



Article Nitrogen Rate, Irrigation Frequency and Volume Differentially Influence Growth, Flowering, and Nutrient Uptake of Container-Grown Rhododendron during the Following Growing Season

Guihong Bi^{1,*}, Carolyn F. Scagel² and David R. Bryla²

- ¹ Department of Plant and Soil Sciences, Mississippi State University, Mississippi State, MS 39762, USA
- ² Horticultural Crops Production and Genetic Improvement Research Unit, Agricultural Research Service, U.S. Department of Agriculture, 3420 NW Orchard Avenue, Corvallis, OR 97330, USA; carolyn.scagel@usda.gov (C.F.S.); david.bryla@usda.gov (D.R.B.)
- * Correspondence: gbi@pss.msstate.edu

Abstract: Sustainable nutrient and water management are critical for optimizing the quality and subsequent landscape performance of nursery plants. In this 2-year study, we investigated the influence of different nitrogen (N) rates [N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH₄NO₃] and irrigation frequencies and volumes [once daily to 50% or 100% container capacity (CC) or twice daily with the same total amount of water as 100% CC] on plant growth, flowering, and nutrient uptake of three rhododendron cultivars, including one deciduous cultivar, Rhododendron 'Gibraltar' and two evergreen cultivar, Rhododendron 'P.J.M.' and Rhododendron 'Catawbiense Album'. In each case, the plants were grown in soilless media in year 1 and transplanted to soil in year 2. Increasing the N rate in year 1 increased plant biomass and N content in both years and improved flowering performance the following year. Furthermore, in year 1, irrigation once daily to 50% CC or twice daily to 100% CC enhanced the uptake of several nutrients in each cultivar and the growth of the evergreen cultivars. Plants that were irrigated more frequently during year 1 performed better in the landscape the following year, while those irrigated to 50% CC only performed better in the deciduous cultivar. In the evergreen cultivars, lower irrigation volume altered nursery plant qualities, resulting in a trade-off between flower production and growth in year 2. Our results indicate that manipulating N rates and irrigation frequency and volume can be used to alter nursery stock qualities and improve subsequent performance in the landscape.

Keywords: landscape performance; nursery production; plant water use

1. Introduction

Nursery production strategies that improve plant survival, growth, and productivity after transplanting can substantially improve the value of plants targeted for specific uses, including reforestation, restoration, row crop transplants, and orchards [1–4]. Production practices that influence consumer preferences in ornamental crops primarily focus on aesthetic attributes (e.g., flowering, size, color, and shape) that influence their purchases, but few studies address the longer-term performance of the plants after transplanting [5–10]. Links between nursery practices, stock qualities, and landscape performance have not been well defined, even though there is increased economic pressure for growers to produce high quality plants that can be established easily and perform well after transplanting [11].

Fertilizer and water are two major inputs in the container production of nursery crops. Sustainable nursery crop production requires optimization of these inputs to achieve growers' economic and environmental goals and requires information on how plants respond to the combined effects of these inputs. Relationships between nutrient availability and water



Citation: Bi, G.; Scagel, C.F.; Bryla, D.R. Nitrogen Rate, Irrigation Frequency and Volume Differentially Influence Growth, Flowering, and Nutrient Uptake of Container-Grown Rhododendron during the Following Growing Season. *Horticulturae* **2022**, *8*, 647. https://doi.org/10.3390/ horticulturae8070647

Academic Editors: Amanda Bayer, Stephanie Burnett and Jongyun Kim

Received: 9 June 2022 Accepted: 12 July 2022 Published: 16 July 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). requirements may result in an additive effect of fertilizer and irrigation management on production costs. While high rates of water and fertilizer application might improve the growth of nursery crops, they can also increase production costs and result in excessive nutrient leaching into the environment [7,12–15]. Furthermore, high fertilizer rates sometimes decrease water availability and increase plant drought stress, resulting in growers applying more water to the plants [16], while more frequent irrigation can improve plant water availability and nutrient uptake in containers and reduce the amount of fertilizer required for optimal growth [17–20].

Decreasing water availability during nursery production may enhance crop quality by preconditioning plants for future performance in stressful environments, such as retail outlets and landscapes [21–23]. Irrigation that allows substrates to dry to 40–75% of container capacity (CC) can produce plants of acceptable consumer quality [7,24–26]. Although with some species, drought treatments during nursery production can increase nutrient accumulation [23], others report that decreasing irrigation may negatively influence plant nutrient reserves that are essential for growth the following year [27,28]. There is little information on how limiting water during container production of *Rhododendron* alters plant nutrition and subsequent long-term plant performance once the plants leave the nursery. This type of information is essential to developing irrigation strategies that improve or maintain the quality of the end product.

Results from several studies suggest that irrigation frequency may alter nutrient availability in the growing substrate or affect the ability of plants to absorb and translocate nutrients and water. For example, high rates of N application have been shown to increase water stress in container-grown *Rhododendron*, resulting in a need for more frequent irrigation to decrease the stress [16]. Irrigation frequency alters the uptake and transfer of water from roots to shoots by altering biomass allocation (root-to-shoot ratios) and stem structure (shoot xylem:leaf area ratios) [23,29]. More frequent irrigation in containers can also improve nutrient use efficiency and net uptake of several nutrients, even when altering irrigation has little influence on plant biomass, and can alter performance (nutrient uptake and flowering) after the plants are transplanted into the landscape [28]; however, little is known about how irrigation frequency alters the performance of *Rhododendron* after transplanting.

Manipulating irrigation frequency and volume alters substrate moisture in nursery production. Reduced irrigation volume combined with increased irrigation frequency decreases drainage and nutrient leaching [30]. Soilless substrates commonly used in nursery production generally have variable water holding capacity and rewetting characteristics that influence how plants respond to irrigation. Porous substrates with low water holding capacity are used in the container production of *Rhododendron*, necessitating growers to commonly apply water daily during hot weather to minimize plant water stress, even though this practice may result in less efficient use of fertilizer.

Rhododendron is a large genus with about 1000 species in the family Ericaceae. Rhododendrons, which include azaleas, are popular for their beautiful flowers and have been extensively used in the landscape. Most of the rhododendrons grown in gardens are hybrids. Rhododendrons are important nursery crops and contribute significantly to the US economy. In 2019, the total sales were over USD 38 M for rhododendron and USD 97 M for azalea [31]. Rhododendrons are also an important component of the Oregon nursery industry, with an annual value of over USD 9.9 M for rhododendron and USD 4.5 M for azalea [31].

The objective of this study was to investigate how altering irrigation frequency or volume affects the transplant performance of deciduous and evergreen cultivars of *Rhododendron* when grown at three different rates of N fertilizer in a commercial soilless substrate mix. Plant responses to treatments were assessed during the first growing season, as well as for 8 months afterward when re-transplanted into soil, to determine how irrigation and N management practices in containers might alter future plant performance in the landscape. We hypothesized that (1) altering N rates and irrigation volume or frequency can affect the growth and nutrient uptake of container-grown *Rhododendron* and can result in varying plant performance in the landscape, and (2) lowering nutrient and water availability in containers may pre-condition plants for better transplant performance.

2. Materials and Methods

2.1. Plant Materials

Two evergreen cultivars of *Rhododendron*, 'P.J.M.', ARS#874 (PJM) and 'Catawbiense Album', RHS#58 (CAT), and one deciduous cultivar, 'Gibraltar', RHS#58 (AZ), were used in this 2-year study. Plants were obtained from a commercial nursery as 1-year-old liners that were clonally propagated and grown in a cell tray (\approx 7 cm × 7 cm cell size) filled with soilless substrate. In Year 1, plants were transplanted on 22 May into 3.8 L containers (18 cm D × 18 cm W × 18 cm H; GL-400; Nursery Supplies, Inc., McMinnville, OR, USA) filled with ~520 g of a substrate mix containing bark (50% by volume), sphagnum peat moss (20%), perlite (15%), vermiculite (15%), dolomitic lime (3.6 kg m⁻³), gypsum (1.2 kg m⁻³), and a proprietary wetting agent (SB-300; Sun Gro Horticulture, Bellevue, WA, USA) and were grown outdoors in Corvallis, Oregon, USA (45°59'04″ N, 123°27'22″ W).

