo, Israel) at a rate of 2 g·L⁻¹ on 7 Sep 2022.

Plants were irrigated using a sensor-based automated irrigation system on 18 Sep 2022 (Chen et al. 2022). The irrigation system included three blocks and two treatments, and substrate volumetric water contents were controlled at 0.40 m³·m⁻³ (control) and 0.20 m³·m⁻³ (drought). Four plants, randomly chosen from each species, were assigned to each treatment within each block. A capacitance sensor (ECH2O 10HS; Meter Group, Pullman, WA, USA) was vertically inserted into the substrate (15 cm deep) of one container randomly selected from the four plants to measure the substrate volumetric water content. A multiplexer (AM 16/32B; Campbell Scientific, Logan, UT, USA) was connected to 18 capacitance sensors and a datalogger (CR1000X; Campbell Scientific). The datalogger scanned the voltage output (mV) of each capacitance sensor every 15 min to calculate the substrate volumetric water content (θ_v) using a substrate-specific calibration equation (θ_v = 10HS voltage × 0.0009 – 0.3688) (Chen et al. 2022). Two relay controllers (SDM-CD16AC; Campbell Scientific) were connected with the datalogger and 18 normally closed 24-V-AC solenoid valves (CPF100; Rain Bird, Azusa, CA, USA). When the measured substrate volumetric water content fell below the corresponding setpoints, the solenoid valve would open for 1 minute to irrigate the four plants in each treatment within each block using pressure-compensated drip emitters at a flow rate of 219.8 ± 16.5 (mean ± SD) mL·min⁻¹.

On 22 Sep 2022, the experiment was initiated after the substrates in containers were irrigated to the substrate volumetric water content of 0.40 m³·m⁻³. Thereafter, the irrigation was controlled at a setpoint of 0.40 or 0.20 m³·m⁻³, which are equivalent to matric potentials of –0.012 and –0.067 MPa, respectively (Chen et al. 2022). The substrates in the containers were maintained at the irrigation setpoint of 0.40 or 0.20 m³·m⁻³ until the experiment was ended on 13 Nov 2022. Apart from the measurements of capacitance sensors throughout the experiment, a handheld soil moisture sensor (HydroSense; Campbell Scientific) was inserted into the substrate of each container to determine the substrate volumetric water content (θ_p) on 14 Oct (3 weeks after experiment

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initiation) and 10 Nov 2022 (end of the experiment). A sensor-specific calibration equation was used to calculate substrate water content as follows: $\theta_p = (0.2923 \times \text{handheld sensor output}) - 0.3855$ (Chen et al. 2022).

Greenhouse environment

Air temperatures inside the greenhouse were maintained at $25.3 \pm 0.8^\circ\text{C}$ (mean \pm SD) during the day and $21.6 \pm 0.3^\circ\text{C}$ (mean \pm SD) at night. Supplemental light was provided using light-emitting diodes (Luxx 200w; Luxx Lighting, Mira Loma, CA, USA) at an intensity of $268.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ 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 photosynthesis photon flux density at the plant canopy height was 264.9 ± 38.7 (mean \pm SD) $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, whereas the daily light integral was $22.7 \pm 4.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, which was recorded using a full-spectrum quantum sensor (SQ-500-SS; Apogee Instruments, Logan, UT, USA).

Data collection

Visual quality assessment. The proportion of visibly wilted leaves was rated weekly using a scale of 1 to 5 (1 = poor quality, >65% of leaves visibly wilted; 2 = unacceptable visual quality, 36% to 65% of leaves visibly wilted; 3 = acceptable visual quality, 11% to 35% of leaves visibly wilted; 4 = good visual quality, up to 10% of leaves visibly wilted; 5 = excellent visual quality, plant fully turgid) (Zollinger et al. 2006). The foliage appearance was also evaluated weekly based on the proportion of visibly damaged leaves using a scale of 1 to 5 (1 = poor foliage quality, >50% of leaves visibly damaged; 2 = unacceptable foliage quality, 26% to 50% of leaves visibly damaged; 3 = acceptable foliage quality, 11% to 25% of leaves visibly damaged; 4 = good foliage quality, up to 10% of leaves visibly damaged; 5 = excellent foliage quality, no leaf visibly damaged) (Reid and Oki 2008).

Morphology and plant growth. The plant height was recorded weekly from the surface of the substrate to the tallest shoot tip. The plant width was measured weekly in perpendicular directions, and the plant growth index $\{[\text{height} + \text{width 1 (the widest point of canopy)} + \text{width 2 (perpendicular width of width 1)}]/3\}$ was calculated (Lalk et al. 2023). The numbers of flowers and shoots longer than 5 cm on each plant were recorded on 14 Oct and 10 Nov 2022. To determine the leaf width at the end of the experiment, five mature leaves were sampled from the second to the sixth node counting downward from the tip of the main shoot of each plant on 10 Nov 2022. The leaf length and width of each plant were estimated by averaging the length and width of the five mature leaves. Three mature leaves were randomly selected from each rosemary plant on 11 Nov 2022. Clear tape was attached to the adaxial surface to sample leaf glandular trichomes. One field of view (9.41 mm^2) at $50\times$ magnification was photographed from each

impression using a dissecting microscope (Wild M5A; Wild Heerbrugg, Heerbrugg, Switzerland) equipped with a camera (DP 74; Olympus Corporation, Tokyo, Japan). The number of glandular trichomes in each field of view was counted manually to determine the trichome density. In contrast, no glandular trichome was observed on the roses and vitexes. On 13 Nov 2022, plants were destructively harvested to quantify the fresh weight (FW) of stems and leaves, and their total leaf area was quantified using a leaf area meter (LI-3100; LI-COR Biosciences, Lincoln, NE, USA). The stems, leaves, and roots were oven-dried at 80°C for 23 d to obtain DWs. The root-to-shoot ratio was calculated as the ratio of the DW of the roots to shoots (stems and leaves), whereas the relative water content of shoots was calculated using the following equation: $[(\text{FW} - \text{DW}) / \text{FW}] \times 100\%$ (Zhou et al. 2021).

