# Irrigation Frequency Alters Nutrient Uptake in Container-grown *Rhododendron* Plants Grown with Different Rates of Nitrogen

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*Abstract.* The influence of irrigation frequency (same amount of water per day given at different times) on nutrient uptake of container-grown evergreen *Rhododendron* 'P.J.M. Compact' (PJM) and 'English Roseum' (ER) and deciduous *Rhododendron* 'Gibraltar' (AZ) grown with different rates of nitrogen (N) fertilizer was evaluated. Increased N application rate increased nutrient uptake and plant dry biomass. Irrigation frequency did not significantly influence total plant dry biomass; however, more frequent irrigation decreased net uptake of several nutrients including phosphorus (P), boron (B), and manganese (Mn) uptake in all cultivars; potassium (K), copper (Cu), and zinc (Zn) uptake in AZ and ER; sulfur (S) uptake in ER and PJM; and iron (Fe) uptake in AZ. Additionally, more frequent irrigation of evergreen cultivars increased calcium (Ca) uptake. Covariate analyses were used to compare nutrient uptake among cultivars and irrigation treatments after accounting for the variability in nutrient uptake attributable to differences in biomass and N uptake. For most nutrients, the influence of irrigation frequency on uptake was partially attributable to differences in biomass and N uptake. After accounting for the variability in nutrient uptake associated with biomass or N uptake, increased irrigation frequency decreased P, S, B, Cu, and Mn uptake only in ER and increased Ca uptake in the two evergreen cultivars. Differences in nutrient uptake among cultivars in response to irrigation treatments were related to water and N availability during production and their combined influence on water stress, nutrient uptake, and biomass partitioning. Estimates of nutrient demand and uptake efficiency using nutrient concentrations and ratios are discussed in relation to nutrient management differences for different cultivars and irrigation treatments.

Large irrigation volumes leach nutrients from containers because the growing substrate used in nursery production generally has low nutrient and water-holding capacity (Arreola et al., 2006; Beeson, 2006; Fare et al., 1994; Huett, 1997). Leaching from containers can be decreased by increasing irrigation frequency but not total volume. Less frequent irrigation may decrease plant growth as a result of nutrient shortage rather than water shortage, and more frequent irrigation may compensate for certain nutrient deficiencies (Buljovcic and Engels, 2001; Scheiber et al., 2008; Silber et al., 2003; Xu et al., 2004).

Many commercially important qualities of container-grown plants are a function of nutrients and water availability during production (Cameron et al., 2008; Sharp et al., 2008). Nitrogen is the primary nutrient that drives growth and therefore demand for other nutrients (Marschner, 1995). One of the largest challenges in container nursery nutrient management is that water availability may have unforeseen impacts on nutrient availability and vice versa. Maintaining a balance of water and nutrient availability to optimize growth

and quality of container plants requires knowledge of how these factors interact. The influence of water and N management on uptake of other nutrients during production for many crops has not been evaluated fully. With some woody perennial plants, growth is enhanced more by minimizing water stress than by increasing fertility (Rose et al., 1999; Tan and Hogan, 1997).

Nitrogen availability influences growth and uptake and storage of N and other nutrients by evergreen and deciduous cultivars of *Rhododendron* spp. (Bi et al., 2007a; Harris et al., 2006; Scagel et al., 2007, 2008a, 2008b). Negative growth responses to excess N can occur from increased salinity, disruption of the balance between N and other nutrients, or increased water stress (Bi et al., 2007b; Cabrera, 2004). Certain N application rates can increase uptake of other nutrients; however, growth of plants with a high N status can be limited by availability of other nutrients if nutrient management strategies are not altered for high N rates. Irrigation scheduling can alter growth of *Rhododendron* (Keever and Cobb, 1985; Million et al., 2007). Improved knowledge of the combined influence of irrigation and nutrient management during nursery production is needed to develop integrated nursery production practices targeted at improving plant quality and decreasing production inputs.

Recently, we described how both N deficiency and high plant N status increase water stress in container-grown *Rhododendron* (Scagel et al., 2011). Watering plants more frequently decreased water stress of plants fertilized with the highest N rate and had little impact on alleviating water stress of N-deficient plants. Altering irrigation frequency changed N availability in the growing substrate or the ability of roots to absorb N. In addition, we found that transitory increases in plant water stress from different irrigation frequencies alters N uptake and use and plant form without detectable changes in total plant biomass. The influence of N rate on the uptake of other nutrients reported in our previous research (Scagel et al., 2008a, 2008b) may have been partially a function of differences in water stress.

The effects of cultural practices on nutrient content can be complicated to interpret in terms of drawing conclusions related to nutrient uptake when plant size is also influenced by the cultural practices and cultivars evaluated. Differences in nutrient uptake between cultivars and treatments can be partially attributable to scaling effects of plant growth on nutrient content (Righetti et al., 2007). For example, the increasing rate of N application can increase total biomass and N content of *Rhododendron* (Bi et al., 2007b; Scagel et al., 2007, 2008a). This indicates that plants absorbed more N at greater N rates (e.g., greater N uptake) but it is not clear whether greater N uptake is solely a function of plant size or a combination of plant size and increased capability to absorb N. Previously, we used covariate analyses to account for differences attributable to plant

size in comparisons of nutrient uptake between cultivars and treatments (Scagel et al., 2008b). Our research on the effects of water stress on N uptake indicated plant size was unaffected by our irrigation treatments (Scagel et al., 2011). Lack of significant biomass response to the low level of water stress achieved by our irrigation treatments allows us to more readily interpret changes in nutrient content as changes in nutrient availability, the efficiency of nutrient uptake, and, in perennial crops, differences in nutrient storage. We report the influence of irrigation frequency and rate of N application on uptake of other nutrients in one deciduous and two evergreen cultivars of *Rhododendron* grown in containers for 1 year. Additionally, we also evaluated whether nutrient concentrations in different structures and ratios of N to other nutrients in leaves and whole plants could be used to detect the influence of irrigation frequency on the relationship between N and other nutrients.

## Materials and Methods

A more detailed description of the experimental methods including analyses and results for N and biomass can be found in Scagel et al. (2011). This experiment used two evergreen cultivars of *Rhododendron*, PJM and ER, and one deciduous cultivar, AZ, obtained from a commercial nursery as 1-year-old liner 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). A summary of the methods given in Scagel et al. (2011) are given subsequently and more detailed methods that pertain to analyses for other nutrients, calculations of nutrient uptake, and statistical analyses are included.

*Nitrogen and irrigation treatments.* Plants were fertilized twice a week from 29 Apr. 2005 to 2 Sept. 2005. Plants in 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 three groups received 250 mL of the N-free fertilizer plus 35 mg·L$^{-1}$, 70 mg·L$^{-1}$, or 140 mg·L$^{-1}$ N from NH$_4$NO$_3$ (N rate; 20 plants per N rate per cultivar). Plants in each N rate were randomly assigned to one of two groups and irrigated daily using drip irrigation from 2 May 2005 to 30 Sept. 2005. Each day 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) (irrigation treatment; 10 plants per N rate per cultivar).

*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 N rate and water 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. Roots were removed from containers and substrate was washed from roots. Leaves, stems, and roots were dried at 65 °C in a forced-air oven (Model 1380FM; Sheldon Manufacturing, Cornelius, OR) until constant weight was achieved, weighed, ground to pass through a 40-mesh screen, and analyzed for nutrient composition.

*Nutrient analyses.* Samples taken for nutrient analyses were analyzed for carbon (C) and N concentrations using combustion (Bi et al., 2007b) and concentrations of other macro- and micronutrients in samples using inductively coupled plasma–optical emission spectroscopy after digestion of dried sample in nitric acid (Scagel et al., 2008a). Reference standard apple leaves (#151, National Institute of Standards and Technology) were run with samples for all procedures to ensure accuracy of results with ± 3% cv.

