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Rate of Nitrogen Application During the Growing Season and Spraying Plants with Urea in the Autumn Alters Uptake of Other Nutrients by Deciduous and Evergreen Container-grown *Rhododendron* Cultivars

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***Abstract*. The influence of fall sprays with urea on the uptake of nutrients other than nitrogen (N) was assessed using 1-year-old container-grown *Rhododendron* L. (*Rhododendron* 'H-1 P.J.M') and azalea (*Rhododendron* 'Cannon's Double') grown with different rates of N. Plants were grown with a complete fertilizer containing different N rates from May to Sept. 2004 sprayed or not with urea in the fall of 2004 and grown with a complete fertilizer containing different N rates in the spring of 2005. Urea sprays altered uptake of nutrients other than just N although fertilizer application with other nutrients ceased before plants were sprayed with urea. Across a wide range of plant sizes and N status, urea sprays increased net phosphorus (P), copper (Cu), and manganese (Mn) uptake and decreased net potassium (K) and magnesium (Mg) uptake during the year of urea application. Spraying plants with urea altered nutrient demand and storage in different plant structures during the winter. For azalea, urea sprays increased P demand by roots, Mn demand by 2004 stems, and Cu demand by stems. Urea also decreased storage of K in roots and 2004 stems of azalea and Mg in roots. For rhododendron, urea sprays increased P demand by 2003 stems and 2004 leaves and Mn demand by 2004 leaves. Urea sprays also decreased storage of K and Mg in 2004 leaves of rhododendron. For both cultivars, urea sprays increased mobilization of iron (Fe) from storage and demand for Fe in stems. Spraying *Rhododendron* with urea in the fall altered uptake and demand for certain nutrients during the following spring. Urea sprays in the fall of 2004 increased uptake and possibly demand for P, K, and sulfur during the spring of 2005 for both cultivars, the uptake of calcium by rhododendron, and the uptake of Mg and Mn by azalea. Our results indicate that when growers spray plants with urea in the fall, spring fertilizer practices may need to be modified to account for increased uptake or demand of certain nutrients.**

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In woody plants, growth in the spring relies on remobilization of nitrogen (N) reserves before substantial root uptake occurs (Cheng et al., 2001; Henry et al., 1992; Millard, 1996). Foliar fertilization with urea in the fall is a common strategy used with fruit tree nursery stock to increase N reserves, improve plant performance the following spring and decrease the potential of N leaching and problems with hardiness sometimes associated with high soil N in the fall (Bi et al., 2003; Dong et al., 2004; Rikala et al., 2004). Most research on fertilizer uptake by container-grown nursery crops has primarily focused on N because it is commonly cited as the most important nutrient for plant growth and losses from nursery production systems have consequences to environmental quality (Cabrera et al., 1993). In addition to N, plants require several other elements for normal vegetative growth and reproduction (Marschner, 1995). Different amounts of each element are required by different plant species and cultivars. Plant growth can be restricted when not enough of one or more elements are present or too much of one or more elements are present and certain elements [e.g., phosphorus (P)] are potential sources of pollution when excess application results in runoff from nursery production areas.

Spraying container-grown *Rhododendron* nursery plants with urea in the fall can increase N storage and improve growth the next spring (Bi et al., 2007). Fall urea sprays can also decrease the amount of N uptake required for new growth in the early spring of some *Rhododendron* cultivars. Research on fall urea sprays has focused on the changes to plant N status and correlating N status with growth, fertilizer demand, and N leaching losses during the following year (del Amor et al., 2007; Dong et al., 2004; Han et al., 1989). Although the influence of fall urea sprays on plant carbohydrate status has been reported (Bi et al., 2004; Xia and Cheng. 2004), the influence of urea sprays on the uptake of other nutrients and their potential influence on plant growth have predominantly been overlooked (Fallahi et al., 2002; Yildirim et al., 2007). Uptake of N from the growing medium by container-grown *Rhododendron* can occur through the fall and into the early winter (Scagel et al., 2007). It is possible that the increased N status of plants sprayed with urea may alter uptake of other nutrients in the fall and the resulting demand for these nutrients from fertilizer the following spring.

Recently, we described the influence of N availability and fall urea sprays on N uptake of *Rhododendron* (Bi et al., 2007). Here we report the influence of fall urea sprays on uptake of other nutrients by *Rhododendron* grown with different rates of N fertilizer. Using deciduous and evergreen cultivars of container-grown *Rhododendron*, our objectives were to determine whether spraying plants with urea in the fall alters 1) uptake of nutrients other than N in the year of application and the following growing season; and 2) allocation of nutrients other than N in the year of application and the following growing season.

