DYNAMICS OF WATER USE IN HYDRANGEA MACROPHYLLA AND GARDENIA JASMINOIDES

by

LUCAS MICHAEL O'MEARA

(Under the Direction of Marc W. van Iersel and Matthew R. Chappell)

ABSTRACT

Daily water use (DWU) of two ornamental species was quantified by changes in plant weights. DWU of two *Hydrangea macrophylla* cultivars 'Pia' and 'Fasan' was similar, ranging from 50-300 mL/plant depending on plant size and environmental conditions. *Gardenia jasminoides* 'Radicans' DWU ranged from 50-560 mL/plant. Daily light integral (DLI) and vapor pressure deficit (VPD) were the most important environmental factors affecting DWU, with DWU increasing with increasing DLI and VPD. The combination of plant age, final leaf area, DLI, and VPD explained 68 to 91% of day-to-day variation in DWU. When grown in a gradually drying substrate, water use by *H. macrophylla* 'Fasan' started to decrease at a higher VWC (0.28 m³·m⁻³) than *G. jasminoides* 'Radicans' (0.20 m³·m⁻³). Plant water uptake stopped at a VWC of 0.16 m³·m⁻³ in 'Fasan' and 0.12 m³·m⁻³ in 'Radicans', indicating that 'Fasan' is less adept at extracting water from a drying substrate than 'Radicans'.

Index words: conductance, load cell, modeling, irrigation, plant available water, transpiration

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DEDICATION

Thank you dad for teaching me to walk softly while keeping my eyes and ears open to the sights and sounds of nature, to find a balance between humor and seriousness, and to approach every task with forethought and commitment. Thank you mom for teaching me the importance of humility and kindness, and for cultivating my attention to detail. Thank you Melanie for your never-ending love and support... your curiosity, creativity, and courage inspire me daily.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Purpose of the Study

With global climate change and population growth on the rise, water availability and usage is becoming an increasingly important issue for the nursery industry (Lea-Cox et al., 2010; Vorosmarty et al., 2000). Large-scale ornamental nurseries can apply over 7,000,000 L of water/ha/yr and may spend around \$160/ha/yr on electricity to power irrigation systems (Anonymous wholesale nursery, personal communication). Due to the lack of quantitative information regarding specific water requirements of commonly grown ornamental plant species, growers often apply more water than their plants need (even when abiding by common water efficiency motifs) (Mathers et al., 2005). Research has shown that efficient irrigation systems and proper scheduling can save significant amounts of irrigation water without adversely affecting crop yield or quality in ornamental production (Bacci et al., 2008; Beeson, 2012; Fereres et al., 2003). A more accurate assessment of plant daily water use (DWU) and how DWU is affected by changes in environmental conditions, as well as limitations in water uptake can help nursery growers to reduce their water usage while still meeting the needs of their plant inventory.

Determination of Substrate Water Content

In a review, Bittelli (2011) discussed the following methods for determining soil/substrate water content: one of the most commonly used methods for directly quantifying substrate water content in a laboratory setting is through thermogravimetric measurement, which is done by weighing the substrate sample before and after being dried in an oven at 105 °C for 24 hours. One thing that makes this approach so accurate is that it accounts for both water held in macropores, in-between soil particles, as well as water bound to micropores within the substrate components.

A more practical method for indirectly determining substrate water content in a nursery environment utilizes soil moisture sensors which measure the dielectric permittivity of liquid water in the substrate. This can be done by either time-domain reflectometry (TDR) in which the time it takes an electromagnetic wave to travel back and forth on the probe is measured, or by measuring the capacitance (ability to hold an electrical charge) of the substrate. The output of these sensors is then used in conjunction with substrate-specific calibration curves to provide the actual volumetric water content (volume of water / volume of substrate; VWC) of the substrate. Another method for indirectly quantifying soil water content is resistivity measurements, where an electric current is sent into the soil through electrodes and the soil resistivity is obtained from the difference in voltage measurements.

A soil's thermal properties can also be used to indirectly assess soil water content in two ways. One is by measuring the rate of heat dissipation from a heated needle imbedded in a porous ceramic probe which equilibrates with moisture content of the media. The other way is by sending a heat pulse into the substrate while measuring the soil temperature in a spot near

the heat pulse. The rate at which the heat pulse reaches the thermocouple sensor is related to the soil's thermoconductivity, and is directly affected by soil water content.

Lastly, neutron probes can be used to release high-energy neutrons from a radiation source into the soil/substrate. As the neutrons collide with other atoms, particularly hydrogen, they lose their energy and slow down to a speed at which they can be counted by an internal detector, thereby providing an indirect measurement of substrate water content. Evett et al. (2012) suggests that neutron probes are the most accurate method of determining soil water content in the field; however, as Bitelli (2011) points out, they are much more expensive to buy, use, and maintain than other soil moisture sensors and one must be licensed to transport/use one of these devices. Furthermore, due to the size of probe, they are simply too large to be used in most ornamental containers.

While the aforementioned methods have their place in quantifying soil water content, they do not directly address the main concerns pertaining to irrigation, which is determining how much water the plant uses, how much of the water in the substrate is available to plants, and how much water the grower needs to apply.

Irrigation in Ornamental Production

Precision irrigation of ornamental plants can be a difficult task for nursery growers due to the lack of quantitative information regarding the specific water needs of different plant species. To prevent drought stress and ultimately crop losses and/or reductions in growth rate due to dehydration, many growers apply excessive amounts of irrigation (Kim et al., 2011; Mathers et al., 2005), despite the fact that over-watering can facilitate the development of

pathogenic disorders in nursery stock such as *Pythium* and *Phytophthora* (Blaker and MacDonald, 1981). This strategy can lead to increased fertilizer/herbicide/fungicide applications, as well as leaching and runoff of fertilizers and pesticides, capable of causing eutrophication of surface water bodies (Majsztrik et al., 2011) or contamination of ground water (Brand et al., 1993; Mangiafico et al., 2009; McAvoy et al., 1992). Majsztrik et al. (2011) and Million et al. (2007) have shown that by reducing leaching of fertilizer from container-grown ornamentals, nurseries can reduce production costs and increase profits.

Best management practices for container nurseries recommend that growers have access to 41,361 L of water per hectare, per day during the peak growing season in order to irrigate at a rate of 1.03 cm/day (Bailey et al., 1999); however, this fails to address differences in DWU among different species or how DWU changes from day-to-day. By using soil moisture sensor-based automated irrigation systems, precision irrigation can be effectively implemented in ornamental plant production (Burnett and van lersel, 2008; Kim and van lersel, 2009; Kim et al., 2011; Nemali and van lersel, 2006; van lersel et al., 2010). Sensor technology has also been used to determine which environmental factors play the largest role in determining plant water use (Kim et al., 2011; van lersel et al., 2010,). By using weighing lysimeters or scales to monitor changes in plant weight throughout the day, whole-plant evapotranspiration rates and volumes can be determined (Earl, 2003), enabling the grower to replenish exactly how much water was lost each day. Knowing the actual DWU volumes and how DWU is affected by environmental conditions can help with the development of more efficient irrigation scheduling protocols for ornamental nurseries and predictive water use models to precisely control irrigation systems.

Modeling Plant Water Use

Beeson (2005) describes irrigation modeling as "estimating how much water should be applied in the upcoming irrigation event, based on conditions that have occurred since the crop was last irrigated." In a review, Beeson (2005) discusses how irrigation modeling began with the development of the basic equation:

$$ET_A = ET_O x Kc$$

where ET_A is the actual evapotranspiration rate, ET₀ is the evapotranspiration rate of a reference crop, and Kc is the crop coefficient. Originally, ET₀ was based on either the evaporation rate of a pan of water or micrometeorology variables and Kc values were shared among plants with similar characteristics. In the 1940s, the Penman-Monteith energy balance equation was developed, which used solar radiation, temperature, relative humidity, and wind speed inputs to estimate plant evapotranspiration (ET₀) rates of agronomic crops (Beeson, 2005). Fitzpatrick (1980) conducted one of the first studies attempting to model the water use of an ornamental species using the Thornthwaite equation to calculate ET₀ for *Ficus benjamina*. However, the resulting model was unable to accurately estimate ET_A of other *Ficus benjamina* specimens, nor for 14 other ornamental species. Problems in the Thornthwaite equation led to the Penman-Monteith equation serving as the backbone for water use modeling.

