Nitrogen Availability Alters Mineral Nutrient Uptake and Demand in Container-grown Deciduous and Evergreen Rhododendron[1]

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Abstract

One-year-old evergreen rhododendron (*Rhododendron* 'H-1 P.J.M.') and deciduous azalea (*Rhododendron* 'Cannon's Double') were grown with (+N) or without (N-deficient) nitrogen (N) from May to September to determine the effects of N-availability on uptake, demand, and allocation of other mineral nutrients. A 7-fold increase in N uptake by rhododendron was associated with a 3 to 4-fold increase in the uptake rate of phosphorus (P), potassium (K), and sulfur (S) and ~2-fold increase in the uptake rate of magnesium (Mg) and calcium (Ca). A 6-fold increase in N uptake by azalea was associated with a 3 to 4-fold increase in uptake rate of K, Mg, and Ca uptake and ~3-fold increase in the uptake rate of P and S. This suggests when altering nutrient management strategies to optimize N uptake, proportional changes in other nutrients may not be required. N-deficiency was also associated with deficiencies in P, K, S and manganese (Mn) for rhododendron and P, K, S, Ca, and Mg for azalea. This suggests N-deficiency decreased the ability of the plant to take up these nutrients; therefore, when altering nutrient management strategies to decrease N fertilizer use, the influence of lower N rates on the ability of plants to take up other nutrients should be considered. Ratios of N to P, K, S, boron (B), and iron (Fe) (N-ratios) for both cultivars were similar when N was not limiting to growth, indicating fertilizers with similar availability ratios for these elements in relationship to N could be used for both cultivars. Cultivars differed in N-ratios for Ca, Mg, Mn, and zinc (Zn) indicating availability of these elements in fertilizer in relationship to N availability may need to be altered for optimal growth of each cultivar. For both cultivars leaf N:P ratio over-estimated P uptake and stem N:P ratio underestimated P uptake; however N:P ratios based on both stems and leaves may be useful for evaluating co-uptake of P in relationship to N. Leaf N:K ratio and N:Ca ratio, and stem N:S ratio for rhododendron varied little during the experiment indicating these ratios may be useful for evaluating co-uptake of K, Ca, and S in relationship to N for rhododendron.

Index words: nutrient uptake, rhododendron, azalea, nursery production, Ericaceae.

Species used in this study: evergreen rhododendron 'H-1 P.J.M.' (*Rhododendron* 'H-1 P.J.M.') and deciduous azalea 'Cannon's Double' (*Rhododendron* 'Cannon's Double').

Significance to the Nursery Industry

The influence of N-availability on uptake and demand for other mineral nutrients by 1-year-old rhododendron (*Rhododendron* 'H-1 P.J.M.') and azalea (*Rhododendron* 'Cannon's Double') was evaluated from May to September. The estimated rates of nutrient uptake in relationship to N-availability will be useful in development of fertilizer management strategies that strive to decrease fertilizer use by synchronizing the availability of nutrients with plant demand. The ratios of N to other mineral nutrients in plants were determined to have potential usefulness in evaluating co-uptake of nutrients in relationship to N. Further research on using N-ratios for predictive purposes in nursery nutrient management could improve understanding of the balance of nutrients required for optimum plant growth.

Introduction

Research on fertilizer uptake by container-grown nursery crops has primarily focused on nitrogen (N) because it is commonly cited as the most important mineral nutrient for plant growth, and losses from nursery production systems have consequences to environmental quality. In addition to N, plants require several other elements for normal vegetative growth and reproduction. Varying amounts of each element are required by different plant species and cultivars. Plant growth can be restricted when not enough or too much of one or more elements are present, and certain nutrients [e.g., phosphorus (P)] are potential sources of pollution when excess application results in run-off from nursery production areas (12).

In addition to amount of a nutrient that is available for plant uptake, the balance between different nutrients can play an important role in development of nutritional problems that limit crop productivity or quality (13). Changing the availability of one nutrient (e.g., N) to a plant can often affect the uptake or transport within the plant of other nutrients (6). Plants need carbon (C), water, and nutrients for growth. Although availability of these components varies dramatically in space and time, a large body of ecology literature discusses how plants usually maintain tissue concentrations of these components within restricted limits (7). Using an economic analogy to study plant resource use, plants act as balanced systems regarding acquisition and use of resources

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(7). Balanced, in this context, means a shortage or excess of a resource will influence the way in which plants acquire or use other resources, and the resulting adjustment optimizes plant performance (3). The term 'nutrient stoichiometry' is used for nutrient ratios of plants (19). Nutrient stoichiometry has potential important physiological and applied consequences 19, 23, 25). To reduce fertilizer waste and pollution and optimize growth, nutrient management of container-grown nursery crops should supply nutrients at rates that both match plant demand and maintain stable internal nutrient ratios.

An awareness of how different plant species respond to different ratios of nutrients in fertilizers is well documented. For example, ratios of N:P:K of 5–1–3 and 8–1–4 have been shown to promote optimum growth of container-grown plants (13). Even though information on the response of plants to different nutrient ratios in fertilizers can be found for many plant species, current understanding of the extent, causes for, and consequences of variation in nutrient composition in plants is limited (23). This is primarily because nutrient ratios in fertilizers do not readily translate into nutrient availability in the growing substrate, particularly when controlled release fertilizers are used. For common species produced in nurseries, little published information exists about how (a) nutrients co-vary, (b) variable nutrient ratios are within a species, (c) growth influences nutrient ratios, and (d) nutrient ratios change with time (19). This information is needed to not only assess the physiological consequences of plant nutrient composition but also to what extent nutrient management practices (and fertilizer formulations) can be altered to balance acquisition and allocation of resources. This is the theory for using demand driven fertilization to increase efficiency of fertilizer use (27).

Information on how the time of N uptake by container-grown nursery plants is related to uptake of other nutrients is limited. Most studies on fertilizer uptake have focused on N and P and have not addressed how plant demand for other nutrients can vary over time. Understanding the relationships between uptake of different nutrients will aid in development of fertilizer management strategies that synchronize nutrient availability with nutrient demand. Recently, we described the influence of N-availability s on growth, N uptake, and N storage by container-grown evergreen and deciduous cultivars of *Rhododendron* spp. L. (Ericaceae) (5). Here we report the influence of N-availability on uptake of other mineral nutrients by *Rhododendron*. Using evergreen and deciduous cultivars of *Rhododendron*, the objectives of this research were to determine whether N-availability in the growing medium alters (A) the rate of uptake of other nutrients; (B) allocation of other nutrients between different plant structures; and (C) plant demand for other nutrients as reflected in ratios of N to other nutrients (N-ratios). To achieve these objectives, nutrient uptake in one deciduous and one evergreen cultivar of *Rhododendron* grown with different amounts of N was assessed from May through September after transplanting liners into larger containers. Additionally, we also wanted to evaluate whether N-ratios describing the relationship between N-uptake and uptake of other nutrients could be useful in development of fertilizer management strategies for this important group of woody nursery crops.