Materials and Methods

A more detailed description of the experimental methods, including analyses for N and biomass, can be found in Bi et al. (2007). Plants used in this experiment were an evergreen rhododendron (*Rhododendron* 'H-1 P.J.M.', ARS #874) and deciduous azalea (*Rhododendron* 'Cannon's Double', ARS #922) obtained from a commercial nursery as 1-year-old liner (112-cm^3 rooting volume) stock grown from tissue-cultured plants. A brief summary of the methods given in Bi et al. (2007) are outlined below and additional methods that pertain to analyses for other nutrients, calculations of nutrient uptake, and statistical analyses are included in more detail.

Plant culture and treatments. Plants were transplanted into 7.6-L polyethylene containers containing a mix of 2 peatmoss:1 pumice:1 sandy loam soil (by volume) in May 2004 and grown outdoors in a lathe house (50% shade) in Corvallis, OR (long. 45°59′04″ N, lat. 123°27′22″ W). Thirty plants of each cultivar were randomly assigned to one of five groups and fertilized two times a week for 5 weeks starting 10 June and then once a week for 5 weeks (N04 treatment). At each fertigation, each group of plants received 250 mL of modified Hoagland's solution (Hoagland and Arnon, 1950) containing one of five different N concentrations (N04 treatments: 0, 5, 10, 15, or 20 mM N). All plants were hand-watered as needed. After terminal bud set, half of the plants in each N04 treatment were randomly selected and sprayed with 3% urea (+U treatment) twice (20 and 29 Oct.) and the remaining plants in each treatment were sprayed with water (–U treatment). In the spring of 2005, after budbreak, half of the plants in each N04 and urea treatment combination were randomly assigned to one of two groups and fertilized two times a week for 8 weeks (N05 treatment). At each fertigation, one group of plants received 250 mL of modified Hoagland's solution containing 10 mM N (+U+N and –U+N treatments) and the remaining group received 250 mL of N-free Hoagland's solution (+U-N and –U-N treatments). These methods allowed us to assess the influence of urea sprays on uptake of nutrients other than N from plants over a wide range of N status.

Measurements. Before transplanting, five plants of each cultivar were randomly selected and divided into roots, stems, and leaves. All samples were washed in double-distilled water, placed in an –80 °C freezer, and freeze-dried until a constant weight was reached. The dry weight of each plant structure was recorded and samples were ground to pass through a 20-mesh screen for nutrient analyses. In Dec. 2004, five randomly selected plants from each N04 and urea treatment combination were harvested. The growing substrate was removed from roots by washing; plants were separated into roots, stems, and leaves; and samples were processed as described previously. Growth was assessed by determining dry weight of different plants structures (e.g., roots, stems, and leaves). For both cultivars, stems were further separated by growing season and for rhododendron leaves were also separated by growing season (e.g., 2003, 2004). Eight weeks after budbreak in 2005, plants were harvested as described previously, except stems of both cultivars and rhododendron leaves were separated by growing season (2003, 2004, and 2005).

Nutrient analyses and calculations. Samples take for nutrient analyses were analyzed for concentrations of N as described in methods from prior research (Bi et al., 2007). Concentrations of other macro- and micronutrients in samples were obtained using inductively coupled plasma-optical emission spectroscopy (ICP-OES) after digestion of dried sample 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 ± 3% CV. The nutrient content of each plant structure was calculated by multiplying the concentration from samples of each structure by the dry weight of each structure. Total content (milligrams or micrograms) of each nutrient was calculated as the sum over all structures. Uptake of nutrients during 2004 was estimated by subtracting the average nutrient content of each cultivar in May from the nutrient content of plants from each N04 and urea treatment combination in Dec. 2004. Uptake of nutrients from spring fertilizer application (N05 treatment) was estimated by subtracting the average nutrient content of plants from each N04 and urea treatment combination in Dec. 2004 from the content of individual plants from each urea, N04, and N05 treatment in the spring of 2005. Allocation of nutrients between different structures was evaluated using the total content of each nutrient in different structures. N uptake ratios were calculated as the ratio of N uptake to the uptake of each other nutrient.

