Effects of Substrate Volumetric Water Content on English Lavender Morphology and Photosynthesis

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Abstract. There is currently little information regarding the impact of soil moisture on morphology and physiology of English lavender (Lavandula angustifolia). Therefore, our goal was to determine the impact of substrate volumetric water content (θ = volume of water ÷ volume of substrate) on this plant. We grew ‘Munstead’ and ‘Hidcote’ lavender at one of four θ: 0.1, 0.2, 0.3, or 0.4 L·L⁻¹ for 54 days using a capacitance sensor-automated irrigation system. Plant height, greatest width, inflorescence number, and total leaf number and area of both cultivars increased with increasing θ. Shoot fresh and dry weight of lavender irrigated at θ ≥ 0.3 L·L⁻¹ was generally twice that of those grown at the lowest θ (0.1 L·L⁻¹). Leaf-level instantaneous net photosynthetic rate (AN) and transpiration (E) of ‘Munstead’ decreased with decreasing θ. This reduction in AN was likely due to the concurrent reduction in stomatal conductance (gs) at lower θ. Similar reductions in AN, E, and gs of ‘Hidcote’ were observed at lower θ (0.2 and 0.3 L·L⁻¹) 5 weeks after the initiation of the study, but not at the end of the study probably due to acclimation of ‘Hidcote’ to mild drought.

English lavender is a popular perennial that is widely used as a landscape ornamental. It is also cultivated for aromatic oil and culinary purposes (Armitage, 2008). This woody shrub is native to the Mediterranean region (Armitage, 2008). Because of the popularity of the plant, English lavender is commonly grown and marketed as a potted herb/flower in greenhouse and nursery production. Irrigation management is difficult for container-grown plants; they are easily susceptible to moisture stress because they are grown in small volumes of substrate. Consequently, there is a limited amount of water available in the root zone. Concern over drought stress may lead producers to overwater container-grown plants. Finding the right balance between these extremes may be of particular concern for English lavender, because irrigation is difficult to manage for this species (Hamrick, 2003). However, little is known about how water impacts growth and physiology of English lavender.

It is of interest to understand how irrigation impacts growth of lavender in greenhouse production because water impacts plant growth, morphology, and physiology (Jones and Tardieu, 1998; Kramer and Boyer, 1995). Plants grown at low-substrate volumetric water contents (θ = volume of water ÷ volume of soil) are exposed to drought stress and often have reduced shoot elongation, leaf area, and biomass production (Burnett and van Iersel, 2008; Garland et al., 2012; van Iersel et al., 2010). Drought stress may also cause wilting, leaf burn, and shoot dieback, thus substantially reducing plants’ visual quality (Nelson, 2012). Another improper irrigation practice in greenhouse operations is overwatering. Overwatering may increase plants’ susceptibility to diseases such as Phytophthora or Pythium (Kramer and Boyer, 1995; Nelson, 2012). Improving irrigation efficiency eliminated plant loss due to pathogens in Gardenia jasminoides ‘Heaven Scent’ (Chappell et al., 2013).

A further benefit of greater irrigation efficiency is that it reduces water and fertilizer waste. In the previously mentioned research, plants that were irrigated when substrates were dry according to measurements from sensors received 83% less irrigation water than those that were conventionally irrigated at a commercial nursery (Chappell et al., 2013). Also, over-irrigation in porous substrates results in leaching of fertilizers, which can be an environmental problem in container production (Bilderback, 2002).

Sensor-automated irrigation systems have been used both in University and on-farm research (Burnett and van Iersel, 2008; Chappell et al., 2013; Lea-Cox et al., 2013). The development of sensor-automated irrigation systems has improved growers’ ability to produce challenging crops such as English lavender. Unfortunately, there is little understanding of how water impacts growth of this perennial. This information would greatly improve growers’ ability to consistently produce high-quality English lavender. Our research uses a capacitance sensor-automated irrigation system (Nemali and van Iersel, 2006) to maintain various substrates at a near constant level. Our objective was to determine how θ (and thus different levels of drought stress) affects morphology and photosynthetic parameters of English lavender ‘Munstead’ and ‘Hidcote’.

Materials and Methods

Prevernalized English lavender ‘Munstead’ and ‘Hidcote’ rooted cuttings in 72-cell plug trays were obtained from a commercial grower (Green Leaf Plants©, Lancaster, PA) and transplanted into round plastic containers (15.2 cm diameter, 1.76 L volume) filled with a commercial soilless substrate (Fafard IP, 80% perlite (v/v); Sun Gro Horticulture, Agawam, MA). Plants were grown in a polycarbonate greenhouse. Slow-release fertilizer (18N–2.6P–10K; Osmocote 18–6–12, 8–9 month release rate at 20 °C; Everris, Marysville, OH) was incorporated into the substrate at rates of 4.9 g L⁻¹ before transplanting. Plants were hand watered for 11 d after transplanting to allow for establishment.