Materials and Methods

Plant culture and treatments. One-year-old liners [262 cm³ (16 in³) containers] of evergreen rhododendron 'H-1 P.J.M.' (*Rhododendron* L. 'H-1 P.J.M.') and deciduous azalea 'Cannon's Double' (*Rhododendron* L.'Cannon's Double') were transplanted into black, #1 [3.8 liter (1 gal)] polyethylene containers (GL-400; Nursery Supplies, Inc., McMinnville, OR) containing a substrate of vermiculite:pumice:sandy loam soil (1:1:1 by vol) in late May 2004 and grown outdoors in a lathe house in Corvallis, OR (lat. 45° 59' 04" N, long. 123° 27' 22" W). The substrate for this study was chosen to minimize N availability to plants. Forty plants of each cultivar were randomly assigned to one of two groups and fertilized twice weekly for 12 weeks starting June 3, 2004. One group of plants of each cultivar (–N treatment) received 250 ml of N-free modified Hoagland's solution (11) at every fertilization; the other group of plants (+N treatment) received 250 ml modified Hoagland's solution with 10 mM (140 ppm) N from NH_4NO_3. All plants were hand-watered as needed throughout the growing season.

Measurements. Approximately every 2 weeks from June 3 to September 1, 2004, five plants of each cultivar by N treatment combination were randomly selected, the substrate was removed from the roots by washing, and plants were separated into roots, stems, and leaves. All samples were washed in doubled distilled (DD) water, placed into an –80C (–112F) freezer then freeze-dried. Dry weights were recorded and samples were ground to pass a 20 mesh screen for mineral nutrient analyses. Growth was assessed by determining biomass (dry weight) of different plant structures (e.g., roots, stems, and leaves). For both cultivars stems were further separated by growing season and for rhododendron 'H-1 P.J.M.' leaves were also separated by growing season (e.g., 2003 and 2004).

Mineral nutrient analyses. Samples taken for nutrient analyses were analyzed for concentrations and content of C and N using procedures described previously (5). Concentrations of phosphorus (P), potassium (K), sulfur (S), calcium (Ca), magnesium (Mg), boron (B), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) in samples were obtained using an inductively coupled plasma optical emission spectrometer (ICP-OES) after digestion of dried samples in nitric acid. Reference standard apple leaves (#1515, National Institute of Standards and Technology) were run with samples for all procedures to ensure accuracy of results within a coefficient of variation of ±3%. The nutrient content of each plant structure was calculated by multiplying the concentration from samples of each structure by the dry weight of the structure. Total content [e.g., milligrams (mg) or micrograms (µg)] of each nutrient was calculated as the sum over all structures. Nutrient allocation to specific plant structures was calculated as a percentage of the total content in the plant. N-ratios (ratios between N and other elements in plants and leaves) were calculated as the ratio of N content to the content of each other element.

Experimental design and statistical analyses. The experiment was a completely randomized design with each treatment unit (container) replicated five times for each N treatment (–N, +N), harvest date (7), and cultivar (rhododendron or azalea). All statistical analyses were performed using Statistica® (Statsoft, Inc., Tulsa, OK). All data were tested for homogeneity of variance using Levene's test and for normality using the Kolmogorov-Smirnov test and trans-

formed if necessary. Where transformation was necessary, back-transformed means and standard errors are presented in tables or figures.

The influence of N-availability on biomass, concentration and content of other nutrients was assessed using MANOVA in a full factorial design with cultivar, N treatment, and time as main effects. Means were separated using Tukey's Studentized range test at $P < 0.05$ ($HSD_{0.05}$). Best subset regression, with Mallow's CP as the criterion for choosing the best subset of predictor effects, was used to assess effects of N-availability on rate of nutrient uptake between May and September. The influence of N-availability on rates of C accumulation and nutrient uptake was assessed by comparing slopes from regression models of content data versus time from a factorial combination of cultivar, N-treatment, and date.

The influence of N-availability on nutrient demand (ratios between N and other elements in plants and leaves) was assessed using MANOVA in a full factorial design with cultivar, N-treatment, and time as main effects. Means between treatments and cultivars were separated using $HSD_{0.05}$. Contrasts within cultivars were used to determine whether the response of N-ratios in leaves to N-availability was different than the response of N-ratios based on total plant nutrient content. The influence of N-availability on nutrient allocation (percentage of total plant nutrient content in different plant structures) in September was assessed using MANOVA in a full factorial deign with cultivar and N-treatment as main effects. Means were separated using $HSD_{0.05}$. Contrasts were used to determine whether nutrient allocation response between different plant structures varied between cultivars.

Results and Discussion

Rate of nutrient uptake or accumulation. Between June and September the relationships between time and total plant content of all elements except copper were best described using simple linear regression models ($P < 0.001$). These linear relationships allowed for uptake or accumulation rates for each element to be estimated from the slope of a linear regression model. Increased N-availability increased the uptake rate of most elements by container-grown *Rho-*

dodendron (Table 1). This is not surprising since, +N plants accumulated C (Table 1) and grew at a greater rate (5) than N-deficient plants; thus, driving demand for increased uptake of other nutrients. The rate of C accumulation is a reflection of photosynthetic rate, and N has been shown to influence the photosynthetic capacity and nutrient use efficiency of *Rhododendron* (16).

There is little available information on the relationship between N availability and uptake rate of other nutrients in container production of *Rhododendron*. Ristvey et al. (26) reported N influences total growth of *Rhododendron* (azalea) and P uptake is a function of P fertilization rate and plant growth — as influenced by N rate. When plants in Ristvey et al. (26) were given a liquid fertilizer with a similar N:P ratio as used for the +N plants in our experiment, they determined N and P uptake from March to May were ~2.8 mg·d^{-1} (9.9E-5 oz·d^{-1}) and P was ~0.28 mg·d^{-1} (9.9E-6 oz·d^{-1}) respectively. In our experiment average N-uptake of +N rhododendron from May to September was 1.4 mg·d^{-1} (4.9E-5 oz·d^{-1}) and +N azalea was 2.7 mg·d^{-1} (9.5E-5 oz·d^{-1}) (5). The rate of N uptake by azalea reported by Ristvey et al. (26) is similar to the average rate of N uptake of the +N azalea in our experiment (5). The rate of P uptake is higher reported by Ristvey et al. (26) is higher than the rate we calculated for azalea possibly due to differences in cultivar and growing conditions, and also time of year.

Pulses of nutrient availability characterize many seasonal environments and can result in a strong asynchrony between nutrient uptake and demand by plants (7). Other researchers have reported seasonal changes in N uptake rates and remobilization of N by *Rhododendron* (15, 18, 24). In most of these reports rates of nutrient uptake and remobilization were probably a response to the seasonality of nutrient availability occurring in natural ecosystems in response to a multitude of abiotic and biotic factors. The linear relationships between time and nutrient uptake from June through September in our study may have been a result of the liquid fertilizer applications decreasing seasonal variation in nutrient availability; thus, resulting in a relatively constant rate of nutrient uptake. The relatively constant rate of nutrient uptake from June through September may also have partially been a result of a steady demand. Seasonal fluctuations in

Table 1. Rate of C, P, K, S, Mg, Ca, B, Fe, Mn, and Zn accumulation or uptake by *Rhododendron* 'H-1 P.J.M.' (rhododendron) and *Rhododendron* 'Cannon's Double' (azalea) grown in containers with (+N) or without (−N) N from May through September 2004.

