

Effects of Irrigation Frequency and Nitrogen Fertilizer Rate on Water Stress, Nitrogen Uptake, and Plant Growth of Container-grown Rhododendron

Carolyn F. Scagel¹

U.S. Department of Agriculture, Agricultural Research Service, Horticultural Crops Research Unit, 3420 NW Orchard Avenue, Corvallis, OR 97330

Guihong Bi

Truck Crops Branch Experiment Station, Mississippi State University, 2024 Experiment Station Road, Crystal Springs, MS 39059

Leslie H. Fuchigami and Richard P. Regan

Department of Horticulture, Oregon State University, Corvallis, OR 97330

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Abstract. The influence of irrigation frequency (same amount of water per day given at different times) and nitrogen (N) fertilizer rate on water stress [stomatal conductance (g_s)], N uptake, and growth (biomass) of container-grown evergreen *Rhododendron* ‘P.J.M. Compact’ and ‘English Roseum’ and deciduous *Rhododendron* ‘Gibraltar’ was evaluated. Both N deficiency and high N rate increased water stress. Water stress was greatest in plants fertilized with the highest N rate and g_s of plants grown with the higher N rates changed more in response to water deficits resulting from irrigation treatments and seasonal climatic changes. Watering plants more frequently decreased water stress of plants fertilized with higher N rates and altering irrigation frequency had little impact on alleviating water stress of N-deficient plants. Increasing irrigation frequency decreased N uptake efficiency (N uptake per gram N applied), increased N use efficiency (growth per gram N uptake) and altered biomass allocation with little influence on total plant biomass. Response of biomass allocation to N rates was similar among cultivars and response of biomass allocation to irrigation frequency varied among cultivars. Altering irrigation frequency changed either the availability of N in the growing substrate or the ability of roots to absorb N. Our results indicate that transitory increases in plant water stress can alter N uptake, N use, and plant form without detectable changes in total plant biomass.

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). Increasing irrigation frequency can increase growth of container-grown plants or have no influence on growth (Beeson, 1992; Fare et al., 1994; Keever

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 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-cm³ 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)

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¹To whom reprint requests should be addressed; e-mail Carolyn.Scagel@ars.usda.gov.

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 group received 250 mL of N-free fertilizer (1.06 mg·mL⁻¹, Cornell No N Eq. 0-6-27; Greencare Fertilizers, Kankakee, IL) and plants in the other groups received 250 mL of the N-free fertilizer plus 35 mg·L⁻¹, 70 mg·L⁻¹, or 140 mg·L⁻¹ N (NH₄NO₃; Sigma Aldrich, St. Louis, MO). The N concentration in irrigation water was measured periodically from May to Oct. 2005 using ion selective electrodes (Thermo Electron Corp., Waltham, MA). Concentrations of nitrate and ammonium in irrigation water were less than 28 mg·L⁻¹ NO₃ and 10 mg·L⁻¹ NH₄, respectively. The N supplied from irrigation water was accounted for in calculating the total amount of N applied to plants.

Irrigation treatments. Plants in each N05 rate were randomly assigned to one of two groups and irrigated daily at two different frequencies (W05 treatment) by drip irrigation from 2 May 2005 to 30 Sept. 2005 using one drip emitter (2 L·h⁻¹ flow rate; Netafim Co., Valley Stream, NY) per container. Plants in one group were irrigated to 100% container capacity at 0800 HR every morning (W100) and plants in the second group received the same amount of water each day as plants in the W100 treatment but in equal volume split applications at 0800 HR and 1430 HR (W50). The irrigation volumes were corrected weekly based on gravimetric determination of the average container capacity measured in three reference plants for each cultivar grown with the highest N05 rate in both irrigation treatments. Climate data were obtained for the duration of the experiment from a U.S. Bureau of Reclamation AgriMet weather station (CRVO) located 5 km from the experimental site. Before irrigation, treatments were started pans were placed below each container to collect runoff from containers. After each irrigation event, any water in pans beneath containers was added back into containers. This procedure was seldom necessary in W100 plants and never necessary in W50 plants.

Harvests. Ten plants of each cultivar were harvested in Apr. 2005 for initial estimates of biomass and nutrient composition, and in Nov. 2005, five plants of each cultivar from each N05 rate and W05 treatment combination were harvested. Shoots were cut at the soil surface, separated into leaves and stems, and divided into 1-year-old and 2-year-old structures, when applicable. Roots were removed from containers and washed from the substrate. Leaves, stems, and roots were dried at 65 °C in a forced-air oven, weighed, ground to pass through a 40-mesh screen, and analyzed for nutrient composition.

