Effects of Substrate Water Content on Morphology and Physiology of Rosemary, Canadian Columbine, and Cheddar Pink

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Additional index words. herbaceous perennial, moisture sensors, photosynthesis, volumetric water content

Abstract. Two experiments were conducted to determine how different substrate volumetric water contents (θ equals volume of water per volume of substrate) affected morphology and physiology of three popular perennials using a capacitance sensor-automated irrigation system. In the first study, rosemary (*Rosmarinus officinalis*) was grown at one of eight θ set points ranging from 0.05 to 0.40 L·L⁻¹. In the second study, Canadian columbine (*Aquilegia canadensis* ‘Pink Lanterns’) and cheddar pink (*Dianthus gratianopolitanus* ‘Bath’s Pink’) were grown at one of nine θ set points ranging from 0.05 to 0.45 L·L⁻¹. Total leaf number and area as well as shoot fresh and dry weight of rosemary plants grown at θ of 0.20 L·L⁻¹ or greater were approximately twice that of those grown at lower θ . Canadian columbine height increased as θ increased. Leaf area of cheddar pink grown at θ of 0.35 L·L⁻¹ or higher was twice that of plants grown at the lowest θ . Shoot dry weight of Canadian columbine was not significantly affected by θ . Shoot dry weight of cheddar pink responded quadratically to increasing θ and peaked at θ of 0.35 L·L⁻¹. θ also significantly influenced photosynthetic activities; net photosynthetic rate (A_N) and stomatal conductance (g_s) of Canadian columbine increased with increasing θ . A_N of cheddar pink also increased as θ increased. Greater water volumes were applied to maintain higher θ set points. Irrigation water use efficiency (IWUE = shoot dry weight ÷ total amount of water applied per plant) of Canadian columbine and cheddar pink was not influenced by θ . Growth of all three plants was reduced when grown at lower θ ; in the case of cheddar pink and Canadian columbine, this was attributable at least in part to reduced A_N .

Greenhouse operations often use high volumes of water for irrigation. In recent years, growers have faced increasing pressure to reduce water input as a result of global water shortages and increasing irrigation costs (Beeson et al., 2004). One way to conserve

water is to irrigate efficiently. However, typical overhead irrigation systems for container production have relatively low irrigation efficiency (volume of water retained in substrate ÷ volume of water applied). Water is frequently lost through spaces between pots and/or leaching from substrates, and leachate volumes increase with excessive irrigation (Bilderback, 2002; Million et al., 2007). In addition, irrigation leachate contains fertilizer and chemicals and may cause nonpoint source pollution in the environment. Stricter environmental regulations of greenhouse water consumption and fertilizer runoff are forcing growers to adopt more efficient irrigation practices such as cyclic, drip, or subirrigation (Beeson et al., 2004; Lea-Cox and Ross, 2001; Tyler et al., 1996).

Proper scheduling of irrigation is critical in greenhouse operations, yet inefficient irrigation strategies are the most frequent cause of reduced plant quality or plant death (Nelson,

2012). Providing plants with the exact amount of water needed can optimize plant growth, improve irrigation efficiency, and increase profitability (Belayneh et al., 2013; Chappell et al., 2013; Lichtenberg et al., 2013). However, irrigation decisions are often affected by factors other than plant water needs such as labor costs, the irrigation system being used, and the way irrigation is automated. In addition, water requirements for most herbaceous perennials remain unclear. As a result of lack of guidelines on how much water should be applied, growers often apply excessive water to reduce the risk of drought-induced crop shrinkage. Overwatering not only increases water waste and nutrient leaching, but also increases plants’ susceptibility to root rot diseases such as *Phytophthora* and *Pythium* (Nelson, 2012).