Experimental design and statistical analyses. The experiment was set up in a completely randomized design. Each treatment unit (pot) replicated five times for each N04 treatment (0, 5, 10, 15, 20 mM N), fall urea treatment (+U, –U), N05 treatment (+N, –N), and cultivar (rhododendron, azalea). All data were tested for homogeneity of variance using Levene's test and for normality using the Kolmogorov-Smirnov test and transformed if necessary. Where transformation was necessary, back-transformed means and arithmetic SES are presented in tables or figures. Data were analyzed using analysis of covariance and regression techniques as described subsequently. Multivariate analysis of covariance (MANCOVA) was used to control experiment-wide error rate before further univariate analysis. The least significant difference method with a Bonferroni correction at $P < 0.05$ was used to make pairwise comparisons between cultivars and urea treatments and to control the overall type I error rate. Linear relationships between variables were assessed using Pearson's correlation coefficient (r) at $P < 0.05$. All statistical analyses were performed using Statistica® (Statsoft, Inc., Tulsa, OK).

Differences in nutrient uptake between cultivars and treatments can be partially attributable to scaling effects of plant growth on nutrient content (Righetti et al., 2007a, 2007b). For example, growth and N uptake data previously reported showed rhododendron accumulated 35% more biomass and 26% more N in 2004 than azalea (19.6 g versus 14.2 g biomass growth; 317 versus 242 mg N) (Bi et al., 2007). Urea treatment had no influence on plant growth in 2004 and plants that were sprayed with urea took up 70% more N than plants that were not sprayed (359 mg versus 211 mg N). The 2004 growth and N uptake responses of the two cultivars to N04 treatments and urea treatments were similar (no cultivar × N04 or cultivar × urea treatment interactions). Therefore, to minimize the influence of differences in plant size (resulting from cultivar and N04 treatment differences) on comparisons of nutrient uptake between cultivars and urea treatments, 2004 growth data and N uptake in 2004 were considered as covariates in analysis of 2004 uptake data. To minimize the influence of plant size resulting from cultivar, N04, and N05 treatment differences on comparisons of nutrient uptake between cultivars and urea treatments, 2005 growth data and N uptake in 2004 and 2005 were considered as covariates in analysis of 2005 uptake data. Similarly, to minimize the influence of differences in biomass partitioning (DW%) on comparisons of nutrient partitioning between cultivars and treatments, 2004 DW% data and N uptake in 2004 were considered as covariates in analysis of 2004 nutrient partitioning data and 2005 DW% data and N uptake in 2004 and 2005 were considered as covariates in an analysis of 2005 nutrient partitioning data.

Linear relationships between covariates and response variables and homogeneity of slopes between categorical variables and continuous variables were verified before analysis; therefore, traditional MANCOVA models were used. Differences in 2004 and 2005 uptake were evaluated with cultivar and urea treatment as factors in a complete factorial model with the covariates described previously and differences in 2004 and 2005 nutrient partitioning were analyzed by structure with cultivar and urea treatment as factors in a complete factorial model with the covariates described previously. Unadjusted means ($\overline{X}$) and means adjusted for the covariates ($\overline{X}_{adj}$) are presented in tables where appropriate. The proportion of effect variance (SS_{effect}) plus error variance (SS_{error}) attributable to the effect from MANOVA was assessed using partial eta-squared values [$\acute{\eta}_p^2 = (SS_{effect}/\{SS_{effect} + SS_{error}\})$] (Pierce et al., 2004). The proportion of total variance (SS_{total})

attributable to the effect from univariate results was assessed using eta-squared values [$\acute{\eta}^2 = (SS_{effect}/SS_{total})$].

Results

Net nutrient uptake in 2004. Regardless of differences in growth and N uptake, spraying either cultivar with urea in the fall of 2004 decreased net K uptake by Dec. 2004 ($\overline{X}$; Table 1). Spraying rhododendron with urea increased net P, calcium (Ca), and manganese (Mn) uptake and spraying azalea with urea decreased net magnesium (Mg) uptake and increased net copper (Cu) uptake (Table 1). Growth in 2004 accounted for over 40% of the variance in net P, potassium (K), Mg, iron (Fe), and Mn uptake in 2004; between 15% to 21% of the variance in net sulfur (S), Ca, and zinc (Zn) uptake; and over 7% of the variance in net Cu uptake. Differences in N uptake in 2004 from N04 treatments accounted for 44% of the variance in net S uptake in 2004, 22% of the variance in net P uptake, and less than 10% of the variance in net uptake of other nutrients.