2.2. Year 1 N Rate Treatments

Plants were fertigated daily from 22 May to 11 Sept. by injecting a nutrient solution through a separate drip irrigation system for each N treatment with one emitter per container (2 L h⁻¹; Netafim USA, Fresno, CA, USA). The nutrient solution contained N-free fertilizer (0 N treatment; Cornell No N Formula 0-6-27, Greencare Fertilizers, Kankakee, IL) or N-free fertilizer plus 7 mg d⁻¹ N (0.5 N; lower N rate treatment) or 14 mg d⁻¹ N (1.0 N; higher N rate treatment) from NH₄NO₃. Electrical conductivity (EC) of the solutions was monitored using an InLab 730 conductivity probe connected to a MultiSeven meter (Mettler Toledo, Columbus, OH, USA) and measured weekly at 25 °C using 35 mL samples collected from three drip emitters in each treatment. During Year 1, EC varied by <8%, and plants received an estimated 0, 766, and 1566 mg N in each treatment, respectively, over the entire growing season.

2.3. Year 1 Irrigation Treatments

In addition to fertigation, the plants were also irrigated with municipal water using separate drip lines and emitters than the ones used for fertilizer applications. Treatments included irrigation to 100% CC (W1 treatment) or 50% CC (W2 treatment) at 0800 HR daily or irrigation with the same amount of water as the W1 treatment but in equal volumes split between 0800 and 1500 HR daily (W3 treatment). The water holding capacity of the substrates was 49% of the container volume and averaged 1370 mL of water at 100% CC. Total irrigation volumes (water and fertigation) were corrected weekly by gravimetric determination in three reference W1 plants per cultivar in the 1.0 N treatment. Based on these measurements, W1 was dried to an average 56–65% CC between irrigations. Daily target volumes in each irrigation treatment accounted for the water from fertigation. Irrigation was monitored weekly by measuring the volume of water and nutrient solution discharged from three fertigation and three irrigation emitters in each treatment. In Year 1, a total of 484-604 mL, 251-319 mL, or 515-637 mL of water was applied per day in W1, W2, and W3, respectively. Pans were placed below containers, and any leachate in the pans was added back into containers. By July, this procedure was seldom necessary in W1 and was never needed in the other irrigation treatments.

2.4. Year 2 Experimental Conditions

On 28 May in Year 2, plants were transplanted into 21 L containers (35 cm D \times 35 cm W \times 25 cm H; GL-2800S; Nursery Supplies, Inc., McMinnville, OR, USA) filled with a Willamette silt loam soil. The soil had a pH of 6.0, a CEC of 22 meq/100 g, and ~4 mg kg⁻¹ NH₄-N, 6 mg kg⁻¹ NO₃-N, 8 mg kg⁻¹ P, 201 mg kg⁻¹ K, 397 mg kg⁻¹ Ca, 80 mg kg⁻¹ Mg, 52 mg kg⁻¹ Fe, 36 mg kg⁻¹ Mn, 0.61 mg kg⁻¹ B, 1.01 mg kg⁻¹ Zn, and 0.8 mg kg⁻¹ Cu

(Central Analytical Lab., Oregon State University, Corvallis, OR, USA). The soil surface was covered with a 6-cm-deep layer of partially decomposed Douglas fir bark chips. At this point, the plants in each treatment were fertilized by hand with N-free fertilizer plus 20 mg N per week until 25 June and irrigated to 100% CC at 0800 HR every 2 d from 28 May to 4 September.

2.5. Plant Growth and Flowering Measurements

Five plants per treatment were harvested destructively on 22 May (prior to treatment) and 11 Dec. (Year 1) and on 4 June, 4 September, and 5 December (Year 2). The harvests in December occurred after leaf fall in AZ; the harvest in June occurred after each cultivar flowered and the leaves had emerged; the harvest in September occurred when the leaves on the AZ plants began to senesce and change color. At each harvest, shoots were cut off at the soil surface, separated into leaves and stems, and, when applicable, were divided into 1-, 2-, and 3-year-old structures. Roots were washed from the growing substrate over a 50-mesh screen, blotted dry with a paper towel, and weighed. The remaining plant samples were dried at 65 $^{\circ}$ C in a forced-air oven (Model 1380FM, Sheldon Manufacturing, Cornelius, OR, USA), weighed and ground to pass through a 40-mesh screen using a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA), and stored in airtight containers until analyzed for nutrients. The date when the first flower was fully expanded on the plants and the number of flowers and inflorescences produced per plant was recorded daily from 5 Mar. to 29 May in Year 2. Spent flowers were collected before 4 June and processed for dry weight (dw) and nutrient analyses.

2.6. Nutrient Analyses

Dried tissue samples were analyzed for P, K, Ca, Mg, S, B, Cu, Fe, Mn, and Zn using an inductively coupled plasma optical emission spectrometer (Optima 8300; PerkinElmer, Inc., Waltham, MA, USA) after digesting them in a microwave (Multiwave Pro; Anton-Paar, Graz, Austria) with 70% (*v*/*v*) nitric acid [32,33]. Apple leaf reference standards (SRM 1515, NIST; Gaithersburg, MD, USA) were included with each analysis to ensure the accuracy of the spectrometry and digestion procedures. Carbon and N in each sample were also measured using a combustion analyzer (Leco Corp., St. Joseph, MI, USA).

2.7. Substrate EC and Moisture

Substrate EC was measured directly using soil probes (FieldScout; Spectrum Technologies, Inc., Aurora, IL, USA) inserted at 2.54 cm and 7.62 cm depths at randomly chosen locations ~2.54 cm from the sidewall of the containers. The measurements were taken at midday (1030 HR and 1430 HR) every 2 weeks from June through September in five containers per treatment. Values were standardized to those obtained using a pour-through method on a fresh substrate [34]. Volumetric water content was measured using moisture sensors (Wet-2; Delta-T Devices, Cambridge, UK) inserted to a depth of 68 mm at three random locations ~2.54 cm from the side wall of the containers and averaged for each container. The measurements were taken once per week at midday in five containers per treatment. Wet sensor output was calibrated to CC for fresh substrate, and data are expressed as %CC.

2.8. Leaf Stomatal Conductance

Stomatal conductance (g_s) was measured periodically at midday on new fully expanded leaves from five plants per treatment using a steady-state porometer (LI-1600; LI-COR, Lincoln, NE, USA) [16]. These were the same plants used for substrate moisture measurements.

2.9. Calculations

Nutrient content was calculated for each plant structure by multiplying the dw of the given structure by its concentration. Total plant nutrient content was calculated as the

sum of each nutrient in all plant parts [35]. Total plant biomass and nutrient content were calculated as the sum of all structures (roots, stems, leaves, and flowers, if present). Total nutrient concentration was calculated by dividing total nutrient content by total biomass for each plant. Nitrogen and biomass allocation were calculated as the percentage of total N and biomass in each plant structure. In year 1, the effects of irrigation on nutrient uptake were calculated relative to the W1 treatment within each N rate (to adjust for any treatment effects on plant size) and expressed as relative uptake. In year 2, percent change in growth and nutrient uptake was calculated as the differences between the total dw or nutrient content at two sequential harvest dates.

2.10. Data Analyses

Containers were arranged in a completely randomized design for each cultivar. Each combination of treatments (3 N treatments \times 3 irrigation treatments) was replicated 20 times for a total of 180 plants per cultivar. All statistical analyses were performed using Statistica^{∞} software (Statsoft, Inc., Tulsa, OK, USA). The data were checked for normality using the Kolmogorov–Smirnov test at $p \le 0.01$ and tested for homogeneity of variance using Levene's test. Allocation data were arcsin-transformed prior to analyses and presented as back-transformed means. Data were analyzed separately for each cultivar. Accumulation and allocation of nutrients and biomass were assessed by ANOVA in a complete factorial design with irrigation treatment and N rate as the main effects, while substrate EC, substrate moisture, and g_s were analyzed by ANOVA in complete factorial designs with date or depth as a repeated measure, when appropriate. Where applicable, means were compared using Tukey's honest significant difference test at $p \le 0.05$ (Tukey HSD_{0.05}). When there was no significant interaction between effects, only the main effects are presented. The effects of irrigation treatment and N treatment on flowering data were assessed using the Kruskal-Wallis ANOVA and means were separated at $p \le 0.05$ (K-W_{0.05}). Correlations between N uptake in Year 1 and response variables were assessed using Pearson product–moment correlation (r) at $p \leq 0.05$.

3. Results

3.1. Effects of Different Nitrogen Rates on Plant Growth and Nutrient Uptake

A higher rate of N application in Year 1 increased the total plant dw and N content of each cultivar at each harvest (Figure 1). Net dw and N accumulation was negligible during the experiment when plants were grown with 0 N. On the other hand, plants treated with 0.5 and 1.0 N accumulated more dw and less N, on average, in Year 2 than in Year 1. Biomass accumulated by the end of Year 1 (December) accounted for 35% to 48% of dw in Year 2 in 0.5 N and 1.0 N plants, while N accumulated in Year 1 accounted for more than 79% of the N accumulated in Year 2. In December, there was a positive linear relationship between N rate and biomass in Year 1 (r > 0.8299; p < 0.0001) and Year 2 (r > 0.8537; p < 0.0001). On average, for every g of N applied, AZ, CAT, and PJM accumulated 9, 11, and 17 g dw, respectively, by December in Year 1 and accumulated 25, 43, and 38 g dw, respectively, by December in Year 2.