Beginning on 19 July 2012, the established plants were irrigated using a capacitance sensor-automated irrigation system similar to the one described by Nemali and van Iersel (2006). Our system differed from Nemali and van Iersel’s in that we used soil moisture sensors (STM; Decagon Devices, Pullman, WA) that measure both θ and substrate temperature. Plants were grown at one of four θ set points: 0.1, 0.2, 0.3, or 0.4 L·L⁻¹ representing a broad range of matric potentials (–45 and –5 kPa for 0.26 L·L⁻¹ and 0.44 L·L⁻¹, respectively; van Iersel et al., 2013). One soil moisture sensor was installed vertically at an angle of about 45° into the substrate of one plant in each experimental unit. The top of the sensor was 5 cm from the side of the pot and 2.5 cm from the substrate surface. The sensor measured θ along the entire length of 5.2 cm long prongs. Sensor outputs were the average θ over ±10 to 5 cm depth range from the substrate surface to the bottom of the container. The neighboring seven plants in that experimental unit were irrigated based on the measurement of that plant’s substrate. The system was automated using sensors. Every 3 min, sensors measured θ. Sensors were connected to a multiplexer (AM 16/32B; Campbell
Scientific, Logan, UT) that was in turn connected to a datalogger (CR-10X; Campbell Scientific), which recorded all data collected from the sensors. The datalogger program converted the sensor output to θ using a peat-based soilless substrate calibration equation that we obtained earlier [θ = (50 × sensor output − 66.35897) × 0.000905]. When θ fell below the set point for each treatment, normally closed solenoid valves (2.54 cm, 24-VAC; Hunter, San Marcos, CA or Netafim, Fresno, CA) connected to a relay driver (SDM-CD16AC 16 Channel Controller; Campbell Scientific) were programmed to open for 1 s. Irrigation was provided using an open-flow photosynthetic system equipped with a leaf chamber fluorometer (LI-6400–40, LI-COR). Reference CO2 while photosynthesis was measured ranged from 375 to 395 mg·L⁻¹. Only plants grown in containers with sensors were used for photosynthesis measurements. Temperature inside the leaf chamber was set at 25 °C and PAR was maintained by blue and red light emitting diodes (LEDs) at 1000 μmol·m⁻²·s⁻¹. Lavender has narrow leaves that would not fill the entire 2 cm² measuring area of the chamber; the actual leaf area inside the chamber was estimated and adjusted in the fluorometer configuration before each measurement. Intact leaves were acclimated to light levels inside the chamber for at least 3 min before gas exchange measurements were taken. Chlorophyll fluorescence of light adapted leaves was measured to estimate quantum efficiency of photosystem II (ΦPSII) under saturating light levels (PAR = 1000 μmol·m⁻²·s⁻¹). Chlorophyll fluorescence of dark-adapted leaves (dark-adapted overnight using tin foil) was measured to estimate maximum capacity for photochemistry of PSII (Fm/Fo). Net photosynthesis (Aₙ), gₛ, and E were also measured. ‘Hidcote’ grown at θ of 0.1 L·L⁻¹ were not measured because leaves from plants grown at that treatment were too small to fit in the leaf chamber. The experimental design was a 2 × 4 factorial (2 cultivars × 4 theta set points) arranged in a randomized complete block design with four blocks. Treatments were arranged in a randomized complete block design with four blocks. We did not intend to analyze the interaction between cultivar and theta level, therefore data from each cultivar were analyzed as separate random- ized complete block designs with four replications (blocks). Each experimental unit contained eight plants arranged in four rows of two containers. Data were only collected from the four plants in the middle to avoid edge effects. These four plants were treated as subsamples, and data collected from these subsamples were averaged before analysis. All data were analyzed using linear or quadratic models in regression and Fisher’s protected least significant difference (LSD) means separation with an alpha level of 0.05 in Statistical Analysis Systems (V9.2; SAS Institute, Cary, NC). The quadratic or linear regression model was selected based on R² and P values.