Kim (2011) points out that, though the Penman-Monteith equation was developed for field crops, modification of specific variables and the development of crop coefficient (Kc) values for ornamental plant species has enabled it to be used to estimate ET_A rates of nursery crops with reasonable accuracy. Differences in plant canopy characteristics have traditionally been a major source of error in ET_A estimates for ornamental crops, but have successfully been

addressed by using measurements of canopy size, relative to the spacing between plants (Beeson, 2010, 2012). Further research utilizing capacitance soil moisture sensors (Kim et al., 2011) and weighing lysimeters (Beeson, 2011, 2012) to quantify ET_A have also shown promise as a means of reducing irrigation volumes in ornamental crops by applying only as much water as the plant needs.

Plant Drought Response

"Stomatal pores, each surrounded by a pair of guard cells, regulate CO₂ uptake and water loss from leaves. Stomatal opening is driven by the accumulation of K⁺ salts and sugars in the guard cells, which is mediated by electrogenic proton pumps in the plasma membrane and/or metabolic activity. Opening responses are achieved by coordination of light signaling, light-energy conversion, membrane ion transport, and metabolic activity in guard cells" (Shimazaki et al., 2007). When plants are exposed to decreasing water availability they respond by progressively closing their stomates to reduce transpiration and prevent dehydration (Sperry et al., 2002; Tezara et al., 1999), though the severity of the drought response is species-specific (Niu et al., 2006). Some drought-tolerant plants are able to undergo osmotic adjustment in the root and leaf tissues that enable the plant to preserve the water potential gradient necessary to facilitate water uptake under drought conditions (Hsiao and Xu, 2000). When drought conditions exist, abscisic acid (ABA) is produced within the plant and elicits the rapid closure of stomata, resulting in reduced transpiration (Kim and van lersel, 2011).

Taiz and Zeiger (2002) point out that cellular expansion in plant tissues is extremely sensitive to water deficit. As the water content within a plant decreases, cells will begin to

loose turgor resulting in decreased leaf expansion and root elongation well before stomatal conductance is affected. Inhibition of leaf expansion leads to decreased light absorption, causing a reduction in whole-plant photosynthesis rates and plant growth. Reduction in total leaf area, through decreased leaf expansion and leaf abscission, serves to reduce the evaporative surface relative to the absorptive surface as a means of preserving hydraulic conductivity (Lambers et al., 1998). However, as water transport ceases and cell turgor approaches zero, the plant's leaves will wilt and gradually desiccate, bringing about plant death.

Water Availability

"Permanent wilting point (PWP) is defined as the largest water content of a soil at which indicator plants, growing in that soil, wilt and fail to recover when placed in a humid chamber" (Tolk, 2003). As further described by Tolk (2003) the assumption that there is no plant available water at a soil water potential < -1.5 MPa is based on research conducted by Furr and Reeve in 1945 on the permanent wilting point of sunflowers (PWP_{sun}). After they found that sunflowers generally do not recover turgor if the soil matric potential is -1.5 MPa or lower, that value (PWP_{-1.5}) became the standard matric potential used to represent the point at which all plants reached PWP. From there, moisture release curves (MRCs) designed to describe the water-holding characteristics of soils by measuring water content over a range of applied pressure/tension were used to determine the VWC at which the matric potential is equal to -1.5 MPa, to determine the PWP_{-1.5} of different soils/substrates (Altland et al., 2010, Tolk, 2003).

dependent upon the species, soil type, and climate (Taiz and Zeiger, 2002; Tolk, 2003). For this reason, the use of PWP_{sun} and PWP_{-1.5} to represent PWP_{field} has been questioned (Tolk, 2003).

When comparing soilless and soil-based substrates, VWC at a matric potential of -1.5 MPa differs significantly between a mineral soil ($0.162 \text{ m}^3 \cdot \text{m}^{-3}$; Cecil clay loam) and a bark-based substrate ($0.215 \text{ m}^3 \cdot \text{m}^{-3}$; 3 bark: 1 sand: 1 peat (v/v/v))(Milks et al., 1989). Drzal et al. (1999) suggested that water present in a soilless substrate at a water potential below -1.5 MPa, is bound within ultramicropores and is unavailable to plants based on the pressure/tension required to extract such water in laboratory setting.

Much of the research on MRCs for soilless substrates is only performed to a pressure/tension of 30 kPa (Altland et al., 2010; Fonteno and Nelson, 1990; Milks et al., 1989a and 1989b; Wallach et al., 1992), at which Milks et al. (1989b) found a pine bark-based substrate to have a VWC of 0.227 m³·m⁻³, compared to a VWC of 0.215 m³·m⁻³ at -1.5 MPa. Given that a specialized pressure plate system is required to apply a pressure/tension as great as 1500 kPa and that an additional pressure/tension of 1470 kPa only serves to extract 1.2% m³·m⁻³ more water from a bark-based substrate, development of MRCs within a range of 0 – 30 kPa has been deemed practically sufficient. However, when applied to actual plant material grown in soilless substrates, moisture release theory may not accurately reflect the ability of plants to take up water from soilless substrates.

In studies conducted on the water requirements of bedding plants in peat-based substrates, a VWC of 0.15 $\text{m}^3 \cdot \text{m}^{-3}$ was not low enough to cause a severe inhibition of growth in vinca (*Catharanthus roseus*), petunia (*Petunia hybrida*) (Nemali and van Iersel, 2005), or

chrysanthemum (*Chrysanthemum x morifolium* Ramat.) (Olson et al., 2002). van Iersel and Dove (2005) also concluded that there was no effect of VWC on whole-plant photosynthesis of abelia (*Abelia x grandiflora*) or hydrangea (*Hydrangea macrophylla*) at a VWC > 0.15 m³·m⁻³ in a bark-based substrate and that wilting did not occur until VWC reached 0.06 m³·m⁻³ for abelia and 0.08 m³·m⁻³ for hydrangea. These findings suggest that MRCs are an inaccurate method of determining plant-available water in soilless substrates and may be improved upon by using actual plants to determine their ability to take up water at different VWCs.

Research Objectives

Irrigation is an essential component of ornamental plant production, yet relatively little is known about how much water nursery crops require for maintaining optimal growth rates. Our objectives were to determine daily water use of *Hydrangea macrophylla* and *Gardenia jasminoides*, quantify how this is affected by environmental conditions, develop a quantitative model describing DWU, and evaluate this model with an independent data set. To address the question of water availability in soilless substrates, we conducted a study to determine the VWC at which transpiration and conductance in *Hydrangea macrophylla* and *Gardenia jasminoides* was inhibited. Our objectives were to determine how much of the water present in a pine bark-based substrate is plant-available and to test whether this is species dependent, as suggested by van lersel and Dove (2005).

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CHAPTER 2

DAILY WATER USE OF HYDRANGEA MACROPHYLLA AND GARDENIA JASMINOIDES AS AFFECTED

BY ENVIRONMENTAL CONDITIONS¹

 $^{^{1}}$ O'Meara, L.M., M.W. van Iersel, and M.R. Chappell. To be submitted to HortScience.