Additionally, precise knowledge of plant water requirements permits growers to control stem elongation and regulate plant form by deliberately growing plants at suboptimal irrigation regimes. Moderate water stress reduces plant growth and elongation in many species and may be used as a substitute for chemical growth retardants in commercial greenhouses. For instance, Burnett and van Iersel (2008) used a capacitance sensor-automated irrigation system to maintain substrates constantly at a range of θ levels and found that gaura (*Gaura lindheimeri*) had shorter branches and was more compact when grown at lower θ , yet some species showed no significant morphological changes when grown under drought conditions such as agastache (*Agastache urticifolia*), cardinal flower (*Lobelia cardinalis*), and lantana (*Lantana camara*) (Niu et al., 2006; Starman and Lombardini, 2006). Other species such as purple coneflower (*Echinacea purpurea*) and Shasta daisy (*Leucanthemum xsuperbum*) had substantially reduced visual quality (i.e., noticeable leaf burn and stem dieback) when exposed to moderate drought (watering at 2-week intervals) (Zollinger et al., 2006). The practice of using water stress to control plant growth might be effective, but it could potentially impair plant quality without a thorough understanding of crop-specific water requirements.

Plants vary in sensitivity to water stress and often differ in their responses to severity and duration of water stress (Kramer and Boyer, 1995). Determining both the morphological and physiological responses of plants grown under various θ levels is key to making proper irrigation decisions, and improved irrigation strategies could reduce water consumption, optimize plant growth, and regulate plant form. To accomplish these goals, accurate control and monitoring of substrate water status is necessary (Jones, 2007). An automated irrigation system using capacitance sensors, developed by Nemali and van Iersel (2006), allows for accurate θ control. Irrigation is automatically activated according to the amount of water lost through evapotranspiration so that substrates are maintained at constant θ set points. Plant morphological and physiological responses to continuous

Received for publication 25 Sept. 2013. Accepted for publication 14 Feb. 2014.

Maine Agriculture and Forestry Experiment Station Publication #3353.

We thank the American Floral Endowment for providing funding to support this research. This work is based on research funded in part by Hatch Multistate Grant #ME0-31401 from the USDA National Institute of Food and Agriculture. We thank Lois Stack, Jonathan Foster, and Marianne Sarrantonio for providing helpful feedback on an early draft of this manuscript. Thank you to Julie Hintz and Bradley Libby for technical support.

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steady-state water stress can be accurately evaluated using this system (Nemali and van Iersel, 2006). This innovative system also shows great potential to reduce or eliminate leaching, thus reducing runoff of fertilizers or pesticides (Burnett and van Iersel, 2008; Garland et al., 2012; Nemali and van Iersel, 2006; van Iersel et al., 2010).

This study explores the effects of water stress on plant morphology and physiology, including the ability of plants to use water to produce biomass. We selected three important horticultural species for which water requirements have not been quantified. Rosemary (*Rosmarinus officinalis*) is an evergreen shrub/subshrub native to the Mediterranean region that is widely used in greenhouse and nursery container plant production [U.S. Department of Agriculture (USDA), 2013]. Canadian columbine (*Aquilegia canadensis* 'Pink Lanterns') and cheddar pink (*Dianthus gratianopolitanus* 'Bath's Pink') are popular herbaceous perennials that are hardy to USDA hardiness zones 3 to 8; they thrive in a wide range of areas in the United States (Armitage, 2008; USDA, 2013). Excellent soil drainage is recommended for both Canadian columbine and cheddar pink (Armitage, 2008). Our objectives were: 1) to determine the optimal θ for growing high-quality and high-yield rosemary in greenhouses; and 2) to determine how θ affects morphology and physiology of Canadian columbine and cheddar pink and quantify the amount of water needed for optimal growth of these two species.

Materials and Methods

Two experiments were conducted in a glass greenhouse from Aug. 22 to 31 Oct. 2011 (rosemary) and from 7 Apr. to 18 June 2012 (Canadian columbine and cheddar pink).