	Uptake or accumulation rate[z]			
	Rhododendron		Azalea	
Element	−N	+N	−N	+N
C (mg·d⁻¹)	17.5 (14.6–20.4)[y]	44.6 (40.2–49.0)	32.0 (27.5–26.5)	73.7 (67.5–79.8)
P (mg·d⁻¹)	0.023 (0.018–0.028)	0.098 (0.084–0.112)	0.062 (0.052–0.071)	0.192 (0.173–0.211)
K (mg·d⁻¹)	0.230 (0.181–0.279)	1.010 (0.906–1.114)	0.394 (0.291–0.497)	1.933 (1.770–2.096)
S (mg·d⁻¹)	0.040 (0.033–0.047)	0.136 (0.125–0.147)	0.095 (0.084–0.105)	0.236 (0.216–0.256)
Mg (mg·d⁻¹)	0.084 (0.072–0.096)	0.204 (0.188–0.220)	0.112 (0.090–0.134)	0.467 (0.421–0.513)
Ca (mg·d⁻¹)	0.175 (0.148–0.201)	0.404 (0.359–0.448)	0.224 (0.190–0.258)	1.081 (0.987–1.174)
B (µg·d⁻¹)	2.5 (1.8–3.1)	3.6 (2.8–4.3)	2.1 (1.2–3.0)	4.7 (3.8–5.6)
Fe (µg·d⁻¹)	3.6 (2.5–4.7)	9.7 (6.4–12.9)	6.0 (3.4–8.6)	16.0 (11.7–20.3)
Mn (µg·d⁻¹)	13.1 (10.6–15.5)	34.6 (30.3–38.9)	22.8 (20.1–25.4)	40.4 (38.2–42.5)
Zn (µg·d⁻¹)	0.65 (0.33–0.85)	1.80 (1.65–1.95)	2.52 (1.82–3.22)	4.91 (3.99–5.82)

[z]Rates calculated based on slopes from linear regression (n = 35). 1 mg = 3.5E − 5 oz. 1 µg = 3.5E − 8 oz.

[y]Mean rate followed by 95% confidence interval estimate in parentheses.

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photosynthesis, particularly related to differences in light, temperature, nutrient availability, and moisture, are well documented. Not surprisingly, the rate of C accumulation in our study was lower in N-deficient plants than +N plants reflecting the influence of N-deficiency on photosynthesis (16). We did not, however, detect any variation in the rate of C accumulation between June and September. The linear relationship between time and C accumulation between June and September may have been result of our water and liquid fertilizer applications decreasing seasonal variation in nutrient and water availability; thus, resulting in a relatively constant rate of C accumulation and demand for nutrients.

Differences in environmental conditions between plants growing in containers and plants in their native habitats or landscape situations have the potential to result in large differences in nutrient availability and resulting nutrient uptake rates. Most information on seasonal variation in nutrient uptake by *Rhododendron* is from research in natural ecosystems and may reflect not only a different magnitude of uptake, but also a different pattern of seasonal variation than found in a production system of a container nursery.

Relationships between N uptake and uptake of other mineral nutrients. Compared to N-deficient plants, increases in N uptake rate in +N plants were not associated with proportional increases in uptake of other nutrients by container-grown *Rhododendron*. With rhododendron, increasing the average rate of N uptake from 0.2 mg·d^{-1} (7.0E-6 oz·d^{-1}) (N-deficient plants) to 1.4 mg·d^{-1} (4.9E-5 oz·d^{-1}) (+N plants) (5) (7-fold increase) were associated with a 3- to 4-fold increase in the rate of P, K and S uptake, a ~2.5-fold increase in the rate of Ca, Mg, Fe, Mn, and Zn uptake and less than 2-fold increase in the rate of B uptake (Table 1). For azalea, increasing the rate of N uptake from an average of 0.5 mg·d^{-1} (1.8E-5 oz·d^{-1}) (N-deficient plants) to 2.7 mg·d^{-1} (9.5E-5 oz·d^{-1}) (+N plants) (5) (5.5-fold increase) was associated with a 4- to 5-fold increase in K, Mg, and Ca uptake, a 2- to 3-fold increase in the rate of P and S uptake, and a ~2-fold increase in the rate of B, Mn and Zn uptake (Table 1). N-availability had no influence on Cu content of either cultivar (P > 0.05), and there was no detectable change in Cu content of plants between June and September (P > 0.05). On average, Cu content of azalea [0.141±0.006 μg/plant (5.0E-9 ± 2.1E-10 oz/plant)] was almost two times greater than rhododendron [0.083 ± 0.004 μg/plant(2.9E-9 ± 1.4E-10 oz/plant).

Combined growth, nutrient concentrations, and content differences between N-deficient and +N plants were used to determine whether N deficiency altered the ability of plants to accumulate other nutrients. Nutrient deficiency is commonly assessed by decreased concentration and content of a specific nutrient with a concomitant decrease in growth (or biomass) (14). Plants of both cultivars that received no additional N from fertilizer had lower biomass and concentrations and content of N than +N plants from late-July to September indicating the –N plants were N-deficient during this time and availability of other nutrients was not limiting to the growth of +N plants (5). For N-deficient plants, other nutrients were considered as potentially limiting to growth when N-deficient plants had lower concentrations and contents of a specific element combined with lower biomass when compared to +N plants. Nitrogen deficiency in rhododendron also resulted in C limitation and potential deficiency in K and S from late-July to September (Table 2, content data not presented). By September, N-deficient rhododendron had lower biomass and P and Mn concentrations and content, suggesting N-deficiency also decreased the capacity of rhododendron to take up P and Mn. N-deficiency in azalea also resulted in potential deficiency in P, K, S, and Ca from mid-July to September (Table 2, content data not presented). By mid-August, N-deficient azalea had lower biomass and Mg concentration and content, suggesting that N-deficiency was also decreasing capacity of azalea to take up Mg. Low soil N conditions has been shown to reduce Mg and Mn uptake in red raspberry (*Rubus idaeus* L.) (6).

The influence of N-deficiency on P and S uptake by rhododendron was primarily a result of decreased biomass and P and S concentrations and content in 2004 stems (data not presented) and the influence of N-deficiency on C and K accumulation was primarily a result of decreased biomass and C and K concentrations and content in 2004 stems and 2004 leaves (Table 3, stem data not presented). Manganese deficiency in rhododendron was primarily a result of decreased biomass and Mn concentration and content in 2004 leaves. The influence of N-deficiency on P, K, S, Mg, and Ca was primarily a result of decreased biomass and nutrient concentrations and contents in 2003 (old) and 2004 (current year) stems and 2004 (current year) leaves (Table 3, stem data not presented).