Abstract

Irrigation is an essential component of ornamental plant production, yet relatively little is known about how much water nursery crops require to maintain optimal growth rates. Our objectives were to determine daily water use (DWU) of Hydrangea macrophylla and Gardenia jasminoides, quantify how this is affected by environmental conditions, develop a quantitative model describing DWU, and evaluate this model with an independent data set. In 2010, we quantified the DWU of two Hydrangea macrophylla cultivars, 'Fasan' and 'Pia'. There was little difference in DWU of the two cultivars, which ranged from 50-300 mL/plant, depending on plant age and weather conditions. In 2010, daily light integral (DLI) was the most important environmental factor affecting DWU, with DWU increasing with increasing DLI. The combination of plant age, final leaf area, DLI, and their interactions explained 83.2 and 90.8% of day-to-day variation in DWU of 'Fasan' and 'Pia', respectively. Vapor pressure deficit and temperature explained only an additional 5.3% of variation in DWU. In July 2011, a follow up study was conducted using Hydrangea macrophylla 'Fasan' and Gardenia jasminoides 'Radicans'. DWU of 'Fasan' ranged from 50-200 mL/plant and DWU of 'Radicans' ranged from 50-560 mL/plant. The lower DWU of 'Fasan' in 2011 compared to 2010 was likely due to stunted growth of the hydrangeas, probably due to excessive heat after transplanting. Interestingly, vapor pressure deficit (VPD) explained more of the daily fluctuations in DWU in 2011, than in 2010. These results suggest there is a complex relationship between DLI and VPD effects on DWU and will require further analysis to better understand their effect on plant water use. Predicting DWU of the 2011 'Fasan' crop using 2011 environmental conditions and a regression model developed using the 2010 data resulted in DWU estimates that were 33-98%

too high, except for five days with the lowest DLI and VPD, which resulted in the model underestimating DWU by 1.2-3.3%. This discrepancy is likely due to the differences in 'Fasan' growth in 2010 and 2011: there was more vegetative growth early in the growing season in 2010 than in 2011, resulting in differences in canopy size between the two years. Likewise, the higher water use of 'Radicans' as compared to 'Fasan' in 2011 was at least partly due to differences in canopy size. We hypothesize that including a measure of plant size, rather than age, into predictive DWU models will improve performance and may help account for growth differences among growing seasons. Including percent canopy closure or light interception may be a simple nondestructive method to do so.

Additional index words: load cell, modeling, ornamental irrigation

Introduction

With global climate change and population growth on the rise, water availability and usage is becoming an increasingly important issue for the nursery industry (Lea-Cox et al., 2010; Vorosmarty et al., 2000). Large-scale ornamental nurseries can apply over 7,000,000 L/ha/year year and may spend around \$160/ha/yr on electricity to power irrigation systems (Anonymous, wholesale nursery, personal communication). A more accurate assessment of plant water needs and the development of quantitative irrigation guidelines can help nursery growers to reduce their water usage while still meeting the needs of their plant inventory.

Growers often apply more water than their plants need (even when abiding by common water efficiency motifs) (Mathers et al., 2005), which in turn leads to increased fertilizer and

pesticide applications and runoff, capable of causing eutrophication of surface water bodies (Majsztrik et al., 2011) or contamination of ground water (Brand et al., 1993; Mangiafico et al., 2009; McAvoy et al., 1992). Overwatering can also facilitate the development of pathogenic disorders in nursery stock such as Pythium and Phytophthora (Blaker and MacDonald, 1981). One hurdle that currently makes more efficient irrigation difficult is the lack of quantitative information regarding the water requirements of plants. Best management practices for container nurseries recommend that growers have access to 41,361 L of water per hectare per day during the peak growing season in order to irrigate at a rate of 1.03 cm/day (Bailey et al., 1999), however, this fails to address differences in DWU between different species or how DWU changes from day-to-day. By using sensors to monitor substrate moisture levels and environmental conditions, researchers are able to re-evaluate how much water different species of plants require for optimal growth and which environmental factors play the largest role in determining plant water use (Kim et al., 2011; van Iersel et al., 2010,). Knowing the actual volume of water lost on a daily basis through evapotranspiration and how DWU is affected by environmental conditions can help with the development of more efficient irrigation scheduling protocols, enabling growers to apply precise volumes of water rather than repeatedly resaturating the substrate.

Much of the work done in regard to modeling plant water use stems from evapotranspiration (ET)-based estimation techniques, derived largely from the Penman-Monteith equation (Jones and Tardieu, 1998). Kim et al. (2011) discuss how this equation was originally designed for agricultural crops but, through the modification of specific variables and the development of crop coefficient (K_c) values for ornamental plant species, has been used to

estimate ET rates of nursery crops. Recent studies using both capacitance soil moisture sensors (Kim et al., 2011) and weighing lysimeters (Beeson, 2011; Earl, 2003) to quantify evapotranspiration (ET_A) have shown promise as a means of reducing irrigation volumes and applying only as much water as the plant needs.

The objectives of this study are to determine DWU of *Hydrangea macrophylla* and *Gardenia jasminoides*, quantify how DWU is affected by environmental conditions, develop a quantitative model describing DWU, and evaluate the hydrangea model with an independent data set.

Materials and Methods

2010: Hydrangea macrophylla

The experiment was conducted in a polyethylene-covered hoop house covered with a 40% shade cloth, at the Center for Applied Nursery Research in Dearing, GA. Thirty two rooted cuttings of *Hydrangea macrophylla* 'Fasan' and 32 cuttings of 'Pia' were transplanted into #2 containers (22.5 cm tall x 22 cm diameter), filled with a composted pine bark medium containing 1.97 kg·m⁻³ lime, 0.74 kg·m⁻³ Micromax (Everris, Dublin, OH), 0.74 kg·m⁻³ gypsum, 1 kg·m⁻³ Talstar (Bifenthrin 0.2%) (FMC Professional Solutions, Philadelphia, PA), and 1.98 kg·m⁻³ Osmocote Pro 18-6-12 (18.0N-2.6P-10.0K) (Everris, Dublin, OH). These two cultivars were chosen to quantify potential differences in DWU between a larger-growing cultivar ('Fasan') and a smaller, more compact cultivar ('Pia'). The plants were irrigated using pressure-compensated drip emitters (2 LPH WPCJ, Netafim USA, Fresno, CA) connected to dribble rings (DR4-12, Dramm, Manitowoc, WI). The system was controlled using a data logger (CR10, Campbell

Scientific, Logan, UT) and multiplexer (AM25T, Campbell Scientific). A rechargeable 12-volt battery was connected to the datalogger to prevent the memory in the data logger from being cleared in the event of a power outage. The weights of eight of the plants, four of each cultivar, were measured using individually calibrated load cells (LSP-10, Transducer Techniques, Temecula, CA) mounted on steel base-plates with the same #2 containers mounted to acrylic platforms on top of the load cells, creating a pot-in-pot system which kept plants from falling over. The plants were weighed at 12:00 am and 10:00 pm each day and the difference in these two weights was used to quantify the amount of water that was lost during the day through evapotranspiration (ET). Thus, DWU was based on water use during a 22 h period, based on the assumption that ET between 10 pm and 12 am was negligible.

The data logger controlled irrigation by opening two solenoid valves (1" NPT Jar Top Valve, Orbit Irrigation Products Inc., Bountiful, UT) at 10:00 pm for 30 minutes, applying 1 L of water, to bring the substrate moisture level to container capacity. Since DWU was well below 1 L at all times, this ensured that water availability would not limit ET. Leachate was allowed to drain for an hour and a half before the plants were weighed at 12:00 am to determine the starting weight for the following day. Photosynthetically active radiation (PAR) was measured every five minutes using a quantum sensor (QSO-sun, Apogee, Logan UT) and integrated at 11:55 pm each night to calculate the daily light integral (DLI), while temperature and humidity were measured using a temperature/humidity probe (HMP50, Vaisala, Woburn, MA). All measurements were taken with the datalogger, which also calculated vapor pressure and vapor pressure deficit (VPD) every 5 min, using temperature and humidity measurements. Maximum, minimum and daily average values were recorded for PAR, temperature, relative humidity, vapor

pressure, saturation vapor pressure, and VPD. On the 48th day of the study, an additional layer of 40% shade cloth was pulled over the hoop house and left in place for the remainder of the study.

After 83 d, the total final leaf area of the eight plants mounted on load cells ('Fasan': $3347 \pm 485 \text{ cm}^3$ [mean \pm sd]; 'Pia': 2912 \pm 601 cm³ [mean \pm sd]) was measured with a leaf area meter (LI-3100, Li-Cor, Lincoln, NE). The containers were soaked in buckets of water for 24 hours, drained for an hour and a half and weighed to determine their weight at container capacity. They were then dried at 80° C for 2 weeks and reweighed to determine the water content at container capacity (2.04 L/container).