Applying N at a higher rate enhanced uptake and concentration of several nutrients in Year 1, including P, Ca, and B in each cultivar, Zn in AZ, Mg and Fe in CAT, and K, S, Fe, and Zn in PJM (Figure S1). Similar to N, uptake of other nutrients showed minor changes when plants were grown without N (data not shown). A higher N rate increased N content in each cultivar in Year 2 (Figure 1); however, N concentrations were similar among the N treatments. In December, there was a positive linear relationship between N uptake and biomass in Year 1 (r > 0.9795; p < 0.0001) and Year 2 (r > 0.7968; p < 0.0001). On average, for every g of N uptake, AZ, CAT, and PJM accumulated 81, 97, and 80 g dw, respectively, by December in Year 1 and accumulated 184, 319, and 167 g dw, respectively, by December in Year 2.

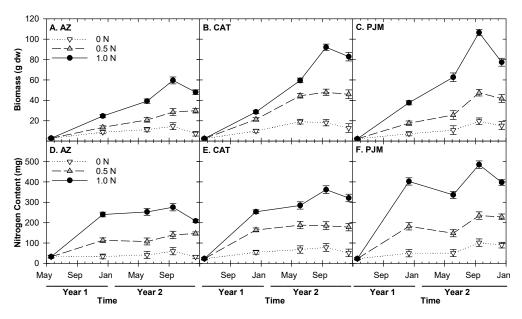


Figure 1. Total biomass (dry weight; dw) and N content of 'Gibraltar' (AZ) (**A**,**D**), 'Catawbiense Album' (CAT) (**B**,**E**), and 'P.J.M.' (PJM) *Rhododendron* (**C**,**F**). In Year 1, plants were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH₄NO₃ and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). In year 2, the plants were transplanted into soil. Data are pooled across irrigation treatments, and error bars represent least significant differences at $p \leq 0.05$.

The effects of the N rate on nutrient uptake varied between the higher N treatments in Year 2 (Figure S2). In general, 0.5 N plants accumulated similar or more biomass and nutrients than 1.0 N plants in late winter and spring (January to June) and less biomass and nutrients in the summer (June to September). In addition, 0.5 N plants of AZ retained more biomass and nutrients in autumn and early winter (September to December) than 1.0 N plants of AZ. Nitrogen application had a similar influence on the content of most nutrients in the plants by December of Year 2, where the higher N rate increased nutrient content but had no effect on nutrient concentrations (data not shown).

3.2. Effects of Irrigation Volume and Frequency on Plant Growth and Nutrient Uptake

The irrigation treatments had no significant effect on growth or nutrient uptake in the 0 N plants (Figure 2). In contrast, when plants were fertilized with 0.5 and 1.0 N, less irrigation (W2 vs. W1) and more frequent water applications (W3 vs. W1) increased biomass in the evergreen cultivars and increased N content in each cultivar.

Compared to the W1 treatment, the W2 and W3 treatments also enhanced uptake of certain nutrients by the 0.5 N and 1.0 N plants during Year 1 (Figure S1). For example, less irrigation in W2 enhanced N uptake in each cultivar, while more frequent irrigation in W3 enhanced N uptake by AZ. With some exceptions, enhanced uptake of nutrients other than N by AZ and CAT primarily occurred at the higher N rate. In PJM, enhanced nutrient uptake generally occurred at both the 0.5 N and 1.0 N rates. Compared to PJM, irrigation volume had a greater influence on nutrient uptake by AZ and CAT. Less irrigation enhanced uptake of K, Fe, Mn, and B by AZ and CAT, as well as uptake of P by PJM and uptake of P and S by CAT. Irrigation frequency, on the other hand, had a greater influence on nutrient uptake by AZ and PJM than by CAT. Specifically, more frequent water applications in W3 enhanced uptake of Mg, B, and Zn by AZ and PJM, uptake of P, K, and Mn by AZ, uptake of S, Ca, and Cu by PJM, and uptake of Ca and Mg by CAT.

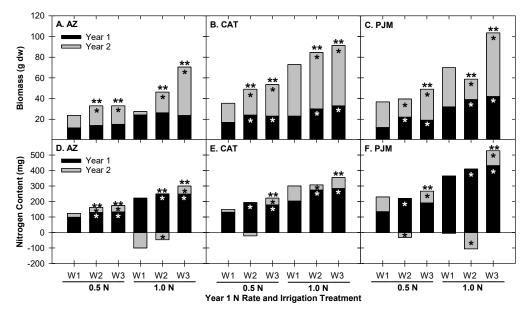
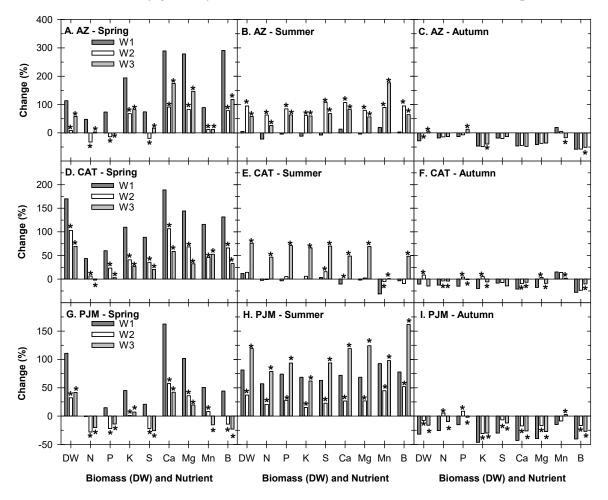


Figure 2. Total biomass (dry weight; dw) and N content of 'Gibraltar' (AZ) (**A**,**D**), 'Catawbiense Album' (CAT) (**B**,**E**), and 'P.J.M.' (PJM) *Rhododendron* (**C**,**F**). In Year 1, plants were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH₄NO₃ and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). In year 2, the plants were transplanted into soil. Segments within each column represent net biomass or N content in December of Year 1 and Year 2. Net biomass and N content within a year and N rate denoted by a single asterisk (*) are significantly different from W1 (*p* < 0.05). Whole columns within an N rate denoted by two asterisks (**) are significantly different from W1 (*p* < 0.05).

During Year 2, irrigation treatments generally had a similar or greater effect on growth and N uptake of 1.0 N plants than they did on 0.5 N plants. The effects of irrigation treatments on growth and nutrient uptake also occurred at different times in Year 2 (Figure 3). Less irrigation (W2) and more frequent water applications (W3) in Year 1 reduced growth and nutrient uptake in each cultivar the following spring but had different effects on growth and nutrient uptake by the following summer and autumn.

By December in Year 2, more frequent water application (W3) increased biomass and N content in all cultivars because of increased growth and N uptake during the summer (all cultivars) and more biomass (AZ and PJM) and N retention (PJM) in the plants in the autumn (Figures 2 and 3). Similar to N, more frequent watering in W3 also increased the content of several other nutrients, even though W3 plants accumulated fewer nutrients than W1 plants during the spring. However, by summer, more frequent irrigation increased the uptake of other nutrients in each cultivar. Furthermore, W3 plants retained more nutrients in the autumn, particularly in evergreen cultivars. Overall, between May of Year 1 and December of Year 2, more frequent irrigation enhanced the uptake of N, P, and K in AZ and the uptake P, Ca, Mg, B, and Cu in the evergreen cultivars.

Irrigation volume differentially altered biomass and nutrient accumulation of each cultivar during Year 2 (Figure 3). By December, less irrigation (W2) in the previous year increased biomass and accumulation of several nutrients in AZ because it increased growth and nutrient uptake the following summer and resulted in greater biomass retention in the autumn. In CAT, the W2 plants had similar growth and nutrient accumulation over the spring and summer as the W1 plants. Therefore, the effects of irrigation volume on biomass and nutrient accumulation in CAT were primarily due to its effects on growth and nutrient uptake in Year 1. In PJM, less irrigation in W2 decreased biomass and nutrient accumulated more nutrients than the W2 plants. In both evergreen cultivars, the W2 plants had similar



or lower content of most nutrients by December of Year 2 than the W1 plants, even though they generally retained more nutrients in the autumn than the W1 plants.