Stomatal conductance measurements. A steady-state porometer (LI-1600; LI-COR, Lincoln, NE) was used to measure water loss from transpiring leaves. All leaves were completely dry before any readings were taken. A leaf sensor head exposing 1 cm² of leaf area

to a dry air stream was used and leaf temperature, cuvette temperature, and cuvette relative humidity were recorded. Leaf transpiration rate (mmol·m⁻²·s⁻¹) was determined from the volumetric flow rate. Stomatal conductance was calculated using the measured values of relative humidity, leaf and air temperature, and flow rate (Cowan, 1977; LI-COR, 1989). Measurements were taken at midday (between 1100 HR and 1300 HR) and in late afternoon (between 1500 HR and 1700 HR) on the same leaves from five plants of each cultivar in each N05 rate and W05 treatment nine times between 17 July 2005 and 22 Oct. 2005. The same plants were used for measurements at each date and sampling was randomized between treatments within each cultivar during measurement periods.

Nitrogen analyses and calculations. Samples taken for nutrient analyses were analyzed for concentrations of N by combustion (Tru Spec CHN; LECO Corp., St. Joseph, MI) (Bi et al., 2007b). Samples of the growing substrate were taken at the beginning of the experiment and analyzed for nutrient composition by standard methods (Berg and Gardner, 1979). Total biomass was calculated as the sum of dry weights overall structures and biomass allocation between different structures was calculated as the proportion (%) of total biomass in different structures. The N content of each plant structure was calculated by multiplying the N concentration (mg·g⁻¹) in samples of each structure by the dry weight of each structure. Total plant content (mg) of N was calculated as the sum overall structures. Net biomass growth and net nutrient uptake between May 2005 and Nov. 2005 (2005 growth and 2005 uptake) were estimated by subtracting the average biomass or nutrient content of each cultivar in May 2005 from the biomass or nutrient content of individual plants harvested in Nov. 2005.

Statistical analyses. Containers were arranged in a randomized design with each treatment unit (container) replicated five times for each N05 rate (0, 35, 70, 140 mg·L⁻¹ N), irrigation treatment (W100, W50), and cultivar (ER, PJM, AZ). All statistical analyses 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 $P < 0.05$ (THSD_{0.05}) 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 g_s was assessed separately at each measurement date using ANOVA in a full factorial design with cultivar, N05 rate, and W05

treatment as between-subject main effects and time of day (midday and late afternoon) as a within-subject repeated measure.

The influence of N05 rate and W05 treatment on biomass, N content, and biomass allocation was assessed using ANOVA in a full factorial design with cultivar, N05 rate, and W05 treatment as main effects. The influence of irrigation 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. Mallows'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 g_s was lower than midday g_s across all cultivars, N05 rates, and W05 treatments and the change in g_s 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 g_s was measured and N05 rate or time of day and W05 treatment. Therefore, data from the midday and late afternoon g_s 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 g_s differed among cultivars. On average, plants of PJM had the highest g_s and ER had the lowest g_s (Fig. 1B). Plant size may play a role in these g_s 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 g_s was higher than late afternoon g_s , and ER had the largest decrease in g_s between midday and late afternoon.

The g_s 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 g_s 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 g_s in evergreen species can recover from summer water deficits (Vaz et al., 2010). The recovery response of g_s varies with plant species and recovery of g_s in plants exposed to greater water stress during the growing season may be lower. Fall recovery of carbon assimilation and g_s 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 g_s between PJM and ER that may be function of plant size can alter the ability of plants to recover from water stress.

The g_s from July to September was similar in ER and AZ, whereas the g_s in September and October was lower in ER than AZ (Fig. 1B). In contrast, the g_s from July to September was greater in PJM than AZ and g_s in PJM and AZ was similar starting in September (Fig. 1B). Differences among cultivars in late-season g_s may be a combined result of plant size, growth habit (e.g., deciduous vs. evergreen), and recovery of g_s after water stress. For example, differences in g_s between ER and AZ in the fall may reflect variation in growth habit (e.g., deciduous vs. evergreen). Leaf g_s changes with plant age and leaf maturation (Bauerle et al., 2004). Senescing leaves can lose their ability to regulate stomatal cells thereby having greater g_s (Herrick and Thomas, 2003). Leaves of AZ started to change color and abscise in October. Thus, differences in g_s 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 g_s 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 g_s was associated with lower photosynthesis in AZ compared with ER; and 2) similar g_s 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 g_s to water availability and plant N status varied among measurement dates. Increasing the frequency of irrigation increased g_s on five of the nine measurement dates (Fig. 2A). Plants grown with 35 mg·L⁻¹ N had the greatest g_s on four of the nine measurement dates and plants grown with the highest N rate had the lowest g_s 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 g_s .