**Results and Discussion**

### Water use

After substrates reached their θ set points, the automated irrigation system maintained substrates close to those set points (Fig. 1A and B). Greater fluctuations in θ observed at lower set points may be the result of decreased hydraulic conductivity in drier substrates (Naasz et al., 2005). Previous studies using similar irrigation control system also reported greater fluctuations in θ at drier treatments (Garland et al., 2012; Nemali and van Iersel, 2006; van Iersel et al., 2010). Low volumes of water were applied to substrates over the 54 d period of the experiment for both cultivars. However, the total amount of irrigation applied to each plant increased with increasing θ (Fig. 1C and D). ‘Munstead’ received 3.8 to 12.3 L·plant of water when grown at θ of 0.1 to 0.4 L·L⁻¹, respectively (Fig. 1C). ‘Hidcote’ used less water compared with ‘Munstead’; plants received 2.1 to 10.6 L/plant during the experiment (Fig. 1D). Other researchers reported that more water was applied when plants were grown at higher θ using similar irrigation systems (Burnett and van Iersel, 2008; Garland et al., 2012; van Iersel et al., 2010). This approach applies only a small amount of water, and water is applied only as needed based on sensor measurements. No leaching was observed from any of the treatments over the entire course of the study. As a result, there was no leachate, which would result in fertilizer run off. This can greatly reduce environmental impacts during plant production. In addition, growers can reduce fertilizer applications because of reduced fertilizer waste, and have increased profitability.

### Daily water use of ‘Munstead’ and ‘Hidcote’

‘Hidcote’ grown at all θ generally increased during the experiment (Zhen, 2013), likely due to an increase in plant size over time. Daily light integral also affected DWU of plants. For example, DWU of ‘Munstead’ grown at 0.4 L·L⁻¹ was significantly correlated with DLI (P = 0.0119; data not shown). In general, both cultivars used less water on days with lower DLI. van Iersel et al. (2010) similarly reported that petunia (Petunia hybrida) used less water when DLI was low. Kim et al. (2011) modeled DWU of petunia based on plant and environmental factors and found that plant size and DLI were the most important factors affecting DWU.

### Plant survival and morphology

‘Munstead’ grown at all θ set points survived. However, ‘Munstead’ grown at the lowest θ (0.1 L·L⁻¹) didn’t reach salable size by the end of this study. By comparison, ‘Hidcote’ had a mortality rate of ≥50% when grown at the θ of 0.1 L·L⁻¹. Further, plants that survived at this θ grew very little during the experiment and were not salable. The higher survival rate of ‘Munstead’ compared with ‘Hidcote’ at the lowest θ indicates that this cultivar may be more drought tolerant.

### Height and width

Plant height and width were positively correlated with θ (Fig. 2). At the end of the experiment, average height of ‘Munstead’ increased from 26.0 to 49.8 cm as...
q increased from 0.1 to 0.4 L·L⁻¹ (Fig. 2A). Average width of 'Munstead' grown at the highest q (0.4 L·L⁻¹) was more than twice that of those grown at the lowest q (0.1 L·L⁻¹) (Fig. 2C). When considering the change in height and width over time, 'Munstead' had a higher growth rate when grown at a higher q. Average height and width of 'Munstead' increased by 17.8 and 19.5 cm, respectively.

Fig. 1. Daily average substrate volumetric water content (θ = volume of water / volume of substrate) throughout the experimental period for ‘Munstead’ (A) and ‘Hidcote’ (B) and total volume of water applied per plant to ‘Munstead’ (C) and ‘Hidcote’ (D) grown at one of four θ set points. In A and B, dashed horizontal lines indicate θ set points. In C and D, data represent mean of four replications with bars representing standard errors (mean ± se). P ≤ 0.05 was considered statistically significant.

Fig. 2. Effects of substrate volumetric water content (θ = volume of water / volume of substrate) on height and width ‘Munstead’ (A and C) and ‘Hidcote’ (B and D). Data represent mean of four replications with bars representing ½ se to avoid overlapping of bars (mean ± ½ se). P ≤ 0.05 was considered statistically significant.