Figure 3. Change in biomass (dry weight; DW) and nutrient content of 'Gibraltar' (AZ) (A–C), 'Catawbiense Album' (CAT) (**D–F**), and 'P.J.M.' (PJM) (**G–I**) *Rhododendron* in the spring, summer, and autumn after transplanting them to soil in Year 2. The previous year, plants from each cultivar were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH₄NO₃ and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). Data are pooled across N treatments, and asterisks indicate the change in biomass or nutrient content was significantly increased or decreased by the W2 or W3 irrigation treatment when compared to the W1 treatment ($p \le 0.05$).

Compared to AZ, irrigation volume had less influence on nutrient uptake in the evergreen cultivars. Overall, between May of Year 1 and December of Year 2, less irrigation in W2 enhanced the uptake of all nutrients by AZ, except Mg. It also enhanced the uptake of P, K, Ca, Mn, and B in CAT but had little influence on any nutrient other than N in PJM.

3.3. Allocation of Plant N and Biomass

Allocation of N and biomass in the plants responded similarly to treatments throughout the experiment (Table 1; biomass allocation not shown). Generally, greater N reduced allocation belowground in each cultivar by December of Year 1 and by spring of Year 2, after which the effects of N rate on allocation varied among the cultivars. By Year 2, the effects of the N rate on allocation by AZ and CAT were similar in September and December (Table 1). In general, greater N reduced allocation to roots in AZ and CAT and increased allocation to the stems. In PJM, greater N increased allocation to roots and stems and decreased allocation to leaves. **Table 1.** Nitrogen (N) allocation in 'Gibraltar' (AZ), 'Catawbiense Album' (CAT), and 'P.J.M.' (PJM) *Rhododendron*. In Year 1, plants from each cultivar were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH_4NO_3 and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). In year 2, the plants were transplanted into soil.

	Allocation (% Total Plant)													
	Cultivar, Time, and S			N Trea	atment		Irrigation Treatment							
		0	N	0.5 N		1.0 N		W1		W2		И	/3	
		Roots	70	a ¹	71	а	58	b	67	а	65	а	61	b
A 77	December Year 1	Stems	30	b	29	b	42	а	33	b	35	b	39	а
ΑZ	December Year 2	Roots	69	а	58	b	50	с	58	а	54	b	52	b
		Stems	31	С	42	b	50	а	42	b	46	а	48	а
		Roots	32	а	25	b	21	С	24	а	23	а	24	а
	December Year 1	Stems	11	b	13	ab	14	а	13	а	14	а	15	а
6 1 T		Leaves	56	b	62	а	65	а	63	а	63	а	61	а
CAT		Roots	48	а	42	b	40	b	41	а	41	а	40	а
	December Year 2	Stems	8	b	17	а	19	а	16	b	20	а	W 61 39 52 48 24 15 61 40 18 42 27 22 52	b
		Leaves	43	а	41	а	41	а	43	а	39	b	42	а
		Roots	34	а	28	b	26	b	27	а	26	а	27	а
	December Year 1	Stems	28	а	23	b	23	b	24	а	25	а	22	а
		$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	49	а	49	а	52	а						
PJM		Roots	34	b	38	а	38	а	41	а	31	b	40	а
	December Year 2	Stems	19	с	29	b	35	а	35	а	30	а	33	а
		Leaves	47	а	33	b	27	с	24	b	39	а	27	b

¹ Means followed by the same letter within a row and response variable are not significantly different at $p \le 0.05$.

Irrigation treatments had similar effects on the allocation of N and biomass when the plants were fertilized with 0.5 N and 1.0 N but had no effect on allocation when they were grown with 0 N (data not shown). By the end of Year 1 (Dec.), more frequent irrigation in W3 reduced the allocation below ground in AZ (Table 1). During Year 2, irrigation treatments had a similar or greater influence on allocation in 1.0 N plants than 0.5 N plants (data not shown). By June, both reduced irrigation (W2) and more frequent irrigation (W3) increased allocation to roots and decreased allocation to leaves in AZ, and both treatments had opposite effects on allocation later in the year. In the evergreen cultivars, only irrigation volume altered allocation. In September and December of Year 2, less irrigation in W2 increased allocation to stems, reduced allocation to leaves in CAT, decreased allocation to roots and stems, and increased allocation to leaves in PJM.

3.4. Flowering

The treatments applied in Year 1 had no effect on the timing of flowering the following spring. Plants flowered within 3 d of 1 May, 10 May, and 12 May in AZ, CAT, and PJM, respectively. More N increased the percentage of plants that flowered on average as well as the number and biomass of flowers produced on the plants (Table 2). In AZ, higher N did not influence the number of inflorescences produced; however, it increased the size of the inflorescences. In contrast, higher N increased the number of inflorescences in CAT. When plants produced flowers in Year 2, the biomass of the inflorescences accounted for <7% of the total biomass of the plants in June that year, while the N content of the inflorescences accounted for <5% of total N in the plants during December of the previous year.

Table 2. Effects of N and irrigation treatments on flowering of 'Gibraltar' (AZ), 'Catawbiense Album' (CAT), and 'P.J.M.' (PJM) *Rhododendron*. In Year 1, plants were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH₄NO₃ and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). In year 2, the plants were transplanted into soil.

0.10	T 7 • 11			N trea	tment				Ir	rigation '	Treatm	ient	
Cultivar	Variable	0 N		0.5 N		1.0 N		W1		W2		W3	
	Plants with flowers (%)	21	c ¹	56	b	86	а	59	b	72	а	84	а
	Flowers/plant	6	с	13	b	30	а	17	b	23	а	25	а
AZ	Flower dry wt (mg)	13	b	17	b	31	а	19	а	16	а	20	а
	Inflorescences/plant	1	а	1	а	3	а	2	а	2	а	2	а
	Flowers/inflorescence	5		12	а								
	Plants with flowers (%)	0	с	39	b	86	а	67	а	67	а	55	а
	Flowers/plant	0	с	10	b	25	а	10	b	19	а	24	а
CAT	Flower dry wt (mg)	0	с	86	b	99	а	91	b	122	а	65	b
	Inflorescences/plant	0	b	2	а	5	а	2	а	3	а	3	а
	Flowers/inflorescence	0	b	7	а	5	а	6	а	7	а	7	а
	Plants with flowers (%)	9	b	97	а	95	а	96	а	92	а	100	а
	Flowers/plant	3	b	4	b	18	а	12	b	23	а	12	b
PJM	Flower dry wt (mg)	38	с	54	b	93	а	38	b	77	а	61	а
	Inflorescences/plant	1	b	2	b	6	а	6	а	5a		6	а
	Flowers/inflorescence	3	а	2	а	3	а	2	а	4a		2	а

¹ Means followed by the same letter within a row and treatment (N or irrigation) are not significantly different at $p \le 0.05$.

In Year 2, reduced irrigation (W2) and more frequent water applications (W3) during the previous year caused similar responses in measured flowering variables in plants fertilized with 0.5 N and 1.0 N in Year 1; however, neither of these treatments had any effect on flowering of the plants treated with 0 N (data not shown). These treatments also had less effect on flowering in the evergreen cultivars than in the deciduous cultivar (Table 2). On average, both treatments enhanced flower production in AZ by increasing the number of plants that flowered, the number of flowers produced, and the size of inflorescences. Both treatments also affected flower production in the evergreen cultivars. In evergreen cultivars, reduced irrigation in W2 increased the number of flowers produced and flower biomass, while more frequent water applications in W3 increased flower biomass, but only increased the number of flowers produced in CAT.

3.5. Electrical Conductivity and Moisture Content of the Substrate

In Year 1, the vertical distribution of EC in the growing substrate was non-uniform and fluctuated over the growing season. On average, salts accumulated deeper in the containers during June and closer to the surface of the substrate during August (Table 3). The greatest differences in substrate EC occurred in August among the N treatments and in June and August among the irrigation treatments. For most of the year, EC was lowest in plants grown with 0 N but was higher in plants fertilized with 0.5 N than with 1.0 N (at least until July, after which EC was similar or lower with 0.5 N than with 1.0 N).

The irrigation treatments had little influence on substrate EC in 0 N plants but, in general, irrigation to 50% CC (W2) increased EC when plants were fertilized with 0.5 N or 1.0 N. In contrast, more frequent irrigation in W3 increased EC at a depth of 2.54 cm in AZ and at depths of 2.54 cm and 7.62 cm in CAT. More frequent irrigation also increased substrate EC in PJM when the plants were fertilized with 1.0 N.

Neither N nor irrigation treatments influenced moisture readings in the substrate until August (Table 3). At that point, plants grown with 0 N or 0.5 N had greater substrate moisture than those grown with 1.0 N. Furthermore, reducing irrigation to 50% CC resulted

in lower substrate moisture readings in AZ and PJM, but it had no influence on moisture readings in CAT. On average, more frequent water applications (W3) increased substrate moisture during August and had the greatest influence on substrate moisture when AZ and CAT were fertilized with 1.0 N. In contrast, irrigation frequency had no influence on substrate moisture when PJM was fertilized at a higher N rate.