Expt. 1

Pre-vernalized rosemary plugs from a commercial grower were transplanted into 1.76-L plastic containers (15.2 cm in diameter) filled with a soilless substrate [Fafard 1p, 80% peat:20% perlite (v/v); Fafard, Agawam, MA]. Slow-release fertilizer (18N-2.6P-10K; Osmocote 18-6-12; Everris, Dublin, OH) was incorporated into the substrate at a rate of 4.9 g·L⁻¹ before transplanting. Plants were hand-watered for 3 weeks to promote plant establishment. After 3 weeks, a capacitance sensor-automated irrigation system similar to the one Nemali and van Iersel (2006) developed was used to control irrigation.

Rosemary was grown at one of eight θ set points: 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, or 0.40 L·L⁻¹. Based on a substrate moisture release curve, θ of 0.26 L·L⁻¹ and 0.44 L·L⁻¹ are equivalent to matric potentials of -45 kPa and -5 kPa, respectively, in the growing substrate used for these experiments (van Iersel et al., 2013). One soil moisture sensor (EC-5; Decagon Devices, Pullman, WA) was inserted vertically at an $\approx 45^\circ$ angle into the substrate of one plant in each experimental unit. Sensor voltage output was measured

every 3 min. Sensors were connected to a multiplexer (AM 16/32B; Campbell Scientific, Logan, UT) connected to a data logger (CR10X; Campbell Scientific). The data logger was programmed to convert voltage to θ using a substrate-specific calibration equation calculated on-site ($\theta = \text{voltage} \times 1.8862 - 0.5624$). When θ fell below the set point for a treatment, a normally closed solenoid valve connected to a relay driver (2.54 cm, 24-VAC solenoid valves) was programmed to open for 1 s. Plants were then irrigated using dribble stakes (Model 1101001-B; Netafim, Fresno, CA) connected to a pressure-compensated emitter (Netafim).

Plant height (from the substrate surface to the tallest point on the plant) and width at the widest point were measured weekly after all substrates reached their θ set points. Only the four plants in the middle of each experimental unit were measured to avoid edge effects. Plants were harvested 10 weeks after initiation of the experiment, when they were considered marketable-sized. The number of leaves per plant was counted and total leaf area (LI-3000A Portable Area Meter; LI-COR Biosciences, Lincoln, NE) was measured on the plants grown in the containers with moisture sensors in each experimental unit. Shoots were cut off at the substrate surface and fresh weight was immediately recorded; shoot dry weight was determined after drying in a soil drying room for 2 weeks.

Treatments were arranged in a completely randomized design for rosemary. Each experimental unit consisted of eight plants (subsamples) in four rows of two containers each. Data were collected from the four plants in the middle to avoid edge effects. There was one replication of each treatment. Data collected from the four subsamples in each experimental unit were averaged before statistical analysis. Data were then analyzed using linear and quadratic regression models in Statistical Analysis Systems (Version 9.2; SAS Institute, Cary, NC). The model that was the best fit was selected based on *P* values and *R*².

Expt. 2

Pre-vernalized Canadian columbine and cheddar pink cuttings were obtained from a commercial grower for the second experiment (72-cell plugs; Green Leaf Plants®, Lancaster, PA). Rooted cuttings were transplanted using the same substrates, fertilizers, and containers described for Expt. 1.

A similar irrigation system was used to control irrigation in Expt. 2. However, for Canadian columbine and cheddar pink, soil moisture sensors that measure both θ and substrate temperature (5TM; Decagon Devices, Pullman, WA) were used rather than sensors that just measure θ . The data logger program converted sensor output (dielectric permittivity) to θ using a substrate-specific calibration equation that was calculated on-site: $\theta = (50 \times \text{dielectric permittivity} - 66.35897) \times 0.000905$, *r*² = 0.98. For the calibration equation, θ was maintained constantly at one of nine set points: 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, or 0.45 L·L⁻¹. The amount of water

applied to each treatment during an irrigation event was measured before the experiment. The data logger counted the number of irrigation events for each experimental unit throughout the course of the experiment. Then, the total irrigation volume applied to each plant was calculated by multiplying the number of irrigation events by the volume of a single irrigation event divided the number of plants in an experimental unit (eight).