Foliar concentrations of nutrients changed from May to September with overlapping values between the two cultivars and N treatments (Table 3). The potential nutrient deficiencies in N-deficient rhododendron indicated by whole plant biomass and nutrient concentrations and content were represented by foliar P, K, S and Mn concentrations of <1.16 mg·g^{-1} (0.018 oz·lb^{-1}), 14.9 mg·g^{-1} (0.238 oz·lb^{-1}), 1.50 mg·g^{-1} (0.024 oz·lb^{-1}), and 397 mg·kg^{-1} (0.006 oz·lb^{-1}), respectively. The potential nutrient deficiencies in N-deficient azalea indicated by whole plant biomass and nutrient concentrations and content were represented by foliar P, K, S, Mg, and Ca concentrations of <1.93 mg·g^{-1} (0.031 oz·lb^{-1}), 20.2 mg·g^{-1} (0.323 oz·lb^{-1}), 1.71 mg·g^{-1} (0.027 oz·lb^{-1}), 3.25 mg·g^{-1} (0.052 oz·lb^{-1}), and 6.68·g^{-1} (0.107 oz·lb^{-1}), respectively. These deficiency values are obviously not only a function of co-limiting nutrients (such as N) but also time of year. For example, leaves of +N rhododendron had P concentrations in August similar to the P concentrations in leaves of N-deficient plants in September and leaves on +N azalea had lower P concentrations in September than N-deficient plants. Mineral nutrient composition of plants change as a plant matures and with the portion of the plant sampled; therefore optimal or sufficient nutrient levels are usually defined for a specific plant structure at a specified stage of maturity. Foliar nutrient analysis is the most common diagnostic method for identifying nutrient deficiencies and imbalances, particularly for long-lived perennials (32). These results highlight the importance of not solely using a single foliar nutrient concentration as an indicator of plant nutrient status without also looking at how nutrients co-vary over time.

Concentrations of nutrients in leaves on evergreen *Rhododendron* change with age (21). The concentrations of N, P, K, Ca, and Mg in leaves of the evergreen cultivar used in our study (*Rhododendron* 'H-1 P.J.M.') were similar to the range reported for *R. maxima* growing under natural conditions. Young leaves (1 month old) of *R. maximum* L. had N, P, K, Ca, and Mg concentrations of 16 mg·g^{-1} (0.256 oz·lb^{-1}), 1.7 mg·g^{-1} (0.027 oz·lb^{-1}), 13.4 mg·g^{-1} (0.214 oz·lb^{-1}), 3.6 mg·g^{-1}

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Table 2. Concentrations C, P, K, S, Mg, Ca, B, Fe, Mn, and Zn in whole plants of *Rhododendron* 'H-1 P.J.M.' (R, rhododendron) and *Rhododendron* 'Cannon's Double' (A, azalea) grown in containers with (+N) or without (0N) N from May through September 2004.

Element	Cultivar	N	June	→	July	→	Aug.	→	Sept.	HSD$_{95\%}$[y]
C (mg·g⁻¹)	R	0N	471	468	469	476	473	472	471	
		+N		470	472	482	480	480	482	(2.64)
	A	0N	458	463	462	463	461	463	463	
		+N		460	463	459	462	459	468	
P (mg·g⁻¹)	R	0N	1.47	1.27	1.02	0.92	0.96	0.89	0.93	
		+N		1.19	1.09	1.08	0.93	1.00	1.21	(0.068)
	A	0N	1.49	1.14	1.06	1.03	1.13	1.04	1.03	
		+N		1.31	1.34	1.25	1.44	1.19	1.26	
K (mg·g⁻¹)	R	0N	9.49	9.88	8.91	8.01	8.53	7.91	7.40	
		+N		9.21	9.28	10.10	10.34	11.23	10.32	(0.537)
	A	0N	11.24	10.00	9.71	8.65	9.37	8.39	7.32	
		+N		10.88	10.36	11.19	11.24	11.66	12.15	
S (mg·g⁻¹)	R	0N	1.53	1.44	1.32	1.20	1.33	1.21	1.24	
		+N		1.69	1.63	1.62	1.48	1.48	1.54	(0.071)
	A	0N	1.21	0.94	0.95	0.97	1.09	1.10	1.29	
		+N		1.33	1.39	1.28	1.54	1.44	1.43	
Mg (mg·g⁻¹)	R	0N	2.04	2.29	2.35	2.07	2.25	2.14	2.30	
		+N		2.38	2.71	2.20	2.34	2.26	2.22	(0.120)
	A	0N	2.27	1.90	2.04	1.89	1.97	1.89	1.77	
		+N		2.03	2.02	2.05	2.12	2.65	2.89	
Ca (mg·g⁻¹)	R	0N	5.98	5.72	4.84	4.79	5.14	4.84	5.27	
		+N		5.60	5.36	4.89	5.22	4.87	4.55	(0.233)
	A	0N	3.68	3.17	3.29	2.92	3.51	3.49	3.18	
		+N		3.61	3.78	4.47	4.61	5.75	6.40	
B (mg·kg⁻¹)	R	0N	112	119	98	91	95	102	80	
		+N		128	89	90	68	62	54	(7.4)
	A	0N	84	68	54	57	56	53	45	
		+N		79	73	49	52	46	41	
Fe (mg·kg⁻¹)	R	0N	213	537	460	190	275	218	226	
		+N		405	495	191	209	152	175	(32.0)
	A	0N	346	378	308	183	185	183	227	
		+N		389	290	136	187	194	155	
Mn (mg·kg⁻¹)	R	0N	455	361	307	320	406	362	357	
		+N		371	335	363	300	329	420	(20.7)
	A	0N	200	140	157	158	203	248	266	
		+N		165	160	172	181	260	232	
Zn (mg·kg⁻¹)	R	0N	43	34	26	27	27	24	26	
		+N		38	37	34	30	24	24	(3.5)
	A	0N	68	52	51	49	55	47	43	
		+N		69	71	55	54	49	36	

[z]Grey highlighted concentrations of 0N plants denote time when plant biomass, and element concentration and content were all lower than +N plants and therefore potentially deficient in the specific nutrient. 1 mg·g⁻¹ = 0.015 oz·lb⁻¹. 1 mg·g⁻¹ = E1.6E − 5 oz·lb⁻¹.

[y]Least significant difference (*P* < 0.05, n = 5)

(0.058 oz·lb⁻¹) and 1.7 mg·g⁻¹ (0.027 oz·lb⁻¹), respectively, while older (6 month old) leaves contained lower concentrations of N [10 mg·g⁻¹ (0.016 oz·lb⁻¹), P [1.3 mg·g⁻¹ (0.021 oz·lb⁻¹)], and K [8.7 mg·g⁻¹ (0.139 oz·lb⁻¹)] and higher concentrations of Ca [10 mg·g⁻¹ (0.016 oz·lb⁻¹)] and Mg [2.9 mg·g⁻¹ (0.046 oz·lb⁻¹)] (21). Other researchers have also reported seasonal increases in Mg and Ca in 1-year-old sun leaves of *Rhododendron* between June and August of 1.3 to 2.25 mg·g⁻¹ (0.021 to 0.036 oz·lb⁻¹) and 7.0 to 10.2 mg·g⁻¹ (0.112 to0.163 oz·lb⁻¹), respectively (10). Reported normal ranges for foliar nutrients in evergreen rhododendron vary; N [14 to 17 mg·g⁻¹ (0.224 to 0.272 oz·lb⁻¹)], P [2 to 3 mg·g⁻¹ (0.032 to 0.048 oz·lb⁻¹)], K [10 to 12 mg·g⁻¹ (0.16 to 0.19 oz·lb⁻¹)], Ca [9 to 12 mg·g⁻¹ (0.144 to 0.0192 oz·lb⁻¹)], Mg [2 to 3 mg·g⁻¹ (0.032 to 0.048 oz·lb⁻¹)], Mn [50 to 500 mg·kg⁻¹ (0.0008 to 0.008 oz·lb⁻¹)], Fe [40 to 80 mg·kg⁻¹ (0.0006 to 0.0013 oz·lb⁻¹)], B [30 to 40 mg·kg⁻¹ (0.0005 to 0.0006 oz·lb⁻¹)], and Zn [15 to 60 mg·kg⁻¹ (0.0002 to 0.0001 oz·lb⁻¹)]. The influence of the deficiency of one nutrient on uptake of others by plants has been well-studied in soil systems; however there is little information on how deficiency in container nursery crops influences uptake of other nutrients. The large ranges of 'normal' concentrations reported for many crops can be a result of cultivar differences, potential deficiencies in one

