The production of high-quality container-grown nursery plants requires adequate nutrients and water during production. Negative growth responses to excess N can occur from increased salinity, disruption of the balance between N and other nutrients, or increased water stress (Cabrera, 2004). Fertilizer application rates commonly used for container-grown crops are based on optimal water availability, a condition that rarely exists in commercial production systems. Fertilizer management effects on plant water use and drought stress during production for many crops has not been evaluated fully (Linder et al., 1987; Tan and Hogan, 1997). With some woody perennial plants it is possible that growth can be enhanced more by minimizing water stress than by increasing fertility (Rose et al., 1999). The soilless substrate used during container production of nursery plants has a low nutrient and water-holding capacity and large irrigation quantities can result in nutrient losses from the container. Maintaining plant-available water near 100% field capacity in the growing substrate is believed to maximize plant growth (Beeson, 1992); however, this objective is impracticable in commercial practice. Reduced irrigation volume in combination with increased irrigation frequency can be used to decrease runoff of nutrients and water in nurseries (Fare et al., 1994). Increased irrigation frequency can increase growth of container-grown plants or have no influence on growth (Beeson, 1992; Fare et al., 1994; Keefer and Cobb, 1985). The growth responses of container-grown plants using deficit irrigation regimes have been investigated and acceptable growth was measured when the growing substrate was allowed to dry to 40% to 75% of container capacity before irrigation (Beeson, 2006; Welsh and Zajicek, 1993). Cumulative actual evapotranspiration was similar between control plants grown at 100% container capacity and plants grown at 40% container capacity (Beeson, 2006), suggesting this range of water stress has little influence on photosynthesis and carbon gain. Nutrient uptake is a function of nutrient availability in the rhizosphere soil solution. Transpiration can cause large differences between the water content in the rhizosphere and that in the bulk growing substrate. Changes of a few percent in water content of a growing substrate can induce 4- to 5-fold decreases in the hydraulic conductivity of the substrate and can potentially limit nutrient acquisition by plants (Raviv et al., 1999). Increasing irrigation frequency may increase availability of nutrients and nutrient uptake efficiency and decrease the amount of fertilizer required for optimal growth. Several researchers suggest increasing irrigation frequency could compensate for certain nutrient deficiencies, and lower yields of plants irrigated less frequently may be a result of nutrient shortage rather than water shortage (Buljovic and Engels, 2001; Silber et al., 2003; Xu et al., 2004).

Recently, we described the influence of N availability on growth and uptake and storage of N and other nutrients by container-grown evergreen and deciduous cultivars of *Rhododendron* spp. (Bi et al., 2007a; Scagel et al., 2007, 2008) and observed an apparent increase in water use with increasing rate of N fertilizer application. Improved knowledge of the combined influence of irrigation and nutrient management during nursery production of container-grown plants is needed to develop integrated nursery production practices that optimize nutrient and water use. The objective of this study was to investigate the influence of water stress (as induced by irrigation frequency) on growth and N uptake of one deciduous and two evergreen cultivars of *Rhododendron* grown with different rates of N fertilizer in containers.

**Materials and Methods**

*Plant culture.* Plants used in this experiment were two evergreen cultivars of *Rhododendron, Rhododendron* ‘P.J.M. Compact’, ARS#874 (PJM), and *Rhododendron* ‘English Roseum’, RHS#58 (ER), and one deciduous cultivar, *Rhododendron* ‘Gibraltar’, RHS#58 (AZ), obtained from a commercial nursery as 1-year-old liner (112-cm2 rooting volume) stock of clonally propagated tissue-cultured plants. Plants were transplanted on 25 Apr. 2005 into 3.8-L (1-gal.) containers (GL-400; Nursery Supplies, Inc., McMinnville, OR) filled with a substrate of bark, sphagnum peatmoss, perlite, vermiculite, dolomitic lime, and gypsum (SB-300; Sun Gro Horticulture, Bellevue, WA).
and were grown outdoors in Corvallis, OR (lat. 45°59′04″ N, long. 123°27′22″ W).