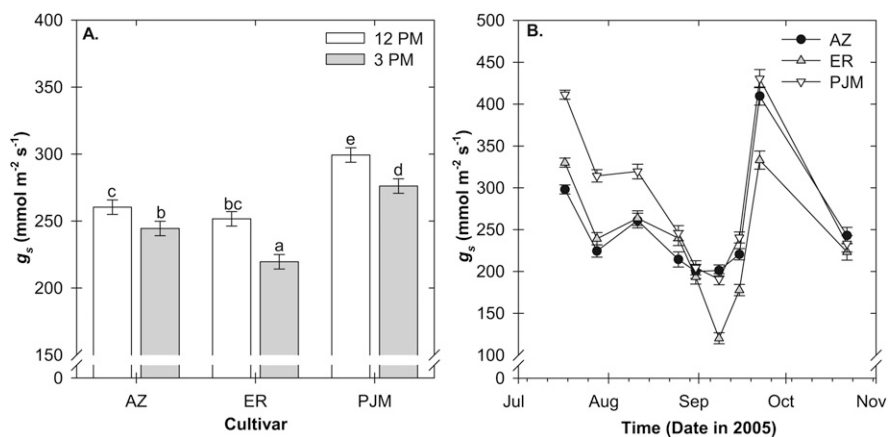


Fig. 1. Stomatal conductance (g_s) in *Rhododendron* ‘Gibraltar’ (AZ), *Rhododendron* ‘English Roseum’ (ER), and *Rhododendron* ‘P.J.M.’ (PJM) grown in containers. Error bars are least significant differences at $P = 0.05$. (A) Mean g_s between 1100 and 1300 HR and 1500 and 1700 HR for each cultivar.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

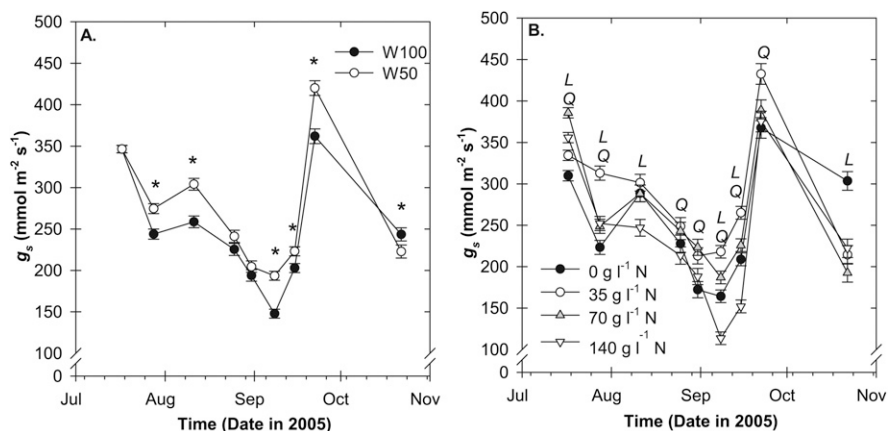


Fig. 2. Stomatal conductance (g_s) in *Rhododendron*. Plants were grown in containers with 0 mg·L⁻¹, 35 mg·L⁻¹, 70 mg·L⁻¹, or 140 mg·L⁻¹ nitrogen (N) fertilizer and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water between May and Sept. 2005. Error bars are least significant differences at $P = 0.05$. Mean g_s 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 a date. (B) Significant ($P = 0.05$) linear (L) and quadratic (Q) response of g_s to N rate within a measurement date indicated above data points.

Effects of nitrogen rate and irrigation frequency on stomatal conductance. Nitrogen application rate altered g_s of container-grown *Rhododendron* and the response of g_s 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 g_s . 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 g_s than plants grown with 140 mg·L⁻¹ N. When plants were irrigated more frequently, our g_s 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 g_s in plants grown with 70 mg·L⁻¹ N and 140 mg·L⁻¹ N and decreased g_s 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 g_s between the two irrigation frequency treatments is a result of the effects of N rate on water availability or

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 at 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 g_s 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 g_s ($\approx 50 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared with $\approx 400 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in well-watered plants). On the dates we measured g_s , it was rarely below $\approx 100 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and seldom above $\approx 400 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. It is possible stronger linear responses of g_s 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 de-

creased 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 g_s 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