*Calculations.* Total biomass was calculated as the sum of dry weights overall structures and biomass allocation between structures was calculated as the proportion (%) of total biomass in specific structures. Biomass and biomass allocation results are presented in Scagel et al. (2011). Nutrient content of each plant structure was calculated by multiplying the nutrient concentration (mg·g$^{-1}$) in samples of each structure by the dry weight of each structure. Total plant nutrient content (mg or μg) was calculated as the sum of overall structures. Average plant nutrient concentration (mg·g$^{-1}$ or μg·g$^{-1}$) was calculated by dividing the total plant nutrient content by total plant dry weight. Net nutrient accumulation (uptake) between May 2005 and Nov. 2005 was estimated by subtracting the average nutrient content of each cultivar in May 2005 from the nutrient content of individual plants in Nov. 2005. Nitrogen ratios (ratios of N to other nutrients) in leaves and total plant were calculated for each plant using concentrations of nutrients in leaves and average plant nutrient concentrations.

*Statistical analyses.* Containers were arranged in a randomized design with each treatment unit (container) replicated five times for each N 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). Based on analysis of variance (ANOVA) results, means for significant effects and their interactions were compared using Tukey's honestly significant difference test at $P < 0.05$.

Differences among cultivars in nutrient status in May 2005 (average plant concentration, concentration in different structures, and total content) were assessed using ANOVA and regression with biomass used as a covariate in analysis of covariance (ANCOVA) to evaluate the contribution of plant size to variance

in nutrient status (Scagel et al., 2008a). The influence of cultivar, N rate, and irrigation treatment on nutrient concentrations in Nov. 2005 and net nutrient uptake between May 2005 and Nov. 2005 were assessed using ANOVA and regression with biomass and N uptake used as covariates in ANCOVA to evaluate the contribution of plant size and N uptake to variance in nutrient concentrations and uptake. Eta-squared [$\eta^2 = (SS_{effect}/SS_{total})$] was used to assess the proportion of total variance attributable to covariates. Unadjusted means ($\overline{X}$) and means adjusted for the covariates ($\overline{X}_{DW}$, $\overline{X}_{NU}$) are presented where appropriate.

The influence of irrigation frequency on relationships between N application rate and uptake of nutrients other than N and the relationships between N uptake and uptake of nutrients other than N were assessed using best subsets regression with Mallow's Cp as 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 irrigation treatment combination. Coefficients from regression models were compared using Z-tests (Paternoster et al., 1998).

Differences among cultivars in leaf and whole plant N ratios in May 2005 were subjected to repeated-measures ANOVA with cultivar as a between-subject factor and structure (leaf and plant) as a within-subject repeated measure. Similarly, the influence of cultivar, N rate, and irrigation treatment on N ratios in Nov. 2005 were assessed using repeated-measures ANOVA with cultivar, N rate, and irrigation treatment as between-subject factors and structure (leaf and plant) as within-subject repeated measure.

## Results and Discussion

*Contribution of biomass and nitrogen uptake to variability in nutrient uptake.* In general AZ had the lowest nutrient uptake between May and November and ER had the greatest nutrient uptake ($\overline{X}$; Table 1). More frequent irrigation decreased P, B, and Mn uptake in all cultivars; decreased K, Cu, and Zn uptake in AZ and ER; decreased S uptake in ER and PJM; decreased Fe uptake in AZ; and increased Ca uptake in ER and PJM. Less frequent irrigation increased water stress and was associated with increased biomass allocation to roots in ER and PJM (Scagel et al., 2011) and increased uptake of specific nutrients by ER and PJM. These results suggest that greater nutrient uptake in W100 ER and W100 PJM than W50 plants may be a result of increased root growth. 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). Increased biomass allocation to roots is a common compensatory mechanism of plants under water or nutrient stress (Chapin, 1991; Kozlowski and Pallardy, 2002) and water stress can alter the timing of resource allocation in the fall (Sanz-Pérez et al., 2009).

Table 1. Net nutrient accumulation (uptake) between May and Nov. 2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM) grown in containers and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water from May to Sept. 2005.

| Nutrient | | AZ W100 | AZ W50 | ER W100 | ER W50 | PJM W100 | PJM W50 | Eta-squared[x] |
|---|---|---|---|---|---|---|---|---|
| Phosphorus (mg) | $\overline{X}$ | 32.1 b[y] | 28.1 a | 56.2 d | 47.3 c | 32.4 b | 28.5 a | |
| | $\overline{X}_{DW}$ | 43.4 d | 42.5 d | 38.0 c | 29.6 a | 37.8 c | 35.4 b | 0.52 |
| | $\overline{X}_{NU}$ | 37.7 b | 36.2 b | 47.4 d | 41.4 c | 32.4 a | 31.6 a | 0.21 |
| Potassium (mg) | $\overline{X}$ | 118 b | 107 a | 307 e | 296 d | 135 c | 130 c | |
| | $\overline{X}_{DW}$ | 182 b | 184 b | 203 d | 194 c | 165 a | 163 a | 0.65 |
| | $\overline{X}_{NU}$ | 148 b | 146 b | 259 c | 263 c | 134 a | 141 ab | 0.15 |
| Sulfur (mg) | $\overline{X}$ | 19.7 a | 18.3 a | 41.4 e | 33.4 d | 30.5 c | 27.5 b | |
| | $\overline{X}_{DW}$ | 27.9 b | 28.0 b | 28.2 b | 20.5 a | 34.4 d | 31.7 c | 0.35 |
| | $\overline{X}_{NU}$ | 23.5 a | 23.2 a | 35.4 c | 29.3 b | 30.5 c | 28.9 b | 0.16 |
| Calcium (mg) | $\overline{X}$ | 49.3 a | 44.1 a | 217.7 d | 233.7 e | 118.4 b | 127.9 c | |
| | $\overline{X}_{DW}$ | 89.2 a | 91.4 a | 153.3 d | 161.0 e | 137.4 b | 146.9 c | 0.38 |
| | $\overline{X}_{NU}$ | 69.3 a | 69.6 a | 186.1 d | 202.4 e | 118.6 b | 133.3 c | 0.11 |
| Magnesium (mg) | $\overline{X}$ | 33.5 a | 31.1 a | 100.3 c | 100.0 c | 48.4 b | 48.3 b | |
| | $\overline{X}_{DW}$ | 51.9 a | 52.8 a | 70.7 c | 71.2 c | 57.1 b | 58.0 b | 0.65 |
| | $\overline{X}_{NU}$ | 42.9 a | 43.0 a | 85.5 c | 90.0 c | 48.5 b | 51.8 b | 0.13 |
| Boron (μg) | $\overline{X}$ | 230 b | 196 a | 846 f | 759 e | 493 d | 467 c | |
| | $\overline{X}_{DW}$ | 374 a | 366 a | 614 d | 533 b | 562 c | 542 b | 0.40 |
| | $\overline{X}_{NU}$ | 303 a | 288 a | 731 d | 681 c | 494 b | 493 b | 0.13 |
| Copper (μg) | $\overline{X}$ | 205 b | 159 a | 344 d | 277 c | 286 c | 290 c | |
| | $\overline{X}_{DW}$ | 305 d | 277 c | 183 b | 120 a | 334 e | 342 e | 0.30 |
| | $\overline{X}_{NU}$ | 263 bc | 233 ab | 252 b | 215 a | 286 cd | 311 d | 0.26 |
| Iron (μg) | $\overline{X}$ | 214 c | 194 b | 139 a | 131 a | 138 a | 142 a | |
| | $\overline{X}_{DW}$ | 6,804 c | 6,359 c | 2,935 a | 2,349 a | 4,527 b | 4,976 b | 0.31 |
| | $\overline{X}_{NU}$ | 5,805 c | 5,293 c | 4,589 b | 4,581 b | 3,434 a | 4,249 b | 0.24 |
| Manganese (μg) | $\overline{X}$ | 8,504 b | 7,494 a | 17,834 f | 15,775 e | 11,232 d | 10,386 c | |
| | $\overline{X}_{DW}$ | 11,419 ab | 10,950 a | 13,129 d | 11,195 ab | 12,618 cd | 11,915 bc | 0.29 |
| | $\overline{X}_{NU}$ | 10,080 ab | 9,506 a | 15,337 e | 14,088 d | 11,244 c | 10,971 bc | 0.13 |
| Zinc (μg) | $\overline{X}$ | 563 b | 500 a | 1,528 e | 1,437 d | 874 c | 861 c | |
| | $\overline{X}_{DW}$ | 887 a | 885 a | 1,004 b | 927 a | 1,028 b | 1,031 b | 0.47 |
| | $\overline{X}_{NU}$ | 717 a | 696 a | 1,285 c | 1,272 c | 875 b | 917 b | 0.15 |

Column header grouping: *Cultivar and irrigation frequency treatment[z]* — AZ (W100, W50), ER (W100, W50), PJM (W100, W50).