Nitrogen treatments. Twenty plants of each cultivar were randomly assigned to one of four groups and fertilized twice a week from 29 Apr. 2005 to 2 Sept. 2005 (N05 rate). During each fertilizer application, one of four groups and fertilized twice a week. Plants and never necessary in W50 plants. The procedure was seldom necessary in W100 valleys. Sprays were performed using Statistica® (Statsoft, Inc., Tulsa, OK). Data were tested for homogeneity of variance using Levene’s test and normality (Kolmogorov-Smirnov test). Allocation (% of total) data were arcsine
transformed before analyses and back-transformed means are presented. Data were analyzed using a combination of analysis of variance (ANOVA) and regression techniques as described subsequently. When appropriate based on ANOVA results, means for significant effects and their interactions were compared using Tukey’s honestly significant difference test at P < 0.05 (THSD0.05) or polynomial contrasts based on N05 rate. Coefficients from regression models were compared using Z-tests (Paternoster et al., 1998).

The influence of N05 rate and W05 treatment on gs was assessed separately at each measurement date using ANOVA in a full factorial design with cultivar, N05 rate, and W05 treatment as main effects. The influence of irradiation frequency on relationships between N05 rate and N uptake (N uptake efficiency) and N uptake and growth (N use efficiency) were assessed using best subsets regression. Mallow’s Cp was the criterion for choosing the best subset of predictor effects from linear and quadratic models. Intercepts and regression coefficients for relationships were calculated for each cultivar and W05 treatment combination.

Results and Discussion

Variation among cultivars in stomatal conductance. Late afternoon gs was lower than midday gS across all cultivars, N05 rates, and W05 treatments and the change in gs between midday and late afternoon varied between cultivars (Fig. 1A; within-subject time by cultivar interaction, P < 0.05). There were no significant interactions between time of day that gs was measured and N05 rate or time of day and W05 treatment. Therefore, data from the midday and late afternoon gs were pooled for each measurement date and analyzed using ANOVA in a full factorial design with cultivar, N05 rate, and W05 treatment as between-subject main effects and date (measurement date) as a within-subject repeated measure.

Daily and seasonal variation in gs differed among cultivars. On average, plants of PJM had the highest gs and ER had the lowest gs (Fig. 1B). Plant size may play a role in these gs differences among cultivars. Larger plants, in general, will have greater demands for water (Augé and Moore, 2002). Plants of ER grew more in 2005 than AZ and PJM (Fig. 4C). For all three cultivars, midday gs was higher than late afternoon gs, and ER had the largest increase in gs between midday and late afternoon. The gs from July through September was greater in PJM than ER (Fig. 1B) suggesting PJM were exposed to less water stress than ER during the growing season. Water stress during the growing season can affect the ability of evergreen plants to assimilate carbon in the fall (Vaz et al., 2010). The recovery of gs in the fall was greater in PJM than ER (Fig. 1B), suggesting that water availability may have decreased late-season carbon assimilation in ER. Others have reported that in the fall, on rewetting, carbon assimilation and gs in evergreen species can recover from summer water deficits (Vaz et al., 2010). The recovery response of gs varies with plant species and recovery of gs in plants exposed to greater water stress during the growing season may be lower. Fall recovery of carbon assimilation and gs compared with activity in the summer highlights the importance of the evergreen habit for whole plant carbon assimilation after summer drought and
therefore, for the accumulation of reserves in roots and stems. Thus, differences in gs between PJM and ER may be function of plant size can alter the ability of plants to recover from water stress.

The gs from July to September was similar in ER and AZ, whereas the gs in September and October was lower in ER than AZ (Fig. 1B). In contrast, the gs from July to September was greater in PJM than AZ and gs in PJM and AZ was similar starting in September (Fig. 1B). Differences among cultivars in late-season gs may be a combined result of plant size, growth habit (e.g., deciduous vs. evergreen), and recovery of gs after water stress. For example, differences in gs between ER and AZ in the fall may reflect variation in growth habit (e.g., deciduous vs. evergreen). Leaf gs changes with plant age and leaf maturation (Bauerle et al., 2004). Senescing leaves can lose their ability to regulate stomatal cells thereby having greater gs (Herrick and Thomas, 2003). Leaves of AZ started to change color and abscise in October. Thus, differences in gs between ER and AZ in the fall may be a function of leaf maturation and not just plant size. In contrast, in the fall when leaves in AZ were losing their ability to regulate their stomatal cells, their gs was similar to that of PJM. If we had measured carbon assimilation in our study, we would have been able to determine whether 1) greater gs was associated with lower photosynthesis in AZ compared with ER; and 2) similar gs was associated with lower photosynthesis in AZ compared with PJM.