After accounting for differences in plant growth and N status from N04 treatments, spraying plants with urea increased net nutrient uptake by 2.2 mg P and 1.2 mg Mn and decreased net nutrient uptake by 15 mg K and 2 mg Mg ($\overline{X}_{adj}$; Table 1). Urea sprays had a greater influence on K uptake by azalea in 2004 than rhododendron. Spraying azalea with urea increased Cu uptake by 44 μg Cu (Table 1). Spraying plants with urea had no influence on net uptake of S, Ca, Fe, or Zn in 2004 (Table 1). Urea treatments in 2004 had the greatest effect on net K uptake in 2004, accounting for over 16% of the variance in net K uptake.

On average, rhododendron took up 3 mg P more than azalea ($\overline{X}$; Table 1); however, after accounting for differences in growth, azalea took up 3.9 mg P more than rhododendron ($\overline{X}_{adj}$; Table 1). Rhododendron took up 43 mg K, 6 mg S, 53 mg Ca, 13 mg Mg, 2.2 mg Fe, and 22 mg Mn more than azalea and after accounting for differences in growth; rhododendron took up 23 mg K, 2 mg S, 37 mg Ca, 7 mg Mg, 1.3 mg Fe, and 7 mg Mn more than azalea (Table 1). Azalea took up 70 μg Cu more than rhododendron and after accounting for differences in growth, azalea took up 74 μg Cu more than rhododendron (Table 1). There was no difference in net Zn uptake between cultivars; on average, plants took up 0.46 to 0.56 mg Zn (Table 1). Differences between cultivars accounted for over 30% of the variance in net Ca, Cu, Mn, K, and Mg uptake in 2004.

Relationships between nutrients in Dec. 2004. There were significant ($P < 0.0001$) positive relationships between N uptake in 2004 and uptake of other nutrients in 2004 (P, r = 0.873; K, r = 0.672; S, r = 0.874; Ca, r = 0.662; Mg, r = 0.606; Cu, r = 0.591; Fe, r = 0.538; Mn, r = 0.541; and Zn, r = 0.569) and significant ($P < 0.001$) positive relationships between net uptake of nutrients other than N (data not shown). Spraying plants with urea in the fall of 2004 increased net N uptake ratios (uptake of N to other nutrients) by Dec. 2004. Plants sprayed with urea had higher N:P (14:1 vs. 9:1), N:K (11:1 vs. 4:1), N:S (19:1 vs. 11:1), N:Ca (9:1 vs. 5:1), N:Mg (19:1 vs. 10:1), N:Cu (1633:1 vs. 1141:1), N:Fe (123:1 vs. 68:1), N:Mn (29:1 vs. 19:1), and N:Zn (779:1 vs. 485:1) than plants that were not sprayed with urea. Rhododendron had greater N:P (13:1 vs. 11:1), and N:Cu (1674:1 vs. 1100:1) than azalea. Azalea had greater N:K (12:1 vs. 4:1), N:S (16:1 vs. 14:1), N:Ca (10:1 vs. 3:1), N:Mg (19:1 vs. 11:1), N:Fe (124:1 vs. 67:1), and N:Mn (32:1 vs. 14:1) than rhododendron. There was no difference between cultivars in N:Zn (602:1).

Nutrient partitioning in Dec. 2004. In general, roots and 2004 stems of azalea contained the greatest proportion of most nutrients and roots and 2004 leaves of rhododendron contained the greatest proportion of most nutrients (Tables 2 and 3). Spraying plants with urea increased net uptake of P, Cu, and Mn between June and Dec. 2004 (Table 1) and altered allocation of these nutrients within plants (Tables 2 and 3). Spraying azalea with urea increased P content and allocation to roots, increased Cu content and allocation to stems, and increased Mn content and allocation to stems and 2004 leaves. Spraying rhododendron with urea increased P content and allocation to 2003 stems and 2004 leaves and Mn content and allocation to stems. Urea sprays decreased allocation of P to stems and Cu and Mn allocation to roots of azalea but not content. Urea sprays decreased allocation of Mn to roots of rhododendron but not content. Spraying rhododendron with urea had no influence on Cu uptake or the content or allocation of Cu to different structures.

Spraying plants with urea decreased Mg uptake (Table 1) and decreased Mg content and allocation to roots (rhododendron) (Table 2). Urea sprays also increased Mg allocation to 2003 stems but not Mg content. Spraying plants with urea decreased net uptake of K (Table 1) and decreased K content in roots, stems, and old leaves; however, urea sprays did not alter allocation of K to these structures (Tables 2 and 3).