[z]Significant ($P < 0.05$) differences between cultivars denoted by different lower case letters within a row (n = 20). Plant biomass and nitrogen data in Scagel et al. (2011).
[y]Means ($\overline{X}$), means adjusted for dry biomass ($\overline{X}_{DW}$), and means adjusted for N uptake between May and Nov. 2005 ($\overline{X}_{NU}$).
[x]Eta-squared ($\eta^2$) is the proportion of total variance attributable to dry biomass or nitrogen uptake. When covariate did not contribute significantly to variance in nutrient accumulation adjusted means and $\eta^2$ not presented.

Plant biomass accounted for greater than 29% of the variance in nutrient uptake, and N uptake between May 2005 and Nov. 2005 accounted for greater than 10% of the variance in nutrient uptake ($\eta^2$; Table 1). The influence of irrigation treatment on P, K, B, Fe, Mn, and Zn uptake in AZ and Mn uptake in PJM were attributable to differences in biomass ($\overline{X}_{DW}$; Table 1). Additionally, the influence of irrigation frequency on Cu uptake in AZ; K and Zn uptake in ER; and P, S, and B uptake in PJM were attributable to differences in N uptake ($\overline{X}_{NU}$; Table 1). Plant biomass and N uptake accounted for a significant portion of the variance in Ca and magnesium (Mg) uptake; however, they only altered the magnitude of the differences in Ca and Mg uptake between irrigation treatments.

The influence of irrigation frequency on nutrient uptake was partially attributable to differences in biomass and N uptake (Table 1).

Biomass in Nov. 2005 increased with increasing N application rate, ER had the greatest biomass and AZ had the lowest biomass, and irrigation frequency had no influence on total plant biomass (Scagel et al., 2011). Nitrogen uptake between May 2005 and Nov. 2005 increased with increasing N application rate, ER had the greatest N uptake and AZ had the lowest, and more frequent irrigation decreased N uptake (Scagel et al., 2011). For some nutrients, differences in uptake between W100 and W50 plants were attributable to differences in biomass or N uptake (e.g., P, K, B, Fe, Mn, and Zn uptake in AZ; Mn uptake in PJM). These results suggest that the lower uptake of these nutrients in W50 plants was possibly the result of a combination of decreased demand and decreased nutrient availability. For other nutrients, differences in uptake between W100 and W50 plants were only attributable to differences in N uptake and not biomass (e.g., K and Zn uptake in ER; P, S, and B uptake in PJM). These results suggest that the lower uptake of these nutrients in W50 plants was possibly the result of decreased nutrient availability. After accounting for the variability associated with biomass and N uptake, increased irrigation frequency decreased P, S, B, Cu, and Mn uptake in ER and increased Ca uptake in ER and PJM. These results indicate that irrigation frequency alters so the ability of plants to take up these nutrients.

Container-grown *Rhododendron* can accumulate significant amounts of Ca in late summer and early fall (Scagel et al., 2007, 2008a). Using stomatal conductance ($g_S$) as an estimate of plant water stress, container-grown *Rhododendron* in the W100 treatment had less access to water than plants in the W50 treatment at certain times of day and at certain times during the growing season (Scagel et al., 2011). High rates of N fertilizer application exacerbated water stress, and some of the water stress resulting from high N rates was alleviated by more frequent irrigation (Scagel et al., 2011). In general, $g_S$ is positively correlated to transpiration rate (curvilinear response) and transpiration rate is positively correlated to uptake of several nutrients that move to roots through mass flow, including N, Ca, and Mg (Xu et al., 2004). Decreasing irrigation frequency in our experimental conditions caused relatively small, transitory increases in plant water stress at different times during the growing season and may have decreased mass flow of Ca to roots of ER and PJM resulting in lower uptake of Ca in the W100 treatment.

*Relationship between nitrogen application rate and nutrient demand.* Increasing rate of N application increased nutrient accumulation and, in general, N rate had the greatest effect on nutrient accumulation in ER and the least effect on nutrient accumulation in AZ ($\beta_N$; Table 2). More frequent irrigation decreased the effect of N rate on P, K, S, and Fe uptake in ER ($\beta_N$; Table 2). Plants of ER in the W50 treatment accumulated less of these nutrients per gram of N applied than plants in the W100 treatment. In contrast, more frequent irrigation increased the effect of N rate on K uptake in AZ; Ca, Mg, and Zn uptake in ER; and Ca, Mg, B, Cu, Fe, Mn, and Zn uptake in PJM ($\beta_N$; Table 2). Plants in the W50 treatment accumulated more of these nutrients per gram of N applied.

The relationship between N application rate and uptake of other nutrients can be interpreted as the influence of N rate on nutrient demand. For example, on average, ER accumulated more P per gram of N applied than AZ and PJM. This suggests that when increasing N rates, ER will have a proportionately greater demand for P than AZ and PJM. This concept can be extended to assess the influence of water stress (from irrigation frequency) on nutrient demand. Irrigation frequency had no influence on the relationship between N rate and nutrient uptake, except K, in AZ. This indicates N rate in AZ did not alter nutrient demands, except for K, under greater

Table 2. Relationships between net nutrient accumulation between May and Nov. 2005 and nitrogen application rate and net nitrogen uptake in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM) grown in containers and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water from May to Sept. 2005.

| Nutrient | | | AZ W100 | AZ W50 | ER W100 | ER W50 | PJM W100 | PJM W50 |
|---|---|---|---|---|---|---|---|---|
| Phosphorus | (mg·g⁻¹) | $\beta_N$ | 40.3 a[y] | 38.7 a | 62.0 d | 51.1 c | 46.3 b | 44.9 b |
| | | $\beta_{NU}$ | 96 c | 103 d | 83 b | 84 b | 82 ab | 80 a |
| Potassium | (mg·g⁻¹) | $\beta_N$ | 169 a | 195 b | 327 d | 304 c | 175 ab | 194 b |
| | | $\beta_{NU}$ | 402 b | 538 e | 445 d | 521 e | 324 a | 369 b |
| Sulfur | (mg·g⁻¹) | $\beta_N$ | 25.1 a | 26.0 a | 57.5 d | 44.8 c | 42.5 b | 43.3 b |
| | | $\beta_{NU}$ | 60 a | 71 bc | 72 bc | 67 b | 75 c | 76 c |
| Calcium | (mg·g⁻¹) | $\beta_N$ | 74 a | 82 a | 250 d | 280 e | 171 b | 221 c |
| | | $\beta_{NU}$ | 186 a | 229 b | 337 c | 420 e | 310 c | 376 d |
| Magnesium | (mg·g⁻¹) | $\beta_N$ | 42 a | 48 a | 107 d | 116 e | 60 b | 71 c |
| | | $\beta_{NU}$ | 106 a | 134 b | 146 c | 185 d | 111 a | 129 b |
| Boron | (µg·g⁻¹) | $\beta_N$ | 375 a | 352 a | 761 d | 702 cd | 573 b | 648 c |
| | | $\beta_{NU}$ | 922 a | 966 ab | 1009 ab | 1213 c | 1055 b | 1157 c |
| Copper | (µg·g⁻¹) | $\beta_N$ | 207 a | 178 a | 308 b | 312 b | 229 a | 296 b |
| | | $\beta_{NU}$ | 539 bc | 515 ab | 444 a | 465 ab | 429 a | 601 c |
| Iron | (mg·g⁻¹) | $\beta_N$ | 6.04 b | 5.56 b | 9.28 c | 6.13 b | 4.17 a | 6.26 b |
| | | $\beta_{NU}$ | 17.1 d | 15.6 d | 13.2 c | 10.2 b | 7.5 a | 11.3 b |
| Manganese | (mg·g⁻¹) | $\beta_N$ | 8.88 a | 8.72 a | 8.86 a | 9.66 a | 8.81 a | 11.13 b |
| | | $\beta_{NU}$ | 20.7 c | 23.1 d | 13.1 a | 19.9 c | 16.7 b | 19.6 c |
| Zinc | (µg·g⁻¹) | $\beta_N$ | 711 a | 619 a | 1544 d | 1654 e | 1091 b | 1302 c |
| | | $\beta_{NU}$ | 1852 ab | 1655 a | 2109 c | 2595 d | 1981 bc | 2199 c |

[z]Significant differences ($P < 0.05$) between cultivars and irrigation treatments denoted by different lower case letters within a row.