Our results indicate that daily plant demand for water was not completely met by our irrigation treatments and suggest ER may have a greater demand for water than AZ and PJM. Thus, ER may have been subjected to more water stress on a daily and seasonal basis than AZ and PJM.

**Seasonal variation in stomatal conductance.**

The response of gs to water availability and plant N status varied among measurement dates. Increasing the frequency of irrigation increased gs on five of the nine measurement dates (Fig. 2A). Plants grown with 35 mg L⁻¹ N had the greatest gs on four of the nine measurement dates and plants grown with the highest N rate had the lowest gs on four of the nine measurement dates (Fig. 2B).

Our results indicate that neither irrigation treatment was able to meet plant water demands by mid- to late August, and plants were exposed to similar levels of water stress during this time regardless of irrigation frequency and N rate. Additionally, plants had a greater demand for water in September than earlier in the year, possibly because they were larger and may have used available water more rapidly because their root systems had penetrated more of the growing substrate. Thus, plants with a higher N status would likely need more water because these plants had more leaves (Fig. 5A) and would have had a higher net transpiration rate. Water deficits resulting from irrigation treatments and seasonal climatic changes would occur more quickly for these plants, causing reductions in their gs.

**Effects of nitrogen rate and irrigation frequency on stomatal conductance.**

Nitrogen application rate altered gs of container-grown Rhododendron and the response of gs to water availability imposed by irrigation frequency (Fig. 3). When irrigated once a day, plants grown in the highest N rate (140 mg L⁻¹ N) had the lowest gs. This suggests higher rates of N application increase plant demand for water and increase the potential for water stress. In contrast, when irrigated more frequently, plants grown with 0 mg L⁻¹ N had similar or lower gs than plants grown with 140 mg L⁻¹ N. When plants were irrigated more frequently, our gs results support the theory that N-deficient plants generally respond to water shortage by more rapid stomatal closure than plants with higher N status (Marschner, 1995).

More frequent irrigation increased gs in plants grown with 70 mg L⁻¹ N and 140 mg L⁻¹ N and decreased gs in plants that received 0 mg L⁻¹ N (Fig. 3). Increased irrigation frequency helped to ameliorate water stress related to high N rates but did not help ameliorate water stress in N-deficient plants. Increasing N availability generally increases plant growth (Ingestad and Lund, 1986) and increasing plant size increases the amount of water plants required for growth (Augé and Moore, 2002). Nitrogen deficiency may limit a plant’s ability to absorb water from the growing substrate, particularly if water distribution within the container is not uniform. Irrigating plants to container capacity once per day may result in a more uniform distribution of water within the growing substrate than more frequent irrigation with the same amount of water.

In general, less frequent irrigation and high N rates increased water stress in container-grown Rhododendron. The differential influence of N rate on gs between the two irrigation frequency treatments is a result of the effects of N rate on water availability or

---

**Fig. 1.** Stomatal conductance (gs) in Rhododendron ‘Gibraltar’ (AZ), Rhododendron ‘English Roseum’ (ER), and Rhododendron ‘P.J.M.’ (PJM) grown in containers. Error bars are least significant differences at \( P = 0.05 \). (A) Mean gs between 1100 and 1300 hr and 1500 and 1700 hr for each cultivar. Columns denoted by the same lower case letter are not significantly different \( (P = 0.05) \). (B) Mean gs for each cultivar on a different measurement date.