θ increased from 0.1 to 0.4 L·L⁻¹ (Fig. 2A). Average width of ‘Munstead’ grown at the highest θ (0.4 L·L⁻¹) was more than twice that of those grown at the lowest θ (0.1 L·L⁻¹) (Fig. 2C). When considering the change in height and width over time, ‘Munstead’ had a higher growth rate when grown at a higher θ. Average height and width of ‘Munstead’ increased by 17.8 and 19.5 cm, respectively.
Reduced cell expansion under drought stress often results not only in reduced height but also in smaller leaf area. Total leaf number of ‘Munstead’ and ‘Hidcote’ at harvest was positively correlated with increasing θ (Fig. 3A). Total leaf area of the two cultivars increased linearly with increasing θ; leaf area of ‘Hidcote’ grown at θ of 0.4 L·L⁻¹ was more than twice that of those grown at θ of 0.2 L·L⁻¹ or lower (Fig. 3B). Average areas of individual leaves (total leaf area ÷ total leaf number) were also larger at higher θ (data not shown). Burnett and van Iersel (2008) and Garland et al. (2012) similarly observed that total leaf area of gaura and coral bells (Heuchera americana) increased linearly with increasing θ. Williams et al. (1999) reported that miniature roses (Rosa ×hybrida) reduced both leaf number and total leaf area by 40% when plants were grown under continuously severe drought (substrate maintained at 60% water availability compared with well-watered control). Other examples of plants that have reduced leaf area when exposed to drought include yarrow (Achillea ‘Moonshine’), lantana (Lantana camara), and abutilon (Abutilon ×hybrida) (Khalil et al., 2008; Kim and van Iersel, 2009).

Biomass production. Similar to leaf number and area, shoot fresh and dry weights of ‘Munstead’ and ‘Hidcote’ English lavender were significantly reduced when plants were grown at lower θ (Fig. 3C and D). ‘Munstead’ fresh weight decreased by 61% and dry weight decreased by 57% when θ decreased from 0.4 to 0.1 L·L⁻¹. Fresh and dry weights of ‘Hidcote’ grown at θ of 0.4 L·L⁻¹ were near or more than triple that of plants grown at θ ≤ 0.2 L·L⁻¹. Many other ornamental plants, including gaura, scarlet sage, coral bells, zonal geranium (Pelargonium ×hortorum), fan flower (Scaevola aemula), and petunia, have reduced shoot dry weight when grown under drought (Burnett and van Iersel, 2008; Eakes et al., 1991; Garland et al., 2012; Sánchez-Blanco et al., 2009; Starman and Lombardini, 2006; van Iersel et al., 2010).

Shoot compactness. Shoot compactness is another morphological feature that affects plant visual appeal. van Iersel and Nemali (2004) defined plant compactness as leaf area or dry mass per unit plant height. Volumetric water content did not affect compactness of ‘Munstead’ (data not shown). Compactness of ‘Hidcote’, calculated as both the ratio of shoot dry weight and leaf area to plant height, increased linearly with increasing θ (Fig. 4A and B). van Iersel and Nemali (2004) reported that African marigold (Tagetes erecta) was smaller but less compact when grown at decreasing moisture levels, which is consistent with the findings for ‘Hidcote’. In contradiction to this, Burnett et al. (2005) found scarlet sage seedlings were more compact when drought stressed. Effects of drought on compactness might be species, even cultivar, specific. Shoot elongation, leaf expansion, and biomass accumulation might vary in sensitivity to drought stress (van Iersel and Nemali, 2004). In this case, drought stress caused about the same degree of reduction in height, leaf area, and dry

![Graphs](Image)
weight of ‘Munstead’, resulting in no difference in shoot compactness. Shoot elongation of ‘Hidcote’ was less sensitive to drought stress than leaf expansion and dry matter production, which could have resulted from higher hydraulic conductivity in stems compared with leaves.

**Floral development.** Volumetric water content also influenced plant development. When plants were harvested, ‘Munstead’ grown at \( \theta = 0.2 \text{ L·L}^{-1} \) only produced vegetative growth, but plants grown at higher \( \theta \) produced flowers. Further, ‘Munstead’ produced more inflorescences when grown at higher \( \theta \) (Fig. 4C). ‘Hidcote’ grown at all \( \theta \) were reproductive, but similar to ‘Munstead’, inflorescence number was greater in substrates maintained at higher \( \theta \) (Fig. 4D). It is not uncommon for drought to impact floral development. Cai et al. (2012) also observed that cyclic drought (re-watering to field capacity when \( \theta = 0.1 \text{ L·L}^{-1} \)) reduced garden rose (Rosa x hybrida) flower number. Rhododendron (Rhododendron ‘Hoppy’) flower number was reduced when plants were exposed to severe drought for 8 weeks (\( \theta \) was maintained between 0.05 and 0.1 L·L\(^{-1}\); Cameron et al., 1999). Petunia, impatiens (Impatiens walleriana ‘Cajun Violet’), and zonal geranium also flower less when grown in drier substrates (Blanusa et al., 2009; Sánchez-Blanco et al., 2009).