Relative chlorophyll content, leaf temperature, and gas exchange parameter. The relative chlorophyll content was recorded for each plant except for rosemary using a chlorophyll meter (SPAD-502; Minolta Camera, Osaka, Japan) on 14 Oct and 10 Nov 2022. The average soil plant analysis development (SPAD) value of five randomly selected leaves was recorded. Four plants were randomly selected from each species at each treatment, and the stem water potential of a matured shoot at the outer canopy was recorded at mid-day using a pressure chamber (PMS Instrument Company, Albany, OR, USA) on 14 Oct and 10 Nov 2022. Top-view thermal infrared images of plant canopies were recorded at mid-day using a thermal image camera (FLIR TG165-X; Teledyne FLIR, Wilsonville, OR, USA) on 14 Oct and 10 Nov 2022, and the leaf-air temperature difference was calculated as the difference between the mid-day leaf temperature and ambient air temperature measured using an air temperature sensor (ST-110-SS; Apogee Instruments), assuming that the leaf emissivity was equal to 1.0.

The gas exchange parameters, including stomatal conductance, leaf-air vapor pressure deficit, transpiration rate, and quantum yield of photosystem II (PhiPSII), were recorded on 13 Oct and 11 Nov 2022 using a porometer/fluorometer (Li-600; LI-COR Biosciences, Lincoln, NE, USA) for all species except for rosemary because of its small leaf size. The parameters of a healthy and fully expanded leaf on the outer canopy of each plant were recorded between 1100 HR and 1300 HR. At the end of the experiment, the net photosynthetic rate was recorded using a portable photosynthesis system (CIRAS-3; PP Systems, Amesbury, MA, USA) with a PLC3 universal leaf cuvette on a sunny day from 1000 HR to 1400 HR. The steady-state gas exchange rate of a matured leaf randomly selected from each plant was recorded after the leaf was enclosed in the cuvette for approximately 1 min. The photosynthetic photon flux density inside the cuvette was set at $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, with 38% red, 37% green, and 25% blue light supplied using light-emitting diodes, whereas

the CO_2 concentration and ambient temperature were controlled at $400 \mu\text{mol}\cdot\text{mol}^{-1}$ and 25°C , respectively.

Data analysis

The experiment was organized in a randomized complete block design with two substrate volumetric water content treatments and three blocks. An analysis of variance procedure was used to test the effects of substrate volumetric water contents on all measured parameters. Correlation analyses were performed to evaluate the relationship between leaf trichome density and leaf width of the rosemary. Means separations among treatments were conducted using the Tukey-Kramer method at $\alpha = 0.05$. Means separations were not conducted among species because of different plant growth habits. All statistical analyses were conducted using the PROC MIXED procedure in SAS Studio 3.8 (SAS Institute, Cary, NC, USA), with a significance level specified at 0.05.

Results

Substrate volumetric water content and visual quality. The substrate volumetric water contents reached their irrigation setpoints 3 weeks after the initiation of the experiment (Fig. 1) and were maintained at their setpoints until the end of the experiment. The substrate volumetric water contents measured using the handheld soil moisture sensor in containers under drought stress were lower than those of the control 3 weeks after experiment initiation and at the end of the experiment (Table 1).

Under the drought treatment, the proportion of visibly wilted leaves of the rose was less than 10% at 1 week after experiment initiation. However, decreases in substrate volumetric water contents from 0.40 to $0.20 \text{ m}^3\cdot\text{m}^{-3}$ increased the proportion of wilted leaves on the roses, and the plants had more than 65% of visibly wilted leaves at the end of the experiment (Figs. 2 and 3). The rosemary plants under drought stress exhibited up to 35% of visibly wilted leaves throughout the experiment. For the vitexes under drought stress, the proportion of visibly wilted leaves was less than 35% at 2 weeks after the experiment was initiated. Nonetheless, decreases in substrate volumetric water contents from 0.40 to $0.20 \text{ m}^3\cdot\text{m}^{-3}$ resulted in more than 65% of visibly wilted leaves on vitexes at the end of the experiment.

Roses under drought stress demonstrated an acceptable foliage appearance 2 weeks after experiment initiation, but they showed more than 50% visible leaf damage at the end of the experiment (Figs. 2 and 3). When substrate volumetric water contents decreased, the proportion of visibly damaged leaves on rosemary was less than 10% throughout the experiment. Vitexes under drought stress had acceptable foliage appearances, and the proportion of visibly damaged leaves was less than 25% at 3 weeks after experiment initiation. Nonetheless, decreases in the substrate