As described in the previous experiment, plant height and widest width were measured weekly after all substrates reached their θ set points. After 10 weeks, plants were harvested, and the number of leaves, leaf area, shoot fresh weight, and shoot dry weight was noted as in Expt. 1. IWUE was calculated using the following equation: IWUE = shoot dry weight (g/plant) ÷ total irrigation (g/plant). As a result of rain events on Day 20 and Day 35, two treatments ($\theta = 0.25$ and $\theta = 0.40$ for the columbine) received additional water that dripped through the greenhouse glazing. For these two treatments, the additional water volume was calculated as follows: (θ after the rain event - θ before the rain event) * 1.76, where 1.76 (L) is the volume of substrate in each container. This value was used to adjust the total irrigation volume and IWUE for those two treatments.

Leaf gas exchange and chlorophyll fluorescence of cheddar pink and Canadian columbine were measured on 13 and 14 June. These measurements were taken on uppermost fully expanded leaves using a portable open-flow photosynthetic system (Li-6400-40, LI-COR, Lincoln, NE) equipped with a leaf chamber fluorometer. The temperature inside the leaf chamber was set at 25 °C and photosynthetically active radiation was maintained at 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Measurements were taken on one or two intact leaves that had acclimated to light levels inside the chamber for at least 3 min. Data represent the average of 10 or 20 measurements taken from these acclimated leaves. Photosynthesis was measured only on plants grown in containers in which sensors were installed. Chlorophyll fluorescence was measured on uppermost fully expanded leaves that were dark-adapted overnight using dark-adapting clips (Li-6400-40; LI-COR). The ratio of variable to maximum fluorescence (F_v/F_m) was measured (Li-6400-40; LI-COR); this is an estimate of the maximum efficiency of photosystem II (PSII) for electron transport. Reduced F_v/F_m indicates damage to PSII, which could be the result of drought stress (Maxwell and Johnson, 2000).

The second experiment (Canadian columbine and cheddar pink) was a two-by-nine factorial design (species $\times \theta$); treatments were arranged in a completely randomized design. Otherwise, the experimental design and analysis was the same as described for the first experiment. For cheddar pink, plants grown at a θ of 0.30 were considered outliers. Data for that treatment were not included in the analysis and are not shown.

Results and Discussion

Expt. 1

Plant morphology. There was a trend for rosemary plants to be larger when they were grown at higher θ . However, it is important to note that rosemary had more than 50% mortality when grown at θ set point of $0.05 \text{ L}\cdot\text{L}^{-1}$

(data not shown). Therefore, this θ should be avoided. Plants grown in drier substrates were smaller, though. Width of rosemary increased with increasing θ , giving rosemary plants grown at a lower θ a narrower, more upright habit (Fig. 1C). Only data collected when plants were harvested are presented. However, there was a trend for width to increase as θ

increased throughout the experiment (data not shown). Rosemary generally had longer, more flexible branches when grown at θ higher than $0.20 \text{ L}\cdot\text{L}^{-1}$, making them much wider and less compact. Other ornamental plants such as gaura and miniature rose (*Rosa ×hybrida*) are more compact when grown under continuous steady-state moisture

Fig. 1. Effects of substrate volumetric water content (θ) on height of Canadian columbine (A) and cheddar pink (B) and width of rosemary (C) and cheddar pink (D). Data were collected in the final week of the experiment. Data represent the mean of four subsamples. $P \leq 0.05$ was considered statistically significant.

Fig. 2. Effects of substrate volumetric water content (θ) on total leaf number of rosemary (A) and cheddar pink (B) and total leaf area of rosemary (C) and cheddar pink (D) at harvest. Data represent the mean of four subsamples. $P \leq 0.05$ was considered statistically significant.

stress (Burnett and van Iersel, 2008; Williams et al., 1999).