Statistical Analysis

The relationship between DWU, environmental conditions (temperature, humidity, VPD, and DLI), final leaf area, time (days from the start of the study) and select interactions were analyzed using Pearson's correlation (Proc CORR, Statistical Analysis Software v. 9.2, SAS, Cary, NC). To develop a model describing DWU, these same factors were combined into a single model and stepwise selection was used in to eliminate non-significant factors (P > 0.05) from the model. Partial R^2 values of the remaining significant factors were used to quantify the effect of various factors on DWU (Proc GLM, SAS).

2011: Hydrangea macrophylla and Gardenia jasminoides

A second experiment was conducted in the same location during the summer and fall of 2011 to investigate differences in DWU of 'Fasan' in two growing seasons (2010 vs. 2011) and to

compare two different ornamental species. Thirty-two rooted cuttings of *Hydrangea macrophylla* 'Fasan' and 32 of *Gardenia jasminoides* 'Radicans' were transplanted into #2 containers, filled with the same pine bark-based substrate as was used before and arranged on the same drip-irrigation system. Four additional load cells were added to the system, enabling DWU to be measured for 6 randomly chosen plants from each species.

The transplanted 'Radicans' crop was placed in the hoop house at the end of April 2011; however, due to problems with propagation, 'Fasan' cuttings were not available until the beginning of July. Data collection began immediately following their arrival and the experiment lasted 145 d until November 27th. To increase variability in DLI, an additional layer of 40% shade cloth was pulled over the hoophouse on day 33 and removed on day 107. After 145 d, the plants were harvested and their leaf area was determined (LI-3100, Li-Cor).

Statistical Analysis

Analysis of the data obtained in the 2011 study was done in much the same way as that of the 2010 data, with a few exceptions. Given that the 2011 study began later in the year and ran for nearly twice the amount of time as the 2010 study, plant growth and corresponding DWU was much more dynamic in response to seasonal changes in environmental conditions. To better account for decreasing light levels and temperatures over the course of the 2011 study, quadratic transformations of environmental and plant parameters (time², DLl², and VPD²) were included in the correlation analysis and stepwise selection (Proc CORR and GLM, SAS). The 2010 model developed for 'Fasan' (including temperature, VPD, DLI x time, DLI x final leaf area, and DLI x time x final leaf area) was evaluated using data from the 2011 study.

Results and Discussion

2010

Average daily temperature and relative humidity ranged from 22.0 - 31.2 $^{\circ}$ C and 51 - 84.5%, respectively (Fig. 2.1A). Daily light integral values ranged from 2.8 - 26.2 mol·m⁻² before the application of an additional layer of shade cloth and between 3.3 - 8.9 mol·m⁻² after. Average daily vapor pressure deficit values were between 0.5 and 2.3 kPa.

The DWU of both cultivars was only 2.5-15% of the water present in the substrate at container capacity, indicating that water use was never limited by water availability in the substrate. Daily water use of both cultivars increased gradually from d 0 to d 48, ranging from 41-369 mL/d (Fig. 2.2), likely mainly as the result of increasing plant size. The application of the shade cloth on d 48 resulted in an immediate and sustained decrease in DWU of both cultivars (Fig. 2.2), with values ranging from 120-358 mL/day. There was a reduction in DLI following the application of the shade cloth, while temperature and VPD remained similar (Fig. 2.1), suggesting that the drop in DWU was caused by lower DLI. The overall mean DWU of 'Fasan' (232 mL/day) was 12% higher than that of 'Pia' (208 mL/day).

Even though there was no correlation between DLI and DWU (Table 2.1), there was a clear effect of DLI on DWU: on days with low DLI DWU was low as well (e.g., day 10, 79, 97, 106, 118). Kim et al. (2011) found that despite a weak or absent correlation between DLI and DWU, DLI was still the most important factor in a model explaining DWU in *Petunia* x *hybrida*. There was, however, a strong correlation between DWU and the interaction of DLI and time in 'Fasan' (Table 2.2), indicating that the effect of DLI on DWU became larger over time. This was expected, since DWU of small plants is low irrespective of DLI, but can vary much more when

plants are larger. The three-way interaction among DLI, time, and final leaf area had the strongest correlation with DWU in 'Pia' (Table 2.3), due to increasing plant size over time and larger differences in final leaf area among plants. Other factors correlated with DWU include time, temperature, VPD, final leaf area, and interactions between time x final leaf area, and DLI x final leaf area ('Pia' only) (Table 2.1).

Most of these correlations make sense from a physiological perspective because after a rooted cutting is transplanted it will increase in size over time, enabling the plant to absorb more sunlight resulting in increased plant growth, transpirational surface area (leaf area), and associated water consumption. The increase in DWU with increasing VPD was expected, because transpiration is primarily driven by the VPD between the stomatal cavity and the surrounding air. The reason for the negative correlation between DWU and final leaf area of 'Fasan' is not clear, but the correlation coefficient was low, indicating that the effect of final leaf area on DWU was small. Temperature is of importance because the vapor pressure of the stomatal cavity (e_s) and surrounding air (e) are functions of temperature and dew point temperature, respectively.

Using stepwise regression, we determined that 90% of day-to-day changes in DWU of 'Fasan' could be explained based on DLI, time, final leaf area, VPD, and temperature (Table 2.2). Of DWU fluctuations of 'Pia', 95% could be explained by the same variables and their specific interactions (Table 2.3). Together, temperature and VPD only explained an additional 4 – 6% of day-to-day changes in DWU, whereas 83 – 85% of day-to-day changes in DWU could be explained based on the effects of DLI. This suggests that a reasonably accurate predictive water use model may be developed with DLI measurements serving as the only environmental input.
Using the effects of DLI, time, final leaf area, VPD, and temperature on DWU, we developed a predictive water use model to be tested for effectiveness in a subsequent study on a different crop of 'Fasan' (Table 2.3).

2011

Average daily temperature and relative humidity ranged from $12.1 - 32.4^{\circ}$ C and 60.1 - 91.9%, respectively (Fig. 2.1B). Before the application of an additional layer of shade cloth, daily light integral values were between $4.7 - 17.4 \text{ mol} \cdot \text{m}^{-2}$. During the 74 d under shade, DLI values ranged from $0.83 - 8.4 \text{ mol} \cdot \text{m}^{-2}$. Over the 39 d following the removal of the shade cloth, DLI values were between $2.0 - 9.1 \text{ mol} \cdot \text{m}^{-2}$. Average daily vapor pressure deficit values ranged from 0.15 - 2.35 kPa.

As was the case in the first study, there was an immediate reduction in light levels in response to the application of the shade cloth, as well as an increase when it was removed (Fig. 2.1B). However, there was also a general reduction in light levels, temperature and VPD over the course of the 145 d study, due to seasonal changes in weather occurring as summer transitioned to fall.

In the first 33 d of the study, average DWU of 'Radicans' exhibited an overall increase from 230 to 570 mL/d as the plants grew rapidly following transplanting (Fig. 2.3) During the 73 d under shade, DWU leveled off with values ranging from 50 to 560 mL/d and in general, decreased as DLI and temperatures dropped. Following the removal of the shade cloth, DWU values temporarily spiked to 275 mL/d, but then gradually tapered to around 100 mL/d.

Daily water use of 'Fasan' ranged from 75 to 200 mL/d over the entirety of the experiment and there were no distinct seasonal changes in DWU (Fig. 2.3). Due to average temperatures reaching over 30 °C for 24 of the first 33 d after the hydrangeas were placed in the hoop house, the 'Fasan' crop did not grow much until fall, explaining the fairly steady daily water use throughout summer. In fall, the growth flush of the plants did not result in increased DWU, probably because light levels and temperatures were dropping at the same time, offsetting the effect of plant growth on water use. Overall, day-to-day changes in DWU of both species responded in a similar manner to changing environmental conditions.