Table 3. Substrate moisture and electric conductivity (EC) in 'Gibraltar' (AZ), 'Catawbiense Album' (CAT), and 'P.J.M.' (PJM) *Rhododendron*. In Year 1, plants from each cultivar were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH_4NO_3 and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). In year 2, the plants were transplanted into soil. EC measured at 2.54 cm and 7.62 cm.

Variable and Irrigation Treatment		AZ								CA	٩T			РЈМ						
		0 N		0.5 N		1.0 N		0 N		0.5 N		1.0 N		0 N		0.5 N		1.0	N	
Substrate Moisture (%CC)																				
	W1	69	a ¹	70	а	65	b	69	а	65	ab	61	b	75	а	73	а	64	b	
Early August	W2	66	ab	68	а	63	b	71	а	67	а	62	b	74	а	71	а	62	b	
	W3	71	ab	74	a *	68	b *	72	а	72	a *	68	b *	77	a *	74	а	65	b	
	W1	63	а	64	а	62	а	65	а	62	а	64	а	68	а	66	а	60	b	
Late August	W2	57	a *	54	a *	55	a *	66	а	65	а	64	а	62	a *	60	b *	64 62 65 60 58 64 864 1682 1038 1645 2188	с	
-	W3	76	a *	73	a *	68	b *	73	a *	75	a *	73	a *	76	a *	71	b *		с	
						Sub	strate	EC (μ	S cm	⁻¹)										
	W1	600	b	536	b	853	а	587	b	608	b	833	а	538	b	542	b	864	а	
$2.54 \times 10^{-2} \mathrm{m}$	W2	702	с	1013	b *	1327	' a *	645	b	1189	a*	1243	a *	633	с	865	b *	1682	a *	
	W3	620	b	865	a *	1068	a *	682	С	854	b *	1139	a *	591	b	718	b	62 65 60 58 64	a *	
	W1	862	с	1331	а	1165	b	1042	b	1147	b'	1344	а	765	с	1112	b	1645	а	
$7.62 \times 10^{-2} \mathrm{m}$	W2	889	b	1321	а	1483	a *	1027	с	1854	b *	2335	a *	907	с	1348	b *	2188	a *	
	W3	927	b	1154	a*	1180	а	1013	b	1644	a *	1748	a *	882	с	1194	b	1941	a *	

¹ Means followed by the same letter within a row and cultivar are not significantly different at $p \le 0.05$, and asterisks (*) indicate that means of W2 or W3 irrigation treatment within a column and response variable are significantly different from W1 at $p \le 0.05$.

3.6. Stomatal Conductance

In each cultivar, plants grown with 0 N had the lowest rates of g_s and were unaffected by the irrigation treatments (Table 4). However, there was no difference in g_s between plants fertilized with 0.5 N and 1.0 N until August, when g_s with 0.5 N was similar to or higher on average than with 1.0 N. Irrigation to 50% CC (W2) increased g_s by mid-July in AZ and CAT and by August in PJM. Irrigation twice daily to 100% CC (W3) also increased g_s on several dates, and this occurred more frequently in CAT than in AZ and PJM. In this case, more frequent irrigation increased g_s of CAT on nearly every measurement date but only increased g_s of AZ and PJM during August. In late August, the effects of irrigation frequency and volume on g_s were similar between plants fertilized with 0.5 N and 1.0 N in AZ and CAT and with 1.0 N in PJM.

By Year 2, the effect of the N rate on g_s in AZ was similar among the irrigation treatments (Table 4). In this case, plants fertilized with 1.0 N had higher g_s by July that year than those grown with 0 N, while those fertilized with 0.5 N had the lowest g_s among the N treatments by August. In contrast to AZ, the effect of the N rate on g_s in the evergreen cultivars differed among the irrigation treatments in July and August. During both months, higher N generally increased g_s when CAT was irrigated daily to 50% to 100% CC (W1 and W2) but reduced g_s when the cultivar was irrigated twice daily to 100% CC (W3). In contrast, higher N generally reduced g_s of PJM in each irrigation treatment during July and August. In July, less irrigation (W2) and more frequent water applications (W3) increased g_s in plants grown with 0 N but had little influence on g_s at other N rates. However, by August, less irrigation reduced g_s in the evergreen cultivars at nearly every N rate, while more frequent water application increased g_s in plants grown with 0 N and reduced g_s when CAT or PJM were fertilized with 0.5 N and/or 1.0 N.

Table 4. Stomatal conductance (g_s) in 'Gibraltar' (AZ), 'Catawbiense Album' (CAT), and 'P.J.M.' (PJM) *Rhododendron*. In Year 1, plants from each cultivar were grown in soilless media with N-free fertilizer (0 N) or N-free fertilizer plus 7 (0.5 N) or 14 (1.0 N) mg N per day from NH₄NO₃ and irrigated once daily to 100% (W1) or 50% (W2) container capacity or twice daily to 100% container capacity (W3). In year 2, the plants were transplanted into soil.

								g _s (mmol	m ⁻² s	s ⁻¹)							
Time and Irrigation			Α	Z					CA	ТУ					PJI	Му		
Treatment ¹	0 N		0.5 N		1.0 N		0 N		0.5 N		1.0 N		0 N		0.5 N		1.0	Ν
	Early August Year 1																	
W1	69	b ¹	143	а	144	а	173	b	284	а	252	а	161	b	334	а	309	а
W2	75	с	246	a *	199	b	198	b	342	a *	312	a *	172	b	337	а	374	a *
W3	95	с	210	a *	204	b	196	b	351	a *	304	a *	188	b	380	a *	401	a *
						La	te Aug	ust Ye	ear 1									
W1	65	b	147	а	157	а	184	b	276	а	232	ab	173	b	270	а	281	а
W2	70	с	252	a *	219	b *	212	с	332	a *	288	b *	190	с	279	b	326	a *
W3	97	b	216	a *	207	a *	210	b	319	a *	297	a *	185	с	259	b	350	a *
							July	Year 2										
W1	106	b	112	ab	128	а	116	b	263	а	246	а	152	а	161	а	86	b
W2	109	b	130	а	134	а	193	с*	247	b	244	а	270	a *	129	b	101	b
W3	102	b	129	ab	142	а	241	a *	260	а	184	b *	238	a *	143	b	110	с
							Augus	t Year	2									
W1	122	а	95	b	121	а	189	с	369	а	297	b	222	а	180	b	101	с
W2	102	а	74	b	106	а	120	b *	216	a *	187	a *	173	a *	97	b *	92	b
W3	115	а	69	b	134	а	396	a *	245	b *	214	b *	324	a *	139	b *	118	b

¹ Means followed by the same letter within a row and cultivar are not significantly different at $p \le 0.05$, and asterisks (*) indicate that means of W2 or W3 irrigation treatment within a column and response variable are significantly different from W1 at $p \le 0.05$.

4. Discussion

4.1. Rate of N Application

A higher rate of N application in soilless media improved the performance (total biomass, nutrient content, and flowering) of container-grown *Rhododendron* the following year when the plants were transplanted into soil. Therefore, increasing the rate of N application improves the qualities of the plants that are important for promoting their growth and survival in the landscape.

A higher N rate also enhanced the nutrient status of 1-year-old container-grown *Rhododendron*. This was expected since N is generally considered the primary driving force for plant growth [36], thus enhancing the demand for nutrients. Improved growth in the first year was also associated with greater concentrations of several nutrients other than N, indicating that better N status in container production enhances the ability of plants to absorb other nutrients. Similar results were found in previous studies on *Rhododendron* [20,28]. In the current study, the effects of the N rate on plant nutrient status in containers were positively correlated with plant growth and nutrient uptake the following year, suggesting that nutrient status was a primary driver of improved plant performance after transplanting.

Seasonal changes in substrate EC suggested that there was differential uptake of nutrients among the cultivars in the present study. For example, in AZ, substrate EC was similar until August, at which point readings were greater when the plants were fertigated at a higher N rate (1.0 N) than at a lower rate (0.5 N). This suggests that the

plants may have benefited from a high N rate initially, but by late summer, the amount of N supplied at the higher rate was greater than the plant's demand for the nutrient. In contrast, substrate EC differed between N rates throughout summer in the evergreen cultivars. This suggests that in evergreen cultivars, the fertilizer rates provided were greater than plant demand while the plants were in the substrate. However, since evergreen cultivars absorbed more N than the deciduous cultivar, evergreen cultivars were either more efficient at N uptake than the deciduous cultivar or N uptake occurred for a longer period of time during the growing season. In the deciduous cultivar, nutrient uptake was low by August compared to the evergreen cultivars, which continued to take up N into winter [37]. These results indicate that, compared to deciduous cultivars, factors that limit nutrient uptake during the summer (e.g., limited water and nutrient availability) may have less impact on nutrient resources required for growth the following year in evergreen cultivars than in deciduous cultivars.