Total leaf number and area of rosemary (Figs. 2A and 2C) increased with increasing θ . Leaf number and area of rosemary grown at θ 0.30 L·L⁻¹ or greater were more than twice that of plants grown at θ 0.15 L·L⁻¹ or less. Reduced leaf expansion is an easily observed symptom of water stress, because turgor pressure is the driving force for cell

elongation (Taiz and Zeiger, 2010). Turgor pressure, in turn, typically decreases with decreasing substrate water availability (Boyer, 1970; Taiz and Zeiger, 2010). Total leaf area of coral bells was reported to increase linearly with increasing θ (Garland et al., 2012) and drought stress reduced leaf area of scarlet sage (*Salvia splendens*), mealycup sage (*Salvia farinacea*), yarrow (*Achillea* 'Moonshine'), lantana (*Lantana camara*), and abutilon

(*Abutilon ×hybridum*) (Eakes et al., 1991; Kim and van Iersel, 2009; Starman and Lombardini, 2006).

Shoot fresh and dry weight of rosemary increased as plants were grown with more water in the substrate. Rosemary plants with the greatest mass were grown in substrates maintained at the highest θ set point (Figs. 3A and 3C). Many other ornamental crops, including gaura, petunia (*Petunia*

Fig. 3. Shoot fresh and dry weight of rosemary (A and C) and cheddar pink (B and D) as a function of substrate volumetric water content. Data represent the mean of four subsamples. $P \leq 0.05$ was considered statistically significant.

Fig. 4. Daily average substrate volumetric water content (θ) and the total amount of water applied per plant over the duration of the experiment for Canadian columbine (A and C) and cheddar pink (B and D), respectively. Dashed horizontal lines indicate θ set points. Data points for θ of 0.30 L·L⁻¹ are not shown here or in the following figures for cheddar pink, because that treatment was considered an outlier. $P \leq 0.05$ was considered statistically significant.

×hybrida), coral bells, dusty miller (*Cineraria maritima*), plumbago (*Plumbago auriculata*), fan flower (*Scaevola aemula*), and zonal geranium (*Pelargonium ×hortorum*), have shown similar reductions in shoot biomass accumulation with decreasing θ (Burnett and van Iersel 2008; Garland et al., 2012; Niu et al., 2006; Sánchez-Blanco et al., 2009; Starman and Lombardini, 2006; van Iersel et al., 2010). We recommend that rosemary growers maintain substrates at θ greater than $0.20 \text{ L}\cdot\text{L}^{-1}$ to obtain the largest overall plants for landscapes or to obtain the greatest yield.

Expt. 2

Substrate water content and total irrigation applied. All substrates reached their θ set points in 4 to 9 d (Fig. 4A–B). The capacitance sensor-automated irrigation system was able to maintain θ close to the set points throughout the remainder of the experiment (Fig. 4A–B). Greater fluctuations in θ observed at set points of $0.25 \text{ L}\cdot\text{L}^{-1}$ or lower were probably caused by decreased hydraulic conductivity of substrates at lower θ (Naasz et al., 2005). Similar fluctuations were previously reported (Burnett and van Iersel, 2008; Garland et al., 2012; Nemali and van Iersel, 2006; van Iersel et al., 2010). Total irrigation volume increased linearly with increasing θ , ranging from 2.6 to 5.4 L/plant (Canadian columbine) and from 4.6 to 15.3 L/plant (cheddar pink) over a period of 70 d (Fig. 4C–D). Previous researchers observed a similar correlation between irrigation applied and θ (Burnett and van Iersel, 2008; Garland et al., 2012). IWUE of Canadian columbine and cheddar pink was not significantly influenced by θ (data not shown).