Changes in average DWU were again closely aligned with DLI, though not well correlated (Table 2.4), with high DWU occurring on days with a high DLI (d 7, 29, 54, 67) (Fig. 2.3). Daily water use also increased and decreased in very close association with daily changes in VPD (Fig. 2.3).

Using stepwise regression, we found that only 40% of the variation in DWU of 'Fasan' was explained by time, final leaf area, and DLI combined (Table 2.4), as compared to 83% in 2010 (Table 2.2). However, by including the effects of VPD, we were able to explain an additional 28% of DWU in 'Fasan'. Of DWU fluctuations in 'Radicans', 57% was explained by the combination of time, final leaf area, and DLI (Table 2.5). By including VPD, we found that an additional 30% of day-to-day changes in DWU of 'Radicans' could be explained.

Our finding that DLI was the most important environmental variable affecting plant water use in the 2010 is consistent with earlier studies conducted on *Lantana camara* and *Abutilon* x *hybridum* (Kim and van Iersel, 2009), *Kalanchoe blossfeldiana* (Löfkvist et al., 2009) and *Petunia* x *hybrida* (van Iersel, et al., 2010). In contrast to 2010, when DLI was the only

environmental variable with a large impact on daily water use, in 2011 both DLI and VPD were important in explaining day-to-day changes in water use by both species. This is likely due to the 2010 study being conducted in spring and early summer, when light levels were steadily increasing, masking the effect of VPD on DWU. The 2011 experiment was conducted from midsummer to late fall, when light levels were decreasing, allowing the effects of VPD to be more clearly seen.

Predicting DWU of the 2011 'Fasan' crop using 2011 environmental conditions and the regression model developed using the 2010 data resulted in DWU estimates that were 33-98% too high, except for five days with the lowest DLI and VPD resulting in the model underestimating DWU by 30-87% (Fig. 2.4). The inability of the 2010 model to accurately predict water use in 2011 is likely due to the differences in 'Fasan' growth in 2010 and 2011: there was more vegetative growth early in the growing season in 2010 than in 2011, resulting in differences in canopy size between the two years. In 2010, days after the start of the study may have been a good proxy for plant size, but this was not the case in 2011. This discrepancy emphasizes the importance of including accurate estimates of plant size into predictive water use models. Leaf area index (LAI) measurements have been used to account for plant size (Baille et al., 1994), but are destructive and time-consuming. Beeson (2012) has recently demonstrated the effectiveness of ETo-based irrigation in conjunction with percent canopy closure measurements. Using such a measurement would be a simple and non-destructive way to track seasonal changes in plant growth rates, likely increasing the accuracy of a plant water use model. Another option would be to measure canopy light interception as a measure of plant size.

Conclusions

Load cells were an accurate way to measure daily water use (DWU) of plants and to quantify environmentally-induced changes in DWU. We found daily light integral (DLI) and vapor pressure deficit (VPD) to be the most influential environmental factors affecting day-today fluctuations in DWU. However, a predictive model developed using the 2010 data did not accurately predict DWU of the 2011 'Fasan' crop, likely as a result of differences in plant growth between the two crops. Therefore, an accurate measure of plant size, such as percent canopy closure or light interception, is necessary to account for seasonal differences in growth. By monitoring plant size and environmental conditions (specifically DLI and VPD), growers can more accurately determine the daily water requirements of hydrangea and gardenia, and irrigate their stock more efficiently. Irrigation volume and/or frequency can be adjusted based on environmental conditions and plant size, improving both economic and environmental aspects of nursery production.

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Table 2.1. The relationship between 2010 daily water use (DWU) of two hydrangea cultivars and various parameters and their interactions, as indicated by Pearson's correlation coefficients (r) and significance (P). Time = days from start of study, DLI = daily light integral, VPD = vapor pressure deficit, LA = final leaf area.

Cultivar	'Fasan'		'Pia'	
	r	Р	r	Р
Time	0.646	<0.0001	0.581	<0.0001
DLI	0.064	0.32	0.077	0.24
Temperature	0.806	<0.0001	0.719	<0.0001
VPD	0.750	<0.0001	0.690	<0.0001
LA	-0.169	0.0085	0.413	<0.0001
Time * DLI	0.885	<0.0001	0.804	<0.0001
Time *LA	0.582	<0.0001	0.721	<0.0001
DLI * LA	0.012	0.85	0.234	0.0002
DLI * LA * Time	0.812	<0.0001	0.923	<0.0001

Table 2.2. The significant components of a model developed using stepwise selection to explain day-to-day fluctuations in daily water use of *Hydrangea macrophylla* 'Fasan' in 2010. The importance of different model components is indicated by the partial coefficient of determination (R^2) and significance (*P*). Time = days from start of study, DLI = daily light integral, VPD = vapor pressure deficit, LA = final leaf area.

Factor	Parameter estimate	Partial <i>R</i> ²	Р
DLI * Time	0.474	0.784	<0.0001
VPD	72.493	0.053	<0.0001
DLI * LA	-0.000372	0.032	<0.0001
DLI * LA * Time	-0.0000735	0.016	<0.0001
Temp	7.936	0.012	<0.0001
Total		0.897	<0.0001

Table 2.3. The significant components of a model developed using stepwise selection to explain day-to-day fluctuations in daily water use of *Hydrangea macrophylla* 'Pia' in 2010. The importance of different model components is indicated by the partial coefficient of determination (R^2) and significance (*P*). Time = days from start of study, DLI = daily light integral, VPD = vapor pressure deficit, LA = final leaf area.

Factor	Parameter	R^2	Р
	Estimate		
DLI * LA * Time	0.0000586	0.851	<0.0001
	62 604	0 022	<0.0001
VPD	03.094	0.033	<0.0001
Time * LA	0.000988	0.020	<0.0001
Timo	2 624	0 025	<0.0001
Time	-2.024	0.055	<0.0001
Temp	5.464	0.007	<0.0001
	0.0110	0.002	0.0024
	-0.0119	0.002	0.0024
Total		0.948	<0.0001

Table 2.4. The significant components of a model developed using stepwise selection to explain day-to-day fluctuations in daily water use of *Hydrangea macrophylla* 'Fasan' in 2011. The importance of different model components is indicated by the coefficient of determination (R^2) and significance (*P*). Time = days from start of study, DLI = daily light integral, VPD = vapor pressure deficit, LA = final leaf area.

	Parameter	Partial	
Factor	Estimate	R^2	Р
DLI * LA	0.00165	0.392	<0.0001
Time * VPD	0.956	0.231	<0.0001
DLI * VPD	2.022	0.048	<0.0001
Time	-0.236	0.008	<0.0001
	-6 000	0.003	0 0059
	0.055	0.005	0.0055
Total		0.682	<0.0001

Table 2.5. The significant components of a model developed using stepwise selection to explain day-to-day fluctuations in daily water use of *Gardenia jasminoides* 'Radicans' in 2011. The importance of different model components is indicated by the partial coefficient of determination (R^2) and significance (*P*). Time = days from start of study, DLI = daily light integral, VPD = vapor pressure deficit, LA = final leaf area.

Factor	Parameter	Parameter Partial	
	Estimate	R^2	
Time*Time	-0.0292	0.522	<0.0001
Time*DLI*VPD	0.202	0.266	<0.0001
Time*LA*VPD	0.000507	0.038	<0.0001
DLI*DLI	-1.689	0.016	<0.0001
DLI*LA*Time	-0.0000358	0.017	<0.0001
DLI*LA	0.00150	0.004	<0.0001
Time	5.087	0.002	0.0011
DLI	52.788	0.004	<0.0001
Time*DLI	-0.335	0.006	<0.0001
Total		0.875	<0.0001





Fig. 2.1. Daily light integral (DLI), average daily temperature, and average daily vapor pressure deficit (VPD) over the 85 d experiment in 2010 (A) and 145 d experiment in 2011 (B). DLI was reduced following the application of an additional layer of 40% shade cloth on day 48 in 2010 (dashed vertical line). DLI was reduced following the application of an additional layer of 40% shade cloth on day 34 and increased after its removal on day 107 in 2011 (dashed vertical lines).