The plant's N status altered the allocation of resources among structures within the plants. In this case, a higher N rate decreased the allocation of resources to roots during the first year of growth. One method of assessing the effect of the growing environment on plant growth is to analyze the allocation of biomass and nutrients to different structures [38]. Plants commonly allocate more N and biomass to roots when they are under nutrient or water stress [39]. In our study, N fertilization increased g_s in two of the cultivars (AZ and CAT), at least until August, after which time plants fertilized with N showed signs of water stress, including lower g_s , in some of the irrigation treatments; however, higher N levels did not appear to have a negative effect on g_s in PJM. These results indicate that greater N can increase water stress and that differences in allocation in response to N is a function of water and nutrient availability in certain cultivars. Resource allocation during container production alters the esthetic qualities of the plants, as well as intrinsic qualities that may alter plant performance in the landscape (e.g., root-to-shoot balance, storage locations for nutrients, etc.). While growing plants without N fertilizer is not practiced in commercial nurseries, some studies have shown that lowering N may improve plant performance after transplanting, particularly if the plants have a larger root system as a result and are storing a larger proportion of their reserves in their roots or other belowground structures [27].

Increased allocation to roots during container production was not associated with plant performance after transplanting in the present study. Less N restricted both plant growth and nutrient uptake of *Rhododendron* after transplanting to soil the following year, indicating that greater resource allocation to roots at lower N rates did not improve plant performance the following year. Similarly, although lowering the N rate increased the allocation of biomass and N to roots of Mediterranean oak (*Quercus ilex*) grown in containers, plants grown with more N performed better than those with less N once the plants were transplanted into the field [40]. In our study, plants flowered just prior to transplanting, which may have affected subsequent root production by depleting reserves in the plants. This suggests that when lower N rates are used in container production of *Rhododendron*, plants may require higher rates of fertilizer after transplanting to minimize the impacts of flowering on reserves.

Limiting N during container production does not appear to pre-condition *Rhododendron* for better performance after transplanting into soil. Under our study conditions, lowering N rates during the first growing season had no pre-conditioning effect on growth or N uptake of any cultivar during the second growing season. Plants grown at the highest N rate in Year 1 grew the most and absorbed the most N the following year. In contrast, plants grown at a lower N rate (0.5 N) generally retained more N (and a higher percentage of total N) by autumn of the second year than those that were grown at a higher N rate (1.0 N), suggesting moderate amounts of N may provide longer-term benefits to transplant performance than higher rates in terms of nutrient retention. Others have shown that lowering fertilizer rates in nursery production can reduce the growth and survival of plants after transplanting into less-than-optimal growing conditions [41,42].

4.2. Irrigation Frequency

Much like higher N rates, more frequent water applications in soilless media improved the performance of container-grown *Rhododendron* the following year when the plants were transplanted into soil. These results indicate that altering the frequency of water application on a daily basis during nursery production can improve plant qualities important to transplant success, without increasing daily water application rates.

More frequent irrigation may improve transplant performance by increasing plant nutrient reserves during the previous growing season. Indeed, more frequent irrigation in the year prior to transplanting increased the growth of evergreen cultivars and enhanced nutrient uptake in all cultivars in the present study. Plants with greater nutrient reserves have greater potential for growth after they are transplanted into nutrient-poor environments [40,41]. Irrigation frequency alters nutrient availability in the growing substrate, thereby affecting nutrient uptake by the plants [16,20,24,43]. Applying more water in a single application each day moves nutrients further down in the container than more frequent irrigations with the same amount of water. Even if there was no appreciable amount of leaching, the nutrients may not be readily available for uptake because the roots of young plants do not have access to nutrients located near the bottom of the containers. Substrate EC is frequently used to assess nutrient availability in container substrates [34]. In our case, more frequent irrigation increased substrate EC, particularly closer to the substrate surface. This suggests that greater nutrient availability may be responsible for the improved plant nutrient status observed with more frequent irrigation. In this study, we did not determine EC at depths lower than 7.62 cm from the substrate surface. Further studies are needed to determine if less frequent irrigation also increases EC near the bottom of the containers.

More frequent irrigation improved plant uptake of certain nutrients during container production of the deciduous cultivar, AZ, even though the irrigation treatments had no influence on its growth. In contrast, increased irrigation frequency had no influence on growth and little influence on nutrient uptake during container production of 'Gibraltar' *Rhododendron* [20]. Compared to the previous study, liners were transplanted into containers later in the growing season in the present study than in the previous study and, therefore, had less time to grow roots into the substrate. A large proportion of nutrient uptake by deciduous *Rhododendron* occurs before July [44]. It is possible that more frequent irrigation provided AZ with greater access to nutrients when the root systems of the plants were small. Thus, altering irrigation frequency on a daily basis during container production of *Rhododendron* may be a useful management strategy to improve plant access to nutrients in the growing substrate.

In evergreen cultivars, more frequent irrigation enhanced the uptake of several nutrients in containers, including Ca. More frequent irrigation was previously reported to increase Ca uptake for two other evergreen *Rhododendron* cultivars and was thought to be a result of enhanced water relations, which improves transpiration and mass flow of Ca in plants [20]. In the present study, this idea was supported by the fact that g_s was greater when twice rather than once daily using the same amount of water. Therefore, even without appreciable leaching losses, altering irrigation frequency on a daily basis can change either the availability or distribution of nutrients in the growing substrate or the ability of roots to absorb the nutrients.

Irrigation frequency altered water availability in the growing substrate both temporally and spatially, which may influence nutrient uptake. Container capacity (CC) is frequently used to manage irrigation and water availability in container substrates even though CC can be influenced greatly by container size and substrate rewetting characteristics [45,46]. In our study, more frequent irrigation increased substrate moisture, particularly during August. Evergreen cultivars of container-grown *Rhododendron* can absorb a large proportion of their annual nutrient uptake in July and August, while the peak nutrient uptake by deciduous cultivars is usually earlier in the growing season [44]. This suggests that greater substrate moisture during peak times for nutrient uptake may be responsible for improved plant nutrient status resulting from more frequent irrigation, at least in evergreen cultivars.

The effect of water availability in the growing substrate on plant growth can also indirectly influence nutrient uptake through its effects on nutrient demand. Stomatal conductance is strongly related to plant metabolism and carbon (C) gain [47]. In our study, more frequent irrigation increased g_s in each cultivar, suggesting that irrigating more frequently improved photosynthesis and C gain in the plants during the first year of production. Increased g_s from more frequent irrigation resulted in more plant growth in the evergreen cultivars and greater nutrient uptake in each cultivar. Others have reported that more frequent irrigation can cause transient increases in g_s that improved nutrient uptake without significantly influencing growth [16,48,49]. On the other hand, high N rates can increase plant water stress in containers when ambient temperature and rates of evapotranspiration are high, while lower N rates may limit photosynthesis through its effects on g_s . Our results indicate that both the N rate and irrigation treatments can alter g_s in *Rhododendron*. In a previous study with *Rhododendron*, we reported that a greater rate of N fertilizer application increased g_s early in the season but decreased it late in the season when temperatures were higher and the plants were larger [16]. Similar to the current study, more frequent irrigation in the previous study decreased water stress in plants grown at higher N rates and had little impact on alleviating water stress of N-deficient plants.

Increasing the frequency of irrigation during container production may be a useful strategy for pre-conditioning *Rhododendron* for better performance in the landscape. Under our study conditions, increasing the frequency of water applied during the first growing season improved the growth and nutrient uptake of all cultivars during the summer of the second growing season when the plants were transplanted to soil. In addition, more frequent irrigation in substrate improved N retention in the evergreen cultivars once they were transplanted to soil. This pre-conditioning effect may be partially explained by the effects of irrigation treatments on plant nutrient status during container production, as well as resource allocation after transplanting.

4.3. Irrigation Volume

Reduced irrigation improved the performance of the deciduous cultivar of *Rhododendron* after transplanting the following year but had the opposite effect on the growth and nutrient uptake of the evergreen cultivars. These results indicate that plant qualities important after transplanting may be negatively impacted by deficit irrigation of evergreen cultivars in the nursery, even though plants may grow similarly or better than those provided with more water.