Plant morphology. Cheddar pink grown at all θ survived, although leaves of plants grown at a θ of $0.05 \text{ L}\cdot\text{L}^{-1}$ were wilting, yellow, and beginning to senesce, which affected their aesthetic value. Like with rosemary, survival of Canadian columbine at the lowest θ ($0.05 \text{ L}\cdot\text{L}^{-1}$) was reduced (50%; data not shown). For both of these species, plants were considered marketable at θ of $0.10 \text{ L}\cdot\text{L}^{-1}$ or higher (Cheddar pink) or θ of $0.15 \text{ L}\cdot\text{L}^{-1}$ or higher (Canadian Columbine). Height of both species and width of Cheddar pink increased with increasing θ (Figs. 1A–B and 1D). Average height of Canadian columbine increased from 30 to 45 cm when grown at θ of $0.05 \text{ L}\cdot\text{L}^{-1}$ and $0.40 \text{ L}\cdot\text{L}^{-1}$, respectively (Fig. 1A). Like with Expt. 1, only the last week of data is shown, but the trend presented in Figure 2 was observed through the duration of Expt. 2 (data not shown).

The reduction in height of Canadian columbine indicates that there is a potential for using irrigation to control height of Canadian columbine. Previous research indicates that chemical growth retardants do not reduce columbine height or width (Latimer and Oetting, 1999). Latimer and Oetting (1999) reported that moisture stress-conditioned plants were larger than controls (Latimer and Oetting, 1999). However, our research indicates that maintaining constant, low θ with moisture sensors reduced Canadian

columbine shoot elongation. Growers who wish to reduce columbine size should consider using sensor-automated irrigation because plant growth retardants are not an option.

Like observed with rosemary, both the leaf number and area of cheddar pink were greater when plants were grown at higher θ (Figs. 2B and 2D). Individual leaves of cheddar pink were visibly larger when grown at higher θ ; total leaf area of plants grown at θ of $0.35 \text{ L}\cdot\text{L}^{-1}$ or higher was twice that of plants grown at θ of $0.05 \text{ L}\cdot\text{L}^{-1}$. Shoot dry weight of cheddar pink responded quadratically to increasing θ and peaked at θ of $0.35 \text{ L}\cdot\text{L}^{-1}$ (Fig. 3D). The responses of cheddar pink biomass production to θ were at least partially caused by an overall reduction in plant photosynthetic surface area at low θ (Fig. 3C–D). Leaf number and area and shoot fresh and dry weight of Canadian columbine were not significantly affected by θ . It is important to note that the slow-release fertilizer used in this experiment would have released more nutrients at higher θ . However, it is

unlikely that nutrition was involved in observed reductions in plant size because nutrient deficiencies were not observed in any plants.

Photosynthesis and chlorophyll fluorescence. Gas exchange and chlorophyll fluorescence data suggest a further, physiological basis for the observed relationships between θ and plant growth. A_N of Canadian columbine and cheddar pink increased with increasing θ (Fig. 5A–B). Decreasing θ from 0.45 to $0.05 \text{ L}\cdot\text{L}^{-1}$ caused A_N to decrease from 28 to $4.83 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (cheddar pink) and from 11.5 to $8.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Canadian columbine) (Fig. 5A–B). g_s of Canadian columbine decreased linearly with decreasing θ (Fig. 5C). There was a trend for g_s of cheddar pink to decrease with decreasing θ as well; however, this trend was not significant (data not shown). When g_s is lower, CO_2 supply for carboxylation in the Calvin cycle can become limiting, which in turn reduces photosynthesis. A reduction in g_s is commonly observed in drought-stressed plants (Cai et al., 2012; Jones and Tardieu, 1998; Nemali and van Iersel, 2008; Niu et al., 2006; Zollinger et al., 2006). Lower

Fig. 5. Net photosynthetic rate (A_N) of Canadian columbine (A) and cheddar pink (B) and stomatal conductance (g_s) of Canadian columbine (C) grown at nine substrate volumetric water content (θ) set points. Data were measured on the upper-most fully expanded leaves. $P \leq 0.05$ was considered statistically significant.

photosynthetic activity likely contributed to the reduced shoot biomass and leaf area observed at lower θ (Figs. 2 and 3).