Spraying plants with urea had no influence on net uptake of S, Ca, Fe, or Zn (Table 1); however, urea sprays altered allocation of these nutrients within plants (Tables 2 and 3). Spraying azalea with urea increased allocation of S to roots, Ca to 2003 stems, and Fe and Zn to stems and decreased allocation of S to stems, Ca to 2004 stems, and Fe and Zn to roots. Spraying rhododendron with urea increased allocation of S to 2003 stems, Ca to 2003 stems, and Fe and Zn to stems and decreased allocation of S to 2004 stems and Fe and Zn to roots. Urea treatments in 2004 had the greatest effect on P ($\acute{\eta}^2 = 0.15$), S ($\acute{\eta}^2 = 0.05$), and Mn ($\acute{\eta}^2 = 0.20$) allocation to roots; K ($\acute{\eta}^2 = 0.25$) and Zn ($\acute{\eta}^2 = 0.19$) allocation to 2004 leaves; and Ca ($\acute{\eta}^2 = 0.06$), Mg ($\acute{\eta}^2 = 0.07$), Cu ($\acute{\eta}^2 = 0.20$), and Fe ($\acute{\eta}^2 = 0.13$) allocation to 2003 stems.

Differences in nutrient uptake between cultivars (Table 1) were reflected by differences

Table 1. Net nutrient uptake of two *Rhododendron* cultivars from June to Dec. 2004 after leaves were sprayed (+U) or not (–U) with urea in the fall of 2004.

	Net uptake from June to Dec. 2004[z]								
	Rhododendron		Azalea		$\acute{\eta}^{2}$[w]				
Nutrient	–U	+U	–U	+U	G04	N04	C	U	C*U
	Unadjusted means[y]								
P (mg)	22.8 a	27.1 b	22.4 a	22.5 a					
K (mg)	69.5 d	63.6 c	34.7 b	13.2 a					
S (mg)	20.8 b	22.3 b	16.1 a	14.7 a					
Ca (mg)	77.4 b	82.4 c	24.8 a	21.9 a					
Mg (mg)	27.1 c	26.7 c	15.6 b	12.8 a					
Cu (μg)	95.6 a	120.5 a	150.2 b	219.9 c					
Fe (mg)	4.4 b	4.5 b	2.4 a	2.3 a					
Mn (mg)	17.9 b	21.3 c	8.3 a	8.0 a					
Zn (μg)	540.6 a	578.9 a	436.7 a	492.2 a					
	Adjusted means[x]								
P (mg)	20.1 a	23.0 b	24.6 b	26.2 c	0.43	0.22	0.10	0.04	NS
K (mg)	62.3 d	51.8 c	43.3 b	23.7 a	0.41	0.03	0.31	0.16	0.02
S (mg)	19.0 b	19.8 b	18.1 a	17.0 a	0.15	0.44	0.04	NS	NS
Ca (mg)	62.4 b	67.9 b	28.9 a	26.2 a	0.21	0.03	0.52	NS	NS
Mg (mg)	25.1 d	23.2 c	18.0 b	15.8 a	0.41	0.06	0.31	0.04	NS
Cu (μg)	80.9 a	95.0 a	168.1 b	242.2 c	0.07	0.09	0.45	0.04	0.02
Fe (mg)	4.1 b	4.0 b	2.7 a	2.8 a	0.46	0.07	0.15	NS	NS
Mn (mg)	16.5 c	18.5 d	10.1 a	11.4 b	0.42	0.05	0.34	0.04	NS
Zn (μg)	491.5 a	485.0 a	499.0 a	573.1 a	0.18	0.08	NS	NS	NS

[z]Cultivars: Rhododendron = *Rhododendron* 'H-1 P.J.M', Azalea = *Rhododendron* 'Cannon's Double'. Urea Treatments: +U = sprayed with 3% urea, –U = sprayed with water.

[y]Unadjusted means. Means followed by the same letter within a row are not significantly different (Bonferroni's test, $P < 0.05$, n = 25).

[x]Means adjusted for 2004 N uptake from N04 treatments and growth in 2004. Means followed by the same letter within a row are not significantly different (Bonferroni's test, $P < 0.05$, n = 25).

[w]Eta-squared ($\acute{\eta}^2$) values for effects from univariate results. G04 = growth in 2004, N04 = N uptake from N04 treatments, C = cultivar, U = urea treatment, C*U = cultivar by urea treatment interaction, NS = nonsignificant effect. Multivariate analysis of covariance partial eta-squared ($\acute{\eta}_p^2$) values for effects of growth: 0.93; 2004 N uptake: 0.73; C: 0.91; U: 0.81; C*U: 0.29.