Fig. 2.2. 2010 daily water use of *Hydrangea macrophylla* 'Fasan' and 'Pia' gradually increasing from the onset of the study until day 48, at which time additional shade cloth was added (dashed vertical line), resulting in lower DWU of both cultivars for the duration of the study.



Fig. 2.3. Daily water use of *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' in the 2011 study. The effect of the application of shade cloth was more pronounced in 'Radicans', resulting in decreased DWU during the period of shading (days 34-106, indicated by dashed lines). Short-term day-to-day changes in daily water use of 'Fasan' and 'Radicans' were closely aligned to fluctuations in daily light integral (DLI), with DWU increasing with increasing DLI.



Fig. 2.4. Daily water use (DWU) of 'Fasan' (closed circles) in 2011 as compared to the predicted water use. Water use predictions are based on the 2010 study when the hydrangeas grew much more in the early part of the study, and thus used more water. On average, the predicted water use is 64% higher than the actual water use, but the model was able to predict day-to-day fluctuations in water use of the plants.

CHAPTER 3

WATER UPTAKE OF HYDRANGEA MACROPHYLLA AND GARDENIA JASMINOIDES IN RESPONSE TO

A GRADUALLY DRYING SUBSTRATE²

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Abstract

Due to the lack of quantitative data regarding specific water requirements of ornamental species, precision irrigation can be a difficult task for nursery growers. One challenge for growers is that it is not clear how much of the water in soilless substrates is actually available for plant uptake. Substrate moisture release curves have been used to predict the amount of plant-available water in soilless substrates, yet there is little information about whether there are differences among species in their ability to extract water from substrates. The objective of this study was to determine how water uptake in Hydrangea macrophylla and Gardenia jasminoides was affected by decreasing substrate volumetric water content (VWC). Growth chambers were used to provide stable environmental conditions that included continuous lighting to prevent diurnal fluctuations in water use. Water use by H. *macrophylla* 'Fasan' started to decrease at a higher VWC (0.28 $m^3 \cdot m^{-3}$) than *G. jasminoides* 'Radicans' (0.20 m³·m⁻³). Plant water uptake stopped completely at a VWC of 0.16 m³·m⁻³ in H. *macrophylla* and 0.12 m³·m⁻³ in *G. jasminoides*. The results show that *H. macrophylla* is less adept at extracting water from a drying substrate than G. jasminoides. Traditionally, plant available water in soilless substrates has been studied using substrate moisture release curves, but our data suggest that there are important differences among species that cannot be detected by utilizing moisture release curves alone.

Additional index words: conductance, load cell, plant available water, transpiration

Introduction

Precision irrigation of ornamental plants can be a difficult task for nursery growers due to the lack of quantitative information regarding the specific water needs of different plant species. To prevent drought stress and ultimately crop losses and/or reductions in growth rate due to dehydration, many growers apply excessive amounts of irrigation (Kim et al., 2011; Mathers et al., 2005). This strategy can lead to leaching and runoff of fertilizer and pesticides from the substrate. Majsztrik et al. (2011) and Million et al. (2007) have shown that by reducing leaching of fertilizer from container-grown ornamentals, nurseries can reduce production costs and increase profits. Previous research has also shown that efficient irrigation systems and proper scheduling can save significant amounts of irrigation water without adversely affecting crop yield or quality in ornamental production (Bacci et al., 2008; Beeson, 2012; Fereres et al., 2003). By using soil moisture sensor-based, automated irrigation systems, precision irrigation can be effectively implemented in ornamental plant production (Burnett and van Iersel, 2008; Kim and van Iersel, 2009; Kim et al., 2011; Nemali and van Iersel, 2006; van Iersel et al., 2010). One critical piece of information for the implementation of soil moisture sensor-based irrigation is the substrate water content at which plants need to be irrigated. Since not all water in substrates is available to plants, it is important to know how much of the water in the substrate can be used by plants. It is generally proposed that plants can no longer take up water from a soilless substrate at a VWC < 0.20 m³·m⁻³ (Drzal et al., 1999; Milks et al., 1989b). However, in past studies we have grown several species of plants below this proposed threshold of water availability and therefore have questions as to how much water plants can actually extract from soilless substrates.

When plants are exposed to decreasing water availability, they respond by progressively closing their stomates to reduce transpiration and prevent dehydration (Sperry et al., 2002; Tezara et al., 1999), though the severity of the drought response is species-specific (Niu et al., 2006). Some of the more drought-tolerant plants can undergo osmotic adjustment in the root and leaf tissues that enable the plant to preserve the water potential gradient necessary to facilitate water uptake under drought conditions (Hsiao and Xu, 2000). As the water content within the plant decreases, cells will begin to loose turgor resulting in decreased leaf expansion and root elongation. When cell turgor approaches zero, the plants leaves will wilt (Taiz and Zeiger, 2002). When the water potential of the substrate becomes too low for a plant to extract water from the substrate, the plant will no longer be able to maintain transpiration, eliciting death of the plant.

"Permanent wilting point (PWP) is defined as the largest water content of a soil at which indicator plants, growing in that soil, wilt and fail to recover when placed in a humid chamber" (Tolk, 2003). As further described by Tolk (2003), the assumption that there is no plant available water at a soil water potential < -1.5 MPa is based on research conducted by Furr and Reeve in 1945 on the permanent wilting point of sunflowers (PWP_{sun}). After they found that sunflowers generally do not recover turgor if the soil matric potential is -1.5 MPa or lower, that value (PWP_{-1.5}) became the standard matric potential used to represent the point at which all plants reached PWP. From there, moisture release curves (MRCs) designed to describe the water-holding characteristics of soils by measuring water content over a range of applied pressure/tension were used to determine the VWC at which the matric potential is equal to -1.5 MPa, to determine the PWP_{-1.5} of different soils/substrates (Altland et al., 2010, Tolk, 2003).

However, the actual water potential threshold for the PWP of different plants (PWP_{field}) is dependent upon the species, soil type, and climate (Taiz and Zeiger, 2002; Tolk, 2003). For this reason, the use of PWP_{sun} and PWP_{-1.5} to represent PWP_{field} has been questioned (Tolk, 2003).

When comparing soilless substrates and soil, VWC at a matric potential of -1.5 MPa differs significantly between a mineral soil (0.162 m³·m⁻³; Cecil clay loam) and a bark-based substrate (0.215 m³·m⁻³; 3 bark: 1 sand: 1 peat (v/v/v)) (Milks et al., 1989b). Drzal et al. (1999) suggested that water present in a soilless substrate at a water potential below -1.5 MPa, is bound within ultramicropores and is unavailable to plants based on the pressure/tension required to extract such water in laboratory setting. However, when applied to actual plant material grown in soilless substrates, moisture release theory may not accurately reflect the ability of plants to take up water from soilless substrates.

In studies conducted on the water requirements of bedding plants in peat-based substrates, a VWC of 0.15 m³·m⁻³ was not low enough to cause a severe inhibition of growth in vinca (*Catharanthus roseus*), petunia (*Petunia hybrida*) (Nemali and van Iersel, 2005), or chrysanthemum (*Chrysanthemum x morifolium* Ramat.) (Olson et al., 2002). van Iersel and Dove (2005) also concluded that there was no effect of VWC on whole-plant photosynthesis of abelia (*Abelia x grandiflora*) or hydrangea (*Hydrangea macrophylla*) at a VWC > 0.15 m³·m⁻³ in a bark-based substrate and that wilting did not occur until VWC reached 0.06 m³·m⁻³ for abelia and 0.08 m³·m⁻³ for hydrangea. These findings suggest that MRCs are an inaccurate method of determining plant-available water in soilless substrates and may be improved upon by using actual plants to determine their ability to take up water at different VWCs. To address this

question, we conducted this study to determine the VWC at which transpiration and conductance in *Hydrangea macrophylla* and *Gardenia jasminoides* was inhibited. Our objectives were to determine how much of the water present in a pine bark-based substrate is actually plant-available and to test whether this is species dependent, as suggested by van lersel and Dove (2005).