Decreased irrigation volume in the year prior to transplanting may have improved the transplant performance of the deciduous cultivar AZ by increasing nutrient reserves during the previous growing season. In AZ, less irrigation increased substrate EC and enhanced nutrient uptake, even though it had no effect on the growth or allocation of biomass and nutrients in the cultivar. Leaf abscission began in late September of Year 1 in AZ, and some plants retained their leaves into late November, particularly when they were irrigated at 50% CC or were fertilized at the higher N rate. This suggests that reducing irrigation may have enhanced N uptake by AZ later in the season. This hypothesis is partially supported by the fact that decreased irrigation volume increased N content and N concentration in December without influencing plant biomass in the cultivar.

Others have reported that reducing irrigation in containers has little impact on the plant growth of certain species [48,49]. In situations where reduced irrigation increased growth, the benefit was attributed to greater nutrient availability as a result of less nutrient leaching [30,48,50]. While some studies have reported that deficit irrigation can improve drought tolerance in the plants after transplanting [40], our results showed that, for AZ, irrigation volume had little influence on g_s after transplanting. This suggests that decreasing irrigation volume during nursery production improves the performance of AZ the following year primarily by improving the nutrient status of the plants.

In evergreen cultivars, even though decreased irrigation volume improved the growth and nutrient status of plants prior to transplanting, these qualities did not translate into improved performance the following growing season. Decreased irrigation volume the previous year decreased growth and nutrient uptake of both evergreen cultivars in the spring and one of the two evergreen cultivars in the summer after transplanting. As with the N rate, flowering in the second growing season before transplanting may account for the poor growth of the W2 plants of evergreen cultivars compared to the W1 plants. Flowering may have depleted reserves in plants and thereby had a greater influence on transplant performance when plants were irrigated with less water during the previous growing season. Water stress was also more frequently observed in W2 plants of evergreen after transplanting. Decreased irrigation increased plant size but did not influence allocation in year 1 by evergreen cultivars, yet these larger plants received the same amount of water as smaller W1 plants after transplanting. Others showed that increased N concentrations of trees in the nursery decrease drought stress tolerance in the landscape [7]. While decreased irrigation volume increased plant N status prior to transplanting, this quality may have also predisposed it to greater drought stress in the landscape. Our results suggest that, at least for evergreen cultivars, when less water is used in container production of *Rhododendron*, plants may require higher rates of fertilizer and water after transplanting to minimize the impacts of flowering on reserves and plant size on water requirements.

5. Conclusions

A higher rate of N application in Year 1 improved the performance (total biomass, nutrient content, and flowering) of container-grown *Rhododendron* in the following year when the plants were transplanted into soil. In contrast, limiting N in Year 1 did not pre-condition the plants for better performance the following year. Less irrigation or more frequent water applications in Year 1 improved the growth of the evergreen cultivars and enhanced the uptake of several nutrients in each cultivar. More frequent water applications also improved the performance of each cultivar in the following year, indicating that altering the frequency of water application on a daily basis can improve plant qualities important to transplant success without increasing water use. Likewise, reduced irrigation volume in Year 1 improved the growth and nutrient uptake of the deciduous cultivar the following year, but it had the opposite effect on the growth and nutrient uptake of the evergreen cultivars. In evergreen cultivars, irrigation volume altered nursery plant qualities resulting in a trade-off between flower production and growth during the second year. Results from this study indicate that manipulating N rates and irrigation frequency and volume during nursery production can be used to alter plant qualities and subsequent landscape performance. Further research on optimal fertilizer rates and irrigation volumes and frequencies will help develop sustainable production practices to optimize nursery stock quality and improve plant survival and performance in the landscape while reducing fertilizer and water inputs.

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/horticulturae8070647/s1, Figure S1: Relative nutrient uptake in Year 1 by 'Gibraltar' (AZ) (A), 'Catawbiense Album' (CAT) (B), and 'P.J.M.' (PJM) (C) Rhododendron.; Figure S2: Change in biomass (dry weight; DW) and nutrient content of 'Gibraltar' (AZ) (A–C), 'Catawbiense Album' (CAT) (D–F), and 'P.J.M.' (PJM) (G–I) *Rhododendron* in the spring, summer, and autumn after transplanting them to soil in Year 2.

Author Contributions: Conceptualization, C.F.S. and G.B.; methodology, C.F.S. and G.B.; formal analysis, C.F.S.; writing—original draft preparation, C.F.S.; writing—review and editing, G.B. and D.R.B. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by USDA-Agricultural Research Service (ARS) projects 2072-21000-055-00D, 2072-21000-053-00D, and 2072-21000-048-00D, and supported by USDA-NIFA Hatch Project MIS-249180. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Acknowledgments: The authors thank Summer Hendricks, Rose Jepson, Jesse Mitchell, Suean Ott, Milt Plocher, Maryann Resendes, and Marj Storm of USDA for technical assistance.

Conflicts of Interest: The authors declare no conflict of interest.

References

- 1. Aghai, M.M.; Pinto, J.R.; Davis, A.S. Container volume and growing density influence western larch (*Larix occidentalis* Nutt.) seedling development during nursery culture and establishment. *New For.* **2014**, *45*, 199–213. [CrossRef]
- Landis, T.D.; Pinto, J.R.; Dumroese, R.K. Light-emitting diodes (LED): Applications in forest and native plant nurseries. *For. Nurs. Notes* 2013, 33, 5–13.
- 3. Oliet, J.A.; Tejada, M.; Salifu, K.F.; Collazos, A.; Jacobs, D.F. Performance and nutrient dynamics of holm oak (*Quercus ilex* L.) seedlings in relation to nursery nutrient loading and post-transplant fertility. *Eur. J. For. Res.* 2009, 128, 253–263. [CrossRef]
- 4. Riikonen, J.; Luoranen, J. Seedling production and the field performance of seedlings. Forests 2018, 9, 740. [CrossRef]
- 5. Currey, C.J.; Lopez, R.G. Cuttings of *Impatiens, Pelargonium*, and *Petunia* propagated under light-emitting diodes and high-pressure sodium lamps have comparable growth, morphology, gas exchange, and post-transplant performance. *HortScience* **2013**, *48*, 428–434. [CrossRef]
- 6. Franco, J.A.; Cros, V.; Bañon, S.; Gonzalex, A.; Abrisqueta, J.M. Effects of nursery irrigation on post-planting root dynamics of *Lotus creticus* in semiarid field conditions. *HortScience* **2002**, *37*, 525–528. [CrossRef]
- 7. Lloyd, J.; Herms, D.A.; Rose, M.A.; Van Wagoner, J. Fertilization rate and irrigation scheduling in the nursery influence growth, insect performance, and stress tolerance of 'Sutyzam' Crabapple in the landscape. *HortScience* **2006**, *51*, 442–445. [CrossRef]
- 8. Marler, T.E. Repetitive pruning of *Serianthes* nursery plants improves transplant quality and post-transplant survival. *Plant Signal. Behav.* **2019**, *14*, 8. [CrossRef]
- 9. McGrath, D.; Henry, J.; Munroe, R.; Williams, C. From propagation to field: Influence of tray design on tree seedling quality and performance. *J. Environ. Hortic.* 2021, 39, 33–40. [CrossRef]
- 10. Wright, A.N.; Warren, S.L.; Blazich, F.A.; Blum, U. Root and shoot growth periodicity of *Kalmia latifolia* 'Sarah' and *Ilex crenata* 'Compacta'. *HortScience* **2004**, *39*, 243–247. [CrossRef]
- 11. Goyette, B.; Piché, M.; Brownbridge, M.; McGrath, D. Impact of handling practices on the quality of bare-root plants: A review. J. *Environ. Hort.* **2014**, *32*, 103–113. [CrossRef]
- 12. Bilderback, T.E. Water management is key in reducing nutrient runoff from container nurseries. *Horttechnology* **2002**, *12*, 541–544. [CrossRef]
- Lea-Cox, J.D.; Bauerle, W.L.; van Iersel, M.W.; Kantor, G.F.; Bauerle, T.L.; Lichtenberg, E.; King, D.M.; Crawford, L. Advancing wireless sensor networks for irrigation management of ornamental crops: An overview. *Horttechnology* 2013, 23, 717–724. [CrossRef]
- 14. Majsztrik, J.C.; Fernandez, R.T.; Fisher, P.R.; Hitchcock, D.R.; Lea-Cox, J.; Owen, J.S.; Oki, L.R.; White, S.A. Water use and treatment in container-grown specialty crop production: A review. *Water Air Soil Pollut.* **2017**, 228, 1–27. [CrossRef]
- 15. Majsztrik, J.C.; Ristvey, A.G.; Ross, D.S.; Lea-Cox, J.D. Comparative water and nutrient application rates among ornamental operations in Maryland. *HortScience* **2018**, *53*, 1364–1371. [CrossRef]
- Scagel, C.F.; Bi, G.; Fuchigami, L.H.; Regan, R.P. Nutrient uptake and loss by container-grown deciduous and evergreen Rhododendron nursery plants. HortScience 2011, 46, 296–305. [CrossRef]
- 17. Cabrera, R.I. Nitrogen balance for two contain-grown woody ornamental plants. Scientia Hort. 2002, 97, 297–308. [CrossRef]
- 18. Raviv, M.; Wallach, R.; Silber, A.; Medina, S.; Krasnovsky, A. The effect of hydraulic characteristics of volcanic materials on yield of roses grown in soilless culture. *J. Amer. Soc. Hort. Sci.* **1999**, 124, 205–209. [CrossRef]
- 19. Mack, R.; Owen, J.S., Jr.; Niemiera, A.X.; Sample, D.J. Validation of nursery and greenhouse best management practices through scientific evidence. *HortTechnology* **2019**, *29*, 700–715. [CrossRef]
- 20. Scagel, C.F.; Bi, G.; Fuchigami, L.H.; Regan, R.P. Irrigation frequency alters nutrient uptake in container-grown *Rhododendron* plants grown with different rates of nitrogen. *HortScience* **2012**, *47*, 189–197. [CrossRef]
- Cameron, R.; Harrison-Murray, R.; Fordham, M.; Wildinson, S.; Davies, W.; Atkinson, C.; Else, M. Regulated irrigation of woody ornamentals to improve plant quality and precondition against drought stress. *Ann. Appl. Biol.* 2008, 153, 49–61. [CrossRef]
- 22. Sánchez-Blanco, M.J.; Ortuño, M.F.; Bañon, S.; Álvarez, S. Deficit irrigation as a strategy to control growth in ornamental plants and enhance their ability to adapt to drought conditions. *J. Hortic. Sci. Biotechnol.* **2019**, *94*, 137–150. [CrossRef]