Table 2. Nutrient content and nutrient partitioning (proportion of total plant content) of roots and stems on two *Rhododendron* cultivars in Dec. 2004 after leaves were sprayed (+U) or not (–U) with urea in the fall of 2004.

	Content and proportion of total plant content[z]							
	Content (mg or µg)[y]				Proportion of total plant content (%)[y]			
	Rhododendron		Azalea		Rhododendron		Azalea	
Nutrient	–U	+U	–U	+U	–U	+U	–U	+U
	—Roots—							
P (mg)	7.6 a[x]	8.4 a	10.7 b	13.2 c	33.4 a	33.8 a	41.2 b	47.2 c
K (mg)	18.3 b	16.2 a	28.5 c	17.4 ab	30.3 a	30.1 a	36.8 b	36.7 b
S (mg)	9.0 a	9.5 a	10.5 b	10.1 b	45.6 a	46.2 a	49.1 b	52.4 c
Ca (mg)	12.6 b	12.8 b	9.1 a	8.6 a	20.3 a	19.8 a	24.8 b	24.1 b
Mg (mg)	9.7 c	8.8 ab	9.4 bc	8.2 a	35.0 a	33.9 a	44.6 b	43.8 b
Cu (µg)	77.5 a	84.7 a	100.2 b	113.1 b	49.3 c	49.2 c	41.1 b	34.0 a
Fe (mg)	3.1 b	3.0 b	2.0 a	1.8 a	62.6 b	58.2 a	70.6 c	61.4 b
Mn (mg)	4.5 d	3.8 c	2.8 b	2.0 a	27.4 b	22.1 a	30.6 c	26.3 b
Zn (µg)	184.8 b	156.6 a	279.3 d	226.8 c	37.3 b	31.5 a	40.6 b	32.8 a
	—2003 stems—							
P (mg)	1.9 a	2.2 b	2.9 c	2.8 c	9.0 a	10.2 b	10.5 b	8.9 a
K (mg)	4.8 a	4.6 a	7.2 b	4.8 a	7.3 a	7.9 a	10.1 b	9.8 b
S (mg)	1.4 a	1.7 b	1.8 c	1.6 b	7.5 a	8.4 b	8.6 b	7.7 a
Ca (mg)	2.1 a	3.8 b	3.5 b	4.3 c	4.4 a	5.3 b	9.1 c	11.0 d
Mg (mg)	1.0 a	1.2 a	1.9 b	1.8 b	4.3 a	5.6 b	7.9 c	8.6 d
Cu (µg)	16.2 a	23.3 a	21.7 a	59.3 b	8.5 a	11.8 a	10.1 a	16.8 b
Fe (µg)	118.5 a	197.8 b	224.6 c	328.3 d	3.8 a	5.9 b	6.2 b	9.1 c
Mn (mg)	1.1 b	1.2 b	0.9 a	0.8 a	7.6 a	7.3 a	10.6 b	10.8 b
Zn (µg)	49.0 a	61.3 b	39.1 a	91.9 b	7.4 a	9.4 b	7.2 a	11.3 b
	—2004 stems—							
P (mg)	6.5 a	6.9 a	9.5 b	9.1 b	28.6 a	27.7 a	32.5 b	28.2 a
K (mg)	17.7 b	15.4 a	25.1 c	18.8 b	24.2 a	23.7 a	33.5 b	34.0 b
S (mg)	5.0 b	4.6 a	5.9 d	5.5 c	25.0 b	22.2 a	26.4 c	24.3 b
Ca (mg)	24.8 bc	22.3 ab	22.8 bc	20.6 a	28.9 b	24.2 a	54.4 d	51.7 c
Mg (mg)	6.5 a	6.7 a	7.6 b	6.9 ab	24.2 a	25.4 a	31.6 b	31.8 b
Cu (µg)	44.7 a	41.7 a	74.1 b	100.9 c	27.1 a	24.7 a	29.8 a	38.9 b
Fe (µg)	512.1 a	556.1 b	511.8 a	744.0 c	12.7 a	13.5 a	14.2 a	20.2 b
Mn (mg)	5.7 c	6.2 d	4.2 a	4.5 b	32.0 a	31.3 a	45.4 b	49.0 c
Zn (µg)	200.1 a	187.9 a	260.5 b	329.1 c	30.8 a	32.2 b	36.8 c	40.6 d

[z]Cultivars: Rhododendron = *Rhododendron* 'H-1 P.J.M', Azalea = *Rhododendron* 'Cannon's Double'. Urea treatments: +U = sprayed with 3% urea, –U = sprayed with water.