Materials and Methods

For this experiment, mature container specimens of *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' were used to determine stomatal responses to declining substrate water content. The plants were potted one year prior to the onset of this study in #2 containers (6.0 L; 22.5 cm. H x 22 cm. D) filled with a typical commercial nursery substrate containing composted pine bark, 1.97 kg·m⁻³ lime, 0.74 kg·m⁻³ Micromax (Everris, Dublin, OH), 0.74 kg·m⁻³ gypsum, 1 kg·m⁻³ Talstar (Bifenthrin 0.2%) (FMC Professional Solutions, Philadelphia, PA), and 1.98 kg·m⁻³ Osmocote Pro 18-6-12 (18.0N-2.6P-10.0K) (Everris, Dublin, OH).

The study took place in two growth chambers (E15 and PGR15; Conviron; Pembina, ND), set to maintain temperature at 25 °C. Overhead banks of fluorescent and incandescent lights were adjusted to a height that provided an above canopy light level of 560 μ mol·m⁻²·s⁻¹. There were minor variations in light intensity, primarily due to differences in plant height between species. Lighting was applied constantly to prevent diurnal fluctuations in water use from obscuring the subtle changes in stomatal conductance expected to occur at low substrate water contents. Light levels were measured at the start of each run using a handheld light bar (SQ-

326; Apogee Instruments; Logan, UT) positioned over the tallest plant in the chamber. The height of the light canopy was adjusted to provide similar light levels in both growth chambers.

Data were collected and stored by a datalogger with two multiplexers (CR10 and AM25T; Campbell Scientific; Logan, UT) to facilitate the various sensors used. Temperature and relative humidity were measured every five minutes using a Rotronic HTO-45D probe (Rotronic; Hauppauge, NY) within each growth chamber and the datalogger calculated vapor pressure deficit (VPD) values from these data.

At the study's onset, containers were submerged in a large tub of water filled to the substrate surface level and soaked for one hour to ensure complete saturation of the substrate and were then allowed to drain for 15 minutes before being placed in growth chambers. Plants were randomly assigned to a load cell and growth chamber location with three load cells within each growth chamber. Plant weight was measured every 10 s using individually calibrated load cells (LSP-10; Transducer Techniques; Temecula, CA) mounted on steel base-plates with an acrylic platform attached to the top of the load cell. The substrate surface was covered with aluminum foil to limit evaporation, to assure that weight changes accurately reflected transpiration. Substrate VWC was also measured every 10 s, using capacitance soil moisture sensors (10HS; Decagon Devices, Pullman, WA). Average plant weight and VWC measurements were stored every five minutes until all plants had died. The remaining water in the substrate was considered to be the plant unavailable water. At that time, the study was repeated.

The difference in hourly average weight was used to calculate whole-plant transpiration rates (T_{wp}). Using T_{wp} , whole-plant conductance rates (g_{wp}) were calculated using the formula:

$$g_{wp} = T_{wp} / (VPD/101)$$

where VPD is the hourly average vapor pressure deficit (kPa) and 101 is the atmospheric pressure (kPa). Above ground biomass of dead plants was removed and the substrate was weighed, dried in an oven at 80 $^{\circ}$ C, and then re-weighed. Difference in plant weight from the start of the replications to the conclusion was used to determine total amount of water lost during the study. Difference in the weight of the substrate at harvest and after oven-drying was used to determine the amount of water still bound in the substrate. The sum of these equaled the amount of water that was present in the substrate at the beginning of the study (container capacity), which averaged 2003 ± 136 mL.

The accuracy of the soil moisture sensor readings was confirmed by the gravimetrically determined VWC values at the start and finish of the study. Soil moisture sensor readings averaged $0.396 \pm 0.027 \text{ m}^3 \cdot \text{m}^{-3}$ at the start of the study and $0.109 \pm 0.013 \text{ m}^3 \cdot \text{m}^{-3}$ at the end. Gravimetrically determined water contents averaged $0.384 \pm 0.032 \text{ m}^3 \cdot \text{m}^{-3}$ at the start of the study and $0.072 \pm 0.017 \text{ m}^3 \cdot \text{m}^{-3}$ at the end. The larger discrepancy between sensor readings and gravimetrically determined VWC at the end of the study was likely due to evaporation from the substrate surface, resulting in a non-uniform distribution of water in the substrate.

Statistical Analysis

The experimental design was a randomized complete block with six replications for each species; three in each run. To determine the VWC threshold values when whole-plant

transpiration and conductance was first limited by VWC and when it stopped, transpiration and conductance were plotted vs. VWC. A spline regression was then performed on the data collected from each plant (Proc NLIN, Statistical Analysis Software v. 9.2, SAS, Cary, NC):

 $Y = b_0 + b_1 \cdot VWC - b_2 \cdot VWCdelta$

VWCdelta = max ((VWC-knot), 0)

where y = transpiration or conductance, b₀, b₁, and b₂ are regression coefficients, and knot is the VWC at which the two regression lines intersect (i.e., the VWC below which transpiration or conductance start to decrease). Using the associated equation for the regression lines, we were able to determine the VWC at which transpiration and plant conductance ceased for each plant. Transpiration and plant conductance were determined to have ceased at a rate of 1.5 mL/h and 75 mL/h, respectively, and subsequent weight loss was attributed to evaporation from the substrate. Threshold values for reduction and cessation of both transpiration and conductance in each plant were analyzed by standard analysis of variance to test for differences between the two species (Proc ANOVA, SAS).

Results and Discussion

Environmental Conditions

Temperature was maintained between $26.0 - 26.5^{\circ}$ C in chamber 1 and $25.2 - 26.0^{\circ}$ C in chamber 2 (Fig. 3.1a). Relative humidity ranged from 8.0 - 56.5% in chamber 1 and 4.3 - 65.1% in chamber 2 (Fig. 3.1b). The VPD fluctuated between 1.48 -3.13 kPa in chamber 1 and 1.15 –

3.09 kPa in chamber 2 (Fig. 3.1c). Although there were small differences in environmental conditions between the two growth chambers, conditions fluctuated in a similar fashion.

Transpiration and Conductance

Plant weights (Fig. 3.2), substrate VWC (Fig. 3.3), and whole-plant transpiration rates (Fig. 3.4) gradually decreased over time as water was lost through evapotranspiration. The rate of weight loss and corresponding transpiration slowed at a higher VWC in hydrangea than in gardenia, as did the rate at which VWC was decreasing. Whole-plant transpiration rates of hydrangea began to gradually decrease at a VWC of 0.277 \pm 0.019 m³·m⁻³ (mean \pm sd), likely due to stomatal regulation in response to decreasing water availability (Fig. 3.5). At a VWC of 0.158 ± 0.013 m³·m⁻³, the transpiration rate neared zero and plateaued at an average rate of 1.5 – 2.0 mL/h. for the duration of the study. This was deemed to be the point where water bound to the substrate was no longer plant-available and subsequent weight loss was attributed to water evaporating from the substrate surface and drain holes in the bottom of the container. Wholeplant transpiration rates of gardenia began to gradually decrease at a VWC of 0.202 ± 0.028 $m^3 \cdot m^{-3}$ and ceased at a VWC of 0.119 ± 0.028 $m^3 \cdot m^{-3}$ (Fig. 3.5). Whole-plant conductance behaved in a similar manner, with a reduction occurring in hydrangea at a VWC of 0.287 ± 0.024 $m^3 \cdot m^{-3}$ and ceasing at a VWC of 0.157 ± 0.006 $m^3 \cdot m^{-3}$ (Fig. 3.6; Table 4.1). In gardenia, the reduction in conductance occurred at a VWC of 0.205 \pm 0.046 m³·m⁻³ and ceased at a VWC of $0.12 \pm 0.009 \text{ m}^3 \cdot \text{m}^{-3}$ (Fig. 3.6; Table 3.1).