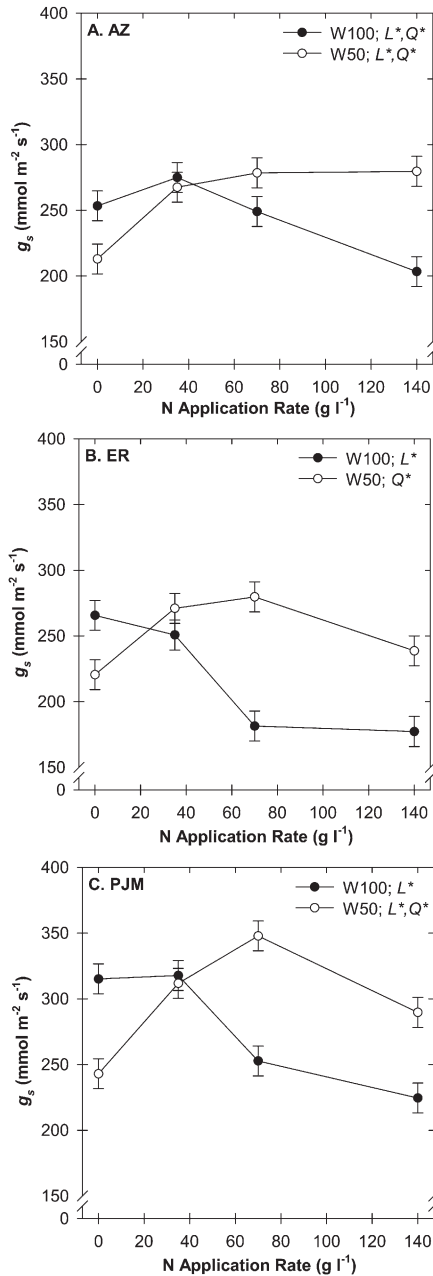


Fig. 3. Stomatal conductance (g_s) in *Rhododendron* 'Gibraltar' (AZ), *Rhododendron* 'English Roseum' (ER), and *Rhododendron* 'P.J.M.' (PJM). Plants were grown in containers with 0 $\text{mg}\cdot\text{L}^{-1}$, 35 $\text{mg}\cdot\text{L}^{-1}$, 70 $\text{mg}\cdot\text{L}^{-1}$, or 140 $\text{mg}\cdot\text{L}^{-1}$ 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 g_s for each cultivar within N rate and irrigation treatment. Differences in significant ($P = 0.05$) linear (L) and quadratic (Q) response of g_s to N rate between irrigation treatments denoted by asterisks (*) in legend.