**Fig. 2.** Stomatal conductance (gs) in Rhododendron. Plants were grown in containers with 0 mg L⁻¹, 35 mg L⁻¹, 70 mg L⁻¹, or 140 mg L⁻¹ nitrogen (N) fertilizer and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water between May and Sept. 2005. Error bars are least significant differences at \( P = 0.05 \). Mean gs for each measurement date and (A) irrigation treatment and (B) N rate. (A) Significant differences \( (P = 0.05) \) between irrigation treatments denoted by asterisks (*) within date. (B) Significant \( (P = 0.05) \) linear \((L)\) and quadratic \((Q)\) response of gs to N rate within a measurement date indicated above data points.
demand (e.g., plant size) and the effects of N rate on the ability of plants to respond to stress. Plants grown with greater N rates may be better able to respond to lower levels of water stress (e.g., our W50 treatment) than plants grown with lower N rates. However, at higher levels of water stress (e.g., our W100 treatment), plants grown at the higher N rates are more sensitive. The level of water stress imposed by our treatments was much lower than the gs reported when deficit irrigation was used with container-grown Rhododendron (Cameron et al., 1999; Sharp et al., 2008). Deficit irrigation treatments in these studies caused large decreases in gs (≈50 mmol m⁻² s⁻¹ compared with ≈400 mmol m⁻² s⁻¹ in well-watered plants). On the dates we measured gs, it was rarely below ≈100 mmol m⁻² s⁻¹ and seldom above ≈400 mmol m⁻² s⁻¹. It is possible stronger linear responses of gs to N rate are more common when plants are under greater water stress.

Growth and nitrogen uptake. Plant growth in 2005 increased linearly with increasing rate of N application. For every gram of N applied, AZ accumulated 21 g to 22 g biomass, PJM accumulated 29 g to 32 g biomass, and ER accumulated 46 g to 51 g biomass by Nov. 2005. Increased irrigation frequency (and decreased water stress) was associated with lower N uptake and N uptake efficiency with no significant influence on plant growth. This resulted in W50 plants having greater N use efficiency than W100 plants (Fig. 4). Decreasing irrigation frequency can transiently decrease gs without influencing growth when the level of water stress imposed is not large enough to significantly influence seasonal carbon gain from photosynthesis (Scheiber et al., 2008). Differences in N uptake and N uptake efficiency among cultivars were related to differences in growth. Between May 2005 and Nov. 2005, ER had the greatest growth, N uptake, and N uptake efficiency and AZ had the lowest (Fig. 4). Plants that grow more rapidly have greater N requirements than plants with slower growth rates, and higher N requirements are usually associated with greater N uptake efficiency (Chapin et al., 1990).

Altering irrigation frequency changed the availability of N in the growing substrate or the ability of roots to absorb N. Increasing the volume of irrigation used in container

Fig. 3. Stomatal conductance (gs) in Rhododendron ‘Gibraltar’ (AZ), Rhododendron ‘English Roseum’ (ER), and Rhododendron ‘P.J.M.’ (PJM). Plants were grown in containers with 0 mg L⁻¹, 35 mg L⁻¹, 70 mg L⁻¹, or 140 mg L⁻¹ nitrogen (N) fertilizer and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water between May and Sept. 2005. Error bars are least significant differences at P = 0.05. Mean gs for each cultivar within N rate and irrigation treatment. Differences in significant (P = 0.05) linear (L) and quadratic (Q) response of gs to N rate between irrigation treatments denoted by asterisks (*) in legend.

Fig. 4. (A) Nitrogen (N) uptake efficiency, (B) N use efficiency, (C) biomass, and (D) N content in Rhododendron ‘Gibraltar’ (AZ), Rhododendron ‘English Roseum’ (ER), and Rhododendron ‘P.J.M.’ (PJM). Plants were grown in containers with 0 mg L⁻¹, 35 mg L⁻¹, 70 mg L⁻¹, or 140 mg L⁻¹ N fertilizer and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water between May and Sept. 2005. First-order regression coefficients for relationships between (A) N application rate in 2005 and net N uptake between May 2005 and Nov. 2005 and (B) N uptake in 2005 and growth between May 2005 and Nov. 2005. (C–D) Mean (n = 20) biomass and N content in May 2005 (May 2005) and net change in biomass and N content between May 2005 and Nov. 2005 (Nov. 2005). Significant differences (P < 0.05) between cultivars and W05 treatments denoted by different lower case letters.
production of nursery crops can increase N leaching from containers and potentially decrease N uptake because N is lost from the growing substrate and unavailable for plant uptake (Cabrera, 2004; Million et al., 2007). Plants in the W100 treatment received more water at one time than plants in the W50 treatment and N uptake by W100 plants was greater than W50 plants (Fig. 4). Additionally, during irrigation events, no water was observed leaving the bottom of containers in the W50 treatment. This suggests that the effect of irrigation frequency on N uptake was not a result of lower N availability in the W50 plants as a result of leaching but instead the ability of roots to absorb N was altered by irrigation frequency.