Our finding that reduction and cessation of whole-plant conductance occurred at different VWCs for hydrangea and gardenia support earlier findings by Nemali and van lersel (2008) and Niu et al. (2006), illustrating species-specific differences in water uptake and drought response. We hypothesize that differences in the morphology and/or anatomy of root systems and xylem vessels may be contributing factors to the differences observed in water uptake. The abundance/distribution of root hairs and level of aquaporin activity has been correlated with differences in hydraulic conductivity among species (Bramley et al., 2009). Small differences in xylem vessel diameter can result in large differences in hydraulic conductivity and susceptibility to cavitation (McElrone et al., 2004; Taiz and Zeiger, 2002). Breakage of the water column within xylem vessels can result in decreased plant conductance and a reduction in the tension required to maintain water uptake at low VWCs.

The persistence of transpiration and stomatal conductance at VWCs well below levels that have been regarded as plant-unavailable suggests that MRCs for soilless substrates may not be as accurate as when applied to soil-based substrates. Research conducted on MRCs for soilless substrates has asserted that plants are unable to extract water at water potentials below -1.5 MPa (Milks et al., 1989a and 1989b) translating to a VWC of 0.215 m³·m⁻³ in a barkbased substrate (Milks et al., 1989b). Much of the research on MRCs for soilless substrates is only performed to a pressure/tension of 30 kPa (Altland et al., 2010; Fonteno and Nelson, 1990; Milks et al., 1989a and 1989b; Wallach et al., 1992), at which Milks et al. (1989b) found a pine bark-based substrate to have a VWC of 0.227 m³·m⁻³. Given that a specialized pressure plate system is required to apply a pressure/tension as great as 1500 kPa and that an additional pressure/tension of 1470 kPa only serves to extract 0.012 m³·m⁻³ more water from a bark-based

substrate, development of MRCs within a range of 0 – 30 kPa has been deemed practically sufficient. Though MRC-related studies conducted over the last 20+ years have claimed to accurately depict limitations in water uptake by plants grown in soilless substrates, our finding that transpiration was maintained until a VWC of 0.16 m³·m⁻³ and 0.12 m³·m⁻³ in hydrangea and gardenia, respectively, is contradictory to the proposed water availability thresholds and is corroborated by the observations of Nemali and van Iersel (2005), Olson et al. (2002) and van Iersel and Dove (2005).

Of the total volume of substrate, we found that 0. 24 m³·m⁻³ consisted of plant-available water for hydrangea and 0.27 m³·m⁻³ was plant-available water for gardenia (Table 3.1), which is less than the amounts proposed by Drzal et al. (0.315 m³·m⁻³, 1999) and Milks et al. (0.30 – 0.45 m³·m⁻³, 1989b). This is likely due to the fact that substrate saturation in MRC studies is often imposed by slowly adding water to the base of the pressure vessel over the course of 24-48 h, expelling any air pockets within the substrate. Since the main objective of this study was to determine the VWC at which transpiration and conductance was inhibited, submersing the containers in water for one hour was deemed to sufficiently represent container capacity. In terms of total water present at container capacity, 60% of the water was available to hydrangea and 69% was available to gardenia (Table 3.1).

Milks et al. (1989) stated that "While 1500 kPa may represent an endpoint for plant survival, the endpoint for optimal plant growth is at a much lower (moisture tension)." While we do not dispute the fact that optimal plant growth occurs at a higher VWC than that which brings about plant death, our results show that both species were able to maintain water uptake until a VWC much lower than what has typically been suggested as the threshold for plant available water. Additional research quantifying the response of whole-plant conductance to decreasing substrate water contents for a broader selection of ornamental species with the added parameters of observing initial wilting points and the analogous VWC, as well as substrate matric potential, could be beneficial to understanding species-dependent limitations of water uptake in soilless substrates.

Conclusions

There were significant differences in VWC thresholds at which transpiration of *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' stopped. Hydrangea was unable to extract water from the pine bark-based substrate at a VWC < 0.16 m³·m⁻³ and gardenia was unable to extract water at a VWC < 0.12 m³·m⁻³. Of the 2003 \pm 136 mL (mean \pm sd) of water held at container capacity, 60% was available to hydrangea and 69% was available to gardenia. This information and subsequent studies like it could be used to increase the precision of deficit irrigation in ornamental production by detailing optimal and minimum VWC thresholds to be maintained for various species. When combined with predictive models used to estimate changes in daily water use based on fluctuations in environmental conditions (Ch. 2), growers could maintain substrate moisture levels in a range that does not hinder plant conductance while applying only as much water as is lost through daily evapotranspiration. Such an irrigation protocol could potentially reduce production costs by reducing water and fertilizer applications, as well as decreasing the likelihood of crop losses due to disease.

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Table 3.1. Volumetric water contents (mean \pm sd) at which a reduction and cessation in wholeplant conductance occurred and plant available water content (vol. at container capacity – vol. at cessation in conductance and VWC at container capacity – VWC at cessation in conductance) for *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans'. Means followed by the same letter are not significantly different ($\alpha = 0.05$).

Species and Cultivar	Reduction in Conductance (v/v)	Cessation of Conductance (v/v)	Plant Available Water (% of total water)	Plant Available Water (% of substrate volume)
Hydrangea macrophylla 'Fasan'	0.287 ± 0.024 a	0.157 ± 0.006 a	60	24
Gardenia jasminoides 'Radicans'	0.205 ± 0.046 b	0.120 ± 0.009 b	69	27


Fig. 3.1. Average vapor pressure deficit, relative humidity, and temperature over the 5 week study. Dotted line indicates when the second run was initiated.



Fig. 3.2. Weights of representative *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' plants decreasing over time.



Fig. 3.3. Volumetric water content of the pine bark-based substrate decreasing over time (measurements from representative *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' plants).



Fig. 3.4. Whole-plant transpiration rates of representative *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' plants over time.



Fig. 3.5. Whole-plant transpiration rates of representative *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' plants in response to decreasing water availability.



Fig. 3.6. Whole-plant conductance rates of representative *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans' plants in response to decreasing water availability.

CHAPTER 4

CONCLUSIONS

Load cells are an accurate way to measure daily water use (DWU) of plants and to quantify environmentally-induced changes in DWU. Daily light integral (DLI) and vapor pressure deficit (VPD) were the most influential environmental factors affecting day-to-day fluctuations in DWU. However, a predictive model developed using the 2010 data did not accurately predict DWU of the 2011 'Fasan' crop, likely as a result of differences in plant growth between the two crops. Therefore, an accurate measure of plant size, such as percent canopy closure or light interception, is necessary to account for seasonal differences in growth. By monitoring plant size and environmental conditions (specifically DLI and VPD), growers can more accurately determine the daily water requirements of their plants, and irrigate their stock more efficiently. Irrigation volume and/or frequency can be adjusted based on environmental conditions and plant size, improving both economic and environmental aspects of nursery production.

Regarding water availability in bark-based substrates, we found significant differences in volumetric water content (VWC) thresholds whereby transpiration and conductance were inhibited in *Hydrangea macrophylla* 'Fasan' and *Gardenia jasminoides* 'Radicans'. Stomatal closure first occurred at a VWC of 0.28 m³·m⁻³ in hydrangea and 0.20 m³·m⁻³ in gardenia. Hydrangea was unable to extract water from the substrate at a VWC < 0.16 m³·m⁻³ and gardenia was unable to extract water at a VWC < 0.12 m³·m⁻³. Of the 2003 ± 136 mL (mean ± sd) of water held at container capacity, 60% was available to hydrangea and 69% was available

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to gardenia. This information, and subsequent studies like it, could be used to increase the precision of deficit irrigation in ornamental production by detailing optimal and minimum VWC thresholds to be maintained for various species. When combined with predictive models used to estimate changes in daily water use based on fluctuations in environmental conditions (Ch. 2), growers could maintain substrate moisture levels in a range that does not reduce plant conductance, while applying only as much water as is lost through daily evapotranspiration. Such an irrigation protocol could potentially reduce production costs by reducing water and fertilizer applications, as well as decreasing the likelihood of crop losses due to disease.