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Table 3. Concentrations of C, P, K, S, Mg, Ca, B, Fe, Mn, and Zn in 2004 leaves of *Rhododendron* 'H-1 P.J.M.' (R, rhododendron) and *Rhododendron* 'Cannon's Double' (A, azalea) grown in containers with (+N) or without (0N) N from May through September 2004.

Element	Cultivar	N	June	→	July	→	Aug.	→	Sept.	HSD$_{95\%}$[y]
C (mg·g⁻¹)	R	0N	485	483	481	486	487	479	476	
		+N		482	483	482	486	488	500	
	A	0N	456	466	462	465	461	464	463	(4.35)
		+N		460	461	455	463	450	476	
P (mg·g⁻¹)	R	0N	2.17	1.57	1.18	1.00	1.07	0.95	1.16	
		+N		1.75	1.32	1.46	1.14	1.09	1.34	
	A	0N	1.75	1.23	1.21	1.22	1.47	1.89	1.93	(0.136)
		+N		1.38	1.33	1.19	1.45	1.22	1.27	
K (mg·g⁻¹)	R	0N	14.5	14.0	12.7	12.9	14.1	13.9	14.9	
		+N		15.3	13.9	16.7	16.9	16.4	15.9	
	A	0N	14.6	12.2	12.7	12.8	17.8	18.3	20.2	(0.84)
		+N		13.2	13.7	15.3	17.5	19.8	24.4	
S (mg·g⁻¹)	R	0N	1.89	1.56	1.38	1.27	1.49	1.31	1.50	
		+N		2.01	1.89	2.05	1.63	1.63	1.71	
	A	0N	1.49	0.95	0.93	0.82	1.00	1.13	1.71	(0.120)
		+N		1.39	1.39	1.24	1.51	1.51	1.60	
Mg (mg·g⁻¹)	R	0N	2.30	2.56	2.27	2.68	3.00	2.89	3.71	
		+N		3.01	2.48	2.82	2.80	2.47	2.62	
	A	0N	3.27	2.55	2.83	2.58	2.85	3.12	3.25	(0.210)
		+N		2.60	2.35	2.23	2.18	3.10	4.30	
Ca (mg·g⁻¹)	R	0N	6.44	6.35	5.43	6.48	6.86	6.77	8.61	
		+N		7.54	6.48	6.90	6.70	5.64	5.61	
	A	0N	4.20	3.78	4.43	4.20	5.49	6.05	6.68	(0.459)
		+N		4.06	4.30	5.13	5.34	8.10	11.02	
B (mg·kg⁻¹)	R	0N	83	130	117	119	125	158	116	
		+N		177	84	74	68	58	53	
	A	0N	95	78	57	66	84	86	97	(15.7)
		+N		61	52	47	60	47	58	
Fe (mg·kg⁻¹)	R	0N	174	385	237	147	191	196	154	
		+N		221	180	147	184	134	128	
	A	0N	133	298	280	142	105	124	298	(87.3)
		+N		197	137	89	110	106	128	
Mn (mg·kg⁻¹)	R	0N	321	295	258	241	355	330	397	
		+N		344	285	373	317	321	477	
	A	0N	157	123	132	145	184	244	307	(31.9)
		+N		149	126	155	172	296	332	
Zn (mg·kg⁻¹)	R	0N	33.9	24.1	18.2	16.5	15.4	15.3	17.5	
		+N		33.7	27.2	28.5	25.3	31.2	18.9	
	A	0N	42.9	31.8	25.1	22.4	18.2	20.5	20.2	(2.63)
		+N		31.2	26.7	24.6	27.9	25.2	24.8	

[z]Grey highlighted concentrations of 0N plants denote time when leaf biomass, and element concentration and content were all lower than +N plants and therefore potentially deficient in the specific nutrient. 1 mg·g⁻¹ = 0.015 oz·lb⁻¹. 1 mg·g⁻¹ = E1.6E–5 oz·lb⁻¹.

[y]Least significant difference ($P < 0.05$, n = 5)

nutrient altering concentration of other nutrients, and time of foliar sampling.

Results herein indicate an increasing rate of N uptake by *Rhododendron* does not cause proportional increases in demand or uptake for other nutrients; therefore, when altering nutrient management strategies to optimize N uptake, proportional changes in other nutrients may not be required. In fact, proportional changes in other nutrients in the fertilizer may lead to excess application of other nutrients, increased nutrient leaching, and increased potential for nutrient toxicity. Results also indicate N-deficiency can increase the potential for deficiency of other nutrients, such as P, K, S, and Mn

for rhododendron and P, K, S, Mg, and Ca for azalea. Thus when altering nutrient management strategies to decrease N fertilizer use, the influence of lower N rates on the ability of plants to take up other nutrients should be considered.

Nutrient allocation. By September 2004, N-availability altered allocation of mineral nutrients to different structures of container-grown *Rhododendron* and the response of nutrient allocation to N-availability varied between cultivars and was not strictly related to the influence of N-availability on biomass (Table 4). Biomass of roots and 2003 (old) leaves of rhododendron were not influenced by N-availability and

Table 4. Biomass and allocation of biomass and elements in structures of *Rhododendron* 'H-1 P.J.M.' (R) and *Rhododendron* 'Cannon's Double' (A) grown in containers with (+N) or without (0N) N from May through September 2004.

		Proportion of total plant content (%)[z]								
		Roots		Leaves			Stems			
				2003	2004		2003		2004	
Element	N Rate	R	A	R	R	A	R	A	R	A
C	0N	28	32	5	32	26§	15	20§	19	22
	+N	14*	19*§	2*	50*	40*§	6*	17§	27*	23§
P	0N	33	30	3	40	48§	8	10	15	11
	+N	20*	23*	1*	52*	40*§	3	13§	23*	23*
K	0N	11	13	8	64	70§	5	7	10	10
	+N	7*	8*	2*	74*	80*§	2	4	15*	8§
S	0N	40	38	4	38	34	8	13	9	16§
	+N	26*	26*	2*	53*	44*§	3	12§	16*	18
Mg	0N	21	31§	6	52	47	5	8	16	15
	+N	14*	15*	2*	56	59*	3	8	24*	18§
Ca	0N	13	15	10	52	53	5	15§	20	17
	+N	8	5*	4*	59*	69*§	3	9*§	25*	17§
B	0N	24	21	11	26	54§	8	8	11	17
	+N	21	14*§	7*	47	57§	5	8	19*	21
Cu	0N	56	46§	3	22	12§	11	27§	9	14
	+N	36*	34*	2	38*	14§	4	32§	20*	20
Fe	0N	61	50§	7	22	34§	5	12	4	4
	+N	47*	44	5	34*	33	4	12	9	10
Mn	0N	14	21§	13	35	29§	9	18§	28	31
	+N	11	9*	3*	54*	57*	4	11*§	27	22*
Zn	0N	47	57§	6	22	12§	13	14	13	16
	+N	32*	35*	4	38*	28*§	7	16§	19	22
Biomass (g)	−N	1.41	3.04§	0.27	1.58	2.44§	0.75	1.96§	0.91	2.14§
	+N	1.34	3.21§	0.22	4.50*	6.47*§	0.62	2.86*§	2.73*	3.82*§