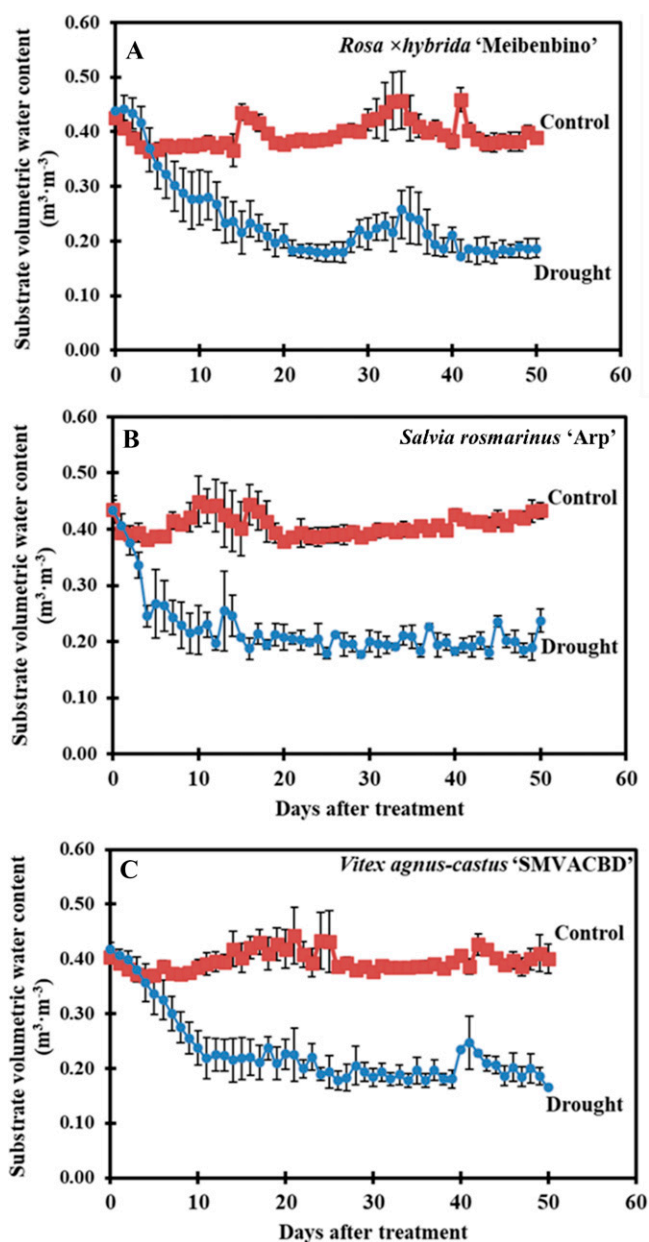


Fig. 1. Daily average volumetric water contents of substrates used for growing *Rosa ×hybrida* 'Meibenhino', *Salvia rosmarinus* 'Arp', and *Vitex agnus-castus* 'SMVACBD'. A substrate volumetric water content of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) was maintained using a sensor-based automated irrigation system with calibrated soil moisture sensors (ECH₂O 10HS; Meter Group, Pullman, WA, USA) during the experiment. Error bars represent the SE of three sensors.

volumetric water contents from 0.40 to $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ increased the proportion of visibly damaged leaves on the vitexes, and the

foliage appearance was graded as 1.6, with more than 50% damaged leaves visible at the end of the experiment.

Plant growth responses and relative chlorophyll contents. Drought treatment reduced the plant growth index of rose plants at 3 weeks after experiment initiation (Fig. 3). By the end of the experiment, decreases in substrate volumetric water contents from 0.40 to $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ reduced the plant growth index of the roses by 30%. Drought stress reduced the plant growth index of rosemary plants at 2 weeks after experiment initiation. At the end of the experiment, the plant growth index of rosemary plants under drought treatment was 30% lower than that of the control. Decreases in substrate volumetric water contents led to reductions in the plant growth indices of the vitexes by 14% at 2 weeks after experiment initiation and by 24% at the end of the experiment.

The shoot numbers of rose and rosemary plants decreased as the substrate volumetric water contents decreased on 14 Oct and 10 Nov 2022 (Table 1). In contrast, the drought treatment only decreased the number of shoots of vitex plants on 10 Nov 2022. On 14 Oct and 10 Nov 2022, the number of flowers per rose plant was greater when grown in substrate with a volumetric water content of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ compared with that of plants grown in substrate with a volumetric water content of $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ (data not shown). The SPAD values of the roses declined from 45 to 41 as the substrate volumetric water contents decreased on 14 Oct 2022. Conversely, drought stress decreased the SPAD values of vitex plants from 35 to 32 at the end of the experiment.

The total leaf area of the rose, rosemary, and vitex plants decreased by 84%, 66%, and 58%, respectively, when the substrate volumetric water contents declined from 0.40 to $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ at the end of the experiment (Table 2). Compared with those of the control, the DWs of leaves, stems, and roots of the roses reduced by 83%, 74%, and 79%, respectively. Decreased substrate volumetric water contents reduced the DWs of leaves, stems, and roots of the rosemary plants by 60%, 44%, and 64%, respectively. In contrast, decreases in substrate volumetric water contents only reduced the leaf and root DWs of the vitex plants by 61% and 22%, respectively, at the end of the experiment. Under drought stress, the vitex plants had a greater root-to-shoot ratio than that of the control. Drought treatments lowered the relative water

Table 1. Substrate volumetric water content (VWC), number of shoots, and relative chlorophyll content [Soil Plant Analysis Development (SPAD) value] of *Rosa ×hybrida* 'Meibenhino', *Salvia rosmarinus* 'Arp', and *Vitex agnus-castus* 'SMVACBD' treated with the VWCs of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) on 14 Oct and 10 Nov 2022. The VWC was measured using a handheld soil water content sensor (HydroSense; Campbell Scientific, Logan, UT, USA), and the number of shoots longer than 5 cm was counted.

| | 14 Oct | | | | | | 10 Nov | | | | | |
|------------------------|--|---------|---------|---------|---------|---------|--|---------|---------|---------|---------|---------|
| | VWC ($\text{m}^3 \cdot \text{m}^{-3}$) | | Shoots | | SPAD | | VWC ($\text{m}^3 \cdot \text{m}^{-3}$) | | Shoots | | SPAD | |
| | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought |
| <i>R. ×hybrida</i> | 0.24 a ⁱ | 0.12 b | 6.4 a | 3.1 b | 45 a | 41 b | 0.30 a | 0.05 b | 10.7 a | 3.0 b | 45 a | 47 a |
| <i>S. rosmarinus</i> | 0.23 a | 0.09 b | 51.1 a | 14.2 b | ii | ii | 0.23 a | 0.12 b | 73.8 a | 10.8 b | ii | ii |
| <i>V. agnus-castus</i> | 0.22 a | 0.09 b | 2.0 a | 1.6 a | 30 a | 27 a | 0.28 a | 0.11 b | 2.2 a | 0.8 b | 35 a | 22 b |

ⁱ Mean with the same lowercase letters within an ornamental species and dependent variable are not significantly different between treatment according to the Turkey-Kramer method, with a significance level specified at 0.05.

ⁱⁱ The relative chlorophyll content was not recorded for *S. rosmarinus* because of its small leaves.

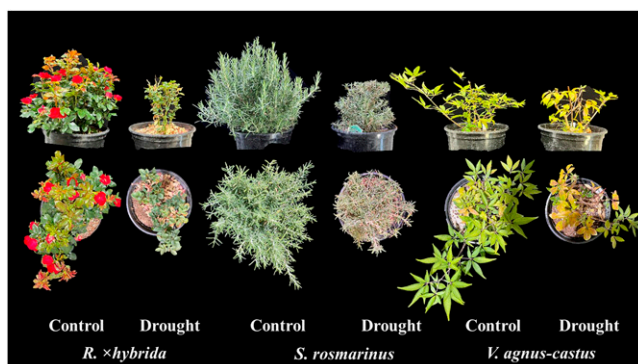


Fig. 2. Representative plants of *Rosa ×hybrida* ‘Meibenhino’, *Salvia rosmarinus* ‘Arp’, and *Vitex agnus-castus* ‘SMVACBD’ grown at the substrate volumetric water content of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) at the end of the experiment (photo taken on 14 Nov 2022).

content of shoots of the rose, rosemary, and vitex plants by 15%, 21%, and 12%, respectively. In addition, their leaf length decreased by 25%, 37%, and 40%, respectively, whereas their leaf width decreased by 19%, 39%, and 30%, respectively, when the substrate volumetric water

content decreased. Compared with the control, the rosemary plants showed higher trichome density on the adaxial surface when the substrate volumetric water contents decreased from 0.40 to $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ at the end of the experiment (Fig. 4). At the substrate volumetric water

content of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$, the adaxial leaf surface of the rosemary plants had 4.9 trichomes/ mm^2 (data not shown). However, the rosemary plants under drought stress had 8.2 trichomes/ mm^2 on the adaxial leaf surface (data not shown). A negative correlation was found between the trichome density on the adaxial leaf surface and leaf width, although the model fit was low ($r^2 = 0.04$, $P = 0.05$) (data not shown).