- 23. Timmer, V.R.; Miller, B.D. Effects of contrasting fertilization and moisture regimes on biomass, nutrients, and water relations of container grown red pine seedlings. *New For.* **1991**, *5*, 335–348. [CrossRef]
- 24. Beeson, R.C., Jr. Relationship of plant growth and actual evapotranspiration to irrigation frequency based on management allowed deficits for container nursery stock. J. Amer. Soc. Hort. Sci. 2006, 131, 140–148. [CrossRef]
- Koniarski, M.; Matysiak, B. Growth and development of potted Rhododendron cultivars 'Catawbiense Boursault' and 'Old Port' in response to regulated deficit irrigation. J. Hort. Res. 2013, 21, 29–37. [CrossRef]
- Welsh, D.F.; Zajicek, J.M. A model for irrigation scheduling in contain-grown nursery crops utilizing management allowed deficits (MAD). J. Environ. Hort. 1993, 11, 115–118.
- 27. Cabrera, R.I.; Devereaux, D. Crape myrtle post-transplant growth as affected by nitrogen nutrition during nursery production. *J. Amer. Soc. Hort. Sci.* **1999**, 124, 94–98. [CrossRef]
- Scagel, C.F.; Bi, G.; Bryla, D.R.; Fuchigami, L.H.; Regan, R.P. Irrigation frequency during container production alters Rhododendron growth, nutrient uptake, and flowering after transplanting into a landscape. *HortScience* 2014, 49, 955–960. [CrossRef]
- 29. Yamg, Q.; Li, F.; Zhang, F.; Lui, X. Interactive effects of irrigation frequency and nitrogen addition on growth and water use of *Jatropha curcas*. *Biomass Bioenergy* **2013**, *59*, 234–242. [CrossRef]
- 30. Fare, D.C.; Gilliam, C.H.; Keever, G.J.; Olive, J.W. Cyclic irrigation reduces container leachate nitrate-nitrogen concentration. *HortScience* **1994**, *29*, 1514–1517. [CrossRef]
- Perdue, S.; Hamer, H. 2019 Census of Horticultural Specialties; United States Department of Agriculture: Washington, DC, USA, 2020; Volume 3, p. 3.
- Gavlak, R.G.; Horneck, D.A.; Miller, R.O. The Soil, Plant and Water Reference Methods for the Western Region, 3rd ed.; Western Regional Extension Publication 125; University of Alaska: Fairbanks, AK, USA, 2005; p. 204.
- Jones, J.B.; Case, V.W. Sample, handling, and analyzing plant tissue samples. In *Soil Testing and Plant Analysis*, 3rd ed.; Westerman, R.L., Ed.; Soil Science Society of America: Madison, WI, USA, 1990; pp. 389–427.
- 34. Scoggins, H.L.; VanIersal, M.W. In situ probes for measurement of electrical conductivity of soilless substrates: Effects of temperature and substrate moisture content. *HortScience* **2006**, *41*, 210–214. [CrossRef]
- Chapin, F.S.; Van Cleve, K. Approaches to Studying Nutrient Uptake, Use and Loss in Plants. In *Plant Physiological Ecology*; Springer: Dordrecht, The Netherlands, 2000; pp. 185–207.
- Chapin, F.S.; Bloom, A.J.; Field, C.B.; Waring, R.H. Plant responses to multiple environmental factors. *BioScience* 1987, 37, 49–57. [CrossRef]
- 37. Bi, G.; Scagel, C.F.; Fuchigami, L.H.; Regan, R.P. Differences in growth, and nitrogen uptake and storage between two containergrown cultivars of *Rhododendron. J. Environ. Hort.* 2007, 25, 13–20. [CrossRef]
- Poorter, H.; Nagel, O. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients, and water: A quantitative review. *Funct. Plant Biol.* 2000, 27, 595–607. [CrossRef]
- 39. Agren, G.I.; Ingestad, T. Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant Cell Environ.* **1987**, 10, 579–586.
- 40. Villar-Salvador, P.; Planelles, R.; Enríquez, E.; Peñuelas Rubira, J.L. Nursery cultivation regimes, plant functional attributes, and field performance relationships in the Mediterranean oak *Quercus ilex* L. *Forest Ecol. Manag.* **2004**, *196*, 257–266. [CrossRef]
- Cuesta, B.; Villar-Salvador, P.; Puértolas, J.; Jacobs, D.F.; Rey Benayas, J.M. Why do large, nitrogen rich seedlings better resist stressful transplanting conditions? A physiological analysis in two functionally contrasting Mediterranean forest species. *For. Ecol. Manag.* 2010, 260, 71–78. [CrossRef]
- Villar-Salvador, P.; Puértolas, J.; Cuesta, B.; Peñuelas, J.L.; Uscola, M.; Heredia-Guerrero, N.; Rey Benayas, J.M. Increase in size and nitrogen concentration enhances seedling survival in Mediterranean plantations. Insights from an ecophysiological conceptual model of plant survival. *New For.* 2012, 43, 755–770. [CrossRef]
- 43. Li, T.; Bi, G.; Harkess, R.L.; Denny, G.C.; Scagel, C.F. Nitrogen fertilization and irrigation frequency affect hydrangea growth and nutrient uptake in two container types. *HortScience* **2019**, *54*, 167–174. [CrossRef]
- 44. Scagel, C.F.; Bi, G.; Fuchigami, L.H.; Regan, R.P. Seasonal variation in growth, nitrogen uptake and allocation by container-grown evergreen and deciduous *Rhododendron* cultivars. *HortScience* 2007, *42*, 1440–1449. [CrossRef]
- 45. Klute, A. Water retention: Laboratory methods. In *Methods or Soil Analysis: Part 1. Physical and Mineralogical Methods*, 2nd ed.; Klute, A., Ed.; ASA and SSSA: Madison, WI, USA, 1986; pp. 635–662.
- 46. White, J.W.; Mastalerz, J.W. Soil moisture as related to container capacity. Proc. Amer. Horticult. Sci. 1966, 89, 758–765.
- 47. Wong, S.C.; Cowan, I.R.; Farquhar, G.D. Stomatal conductance correlates with photosynthetic capacity. *Nature* **1979**, *282*, 424–426. [CrossRef]
- 48. Pershey, N.A.; Cregg, B.M.; Anresen, J.A.; Fernandez, R.T. Irrigation based on dialy water use reduces nursery runoff volume and nutrient load without reducing growth of four conifers. *HortScience* **2015**, *50*, 1553–1561. [CrossRef]
- Warsaw, A.L.; Fernandez, R.T.; Cregg, B.M.; Andresen, J.A. Water conservation, growth, and water use efficiency of containergrown woody ornamentals irrigation based on daily water use. *HortScience* 2009, 44, 1308–1318. [CrossRef]
- 50. Karam, N.S.; Niemiera, A.X. Cyclic sprinkler irrigation and pre-irrigation substrate water content affect water and N leaching from containers. *J. Environ. Hort.* **1994**, *12*, 198–202. [CrossRef]