[y]Content means adjusted for 2004 N uptake from N04 treatments and growth in 2004. Partitioning means adjusted for 2004 N uptake from N04 treatments and biomass partitioning in 2004.

[x]Means followed by the same letter within a row and variable (content or partitioning) are not significantly different (Bonferroni's test, $P < 0.05$, n = 25). For content in roots, 2003 stems, and 2004 stems, respectively, multivariate analysis of covariance (MANCOVA) partial eta-squared ($\acute{\eta}_p^2$) values for effects of growth: 0.92, 0.87, 0.89; 2004 N uptake: 0.75, 0.29, 0.62; cultivar (C): 0.80, 0.86, 0.85; urea treatment (U): 0.87, 0.86, 0.59; C*U: 0.74, 0.70, 0.25. For partitioning to roots, 2003 stems, and 2004 stems, respectively, MANCOVA $\acute{\eta}_p^2$ values for effects of biomass partitioning: 0.87, 0.77, 0.94; 2004 N uptake: 0.43, 0.61, 0.29; C: 0.57, 0.63, 0.92; U: 0.69, 0.57, 0.61; C*U: 0.37, 0.32, 0.46.

in content and allocation of nutrients to roots and stems (Table 2). Net uptake of K, S, Ca, Mg, and Fe by rhododendron in 2004 was greater than azalea; however, in general, azalea content and allocation of these nutrients to roots (K, S) and stems (K, S, Ca, Mg, Fe) was greater than rhododendron. Net uptake of P and Cu by azalea in 2004 was greater than rhododendron and azalea content, and allocation of these nutrients to roots (P) and stems (P, Cu) was greater than rhododendron. Net uptake of Mn by rhododendron in 2004 was greater than azalea; however, in general, rhododendron Mn content in roots and stems was higher than azalea and Mn allocation to roots and stems was lower than azalea. Differences between cultivars had the greatest effect on P ($\acute{\eta}^2 = 0.14$), Mg ($\acute{\eta}^2 = 0.18$), and Cu ($\acute{\eta}^2 = 0.06$) allocation to roots, and K ($\acute{\eta}^2 = 0.24$), S ($\acute{\eta}^2 = 0.04$) Ca ($\acute{\eta}^2 = 0.68$), Fe ($\acute{\eta}^2 = 0.18$), Mn ($\acute{\eta}^2 = 0.52$), and Zn ($\acute{\eta}^2 = 0.12$) allocation to 2004 stems.

Nutrient uptake in the spring of 2005. Regardless of differences in growth and N uptake, spraying either cultivar with urea in the fall of 2004 increased net P, K, S, and Ca uptake and decreased net Fe uptake in 2005 ($\overline{X}$; Table 4). Spraying azalea with urea increased net Mg, Mn, and Zn uptake and spraying rhododendron with urea decreased net Mn uptake. After accounting for the differences in plant growth and N uptake, spraying plants with urea in 2004 increased net nutrient uptake by 10 mg P, 100 mg K, and 25 mg S in 2005 and decreased net uptake by 32 mg Fe ($\overline{X}_{adj}$; Table 4). Urea sprays had a greater influence on S and Fe uptake by rhododendron in 2005 than azalea. Spraying azalea with urea increased Mg and Mn uptake in 2005 and decreased Cu uptake (Table 4). Spraying rhododendron with urea decreased Mn uptake in 2005 (Table 4). Urea sprays in 2004 had no effect on uptake of Ca or Zn in 2005. Urea treatments in 2004 had the greatest effect on S uptake and Fe uptake in 2005, and differences between cultivars in response to urea sprays were greatest for Mn uptake in 2005.

On average, azalea took up 217 mg K, 61 mg Mg, 857 µg Cu, and 1.5 mg Zn more than rhododendron; and rhododendron took up 173 mg Ca, and 17 mg Mn more than azalea ($\overline{X}$; Table 4). When differences in plant growth were accounted for, azalea took up 166 mg K, 47 mg Mg, 768 µg Cu, and 1.3 mg Zn more than rhododendron; and rhododendron took up 11 mg P, 14 mg S, 199 mg Ca, 11 mg Fe, and 14 mg Mn more than azalea ($\overline{X}_{adj}$; Table 4). Differences between cultivars had the greatest effect on net K, Ca, Mg, Cu, and Zn uptake in 2005.