Stem water potential, leaf temperature, and physiological responses. On 14 Oct 2022, the drought treatment decreased the stem water potentials of the rose, rosemary, and vitex plants by 1.5 , 1.5 , and 1.2 MPa, respectively, compared with that of the control (Table 3). By the end of the experiment, the stem water potentials of rose, rosemary, and vitex plants decreased from -0.9 to -2.7 MPa, -1.0 to -2.4 MPa, and -1.3 to -2.4 MPa, respectively, when substrate volumetric water contents decreased from 0.40 to $0.20 \text{ m}^3 \cdot \text{m}^{-3}$. The leaf temperatures of the rose and rosemary plants under drought stress were 4.5°C and 2.4°C greater than that of the control, respectively, whereas vitexes did not show an

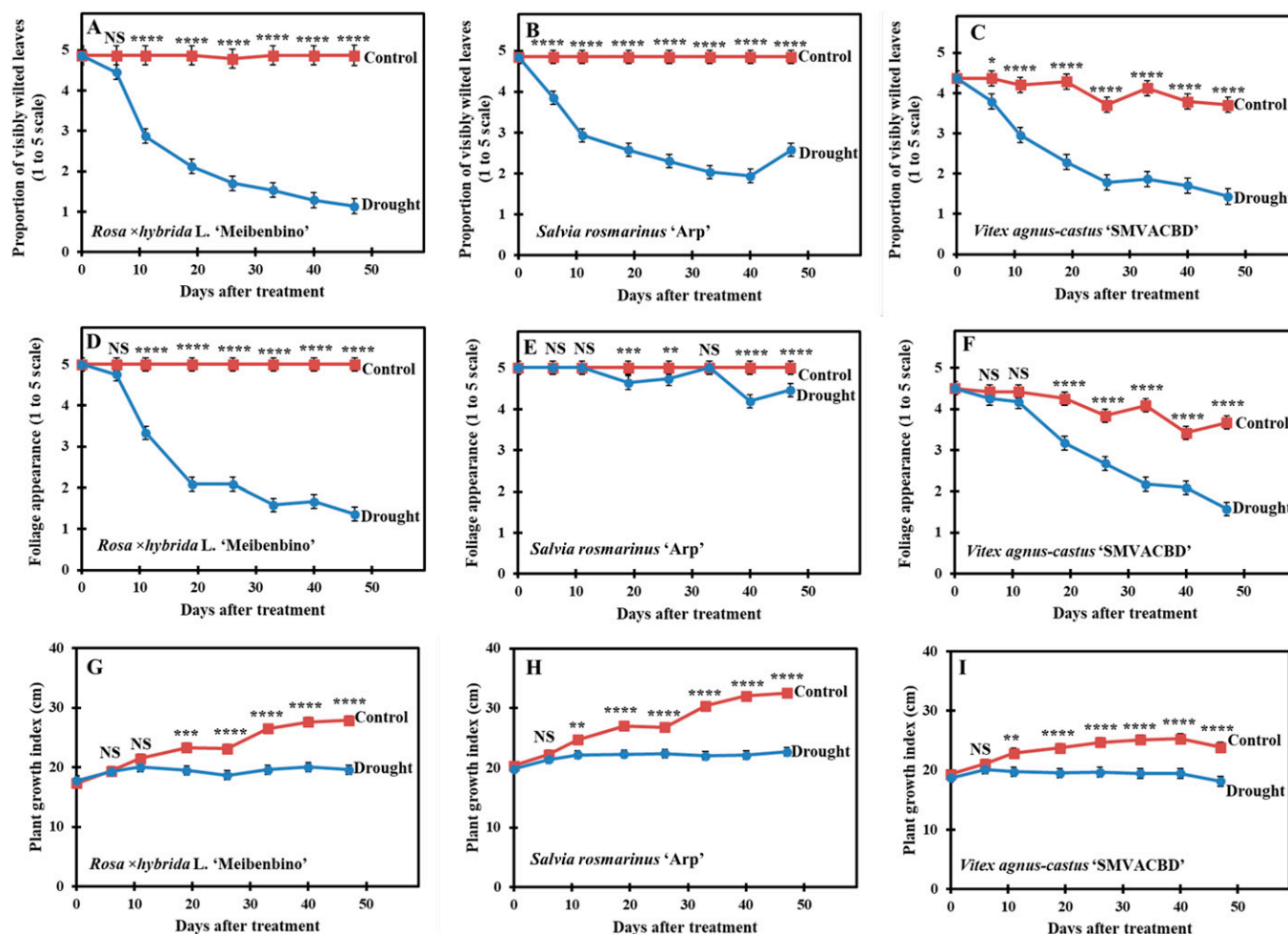


Fig. 3. Proportion of visibly wilted (A–C) and damaged (D–F) leaves and plant growth index (G–I) [(height + width 1 (the widest point of canopy) + width 2 (perpendicular width of width 1))/3] of *Rosa ×hybrida* ‘Meibenhino’, *Salvia rosmarinus* ‘Arp’, and *Vitex agnus-castus* ‘SMVACBD’ grown at the substrate volumetric water contents of $0.40 \text{ m}^3 \cdot \text{m}^{-3}$ (control) and $0.20 \text{ m}^3 \cdot \text{m}^{-3}$ (drought) during the experiment. The proportion of visibly wilted leaves was rated using a scale of 1 to 5 (1 = more than 65% of leaves wilted; 5 = plant fully turgid) (Zollinger et al. 2006). The foliage appearance was determined by the proportion of visibly damaged leaves (i.e., leaf edge burn, curling, necrosis, etc.) using a scale of 1 to 5 (1 = more than 50% of leaves visible damaged; 5 = no leaves visible damaged) (Reid and Oki 2008). Error bars represent the *SE* of eight plants. NS, *, **, ***, **** represent nonsignificant, and significant at $\alpha \leq 0.05$, 0.01 , 0.001 , or 0.0001 , respectively.