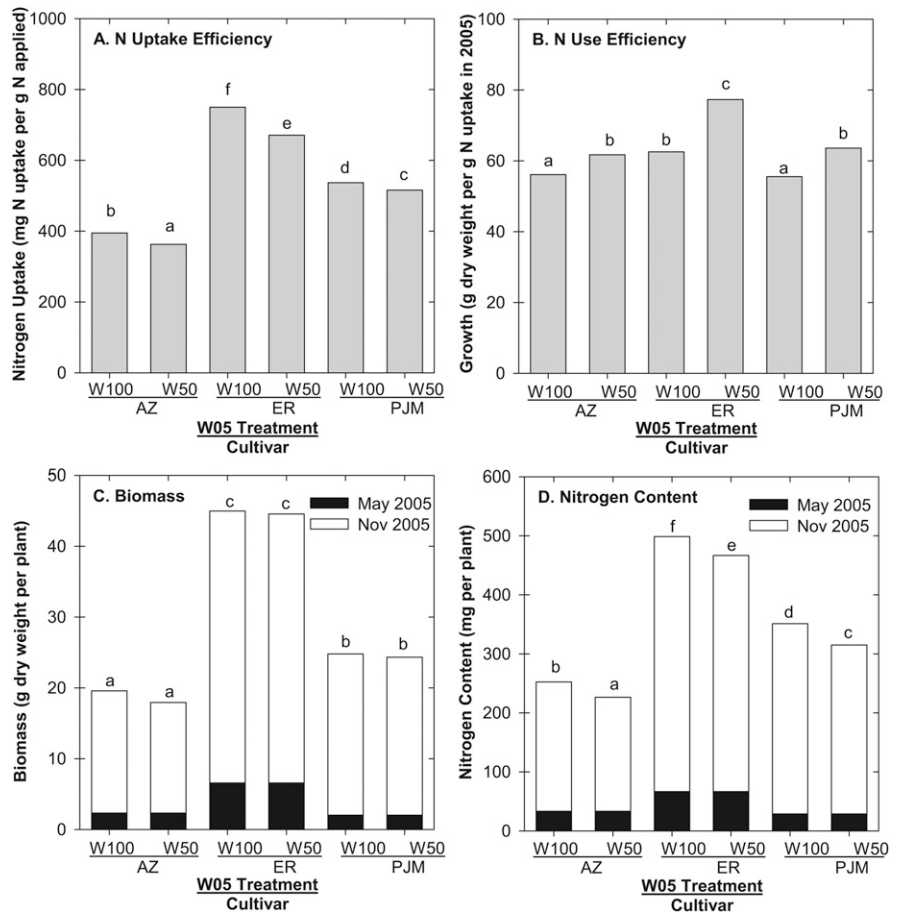


Fig. 4. (A) Nitrogen (N) uptake efficiency, (B) N use efficiency, (C) biomass, and (D) N content in *Rhododendron* 'Gibraltar' (AZ), *Rhododendron* 'English Roseum' (ER), and *Rhododendron* 'P.J.M.' (PJM). Plants were grown in containers with 0 $\text{mg}\cdot\text{L}^{-1}$, 35 $\text{mg}\cdot\text{L}^{-1}$, 70 $\text{mg}\cdot\text{L}^{-1}$, or 140 $\text{mg}\cdot\text{L}^{-1}$ 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 of ER 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).

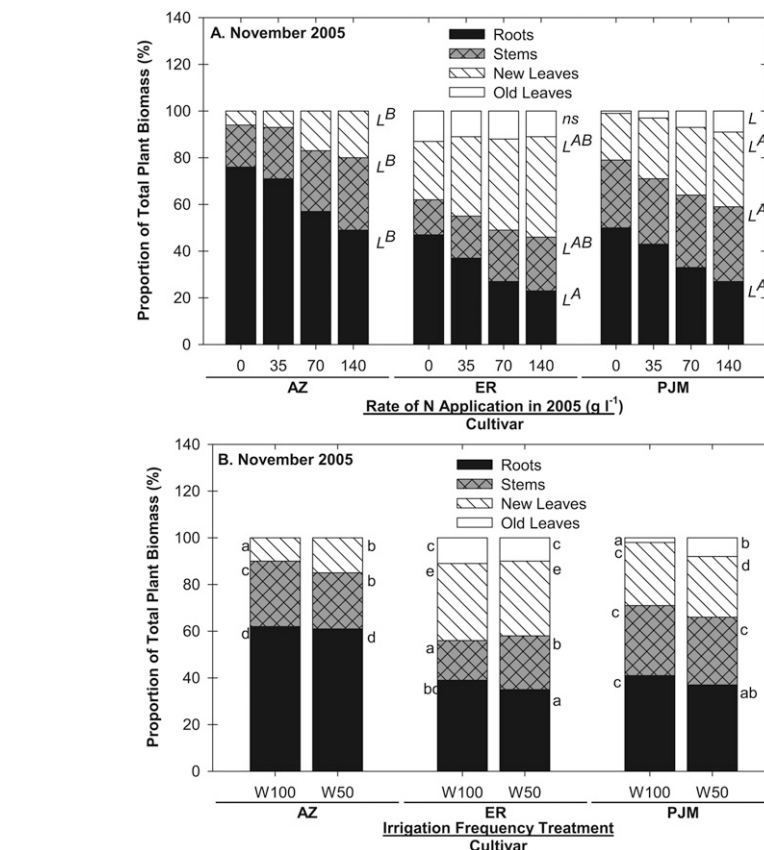


Fig. 5. Biomass allocation in Nov. 2005 in *Rhododendron* ‘Gibraltar’ (AZ), *Rhododendron* ‘English Roseum’ (ER), and *Rhododendron* ‘P.J.M.’ (PJM). Plants were grown in containers with 0 mg·L⁻¹, 35 mg·L⁻¹, 70 mg·L⁻¹, or 140 mg·L⁻¹ nitrogen (N) fertilizer and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water between May and Sept. 2005. New stems and new leaves originated in 2005 and old stems and old leaves originated before 2005. Non-significant (ns) and significant ($P < 0.05$) linear (L) relationships between N05 rate and response variable indicated adjacent to structure within a cultivar and differences between cultivars in L response to N05 rate denoted by upper case superscript letters following L within a structure (A). Significant differences ($P < 0.05$) between cultivars and W05 treatments for each response variable denoted by different lower case letters within a structure (B).

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 (Ågren and Ingestad, 1987; Tan and Hogan, 1997). Drought stress and N deficiency have similar effects on g_s , 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 g_s 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.

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