[y]First-order regression coefficients for relationships between nitrogen application rate (g) and net nutrient accumulation (mg or µg) ($\beta_N$) and between net nitrogen uptake (g) and net nutrient accumulation ($\beta_{NU}$).

water stress. In contrast, irrigation frequency altered the relationship between N rate and nutrient uptake for several nutrients in ER and PJM. For example, PJM in the W100 treatment accumulated less Ca, Mg, B, Cu, Fe, Mn, and Zn per gram of N applied. This suggests that demand for these nutrients will be less under greater water stress when increasing N rates in PJM (Table 2). Similarly, increased N rate decreased ER demand for Ca, Mg, and Zn under greater water stress. In contrast, increased N rate increased ER demand for P, K, S, and Fe under greater water stress. Water stress can decrease plant growth and therefore nutrient requirements for growth (Singh and Singh, 2009). In our study, irrigation frequency did not significantly influence plant biomass (Scagel et al., 2011) but altered net nutrient uptake for several nutrients and nutrient demand in relationship to N supply. This information is important for understanding whether altering N management for different cultivars or irrigation strategies will alter plant requirements for other nutrients.

*Relationship between nitrogen uptake and nutrient uptake efficiency.* In general, ER accumulated the most K, Ca, Mg, and Zn per gram of N uptake and the least Cu and Mn per gram of N uptake ($\beta_{NU}$; Table 2). Plants of AZ accumulated most P, Fe, and Mn per gram N uptake and the least S, Ca, Mg, B, and Zn ($\beta_{NU}$; Table 2). Plants of PJM accumulated the most S, B, and Cu per gram N uptake and the least K and Fe uptake per gram N uptake ($\beta_{NU}$; Table 2). More frequent irrigation decreased the influence of N uptake on Fe uptake in ER. Plants of ER in the W50 treatment accumulated less Fe per gram of N uptake than plants in the W100 treatment. In contrast, ER in the W50 treatment accumulated more K, Ca, Mg, B, Mn, and Zn per gram of N uptake than plants in the W100 treatment ($\beta_{NU}$; Table 2). Similarly, AZ in the W50 treatment accumulated more P, K, S, Ca, Mg, and Mn per gram of N uptake than plants in the W100 treatment and PJM in the W50 treatment accumulated more K, Ca, Mg, B, Cu, Fe, and Mn per gram of N uptake than plants in the W100 treatment.

Net nutrient uptake varied among cultivars (Table 1). Differences among cultivars in nutrient uptake were related to nutrient demands for plant growth and how efficiently cultivars use nutrients for growth. Plants of ER grew more in 2005 than AZ and PJM, for every gram of N applied ER accumulated more biomass, and ER had the highest net N and nutrient uptake (Scagel et al., 2011). Plants of ER also had lower N ratios for specific nutrients (e.g., K, Ca, Mg, B, Zn) (Table 3). These results indicate that ER was more efficient at using N and possibly some other nutrients for growth and that growth per se was not the only reason for uptake differences among cultivars.

Irrigation frequency altered the relationships between N uptake and uptake of several nutrients ($\beta_{NU}$; Table 2). There were linear relationships between N application rate and N uptake for all cultivars and irrigation treatments; however, these relationships differed among cultivars and irrigation treatments (Scagel et al., 2011). For example, on average, AZ accumulated more P per gram of N uptake than ER and PJM. This suggests greater N uptake may require proportionately more P uptake in AZ than in ER and PJM or conversely ER and PJM are more efficient at P uptake than AZ. This concept can be extended to assess the influence of water stress (from irrigation frequency) on nutrient uptake. Irrigation frequency had no influence on the relationship between N uptake and uptake of most micronutrients in AZ, suggesting N uptake in AZ did not alter uptake efficiency (or ability) for these nutrients under greater water stress. In contrast, AZ in the W100 treatment accumulated less P, K, S, Ca, Mg, and Mn per gram of N uptake. This suggests that increased N uptake in AZ will decrease uptake efficiency for these nutrients under greater water stress. Similarly, increased N uptake in ER and PJM decreased uptake efficiency for many nutrients under greater water stress. In contrast, increased N uptake in ER increased uptake efficiency for Fe in ER under greater water stress.

*Variation in nutrient status in May 2005.* Nutrient status (concentrations and contents) differed among cultivars in May ($\overline{X}$; Table 4). Carbon concentrations were similar among cultivars and C content was greatest in ER (data not shown). Similarly, biomass of ER was greatest in May (Scagel et al., 2011). Plant biomass accounted for a significant but low portion ($\eta^2 < 0.05$) of the variance in Ca, Cu, Mn, and Zn concentration among cultivars and only altered the magnitude of the differences among effects and not the trends or significant effects from ANOVA. Plant biomass accounted for greater than 30% of the variance in nutrient content ($\eta^2$; Table 4). After accounting for the variance in nutrient concentration and content attributable to plant dry biomass, B status was similar among cultivars; AZ had the greatest P, S, Fe, and Mn status; and ER had the greatest Ca and Zn status ($\overline{X}_{DW}$; Table 4). Additionally, PJM had a greater S status than ER, a greater Ca status than AZ, and a lower P status than ER ($\overline{X}_{DW}$; Table 4).

Nutrient concentrations in roots, stems, and leaves differed among cultivars (Table 5). Biomass accounted for a significant portion of the variance in P, K, B, Fe, and Zn concentrations in roots among cultivars ($\eta^2$, data not shown); however, it only altered the magnitude of the differences among effects and not the trends or significant effects from ANOVA. Biomass did not account for a significant portion of the variance in nutrient concentrations in stems and leaves (data not shown). In general, AZ had the greatest P, K, Fe, and Mn concentrations in all structures; PJM had the lowest P and K concentrations in all structures; and ER had the lowest Mn concentrations in

Table 3. Nitrogen ratios of leaves and total plant in Nov. 2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM) grown in containers and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water from May to Sept. 2005.