Table 2. Total leaf area, dry weights (DWs) of leaves, stems, and roots, root-to-shoot ratio (R/S), shoot relative water content (RWC), leaf width and length, and trichome density of *Rosa × hybrida* 'Meibenhino', *Salvia rosmarinus* 'Arp', and *Vitex agnus-castus* 'SMVACBD' treated with the substrate volumetric water contents of 0.40 m³·m⁻³ (control) and 0.20 m³·m⁻³ (drought) at the end of the experiment.

| | Total leaf area (cm ²) | | Leaf DW (g) | | Stem DW (g) | | Root DW (g) | | R/S (g·g ⁻¹) ⁱ | | Shoot RWC (g·g ⁻¹) ^j | | Leaf length (cm) ⁱⁱ | | Leaf width (cm) ⁱⁱ | |
|------------------------|------------------------------------|---------|-------------|---------|-------------|---------|-------------|---------|---------------------------------------|---------|---|---------|--------------------------------|---------|-------------------------------|---------|
| | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought |
| <i>R. × hybrida</i> | 1360 a ⁱⁱⁱ | 223 b | 19.0 a | 3.2 b | 14.3 a | 3.8 b | 13.6 a | 2.9 b | 0.42 a | 0.42 a | 0.64 a | 0.55 b | 3.37 a | 2.54 b | 1.82 a | 1.48 b |
| <i>S. rosmarinus</i> | 859 a | 296 b | 46.3 a | 18.6 b | 25.0 a | 14.1 b | 53.5 a | 19.5 b | 0.75 a | 0.63 a | 0.59 a | 0.46 b | 3.15 a | 1.99 b | 0.30 a | 0.18 b |
| <i>V. agnus-castus</i> | 434 a | 183 b | 6.2 a | 2.4 b | 9.2 a | 7.5 a | 45.4 a | 35.3 b | 2.98 b | 3.72 a | 0.50 a | 0.44 b | 4.69 a | 2.79 b | 1.34 a | 0.94 b |

ⁱ The R/S was calculated using the DW of roots and shoots (leaves and stems), whereas the shoot RWC was calculated using the following equation: [fresh weight (FW) – dry weight (DW)]/FW.

ⁱⁱ The leaf length and width of a plant were determined by averaging the length and width of five mature leaves.

ⁱⁱⁱ Mean with the same lowercase letters within an ornamental species and dependent variable are not significantly different between treatments according to the Turkey-Kramer method, with a significance level specified at 0.05.

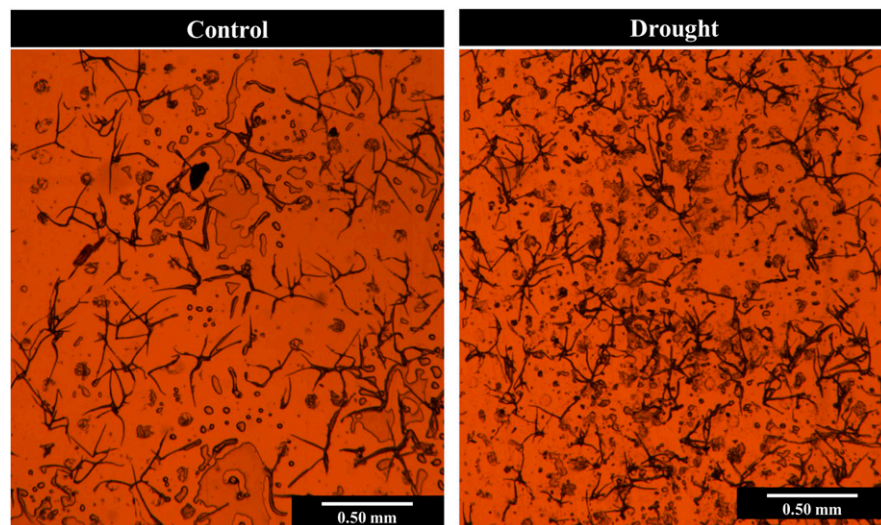


Fig. 4. The dissecting microscope images of glandular trichomes sampled from the leaf adaxial surface of *Salvia rosmarinus* 'Arp' grown at the substrate volumetric water content of 0.40 m³·m⁻³ (control) and 0.20 m³·m⁻³ (drought).

increase in leaf temperature when the substrate volumetric water contents decreased on 14 Oct 2022. Similarly, decreased substrate volumetric water contents led to increased leaf temperatures on the rose and rosemary plants, whereas the leaf temperature of the vitex plants was unaffected by the drought treatment at the end of the experiment.

Decreases in substrate volumetric water contents resulted in a greater leaf–air temperature difference in the roses than that in the control on 14 Oct 2022. Similarly, drought stress increased the leaf–air temperature differences of the rose and rosemary plants at the end of the experiment. For plants subjected to drought stress, their leaf–air temperature differences increased from 14 Oct to 10 Nov 2022. Decreases in the substrate volumetric water content reduced the PhiPSII value of the rose plants on 14 Oct 2022, whereas the PhiPSII value of the vitex plants reduced with the decreasing substrate volumetric water content on 10 Nov 2022.

Compared with the control, the stomatal conductance of the rose and vitex plants under drought stress decreased by 77% and 81%, respectively, on 14 Oct 2022 (Table 4). Decreasing the substrate volumetric water content from 0.40 to 0.20 m³·m⁻³ reduced stomatal conductance of the rose and the vitex plants by 58% and 60%, respectively, at the end of the experiment. Drought stress reduced the transpiration rates of the rose and vitex plants by 5.0 and 1.7 mmol·m⁻²·s⁻¹, respectively, on 14 Oct. By the end of the experiment, the transpiration rates of the rose and vitex plants under drought stress were 68% and 55% lower than that of the control. Compared with the control, drought stress led to a higher leaf–air vapor pressure deficit of the rose plants on 14 Oct and 10 Nov 2022. The CO₂ assimilation rates of the rose and vitex plants decreased by 8.8 and 8.6 μmol·m⁻²·s⁻¹, respectively, when the substrate volumetric

water contents decreased from 0.40 to 0.20 m³·m⁻³ at the end of the experiment.