Irrigating plants more frequently may result in higher salt accumulation in containers because of reduced leaching. Compared with overhead irrigation, subirrigation more completely saturates the container substrate and has lower pour-through electrical conductivity (EC) resulting in improved N uptake ability by azalea at lower N fertilizer rates (Million et al., 2007). It is possible N uptake by plants in our W50 treatment was restricted as a result of higher substrate EC, which could also influence uptake of potassium and calcium (Marschner, 1995).

Irrigating plants less frequently and increasing N fertilizer application rate can increase water stress in container-grown *Rhododendron* and plants may respond by altering N accumulation and efficiency of N use without influencing growth. Plant N status in the fall is frequently correlated with plant performance during the next growing season (Millard, 1996). Low levels of water stress during container production of *Rhododendron* may not impact net total carbon gain but has the potential to alter N uptake and thus influence plant performance during the next growing season.

**Biomass allocation.** Cultivars preferentially allocated biomass to different structures in the fall (Fig. 5). On average, biomass allocation to roots was highest in AZ and lowest in ER, biomass allocation to stems was highest in PJM and lowest in ER, and biomass allocation to leaves was highest in ER and lowest in AZ. In the fall, deciduous plants generally store reserves in roots and evergreen plants store reserves in different structures depending on the cultivar (Ingestad, 1991; Millard, 1996). Our results suggest AZ preferentially allocated biomass to roots and ER to leaves. Plants of PJM generally store more reserves in roots and stems than ER and ER generally stores more reserves in leaves than PJM (Scagel et al., 2007). The effects of irrigation treatments and N rate on biomass allocation may be related to where and when cultivars preferentially allocate resources.

Irrigating ER and PJM more frequently decreased biomass allocation to roots and increased biomass allocation to stems and leaves of PJM (Fig. 5B). Increasing rate of N application decreased biomass allocation to roots of all cultivars and increased biomass allocation to aboveground structures (Fig. 5A).

Increased allocation of biomass to roots is a common plant response to nutrient and water deficits. Nutrient uptake by roots, even in the constraints of a container, is greater when plants have larger root systems (Agren and Ingestad, 1987; Tan and Hogan, 1997). Drought stress and N deficiency have similar effects on gs, root/shoot ratios, and abscisic acid levels in plants (Marschner, 1995). All cultivars allocated more biomass to roots in response to N limitation but only ER and PJM allocated more biomass to roots in response to decreased irrigation frequency. Less frequent irrigation increased water stress and was associated with increased N uptake and biomass allocation to roots in ER and PJM. This suggests that greater N uptake in W100 ER and PJM may be a result of increased biomass allocation to roots.

More frequent irrigation in AZ had no influence on biomass allocation to roots, decreased biomass allocation to stems, and increased allocation to leaves (Fig. 5B). Many woody deciduous plants store reserves for the next growing season in roots (Millard, 1996) and nutrient and biomass import to roots of AZ can occur as early as September (Scagel et al., 2007). Water stress can decrease accumulation of reserves and promote early nutrient mobilization to storage (Sanz-Pérez et al., 2009). Leaves in W100 AZ changed color and abscised earlier in the fall than leaves in W50 AZ (data not shown). Water stress may have decreased reserve storage in AZ roots; however, the timing of our harvest in the fall may not reflect these effects as a result of how irrigation treatments influenced the timing of mobilization.

Irrigating plants less frequently can increase water stress of container-grown *Rhododendron* and plants may respond by altering plant form (biomass allocation) without a detectable change in growth (total plant biomass). Plant form can be as important to nursery stock quality as plant growth (Cameron et al., 2008; Sharp et al., 2008; Tan and Hogan, 1997). Our results indicate water stress from irrigation frequency may not impact total growth but has the potential to alter biomass allocation and thus influence plant form (e.g., leaf retention, stem growth, etc.) and N uptake and N use efficiency.

In conclusion, using gs as an estimate of plant water stress, our results indicate that decreasing the frequency of irrigation increases water stress of container-grown
*Rhododendron* and plants grown with high rates of N fertilizer are more susceptible to water stress, particularly when plant water requirements are highest as a result of growth and environmental conditions. Additionally, relatively small, transitory increases in plant water stress at different times during the growing season can alter N uptake and plant form without impacting total plant biomass.

**Literature Cited**