| N ratio[z] | | Cultivar and irrigation frequency treatment[y] | | | | | |
|---|---|---|---|---|---|---|---|
| | | AZ | | ER | | PJM | |
| | | W100 | W50 | W100 | W50 | W100 | W50 |
| N/P | Leaf | 9.3 aB | 16.4 cB | 9.3 aA | 10.0 abA | 11.0 bA | 10.8 bA |
| | Plant | 7.5 aA | 7.4 aA | 8.7 bA | 9.3 bA | 10.6 cA | 10.4 cA |
| N/K | Leaf | 0.5 aA | 0.9 bA | 1.5 cdA | 1.4 cA | 1.9 dA | 1.8 cdA |
| | Plant | 2.3 bB | 2.4 bB | 1.6 aA | 1.5 aA | 2.6 bB | 2.5 bB |
| N/S | Leaf | 11.0 aA | 16.2 dB | 13.3 bA | 14.8 cA | 11.6 aA | 11.5 aA |
| | Plant | 12.5 bB | 11.9 abA | 12.6 bA | 14.0 cA | 11.4 aA | 11.7 abA |
| N/Ca | Leaf | 1.5 aA | 2.0 bA | 1.8 abA | 1.7 abA | 2.7 cA | 2.6 cA |
| | Plant | 5.5 dB | 5.8 dB | 2.2 abA | 2.0 aA | 2.9 cA | 2.6 bcA |
| N/Mg | Leaf | 3.4 aA | 4.5 bA | 4.6 bA | 4.3 bA | 6.4 dA | 5.9 cA |
| | Plant | 7.3 dB | 7.2 dB | 4.8 aA | 4.4 aA | 6.9 cdB | 6.4 bB |
| N/B | Leaf | 331 aA | 466 dA | 415 bcA | 419 cA | 399 cA | 367 bA |
| | Plant | 1209 dB | 1284 eB | 558 aB | 567 aB | 683 cB | 648 bB |
| N/Cu | Leaf | 2916 aB | 4126 bB | 5910 dB | 5180 cB | 6215 eB | 6019 deB |
| | Plant | 1195 bA | 1369 cA | 1433 cA | 1556 dA | 1146 abA | 1054 aA |
| N/Fe | Leaf | 72 aA | 101 bB | 131 cB | 118 cB | 169 eB | 145 dB |
| | Plant | 61 aA | 69 aA | 79 bA | 80 bcA | 98 dA | 88 cA |
| N/Mn | Leaf | 12.0 aA | 16.8 bA | 28.0 cA | 31.1 dA | 27.4 cA | 26.9 cA |
| | Plant | 15.3 aB | 20.1 bB | 31.3 dB | 34.4 eB | 29.1 cA | 28.0 cA |
| N/Zn | Leaf | 524 aB | 681 cB | 587 bB | 576 bB | 700 cB | 678 cB |
| | Plant | 438 cA | 444 cA | 325 aA | 314 aA | 386 bA | 372 bA |

[z]Ratios of N concentrations (mg·g⁻¹) to concentrations of other nutrients (mg·g⁻¹) in leaves (Leaf) and total plant (Plant).

[y]Significant ($P < 0.05$) differences between cultivars within a structure (leaf or plant) denoted by different lower case letters within a row and differences between structures within a cultivar denoted by different upper case letters within a column and ratio (n = 10). Nitrogen data in Scagel et al. (2011).

N = nitrogen; P = phosphorus; K = potassium; S = sulfur; Ca = calcium; Mg = magnesium; B = boron; Cu = copper; Fe = iron; Mn = manganese; Zn = zinc.

all structures. Differences in S and B concentrations among cultivars were only detectable aboveground where AZ had the greatest S and B concentrations in leaves and ER had the lowest. Differences in Ca, Mg, and Zn concentrations among cultivars varied between structures. Plants of AZ had the lowest Ca concentrations in all structures; PJM had the highest stem and root Ca concentrations, and ER had the highest leaf Ca concentrations. Leaves in AZ had the greatest Mg concentrations and stems and roots had the lowest Mg concentrations. Stems in AZ had the greatest Zn concentrations and roots had the lowest Zn concentrations.

Cultivars differed in nutrient status (whole plant nutrient concentrations and contents) in May (Table 4). For specific nutrients, differences among cultivars in total plant nutrient concentrations were similar to differences among cultivars in nutrient concentrations in all structures (Table 5) and were representative of cultivar differences in total nutrient content after accounting for differences in biomass (Table 4). For example, differences in total plant P concentrations and content among cultivars were similar to differences between cultivars in P concentrations in different structures. These results suggest that for certain nutrients such as P, samples from any

structure in the spring are good estimates of differences in P status among these cultivars. Additionally, although biomass allocation preferentially allocated biomass to different structures (Scagel et al., 2011), distribution of P was similar among cultivars. Similar distribution of P among cultivars in the spring may be a result of high P demand from growth. Phosphorus, like N, has a strong relationship to spring growth when it is a limiting factor (Ristvey et al., 2007).

For certain nutrients, samples from specific structures in the spring were good estimates of differences in nutrient status among all cultivars. Using a similar rationale as stated previously, our data indicate that differences in P, K, S, Ca, B, and Fe status among all cultivars in the spring can be estimated by P concentrations in all structures, K concentrations in roots, Ca concentrations in leaves, S and Fe concentrations in stems and leaves, and B concentrations in roots. For certain nutrients, samples from specific structures in the spring were good estimates of differences in nutrient status among two of the three cultivars. Our data indicate that differences in Mg, Cu, Mn, and Zn status in the spring between AZ and ER are estimated by Mn concentration in all structures, Mg concentrations in roots and stems, Zn concentrations in leaves, and Cu

concentrations in stems; differences in Mg, Cu, Mn, and Zn status between AZ and PJM are estimated by concentrations in leaves; and differences in Mg status between ER and PJM are estimated by Mg concentrations in leaves, Cu concentrations in roots, and Zn concentrations in roots and leaves.

Concentrations of nutrients in leaves are commonly used to determine plant nutrient status. Our results suggest that leaves are not always an adequate representation of whole plant nutrient status when comparing cultivars. Especially with the evergreen cultivars, this may be a result of preferential storage of nutrients in leaves by some cultivars (Scagel et al., 2008a) or species (Pasche et al., 2002).

*Variation in nitrogen ratios in May 2005.* In May, PJM had the greatest leaf and total plant N/P, N/K, and N/Mg ratios; AZ had the greatest leaf and plant N/Ca; and ER had the lowest leaf and plant N/K, N/Ca, N/Mg, and N/Zn (Table 6). Plant N/K ratios were similar to N/K ratios in leaves for all cultivars. Leaf N ratios in ER were similar to plant N ratios for all nutrients except N/Ca and N/Mg, which were lower in leaves. Leaf N ratios in PJM were greater than plant N ratios for all nutrients except N/K, N/Ca, and N/B. In PJM, leaf N ratios were lower than plant N/B and similar to plant N/K and N/Ca. In AZ, leaf N ratios were similar to plant N/P, N/K, N/S, N/Fe, and N/Mn; lower than plant N/Ca, N/Mg, and N/B; and greater than plant N/Cu and N/Zn.

One method of estimating differences in nutrient status or demand between cultivars is to use N ratios, the ratio of N to nutrients other than N (Scagel et al., 2008b). For example, PJM had greater leaf and plant N/P ratios than AZ and ER (Table 6). Plants of PJM not only have a lower P status than AZ and ER (Table 4), but also a lower demand for P in relationship to N as indicated by N/P ratios. In contrast, ER had a lower P status than AZ and ER and AZ had similar leaf and plant N/P ratios. This combined interpretation of nutrient status and N ratios can be useful when estimating differences in fertilizer requirements among cultivars. For example, the results presented here suggest that PJM will grow more efficiently with fertilizers containing less total P (available P) and greater N/P ratios than AZ and ER and that ER will grow more efficiently with fertilizers containing less total P with similar N/P ratios than AZ.

Combined interpretation of our nutrient status and N ratio data from May 2005 suggests that compared with AZ, PJM can be grown in cultural conditions with greater availability of Ca and less total P, K, Mg, and B; compared with AZ, ER can be grown in cultural conditions with greater availability of K, Ca, Mg, and Zn; and compared with PJM, ER can be grown in cultural conditions with greater availability of P, K, Ca, Mg, and Zn. Differences in N/S, N/Cu, N/Fe, and N/Mn ratios between AZ and PJM were only in leaves and therefore may be more associated with differences in nutrient distribution between cultivars. Similarly, differences in N/B and N/Cu ratios between AZ and ER and in N/S and N/Cu ratios between ER and PJM were considered to

Table 4. Total plant nutrient concentrations (per gram dry weight) and total nutrient accumulation in May 2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM).