Discussion

Drought treatment reduced the volumetric water content compared with that of the control, as evidenced by both capacitance and handheld sensors. However, readings differed between these methods (Table 1; Fig. 1). This discrepancy likely resulted from differences in the measurement scope and nonuniform water distribution within containerized substrates. Capacitance sensors, which were used for irrigation control, measured one-quarter of the plants, whereas handheld sensors covered all plants. Heterogeneous greenhouse microclimates led to differences in water use and the substrate moisture content (Wang et al. 2013), thus contributing to discrepancies between capacitance and handheld sensor measurements. Water distributes nonuniformly within each containerized substrate (van Iersel et al. 2011). This nonuniform distribution further contributes to discrepancies in soil moisture measurements because sensors only measure the substrate water content through the substrate surrounding their rods (Patrignani et al. 2022).

Decreases in plant-available water from 0.40 to 0.20 m³·m⁻³ impaired the aesthetic quality of the three landscape plant species because of increases in the proportion of visibly wilted and damaged leaves by water stress. The first visible sign of water stress on ornamental plants is often leaf wilting, followed by leaf burn, chlorosis, and restriction in flower growth; all of these impair plant aesthetic quality (Percival and Sheriffs 2002). Drought-tolerant plants often exhibit better visual quality than that of drought-sensitive plants because of their capacity to modify morphology and physiology to mitigate heat and water stress. For instance, when substrates were dried-down from volumetric

Table 3. Stem water potential (WP), leaf temperature, leaf–air temperature difference, and quantum yield of photosystem II (PhiPSII) of *Rosa ×hybrida* ‘Meibenhino’, *Salvia rosmarinus* ‘Arp’, and *Vitex agnus-castus* ‘SMVACBD’ treated with the substrate volumetric water content of 0.40 m³·m⁻³ (control) and 0.20 m³·m⁻³ (drought) on 14 Oct and 10 Nov 2022.

| | 14 Oct | | | | | | 10 Nov | | | | | |
|------------------------|---------------|---------|----------------|---------|--|---------|---------|---------|---------------|---------|----------------|---------|
| | Stem WP (MPa) | | Leaf temp (°C) | | Leaf–air temp difference ⁱ (°C) | | PhiPSII | | Stem WP (MPa) | | Leaf temp (°C) | |
| | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought |
| <i>R. ×hybrida</i> | -1.2 a | -2.7 b | 24.2 b | 28.7 a | -2.0 b | 2.4 a | 0.46 a | 0.21 b | -0.9 a | -2.7 b | 23.5 b | 26.7 a |
| <i>S. rosmarinus</i> | -1.0 a | -2.5 b | 26.2 b | 28.6 a | -0.1 a | 2.3 a | 0.46 a | 0.21 b | -1.0 a | -2.4 b | 22.2 b | 27.2 a |
| <i>V. agnus-castus</i> | -0.9 a | -2.0 b | 27.9 a | 28.6 a | 1.6 a | 2.3 a | 0.33 a | 0.32 a | -1.3 a | -2.4 b | 24.8 a | 25.3 a |

ⁱ The canopy–air temperature difference is the deviation of the leaf temperature from the ambient air temperature during the measurement.

ⁱⁱ Mean with the same lowercase letters within an ornamental species and dependent variable are not significantly different between treatments according to the Turkey–Kramer method, with a significance level specified at 0.05.

ⁱⁱⁱ The PhiPSII was not recorded for *S. rosmarinus* because of its small leaf size.

water contents of 0.35 to 0.15 m³·m⁻³, the proportion of visibly wilted leaves on mesic *Penstemon digitalis* ‘TNPENDB’ (Dakota™ Burgundy beardtongue) increased by 35% (Chen et al. 2023a). In contrast, less than 10% of leaves on xeric *Penstemon strictus* (Rocky Mountain penstemon) were visibly wilted when substrates were dried-down to the same level (Chen et al. 2023a). Similarly, decreases in the soil moisture content by 60% did not affect the number of flowers of drought-tolerant *Pelargonium peltatum* (ivy leaf geranium), whereas the number of flowers of drought-sensitive *Gazania rigens* (treasure flower) decreased when the same treatment was used (Rydlová and Püschel 2020). During our study, the rose plants showed a greater proportion of visibly wilted and damaged leaves compared with those of the rosemary and vitex plants at the end of the experiment. This suggests that the rose plants might be susceptible to the decreased substrate volumetric water contents. Abbaszadeh et al. (2020) reported that the rosemary cultivar tested during our study was one of the most drought-resistant plants and required lower amounts of irrigation water to sustain growth compared with that required by the other plant species. The previous literature also found that the vitex species was suitable for xeriscaping because it is native to arid and semi-arid regions in Mediterranean Europe and western Asia (Dogan et al. 2011). In contrast, the drought tolerance of rose plants is highly variable between cultivars (Cai et al. 2012). Drought-sensitive rose cultivars, such as Marie Pavie, exhibited poor visual quality and severe growth reduction when the substrate volumetric water content decreased (Cai et al. 2012). Because of severe leaf burn and wilting, the rose cultivar tested during our research, Meibenhino, might be sensitive to drought stress.

Apart from visual quality, decreased substrate water contents negatively affected plant growth by restricting shoot elongation and leaf expansion of three ornamental plant species. Decreased soil water potentials and higher leaf evaporative demands could decline cell turgor pressures and limit cell expansion, thus restricting the expansive growth of plants (Litvin et al. 2016). During our research, the stem water potential declined under water stress, suggesting that cell turgor pressure might be reduced as the substrate water contents decreased. Compared with other plant tissues, immature shoots and leaves were more sensitive to water stress, and minor drought stress could constrain the expansive growth of young leaves and shoots (Raviv and Blom 2001). Therefore, water-stressed plants often developed fewer shoots and leaves compared with those of well-watered plants. For instance, the number of shoots on *Shepherdia ×utahensis* (hybrid buffaloberry) decreased by 58% when the substrate volumetric water contents declined from 0.40 to 0.10 m³·m⁻³ (Chen et al. 2022). Similarly, *Dianella revoluta* ‘Breeze’ (‘Breeze’ blueberry lily) and *Orthosiphon aristatus* (cat’s whiskers) decreased