**Photosynthetic responses**

Leaf-level photosynthesis of ‘Munstead’ and ‘Hidcote’ was limited at lower \( \theta \) (Fig. 5), which might partially account for reduced biomass and leaf area accumulation. \( A_N, g_S, \) and \( E \) of both cultivars measured on the first dates (d 37 and 38) increased linearly as \( \theta \) increased (Fig. 5A–F). Net photosynthetic rate of ‘Munstead’ measured on the second date (d 52) increased linearly with increasing \( \theta \), whereas \( g_S \) and \( E \) increased quadratically with increasing \( \theta \) (Fig. 5A–C). For ‘Hidcote’ plants, \( A_N, g_S, \) and \( E \) measured on the second date didn’t significantly differ among treatments. It is important to note that on the second date, only plants grown at \( \theta = 0.2 \text{ to } 0.4 \text{ L·L}^{-1} \) were measured, since, ‘Hidcote’ plants grown at 0.1 L·L\(^{-1} \) had small leaves or were dead (data not shown). The lack of correlation between photosynthetic parameters and \( \theta \) for ‘Hidcote’ on the second date might indicate that these plants acclimated to drought stress by this later date. Similarly, whole plant net carbon assimilation of a related species (Lavandula stoechas) decreased when plants were drought stressed for 10 d, rather than an entire cropping cycle (Nogués et al., 2001). Petunia similarly acclimated to mild, continuous water stress (substrate \( \theta \) of 0.2 or 0.3 L·L\(^{-1}\); Kim et al., 2011). However, it is important to note that water stress increased mortality and reduced ‘Hidcote’ growth, despite this physiological acclimation to drought.

Limiting \( g_S \) reduces the amount of CO\(_2\) diffusing through stomata into the leaves, thus slowing down carbon fixation. Limitation of \( g_S \) (thereby increased leaf stomatal resistance to transpirational water loss) could be one of the reasons that plants had lower \( E \) when grown in drier substrates, therefore, lowering the risk of dehydration under drought. Drought-induced reductions in \( g_S \) and \( A_N \) have been reported with many other horticultural species, including bottlebrush (Callistemon citrinus), garden rose, bell pepper (Capsicum annum), purple coneflower, and beardlip penstemon (Alvarez et al., 2011; Cai et al., 2012; Delfine et al., 2001; Zollinger et al., 2006).

Quantum efficiency and maximum efficiency of PSII (\( F_{v}/F_{m} \)) did not differ among treatments (data not shown), suggesting no detectable drought-induced damage to PSII. Similar findings have been reported elsewhere (Alvarez et al., 2011; Delfine et al., 2001; Sánchez-Blanco et al., 2009). Nogués and Alegre (2002) reported that damage to PSII is a relatively late effect of drought stress in drought-tolerant field-grown Mediterranean plants including rosemary (Rosmarinus officinalis) and a related species of lavender (L. stoechas). It is likely that in our experiment, drought induced by sensor-automated irrigation was too mild to damage PSII.

**Conclusion**

Use of sensor-automated irrigation reduces water and fertilizer waste and provides more precise substrate moisture control. Volumetric water content impacts growth and morphology of English lavender ‘Munstead’...
and ‘Hidcote’. Both cultivars produced the greatest amount of biomass and had the greatest total leaf area and inflorescence number at the highest \( q \) (0.4 L·L\(^{-1}\)). A reduction in photosynthesis at lower \( q \) could be one reason that English lavender were smaller when grown with less water. ‘Munstead’ tolerates severe drought (\( q \) of 0.1 L·L\(^{-1}\)); however, survival of ‘Hidcote’ is reduced to only 50% at this \( q \), indicating that ‘Munstead’ could be more drought tolerant than ‘Hidcote’. Nonetheless, neither of the two cultivars grown at \( q \) of 0.1 L·L\(^{-1}\) were considered salable. Reducing irrigation could be an effective way to control height of ‘Munstead’, as plant height decreased linearly with decreasing \( q \). Decreasing \( q \) from 0.4 to 0.2 L·L\(^{-1}\) didn’t significantly reduce height of ‘Hidcote’, but rather lowered plant quality by decreasing shoot compactness and floral and biomass production. Thus we recommend lowering \( q \) to no less than of 0.2 L·L\(^{-1}\) if height control of ‘Munstead’ is needed, and growing ‘Hidcote’ at \( q \) of 0.3 to 0.4 L·L\(^{-1}\) to obtain high-quality plants.

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**Fig. 5.** Net leaf photosynthetic rate (\( A_N \)), instantaneous stomatal conductance (\( g_S \)), and transpiration rate (\( E \)) of ‘Munstead’ (A–C) and ‘Hidcote’ (D–F). In A–C, only the upper or lower standard error bar is shown (mean + SE or mean – SE). In D–F, data represent mean of measurements from four replications with bars representing standard errors. \( P \leq 0.05 \) was considered statistically significant.
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