| Nutrient | | $\overline{X}$ AZ | $\overline{X}$ ER | $\overline{X}$ PJM | $\overline{X}_{DW}$ AZ | $\overline{X}_{DW}$ ER | $\overline{X}_{DW}$ PJM | Eta-squared[y] |
|---|---|---|---|---|---|---|---|---|
| Phosphorus | (mg·g⁻¹) | 2.12 c | 1.50 b | 1.09 a | — | — | — | NS |
| | (mg) | 4.90 b | 9.82 c | 2.21 a | 6.77 c | 5.67 b | 4.87 a | 0.60 |
| Potassium | (mg·g⁻¹) | 6.43 b | 6.76 b | 4.66 a | — | — | — | NS |
| | (mg) | 14.7 a | 44.6 b | 9.4 a | 23.4 ab | 25.3 b | 20.0 a | 0.76 |
| Sulfur | (mg·g⁻¹) | 1.24 c | 0.76 a | 1.00 b | — | — | — | NS |
| | (mg) | 2.86 a | 4.98 b | 2.02 a | 3.86 c | 2.78 a | 3.23 b | 0.73 |
| Calcium | (mg·g⁻¹) | 3.12 a | 7.52 c | 5.81 b | 2.93 a | 7.95 c | 5.57 b | 0.02 |
| | (mg) | 7.3 a | 49.0 b | 11.8 a | 14.8 a | 32.4 c | 20.9 b | 0.41 |
| Magnesium | (mg·g⁻¹) | 2.27 b | 2.71 c | 1.72 a | — | — | — | NS |
| | (mg) | 5.29 a | 17.75 b | 3.47 a | 8.54 ab | 10.52 b | 7.45 a | 0.74 |
| Boron | (µg·g⁻¹) | 30 a | 23 a | 25 a | — | — | — | NS |
| | (µg) | 69 a | 152 b | 50 a | 97 a | 90 a | 84 a | 0.72 |
| Copper | (µg·g⁻¹) | 11 b | 8 a | 12 b | 12 b | 7 a | 12 b | 0.03 |
| | (µg) | 27 a | 56 b | 24 a | 41 b | 26 a | 39 b | 0.81 |
| Iron | (µg·g⁻¹) | 198 b | 96 a | 98 a | — | — | — | NS |
| | (µg) | 469 b | 624 c | 199 a | 598 b | 338 a | 356 a | 0.34 |
| Manganese | (µg·g⁻¹) | 240 c | 109 a | 172 b | 232 b | 128 a | 162 a | 0.02 |
| | (µg) | 553 b | 704 c | 352 a | 660 b | 467 a | 478 a | 0.30 |
| Zinc | (µg·g⁻¹) | 39 a | 42 a | 43 a | 36 a | 49 b | 40 ab | 0.04 |
| | (µg) | 90 a | 275 b | 86 a | 128 a | 190 b | 133 a | 0.49 |

[z]Means ($\overline{X}$) and means adjusted for dry biomass ($\overline{X}_{DW}$). Significant ($P < 0.05$) differences between cultivars denoted by different lower case letters within a row and mean (n = 10). Plant biomass and nitrogen data in Scagel et al. (2011).
[y]Eta-squared ($\eta^2$) is the proportion of total variance attributable to dry biomass. When covariate did not contribute significantly (NS) to variance in nutrient concentration the adjusted means and $\eta^2$ not presented.

Table 5. Nutrient concentrations (per g dry weight) of roots, stems, and leaves in May 2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM).

| Nutrient | | Roots AZ | Roots ER | Roots PJM | Stems AZ | Stems ER | Stems PJM | Leaves AZ | Leaves ER | Leaves PJM |
|---|---|---|---|---|---|---|---|---|---|---|
| Phosphorus | (mg·g⁻¹) | 1.81 c | 1.21 b | 0.97 a | 1.73 c | 1.20 b | 0.96 a | 2.91 c | 1.77 b | 1.27 a |
| Potassium | (mg·g⁻¹) | 2.96 b | 3.03 b | 2.21 a | 6.68 b | 7.88 c | 5.57 a | 10.78 b | 7.63 a | 6.11 a |
| Sulfur | (mg·g⁻¹) | 1.05 a | 0.88 a | 0.98 a | 0.96 c | 0.57 a | 0.72 b | 1.76 c | 0.82 a | 1.19 b |
| Calcium | (mg·g⁻¹) | 1.31 a | 1.58 b | 1.85 c | 2.87 a | 4.93 b | 7.16 c | 5.86 a | 11.14 c | 8.36 b |
| Magnesium | (mg·g⁻¹) | 0.76 a | 1.12 b | 1.02 b | 1.55 a | 1.94 b | 1.80 b | 4.93 c | 3.72 b | 2.17 a |
| Boron | (µg·g⁻¹) | 4 a | 5 a | 7 a | 7 a | 27 c | 14 b | 84 c | 28 a | 47 b |
| Copper | (µg·g⁻¹) | 14 a | 13 a | 27 b | 18 b | 7 a | 5 a | 2 a | 7 b | 3 a |
| Iron | (µg·g⁻¹) | 260 a | 188 a | 201 a | 163 b | 79 a | 50 a | 170 b | 72 a | 43 a |
| Manganese | (µg·g⁻¹) | 159 b | 56 a | 105 a | 241 b | 93 a | 216 b | 352 c | 137 a | 206 b |
| Zinc | (µg·g⁻¹) | 29 a | 56 b | 59 b | 54 c | 44 b | 31 a | 41 a | 37 a | 35 a |

[z]Significant ($P < 0.05$) differences between cultivars denoted by different lower case letters within a row and structure (n = 10). Plant biomass, biomass allocation, and nitrogen data in Scagel et al. (2011).

be related to differences between cultivars in nutrient distribution and not demand per se.

*Variation in nutrient concentrations in Nov. 2005.* In general, AZ had the greatest P and Fe concentrations; ER had the greatest K, Ca, and Mg concentrations; and PJM had the greatest S, B, Cu, Mn, and Zn concentrations in November (Table 7). Increasing irrigation frequency decreased concentrations of several nutrients, including P (ER, PJM), K (AZ), S (ER, PJM), B (ER), Fe (AZ), Mn (ER, PJM), and increased concentrations of Ca (ER, PJM) (Table 7). Plant biomass accounted for a significant but low portion of the variance in P, S, B, Fe, and Mn concentration ($\eta^2$; Table 7) and plant N status (N uptake) accounted for a significant but low portion of the variance in P, S, B, and Mn concentration ($\eta^2$, data not shown). Covariates only altered the magnitude of the differences among effects and not the trends or significant effects from ANOVA (Table 7).

Increased irrigation frequency increased concentrations of several nutrients in leaves in November, including K (AZ), S (AZ), Ca (AZ), Mg (AZ), B (AZ), Fe (AZ, PJM), Mn (AZ), and Zn (AZ) (Table 8). In contrast, increased irrigation frequency decreased concentrations of P (ER, PJM), S (ER, PJM), B (ER), and Mn (ER, PJM) in leaves. Irrigating more frequently decreased concentration of several nutrients in roots, including P (ER), K (ER), S (ER, PJM), Ca (AZ, ER, PJM), Cu (AZ, ER), Fe (AZ, ER), Mn (ER, PJM), and Zn (ER). More frequent irrigation decreased concentrations of several nutrients in stems, including P (PJM), S (ER, PJM), and Mn (ER, PJM). In contrast, more frequent irrigation increased concentrations of K (ER), Ca (ER, PJM), Mg (ER), Fe (AZ, ER, PJM), and Zn (AZ) in stems. Biomass accounted for a significant but low portion of the variance in root P, S, and Fe concentrations and stem K and Mn concentrations ($\eta^2$, data not shown); however, it only altered the magnitude of the differences among effects and not the trends or significant effects from ANOVA. Biomass did not account for a significant portion of the variance in concentrations of other nutrients in the different structures (data not shown).

For some nutrients, differences in total plant nutrient concentrations among cultivars in November were reflected in nutrient concentrations in specific structures (Tables 4 and 5). For example, AZ had the greatest total plant Fe concentrations as a result of greater Fe concentrations in all structures. For other nutrients, differences in total plant nutrient concentrations among cultivars were reflected in nutrient concentrations in specific structures and could be partially a result of differences in allocation among cultivars. For example, AZ had the greatest total plant P concentration as a result of greater root and stem P concentrations than ER and PJM. In the fall, deciduous woody perennial plants move several nutrients from leaves to storage in stems and roots, whereas evergreen plants may retain similar nutrients in leaves (Millard, 1996). Evergreen *Rhododendron* plants can store P in stems and leaves over winter (Scagel et al., 2008a). Greater P concentrations in roots and stems in AZ may partially be a result of differences in fall allocation between cultivars. Similarly, greater P concentrations in leaves of ER than PJM and greater P concentrations in stems of PJM than ER may be partially attributed to nutrient allocation differences between these cultivars. Plants of ER preferentially store certain nutrients in leaves compared with stems, whereas PJM preferentially store more certain nutrients in stems compared with leaves (Scagel et al., 2008a).