their water potentials and leaf expansion in response to the decreasing soil water available (Kjelgren et al. 2009). However, drought-sensitive plants often showed a greater reduction in water potential and expansive growth compared with those of drought-tolerant plants (Oki and Lieth 2004). At the end of the experiment, the rose and rosemary plants in this research exhibited a greater decline in their stem water potential compared with that of the vitex plants. This led to greater reductions in plant growth indices, and the number of shoots of the rose and rosemary plants decreased as the substrate water content reduced. Apart from the restriction of expansive growth, the accumulation of photosynthetic products was limited, leading to lower DWs of stems, leaves, and roots under water stress. During this research, chlorosis shown under drought stress could negatively affect net photosynthetic rate because of a lack of photosynthetic pigments on the canopy (Chen et al. 2023a). Furthermore, stomatal conductance decreased to a value close to zero under drought stress, thus restricting the efficiency of the plant to use atmospheric CO₂ for photosynthesis because stomata also regulate the intake of CO₂ (Flexas and Medrano 2002). Zollinger et al. (2006) reported that *Gaillardia aristata* (common blanket flower) reduced its net photosynthetic rate along with decreased stomatal conductance when the irrigation frequency decreased from once every week to once every 4 weeks. Munné-Bosch et al. (2001) also found that *Lavandula stoechas* (lavender) decreased its leaf chlorophyll contents and net photosynthetic rates along with its decreased shoot water potentials. Compared with the rosemary and vitex plants, the rose plants in this experiment experienced greater reductions in the DWs of leaves, stems, and roots as the substrate volumetric water contents decreased during our experiment, indicating that it might not be suitable for xeriscaping uses.

In addition to cell dehydration, canopy overheating under drought stress could impair plant growth and visual quality of the three landscape plant species because mid-day leaf temperatures became higher under drought stress. Transpirational cooling was restricted when stomatal conductance was reduced under water stress, leading to high canopy temperatures and high leaf–air vapor pressure deficits, both of which could exacerbate leaf wilting (Devi et al. 2015). Similar results were discovered in the literature; well-watered plants with a stomatal conductance of 0.50 mol·m⁻²·s⁻¹ had lower leaf temperatures than that of plants under drought stress, which had a stomatal conductance of 0.10 mol·m⁻²·s⁻¹ (Nelson and Bugbee 2015). In a greenhouse, because the highest solar radiation occurs at midday, plants were most water-stressed with the highest leaf temperatures at noon (Chen et al. 2023a). Heat stress could disturb the biochemical functions of enzymes and destabilize membranes and proteins in plants (Hasanuzzaman et al. 2013), thus impairing the photosystem II and leading to decreased PhiPSII values when the substrate

Table 4. Stomatal conductance (g_s), transpiration rate (E), leaf–air vapor pressure deficit (VPD), and net assimilation rate (P_n) of *Rosa ×hybrida* ‘Meibebino’ and *Vitex agnus-castus* ‘SMVACBD’ treated with the substrate volumetric water contents of 0.40 $\text{m}^3\cdot\text{m}^{-3}$ (control) and 0.20 $\text{m}^3\cdot\text{m}^{-3}$ (drought) on 14 Oct and 10 Nov 2022. These parameters were not recorded for *Salvia rosmarinus* ‘Arp’ because of its small leaf size.

| | 14 Oct | | | | | | 10 Nov | | | | | | | |
|------------------------|---|---------|--|---------|--------------|---------|---|---------|--|---------|--------------|---------|--|---------|
| | g_s | | E | | Leaf–air VPD | | g_s | | E | | Leaf–air VPD | | P_n^i | |
| | (mol·m ⁻² ·s ⁻¹) | | (mmol·m ⁻² ·s ⁻¹) | | (kPa) | | (mol·m ⁻² ·s ⁻¹) | | (mmol·m ⁻² ·s ⁻¹) | | (kPa) | | (μmol·m ⁻² ·s ⁻¹) | |
| | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought | Control | Drought |
| <i>R. ×hybrida</i> | 0.49 a ⁱⁱ | 0.11 b | 5.3 a | 0.3 b | 1.5 b | 2.5 a | 0.33 a | 0.14 b | 4.7 a | 1.5 b | 1.8 b | 2.5 a | 11.4 a | 2.6 b |
| <i>V. agnus-castus</i> | 0.38 a | 0.07 a | 3.5 a | 1.8 b | 2.2 a | 2.3 a | 0.11 a | 0.04 b | 2.5 a | 1.1 b | 2.1 a | 2.2 a | 10.5 a | 1.9 b |

ⁱ The P_n was only recorded at the end of the experiment.

ⁱⁱ Mean with the same lowercase letters within an ornamental species and dependent variable are not significantly different between treatments according to the Turkey-Kramer method, with a significance level specified at 0.05.

volumetric water content declined during this research. Because of the relationship between the leaf temperature and drought stress, leaf–air temperature differences have been used to quantify the plant water status (Nelson and Bugbee 2015; Rafi et al. 2019). The model proposed by Nelson and Bugbee (2015) suggested that the leaf–air temperature differences of water-stressed plants were often 2 °C greater than the ambient temperature in a glass greenhouse. Our results were consistent with those of this previous study, and the three landscape plant species under drought stress showed leaf–air temperature differences greater than 2.0 °C during the experiment. In contrast, control plants had leaf–air temperature differences ≤ 2.0 °C. The leaf–air temperature differences of plants under drought stress increased from 14 Oct to 10 Nov 2022, indicating that the plants became more water-stressed under continuous drought conditions. However, drought-tolerant plants often had lower leaf–air temperature differences than those of drought-sensitive plants when they received the same level of deficit irrigation treatment. For instance, *Malva sylvestris* (common mallow), a high water-use landscape plant, exhibited a greater leaf–air temperature difference than that of drought-tolerant *Rudbeckia hirta* (black-eyed susan) when it received deficit irrigation at 50% ET_O (Rafi et al. 2019). Compared with the rose and rosemary plants, the vitex plants might have mechanisms to avoid heat stress when the substrate water content is decreased because it showed a lower leaf–air temperature difference.