[z]Means from September 2004 (n = 5). Asterisks (*) by +N means within a cultivar denote significant differences in allocation between +N and −N treatments within an element (THSD$_{0.05}$). Symbol (§) by azalea means within N treatment denote significant differences in allocation between cultivars treatments within an element (THSD$_{0.05}$). 1 g = 0.035 oz.

roots on +N rhododendron contained lower proportions of total plant P, K, S, Mg, Cu, Fe, and Zn compared to roots on N-deficient plants and 2003 leaves contained lower proportions of total plant P, K, S, Ca, Cu, Fe, Mn, and Zn. Decreased allocation of these nutrients to rhododendron roots and 2003 leaves was associated with increased allocation of biomass and nutrients to 2004 leaves and 2004 stems. N-availability had no influence on biomass or nutrient allocation to 2003 stems of rhododendron. Biomass of roots of azalea were not influenced by N-availability and roots on +N azalea contained lower proportions of P, K, S, Mg, Ca, B, Cu, Mn, and Zn compared to roots on N-deficient plants. Decreased allocation of these nutrients to azalea roots was associated primarily with increased allocation of biomass and nutrients to 2004 leaves. N-availability had little influence on nutrient allocation to azalea stems, even though +N azalea had greater stem biomass.

Accumulation and remobilization of nutrients in structures of perennial plants are highly dynamic processes. Nutrients are constantly imported into and exported from branches, leaves, and roots as a function of multiple factors. The source-sink strength of different structures varies with plant age, structure or organ age, nutrient availability, and growth requirements. Maintaining a balance between mineral nutrient resources requires adjustment of nutrient concentrations over time by alteration of factors such as the root:shoot ratio, uptake efficiency of scarce or overabundant nutrients, and nutrient allocation patterns (7). In our study N-availability had no influence on root biomass by September and N-deficient plants allocated a greater proportion of total biomass to roots (Table 4). This increase in biomass allocation to roots in response to N-limitation also resulted in concomitant increases in allocation of most nutrients to roots. For *Rhododendron* and other plant genera, N-deficiency has been reported to increase root:shoot ratios (1, 5, 28) and is believed to be a mechanism to optimize available resources by allocating more resources to the acquisition of nutrients when they limit growth (2). Our results indicate N-deficiency does not alter nutrient content in roots but increases allocation of most nutrients to roots, even though N was supposedly the only nutrient limiting growth. This suggests that under N-deficiency, roots have a proportionately greater demand for other nutrients than when N-availability is not limiting to growth.

The combination of increased biomass and nutrient allocation to different plant structures can be used to assess the influence of N-availability on nutrient demand or storage by different structures. For example, the influence of N-availability on allocation of biomass and P, K, S, Ca, and Cu to 2004 leaves and stems on rhododendron suggests new stems and leaves on +N plants had a higher demand or storage of these nutrients compared to the same structures on N-deficient plants. Similarly, 2004 leaves on +N azalea had a higher demand or storage of P, K, S, Mg, and Ca compared to new leaves on N-deficient azalea.

Evergreen and deciduous plants use various methods for storing mineral nutrients depending on leaf phenology and developmental stage (15). In our study, the influence of N-

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deficiency on nutrient allocation in September to stems and leaves varied with element, plant structure, and cultivar. In general the allocation of nutrients to stems of rhododendron was more sensitive to N-deficiency than allocation of nutrients to stems of azalea. Nutrient allocation to stems of azalea may be less sensitive to N-deficiency due to their role in nutrient storage. Storage of N in leaves is a common strategy in evergreen *Rhododendron* (18, 24, 28) whereas deciduous species store a greater proportion of N in roots and stems (28). In September, stems of +N rhododendron contained ~13% of total plant N and leaves contained ~70% (5). In contrast, stems of +N azalea contained ~34% of total plant N and leaves ~36% (5). Between August and September the proportion of total plant N in azalea leaves decreased and the proportion of total plant N in stems increased (5). Decreased allocation of N to leaves in September with concomitant increases in allocation of N to stems and roots during this time suggests N was being actively conserved or stored.

Changes in allocation of P, K, S, Mg, and Ca between different structures observed during this study were similar to those observed for N (5). In perennial plants N is often conserved between growing seasons and in deciduous plants this involves removal of N from leaves prior to abscission. No change in allocation to leaves at the end of the growing season in deciduous plants suggests that the nutrient was either poorly mobile or in excess of plant requirements and not generally stored (7). For example, between August and September the proportion of total plant P and K in azalea leaves decreased and the proportion of total plant P, K, and S in stems of +N plants or roots of N-deficient plants increased (data not presented). Plants store P in structures for use during the following growing season (7) and in this particular deciduous cultivar of *Rhododendron* storage locations (structures) and timing of storage for N, P, K, and S appear to be similar.

Increased allocation to leaves at the end of the growing season in evergreen plants suggests the nutrient is either poorly mobile, leaves serve as a storage location for the nutrient, or there is a high demand for the nutrient in leaves during the winter (7, 20). For example, between August and September the proportion of total plant P, K, and S in rhododendron increased and the proportion of total plant P, K, and S in roots decreased and the allocation of P to stems was relatively stable (data not presented). A similar increased allocation of Ca and Mg to rhododendron leaves also occurred during this time (data not presented). In evergreen perennial plants, cations such as K, Ca, and Mg play an important role in cold tolerance of plant structures or organs (31). It is possible K, Ca, and Mg accumulation in leaves is a preliminary step in increasing cold tolerance of leaves before winter.

N-ratios. One of the first steps in determining fertilizer application rates for any crop is to know the rate at which the crop will take up nutrients. The most efficient uptake of fertilizer will occur when nutrient availability from fertilizer best matches the rate of uptake. Unfortunately, the rate of uptake of one nutrient (N for example) can differentially alter the rate of uptake of other nutrients. This differential influence of N availability on uptake of other nutrients is reflected in the ratios of N to these other nutrients (N-ratios) (Figs. 1 and 2). Results from nutrient analysis can be used to indicate absolute nutrient levels in the plant (e.g., in relationship to optimal or sufficiency levels) or as different types of

ratios of one nutrient against another (i.e., nutrient balance; 4, 17). The N-deficient plants had lower N-ratios for most nutrients indicating either a lower demand for most nutrients per milligram of N uptake or a decreased ability to accumulate these nutrients due to N-deficiency. The average N:C, N:P, N:K, N:S, N:Mg, N:Fe, and N:Mn ratios between May and September for N-deficient plants of both cultivars were similar (N:C, N:Fe, and N:Mn ratios not presented). The average N:C, N:P, N:K, N:S, N:B, and N:Fe ratios between May and September for +N plants of both cultivars were similar (N:B and N:Fe ratios not shown). Similar uptake ratios for both cultivars when N was not limiting to growth suggests demand for P, K, S, B, and Fe by both cultivars was similar and fertilizers with similar availability ratios for these elements in relationship to N could be used with both cultivars. Cultivar differences in N/Ca, N/Mg, N/Mn, and N/Zn ratios suggests availability of Ca, Mg, Mn, and Zn in the fertilizer in relationship to N availability may need to be altered for optimal growth of each cultivar.