Table 6. Nitrogen ratios (N ratios) of leaves and total plants in May 2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM).

| N ratio[z] | | Cultivar[y] AZ | ER | PJM |
|---|---|---|---|---|
| N/P | Leaf | 7.9 aA | 6.6 aA | 16.1 bB |
| | Plant | 6.7 aA | 6.8 aA | 13.2 bA |
| N/K | Leaf | 2.1 bA | 1.5 aA | 3.4 cA |
| | Plant | 2.3 bA | 1.5 aA | 3.1 cA |
| N/S | Leaf | 13.0 aA | 14.1 abA | 17.1 bB |
| | Plant | 11.6 aA | 13.3 aA | 14.5 aA |
| N/Ca | Leaf | 3.9 cA | 1.0 aA | 2.4 bA |
| | Plant | 4.6 cB | 1.4 aB | 2.5 bA |
| N/Mg | Leaf | 4.6 bA | 3.1 aA | 9.3 cA |
| | Plant | 6.3 bB | 3.8 aB | 8.4 cB |
| N/B | Leaf | 268 aA | 413 bA | 427 bA |
| | Plant | 480 aB | 440 aA | 598 bB |
| N/Cu | Leaf | 9870 cB | 1616 aA | 6803 bB |
| | Plant | 1272 aA | 1200 aA | 1235 aA |
| N/Fe | Leaf | 152 aA | 162 aA | 495 bB |
| | Plant | 75 aA | 105 aA | 148 aA |
| N/Mn | Leaf | 65 aA | 87 abA | 103 bB |
| | Plant | 61 aA | 94 bA | 85 abA |
| N/Zn | Leaf | 544 bB | 317 aA | 592 bB |
| | Plant | 375 bA | 241 aA | 359 bA |

[z]Ratios of N to other nutrients in leaves (Leaf) and total plant (Plant).
[y]Significant ($P < 0.05$) differences between cultivars within a structure (leaf or plant) denoted by different lower case letters within a row and differences between structures within a cultivar denoted by different upper case letters within a column and ratio (n = 10). Nitrogen data in Scagel et al. (2011).
P = phosphorus; K = potassium; S = sulfur; Ca = calcium; Mg = magnesium; B = boron; Cu = copper; Fe = iron; Mn = manganese; Zn = zinc.

Table 7. Total plant nutrient concentrations (per gram dry weight) in Nov.2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM) grown in containers and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water from May to Sept. 2005.

| Nutrient[z] | | Cultivar and irrigation frequency treatment[y] AZ W100 | AZ W50 | ER W100 | ER W50 | PJM W100 | PJM W50 | Eta-squared[x] |
|---|---|---|---|---|---|---|---|---|
| Phosphorus (mg·g⁻¹) | $X$ | 1.59 d | 1.60 d | 1.22 bc | 1.06 a | 1.24 c | 1.17 b | |
| | $\overline{X}_{DW}$ | 1.55 d | 1.54 d | 1.28 c | 1.12 a | 1.22 b | 1.15 a | 0.02 |
| Potassium (mg·g⁻¹) | $\overline{X}$ | 5.54 b | 5.19 a | 6.66 c | 6.63 c | 5.13 a | 5.00 a | |
| Sulfur (mg·g⁻¹) | $\overline{X}$ | 0.97 c | 0.99 cd | 0.85 b | 0.70 a | 1.16 e | 1.06 d | |
| | $\overline{X}_{DW}$ | 0.93 b | 0.94 bc | 0.92 b | 0.76 a | 1.15 d | 1.04 c | 0.03 |
| Calcium (mg·g⁻¹) | $\overline{X}$ | 2.30 a | 2.15 a | 4.77 c | 4.91 d | 4.57 b | 4.75 c | |
| Magnesium (mg·g⁻¹) | $\overline{X}$ | 1.65 a | 1.64 a | 2.18 c | 2.19 c | 1.90 b | 1.92 b | |
| Boron (μg·g⁻¹) | $\overline{X}$ | 10 a | 10 a | 20 c | 17 b | 20 c | 19 c | |
| | $\overline{X}_{DW}$ | 10 a | 9 a | 22 c | 19 b | 19 b | 18 b | 0.01 |
| Copper (μg·g⁻¹) | $\overline{X}$ | 10 c | 9 bc | 8 b | 6 a | 12 d | 12 d | |
| Iron (μg·g⁻¹) | $\overline{X}$ | 214 c | 194 b | 139 a | 131 a | 138 a | 142 a | |
| | $\overline{X}_{DW}$ | 234 d | 217 c | 108 a | 100 a | 147 b | 153 b | 0.03 |
| Manganese (μg·g⁻¹) | $\overline{X}$ | 438 b | 427 b | 459 c | 400 a | 498 d | 464 c | |
| | $\overline{X}_{DW}$ | 392 a | 373 a | 532 d | 472 c | 477 c | 440 b | 0.06 |
| Zinc (μg·g⁻¹) | $\overline{X}$ | 27 a | 28 a | 33 bc | 31 b | 34 c | 34 c | |

[z]Means ($\overline{X}$) and means adjusted for dry biomass ($\overline{X}_{DW}$).
[y]Significant ($P < 0.05$) differences between cultivars denoted by different lower case letters within a row (n = 20).
[x]Eta-squared ($\eta^2$) is the proportion of total variance attributable to dry biomass. When covariate did not contribute significantly to variance in nutrient concentration the adjusted means and $\eta^2$ not presented.

Nutrient concentrations in leaves are commonly used to describe differences in plant nutrient status as an result of experimental treatments. Irrigation frequency altered biomass allocation of all cultivars (Scagel et al., 2011); therefore, the influence of irrigation frequency on total nutrient concentrations may not be well estimated by concentrations in certain structures. Our results indicate that differences in total plant nutrient concentrations between W100 and W50 AZ can be estimated by P concentrations in all structures; S, Mg, B, and Mn concentration in roots and stems; Ca concentration in stems; Cu concentrations in stems and leaves; and Fe and Zn concentrations in roots. Differences in total plant nutrient concentration between W100 and W50 ER can be estimated by S and Mn concentrations in all structures; P and Mg concentrations in roots and leaves; Cu concentrations in roots; Ca concentration in stems; K, B, and Fe concentrations in leaves; and Zn in stems and leaves. Differences in total plant nutrient concentration between W100 and W50 PJM can be estimated by K, S, Mg, B, Cu, Mn, and Zn concentrations in all structures;

Fe concentrations in roots; Ca concentrations in stems; and P in stems and leaves.

*Variation in nitrogen ratios in Nov. 2005.* In November, leaf N/P, N/S, N/Cu, N/Fe, and N/Zn ratios were generally greater than total plant ratios for these nutrients and leaf N/K, N/Ca, N/Mg, N/B, and N/Mn ratios were lower than plant ratios for these nutrients (Table 3). Differences in plant N/S, N/Fe, and N/Mn ratios among cultivars were similar for leaf N ratios for these nutrients. On average, AZ had the greatest plant N/Ca, N/Mg, N/B, and N/Zn ratios and the lowest plant N/P and N/Fe ratios; ER had the greatest plant N/S, N/Cu and N/Mn ratios and the lowest plant N/K, N/Ca, N/Mg, N/B, and N/Zn ratios; and PJM had the greatest plant N/P, N/K, and N/Fe ratios and the lowest plant N/S and N/Cu ratios.

Irrigation frequency altered the leaf N ratios for all nutrients in AZ and only influenced N ratios for three of the 10 nutrients for ER and PJM. More frequent irrigation increased leaf N ratios for all nutrients and plant N/B, N/Cu, and N/Mn ratios in AZ and decreased plant and leaf N/Mg, N/B, and N/Fe ratios in PJM. In contrast, more frequent irrigation increased plant and leaf N/S and N/Mn ratios and plant N/Cu ratio and decreased leaf N/Cu ratio in ER. Irrigation frequency had no influence on plant and leaf N/P, N/K, N/Ca, and N/Zn ratios in ER and PJM.