The stomatal conductance of the rose and vitex plants declined when plants were dehydrated under drought stress, indicating their ability to modify the stomatal conductance to limit transpirational water loss and avoid further dehydration. The degree of stomatal closure was positively correlated with the plant water status (Zhang et al. 2013). Hence, stomatal conductance decreased as the stem water potential decreased during our research. Decreases in stomatal conductance allowed ornamental plants to maintain lower proportions of visibly wilted leaves; however, CO₂ uptake for photosynthesis was limited (Kjelgren et al. 2000; Zollinger et al. 2006). In addition, small leaves that developed under drought stress were the result of restricted expansive growth (Alem et al. 2015). A smaller leaf size could promote convective heat exchange with

the air because the efficacy of sensible heat loss was related to leaf width (Devi et al. 2015). For instance, the leaf size of *S. utahensis* reduced from 1.97 to 0.97 cm² as the substrate dried-down from the volumetric water contents of 0.40 to 0.05 $\text{m}^3\cdot\text{m}^{-3}$ to enhance sensible heat loss (Chen et al. 2022). Mediterranean ornamental plants, including *Bougainvillea ×buttiana* (bougainvillea) and *Pelargonium ×hortorum* (garden geranium), produced small leaves as the substrate moisture contents declined from 100% to 30% of the container capacity (Toscano et al. 2019). Our results were in agreement with the previous findings because the rose, rosemary, and vitex plants all developed smaller leaves to regulate leaf temperatures when latent heat loss was constrained under drought stress.

The three landscape plant species in this research defoliated under drought stress, which reduced the surface area for transpiration and minimized canopy light interception (Kjelgren et al. 2000; Toscano et al. 2019). The reduction in the total leaf area was a drought acclimation strategy used by various landscape plant species to avoid water stress (Chen et al. 2023a; Kjelgren et al. 2009; Zollinger et al. 2006). For example, *Echinacea purpurea* reduced its total leaf area by 50% to tolerate drought stress caused by decreased irrigation frequency (Zollinger et al. 2006). Summer dormancy was also a drought-tolerant mechanism whereby plants rapidly reduced the leaf area to avoid heat stress and water stress during summer (Balachowski et al. 2016). For example, the mature leaves of *Poa bulbosa* (bulbous bluegrass) and *Poa secunda* (sandberg bluegrass) completely senesced and defoliated during hot and dry summers (Balachowski et al. 2016). The vitex plants promoted root growth, but the shoot growth was inhibited, leading to a higher root-to-shoot ratio to enhance water uptake under drought stress. Similarly, *Vitex negundo* (Chinese chastetree), a drought-tolerant species used for vegetation restoration (Li et al. 2008), increased its root-to-shoot ratio as soil moisture contents decreased by 50% (Du et al. 2010). Compared with the rose and rosemary plants, the vitex plants showed a higher root-to-shoot ratio, which might help maintain a lower leaf–air temperature difference under drought stress. Similarly, Chen et al. (2023a) reported that *P. strictus*, which had a root-to-shoot ratio of 4.8, exhibited lower leaf–air temperature differences compared with those

of *Penstemon ×mexicali* ‘P007S’ (Pikes Peak Purple[®] penstemon), which had a root-to-shoot ratio of 0.9.

The rosemary plants acclimated to drought stress by modifying glandular trichomes on the leaf adaxial surface. Increases in leaf trichome density can enhance leaf reflectance and add additional resistance to transpirational water loss (Ehleringer 1982). Previous studies have shown that a variety of species can increase leaf trichome density when dehydrated (Ehleringer 1988). For example, when the leaf water potential of *Lotus creticus* (cretan trefoil) decreased from −0.69 to −1.23 MPa, the trichome density on the abaxial surface of leaves increased from 138.89 to 164.84 per mm² (Bañón et al. 2004). Similarly, water stress resulting from reduced atmospheric humidity increased trichome density on the adaxial leaf surface of *Cucumis sativus* (cucumber) from 255 to 463 trichomes per cm² (Shibuya et al. 2016). Leaf trichomes are broad-spectrum reflectors (Bickford 2016), and increased trichome density enhances the reflectance of photosynthetic active radiation of a leaf. *Shepherdia ×utahensis* and *Salix commutata* (undergreen willow) enhanced leaf reflectance by increasing trichome density to protect the canopy from overheating under drought stress (Chen et al. 2022; Mershon et al. 2015). Densely packed trichomes also increase resistance to water vapor diffusion from leaf to air by adding an atmospheric boundary layer to maintain the leaf water status in hot and arid climates (Domanda et al. 2023). Decreased turgor pressure might be the mechanism the rosemary plants used to regulate leaf trichome density. Under drought stress, the decreased stem water potential caused a reduction in cell size, thus minimizing the space between trichomes and increasing trichome density (Chen et al. 2022). Previous research reported that turgor pressure-driven cell expansion allows plants to rapidly modify leaf anatomy in response to abiotic stress without compromising whole-leaf function (Brodribb et al. 2013). Because a negative correlation was observed between leaf width and trichome density of the rosemary plants, turgor pressure-driven cell expansion might be used to regulate the trichome density in response to drought stress.

Conclusions

The rose, rosemary, and vitex plants increased the proportion of visibly wilted and

damaged leaves as the substrate volumetric water contents decreased from 0.40 to 0.20 m³ m⁻³, thus impairing the aesthetic quality. Under drought stress, plant dehydration decreased stem water potential and limited the net photosynthetic rate, resulting in decreases in the DWs of leaves, stems, and roots. Although three landscape plants closed stomata to reduce transpiration, the leaf temperatures and leaf-air temperature differences of the rose and rosemary plants increased when the drought treatment was received. The vitex plants, which had a greater root-to-shoot ratio, maintained a cooler leaf temperature and a lower leaf-air temperature difference when the substrate volumetric water contents decreased. Compared with the rose plants, the rosemary plants maintained a better aesthetic quality and growth under drought stress. This might be related to the fact that the rosemary plants could increase trichome density on the leaf adaxial surface to enhance leaf reflectance and maintain leaf water status to avoid heat and water stress. Three landscape plants decreased the leaf size to promote sensible heat loss and reduced the total leaf area to reduce net radiation absorbance under water stress. Under the reduced substrate volumetric water content, the rosemary and vitex plants were able to maintain better aesthetic quality and growth compared with those of the rose plants because of dense leaf trichomes for the rosemary plants and high root-to-shoot ratio for the vitex plants.

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