If drought limits the ability of photosynthesis to use captured light energy by restricting CO_2 supply and non-photosynthetic dissipation pathways are insufficient to quench the excess light energy, plant photosystems can suffer damage. This damage can be detected by differences in chlorophyll fluorescence between healthy and stressed plants, particularly the difference in F_v/F_m (Maxwell and Johnson, 2000). In this study, θ treatments did not affect F_v/F_m for Canadian columbine, indicating that PSII was not damaged. In cheddar pink, there was a modest reduction in F_v/F_m that ranged from 0.803 to 0.84 at θ of 0.10 and 0.45 $\text{L}\cdot\text{L}^{-1}$, respectively. The lowest F_v/F_m (0.786) was measured at the lowest θ (0.05 $\text{L}\cdot\text{L}^{-1}$). These results suggest that Canadian columbine may possess a slightly greater capacity to counter photodamage through alternative mechanisms when photochemistry is stomatal-limited such as increased photorespiration (Voss et al., 2013).

For cheddar pink, although F_v/F_m may indicate drought stress in some cases, it is not as sensitive as other physiological and morphological indicators (Maxwell and Johnson, 2000). Small differences in F_v/F_m (in this case 4%) may be hard to correlate with lower photosynthetic rates when water stress is not severe (Karukstis, 1991). In this experiment, plants were gradually exposed to low rates of drought stress that reduced photosynthesis and g_s but had only a modest impact on F_v/F_m for cheddar pink and no detectable differences for Canadian columbine. Previous researchers have reported small or no differences in F_v/F_m when plants were drought-stressed. Starman and Lombardini (2006) reported that drought did not affect F_v/F_m when mealycup sage and fan flower were exposed to two subsequent 10-d drought cycles (θ of the upper 6 cm of substrate reached 0.13 $\text{L}\cdot\text{L}^{-1}$), whereas F_v/F_m of lantana was reduced by 2.4% compared with the control on Day 8 of the first drought cycle. Niu et al. (2008) exposed two cultivars and two breeding lines of oleander (*Nerium oleander*) to 12-week cyclic drought stress, and decreases in F_v/F_m of drought-stressed plants were observed in only two of the four clones. Sánchez-Blanco et al. (2009) observed no drought-induced damage to PSII of zonal geranium.

Conclusion

Substrate volumetric water content (θ) affected growth and morphology of rosemary, Canadian columbine, and cheddar pink. Shoot fresh weight of rosemary increased as plants were grown at a higher θ . If crops are to be harvested fresh, we recommend growing rosemary at θ greater than 0.20 $\text{L}\cdot\text{L}^{-1}$ up to a maximum θ of 0.4 $\text{L}\cdot\text{L}^{-1}$ to obtain high yield (i.e., fresh weight). Substrate θ did not affect biomass production of Canadian columbine. However, Canadian columbine height was reduced when plants were grown in drier

substrates. Therefore, it is possible to use drought as a substitute for chemical growth retardants in production of Canadian columbine. Cheddar pink had the highest biomass production at θ of 0.35 $\text{L}\cdot\text{L}^{-1}$; increasing θ above this set point did not increase plant growth. Reductions in overall size of Canadian columbine and cheddar pink at lower θ were caused at least in part by reductions in leaf-level A_N .

Sensor-automated irrigation systems conserve water, and no leaching was observed during the experiment. Canadian columbine used less than 5.5 L of water even when grown at the highest θ (0.45 $\text{L}\cdot\text{L}^{-1}$) for 10 weeks. Low quantities of water were used to grow all cheddar pink; even the largest plants were irrigated with no more than 15 L of water during the entire experiment. IWUE was not influenced by θ for both species. High-quality plants may be grown in a sensor-automated irrigation system using relatively low quantities of water.

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