More frequent irrigation increased net uptake of Ca in ER and PJM (Table 1) but did not influence leaf or plant N/Ca ratios (Table 3). More frequent irrigation decreased net P, K, B, Cu, Fe, Mn, and Zn uptake in AZ with

corresponding increases in leaf and plant N/B, N/Cu, and N/Mn ratios. The influence of irrigation frequency on N/P, N/K, N/S, N/Ca, N/Mg, N/Fe, and N/Zn ratios was considered to be more associated with differences in nutrient distribution between irrigation treatments and not demand for these nutrients. More frequent irrigation decreased net P, K, S, B, Cu, Mn, and Zn uptake in ER with corresponding increases in N/S, N/Cu, and N/Mn. Increased irrigation frequency (and decreased water stress) was associated with greater N use efficiency in AZ and ER (grams growth per milligram N uptake; Scagel et al., 2011). These results indicate that a low level of water stress can increase a plant's ability to grow with less of these nutrients and when grown with a low level of water stress plants may be grown with lower availability of these nutrients in relationship to N.

More frequent irrigation decreased net P, S, B, and Mn uptake in PJM with no increase in N ratios. The influence of irrigation frequency on N/Mg, N/B, and N/Fe ratios in PJM were similar for leaves and plants. Increased irrigation frequency (and decreased water stress) was also associated with lower N uptake efficiency in PJM (N uptake per amount of N applied; Scagel et al., 2011). These results suggest that a low level of water stress alters the ability of PJM to absorb N and subsequently plant uptake for Mg, B, and Fe nutrients in relation to N. The greater N ratios for these nutrients indicate plants may require fertilizers containing higher ratios for these nutrients to optimize growth when

Table 8. Nutrient concentrations (per gram dry weight) of roots, stems, and leaves in Nov. 2005 in *Rhododendron* 'Gibraltar' (AZ), R. 'English Roseum' (ER), and R. 'P.J.M' (PJM) grown in containers and irrigated once a day (W100) or twice a day (W50) to receive the same total daily amount of water from May to Sept. 2005.

| Nutrient | | | AZ W100 | AZ W50 | ER W100 | ER W50 | PJM W100 | PJM W50 |
|---|---|---|---|---|---|---|---|---|
| Phosphorus | (mg·g⁻¹) | Roots | 1.72 d | 1.73 d | 1.27 c | 1.07 a | 1.21 bc | 1.13 ab |
| | | Stems | 1.54 d | 1.50 d | 0.72 a | 0.69 a | 0.97 c | 0.91 b |
| | | Leaves | 0.93 a | 0.97 a | 1.41 c | 1.23 b | 1.60 e | 1.50 d |
| Potassium | (mg·g⁻¹) | Roots | 3.44 b | 3.51 b | 3.90 d | 3.74 c | 3.17 a | 3.00 a |
| | | Stems | 4.27 b | 4.11 b | 6.04 c | 6.30 d | 3.08 a | 3.00 a |
| | | Leaves | 15.7 b | 18.9 c | 9.0 a | 8.9 a | 9.6 a | 9.1 a |
| Sulfur | (mg·g⁻¹) | Roots | 1.05 c | 1.04 c | 0.91 b | 0.72 a | 1.20 d | 1.06 c |
| | | Stems | 0.81 e | 0.82 e | 0.58 b | 0.46 a | 0.75 d | 0.68 c |
| | | Leaves | 0.78 a | 0.96 b | 0.98 b | 0.83 a | 1.56 d | 1.42 c |
| Calcium | (mg·g⁻¹) | Roots | 1.29 b | 1.09 a | 2.22 e | 2.07 cd | 2.14 d | 1.95 c |
| | | Stems | 2.69 a | 2.91 a | 4.28 b | 5.00 c | 5.42 d | 6.08 e |
| | | Leaves | 5.46 a | 7.75 c | 6.98 b | 7.01 b | 6.65 b | 6.67 b |
| Magnesium | (mg·g⁻¹) | Roots | 1.33 a | 1.31 a | 1.59 c | 1.52 bc | 1.45 b | 1.48 b |
| | | Stems | 1.69 a | 1.65 a | 1.82 b | 1.95 c | 1.60 a | 1.62 a |
| | | Leaves | 2.48 a | 3.49 c | 2.78 b | 2.83 b | 2.73 b | 2.74 b |
| Boron | (µg·g⁻¹) | Roots | 7 ab | 6 ab | 6 ab | 5 a | 8 b | 7 ab |
| | | Stems | 10 ab | 11 b | 10 ab | 10 ab | 9 a | 9 a |
| | | Leaves | 26 a | 34 c | 34 c | 31 b | 46 d | 44 d |
| Copper | (µg·g⁻¹) | Roots | 13 bc | 11 a | 19 d | 14 c | 24 e | 25 e |
| | | Stems | 7 b | 7 b | 3 a | 4 a | 8 b | 8 b |
| | | Leaves | 3 a | 4 a | 2 a | 2 a | 3 a | 3 a |
| Iron | (µg·g⁻¹) | Roots | 265 b | 182 a | 256 b | 202 a | 207 a | 181 a |
| | | Stems | 102 b | 182 c | 48 a | 99 b | 78 a | 106 b |
| | | Leaves | 151 c | 200 d | 99 a | 106 a | 109 a | 130 b |
| Manganese | (µg·g⁻¹) | Roots | 297 b | 290 b | 307 bc | 267 a | 355 d | 317 c |
| | | Stems | 560 c | 571 c | 625 d | 566 c | 474 b | 439 a |
| | | Leaves | 747 d | 984 e | 515 b | 425 a | 719 d | 671 c |
| Zinc | (µg·g⁻¹) | Roots | 27 a | 23 a | 59 c | 52 b | 48 b | 47 b |
| | | Stems | 34 b | 47 c | 22 a | 26 ab | 27 ab | 27 ab |
| | | Leaves | 16 a | 24 cd | 22 bc | 21 b | 26 d | 25 d |

[z]Significant ($P < 0.05$) differences between cultivars denoted by different lower case letters within a row (n = 20). Plant biomass, biomass allocation, and nitrogen data in Scagel et al. (2011).

grown with a low level of water stress. The combined influence of water stress and N limitation can alter plant demands for other nutrients because of increased stress-related metabolism (Chapin, 1991).

Irrigation frequency had no influence on plant N/P, N/K, N/Ca, and N/Zn ratios for all cultivars although increased irrigation frequency decreased N uptake (Scagel et al., 2011). These results suggest water stress may result in luxury consumption or increased storage of specific nutrients and when grown with a low level of water stress, plants may not require more of these nutrients for growth but may have requirements for these nutrients unrelated to growth.

## Conclusions

Nutrient uptake is a function of multiple factors including root morphology, plant growth rate, nutrient absorption capability, plant nutrient demand, and nutrient availability. Nutrient availability is a function of the total amount of nutrient in a substrate, whether the nutrient is in a form or physical location available for uptake. Our results indicate that irrigating plants once per day to container capacity early in the growing season may be more beneficial for nutrient uptake than irrigating plants more frequently. Additionally, increasing irrigation frequency later in the growing season when plants are grown in conditions with greater potential for water stress may improve uptake of certain nutrients.

Nitrogen availability can influence the uptake of other nutrients and in combination with water stress can increase or decrease demand for other nutrients. Our results indicate that changes to irrigation strategies and N fertilizer rates that cause low levels of water stress during container production of *Rhododendron* can alter nutrient uptake and use without restricting growth. To optimize efficiency of fertilizer use, fertilizer formulations may need to be adjusted when altering irrigation or N rate in container production of *Rhododendron*.

Plant nutrient status in the spring and fall is reflected by concentrations of nutrients in specific structures as a result of differences in resource allocation between cultivars and in response to irrigation frequency. Our results indicate that a combination of nutrient concentrations and N ratios from specific structures can be used to estimate plant nutrient status. This information has potential use in modifying nutrient management when N or irrigation frequency is altered during production.

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