One potential drawback of using total plant N-ratios (plant N-ratios) for assessing uptake relationships between nutrients is the destructive and time consuming nature of gathering data on total plant nutrient uptake. Just as leaf nutrient concentrations are commonly used for assessing plant nutrient status, it is possible leaf or stem nutrient ratios could have a similar predictive ability. Correlations ($P < 0.05$) between uptake ratios and ratios of N to other nutrients in 2004 leaves and stems (leaf or stem N-ratios) do not imply N-ratios in these structures are representative of total plant uptake ratios. Therefore, plant N- ratios were compared to leaf and stem N-ratios to assess whether the response of leaf or stem N-ratios to N-availability were similar as the response of plant N-ratios (Figs. 1 and 2).

By definition N-ratios are a direct function of N uptake and an inverse function of the uptake of the other nutrient in the ratio (9). In general N-ratios changed less between May and September in N-deficient plants than in +N plants. For both cultivars leaf N:P ratio under-estimated P uptake and stem N:P ratio over-estimated P uptake compared to plant N:P ratio at most harvest dates. This suggests when plant N:P ratios are not available, N:P ratios based on both stems and leaves could be used for evaluating co-uptake of these nutrients. Leaf N:K ratios generally over-estimated K uptake of both cultivars and leaf N:S ratios generally under-estimated S uptake compared to same plant N-rations at most harvest dates. There was very little change in plant and leaf N:K ratios for +N rhododendron between May and September and very little difference in plant and leaf N:K ratios. Similarly there was very little change in plant and stem N:S ratios for +N rhododendron between May and September and very little difference in plant and stem N:S ratios. Plant and leaf N:Ca ratios for +N rhododendron increased between May and September; however there was very little difference in plant and leaf N:Ca ratios. This indicates rhododendron leaf N:K, leaf N:Ca and stem N:S ratios may be reasonable diagnostic tools for evaluating co-uptake of these nutrients. Leaf N:K and leaf N:Ca ratios of +N azalea were not similar to plant N-ratios during the later part of the summer suggesting leaf N:K and leaf N:Ca ratios may not be useful for evaluating co-uptake for deciduous plants when plants may be starting to reallocate nutrients for winter storage. Depending on the harvest date, leaf N:Mg ratio generally under-estimated Mg uptake and stem N:Mg ratio over-estimated Mg uptake.
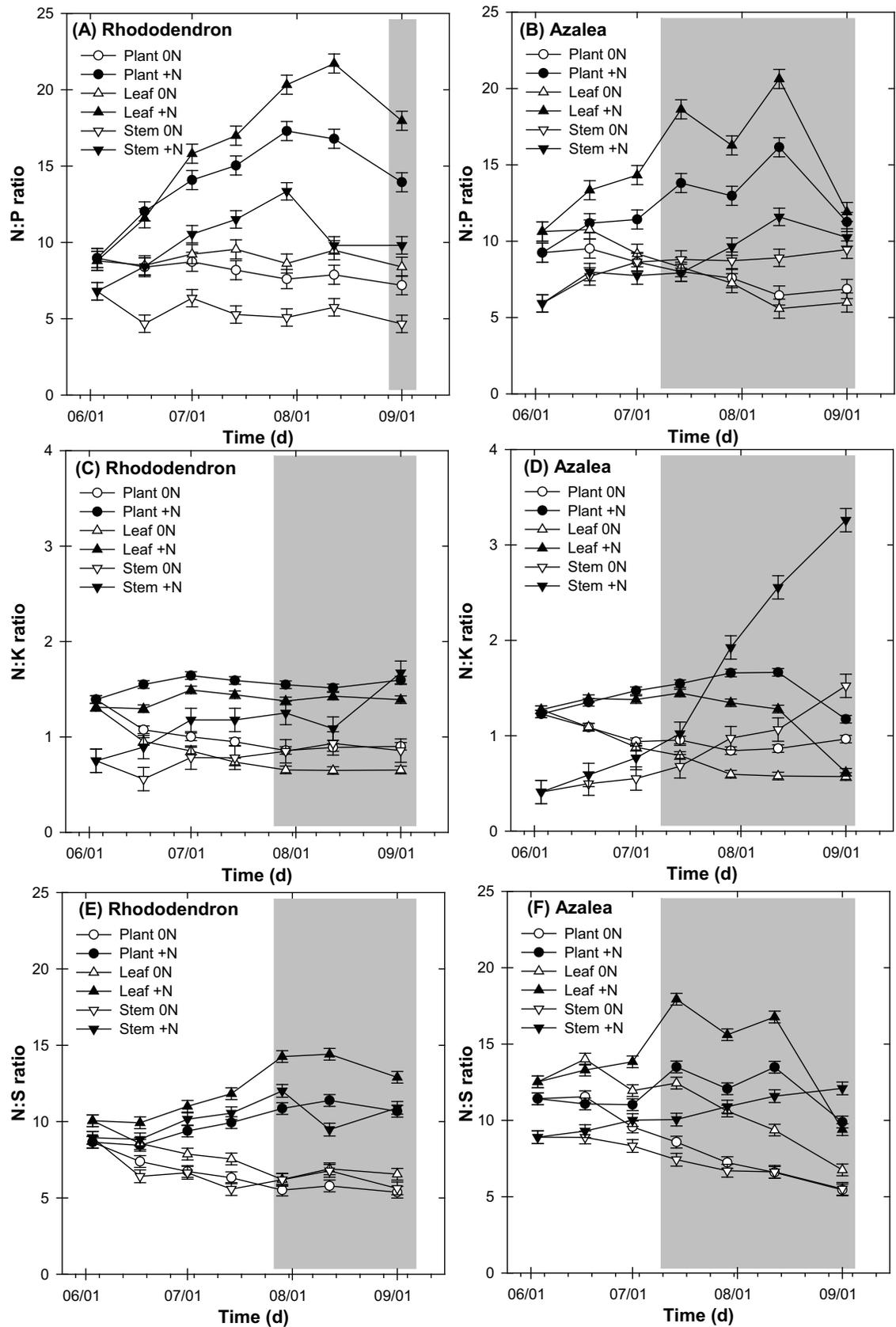
Fig. 1. Ratios of N:P, N:K, and N:S in whole plants (Plant), 2004 leaves (Leaf) and 2004 stems (Stem) of *Rhododendron* 'H-1 P.J.M.' (Rhododendron) and *Rhododendron* 'Cannon's Double' (Azalea) grown in containers with (+N) or without (0N) N from May through September 2004. Symbols represent means and error bars 95% confidence intervals (n = 5). Grey box indicates dates when N-deficient plants (0N) were also deficient in P, K, and S.
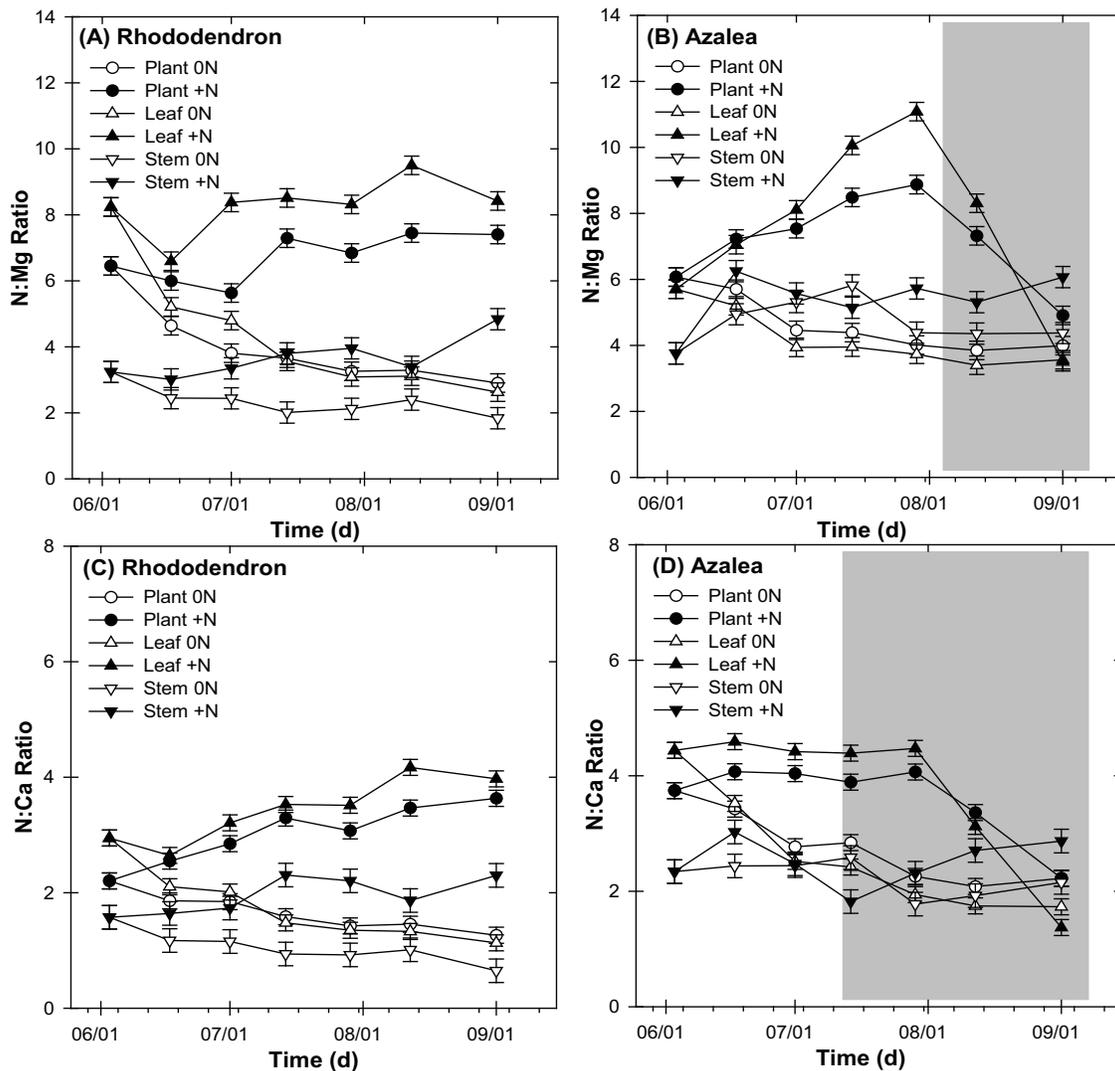
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Fig. 2. Ratios of N:Mg and N:Ca in whole plants (Plant), 2004 leaves (Leaf) and 2004 stems (Stem) of *Rhododendron* 'H-1 P.J.M.' (Rhododendron) and *Rhododendron* 'Cannon's Double' (Azalea) grown in containers with (+N) or without (0N) N from May through September 2004. Symbols represent means and error bars 95% confidence intervals (n = 5). Grey box indicates dates where N-deficient plants (0N) were also deficient in Mg and Ca.

The N:P ratios in both cultivars at harvest dates when N-deficient plants were also hypothesized as being P-deficient were <10 and plant N:P ratios of +N plants were between 11 and 16. The N:P ratio has been suggested as a tool for analyzing nutrient limitations and determining fertilizer requirements in agriculture and forestry (9, 17, 30). Variation in N:P ratios is determined primarily by variation in N for woody plants (8). In terrestrial ecology literature vegetation N:P ratios of <10 are indicative of N-limited environments (9), and in certain agronomic crops N:P ratios <5 are indicative of N-limited growing conditions (8). While there is agreement that low N:P ratios indicate N limitation there is no consistent interpretation of high N:P ratios (9) and the range of N:P ratios that occur across species and time has not been evaluated for nursery crops. An important limitation of N:P ratios as predictors of nutrient limitation is they can only be applied to plants that are not limited by factors other than N or P (17). In most environmental applications, this restriction does not constitute a major problem since a majority of natural soils are usually only N- and/or P-limited.

In container nursery production systems where other nutrients may also be limiting, their limitation may influence the predictive value of N:P.

Beyond the N:P ratio, other nutrient ratios indicating nutrient covariation have also been proposed for use in plant production (22, 29). The N:K ratios in both cultivars at harvest dates when N-deficient plants were also hypothesized as being K-deficient were <1.0 and for +N plants at the same dates was 1.0 to 1.5. Similarly the N:S ratios in both cultivars at harvest dates when N-deficient plants were also hypothesized as being S-deficient were approximately 10 lower than N:S ratios in +N plants at the same dates. Although these differences in N:K and N:S between N-deficient and +N plants are small, further investigation may be warranted to determine whether these ratios can also be used as an indicator of imbalance in N:K and N:S nutrition. The N:Mg and N:Ca ratios in azalea at harvest dates when N-deficient plants were also hypothesized as being Mg and Ca deficient were <4.0; however, for +N azalea plant N:Mg and N:Ca ratios were not stable between the same dates. This rapid decrease

in N:Mg and N:Ca ratios at the end of the summer suggests these ratios may not be useful for determining imbalances in N:Mg and N:Ca ratios in the later part of the summer.

Optimal levels of plant nutrients as well as the balance between nutrients can not be derived from a single experiment, particularly for perennial plants. Results of numerous experiments over many years and various locations are required. According to the theory of optimum nutrition (14) maximum plant growth occurs when internal nutrient concentrations and ratios are stable and nutrient addition rates match uptake rates. Characterizing changes in nutrient ratios over time has potential to improve understanding of the balance of mineral nutrients required for optimum growth and aid in development of nutrient management strategies that synchronize availability of nutrients with plant demand.

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