Relationships between nutrients in 2005. There were significant ($P < 0.01$) positive relationships between N uptake in 2004 and uptake of nutrients other than N in 2005 (P, r = 0.444; K, r = 0.453; S, r = 0.464; Ca, r = 0.635; Mg, r = 0.525; Cu, r = 0.425; Fe, r = 0.476; Mn, r = 0.687; and Zn, r = 0.416), significant ($P < 0.001$) positive relationships between N uptake in 2005 and uptake of nutrients other than N in 2005 (P, r = 0.897; K, r = 0.706; S, r = 0.835; Ca, r = 0.599; Mg, r = 0.655; Cu, r = 0.558; Fe, r = 0.458; Mn, r = 0.510; Zn, r = 0.572), and significant ($P < 0.001$) positive relationships between net uptake of nutrients other than N in 2005 (data not shown). Spraying plants with urea in the fall of 2004 decreased net N uptake ratios for most nutrients between Dec. 2004 and June 2005. Plants sprayed with urea in the fall of 2004 had lower N:P (6:1 vs. 8:1), N:K (0.6:1 vs. 0.8:1), N:S (5:1 vs. 8:1), N:Ca (0.9:1 vs. 1.1:1), N:Mg (2:1 vs. 3:1), N:Mn (7:1 vs. 9:1), and N:Zn (163:1 vs. 193:1). Urea sprays in 2004 had no influence on N:Cu (663:1) or N:Fe (9:1) between Dec. 2004 and June 2005. Rhododendron had lower N:P (6:1 vs. 8:1), N:Ca (0.8:1 vs. 1.2:1) and higher N:K (0.8:1 vs. 0.5:1), N:Mg (3:1 vs. 2:1), N:Cu (1023:1 vs. 310:1), N:Fe (9:1 vs. 6:1), and N:Zn (239:1 vs. 116:1) than azalea. There were no differences between cultivars in N:S (7:1) or N:Mn (9:1) between Dec. 2004 and June 2005.

Nutrient partitioning in June 2005. In general, 2005 leaves and roots contained the greatest proportion most nutrients (Tables 5 and 6). Old leaves on rhododendron accounted for more than 20% of total plant Ca and Mn; between 10% to 20% of total plant P, K, Mg, Cu, and Zn; and less than 10% of total plant S and Fe (Table 3). Between Dec. 2004 and June 2005, the Ca, Mg, and Mn content of 2003 leaves on rhododendron increased and the S content decreased (Table 3). Between Dec. 2004 and June 2005, the Ca, Mg, and Mn content of 2004 leaves on rhododendron increased and the P and S content decreased (Table 3). Spraying rhododendron with urea decreased the Fe content on 2003 and 2004 leaves in June 2005.

Spraying rhododendron with urea increased net uptake of P, K, and S between Dec. 2004 and June 2005 (Table 4), increased P content and allocation to 2005 stems and 2005 leaves, and increased S content and allocation to 2005 leaves (Tables 5 and 6). Urea increased K content of 2004 and 2005 stems of rhododendron and S content of 2005

Table 3. Nutrient content and nutrient partitioning of 2003 and 2004 leaves on *Rhododendron* 'H-1 P.J.M' in Dec. 2004 and June 2005 after leaves were sprayed (+U) or not (–-U) with urea in the fall of 2004.

	Content and proportion of total plant content[z]							
	Content (mg or μg)[y]				Proportion of total plant content (%)[y]			
	Dec. 2004		June 2005		Dec. 2004		June 2005	
Nutrient	–U	+U	–U	+U	–U	+U	–U	+U
—2003 leaves[y]—								
P (mg)	2.7 aA[x]	2.8 aA	1.7 aA	1.7 aA	9.5 a	9.4 a	3.3 a	3.0 a
K (mg)	11.9 bB	9.8 aA	14.3 aC	13.6 aC	12.2 a	12.4 a	4.6 a	4.2 a
S (mg)	1.9 aB	1.9 aB	1.1 aA	1.2 aA	8.0 a	8.2 a	2.2 a	2.3 a
Ca (mg)	11.3 aA	12.4 aA	25.2 aB	24.7 aB	12.8 a	12.6 a	7.0 a	6.4 a
Mg (mg)	2.6 aA	2.1 aA	4.7 aB	4.2 aB	11.2 a	10.8 a	4.6 a	4.3 a
Cu (μg)	12.3 aA	17.0 aA	16.0 aA	15.6 aA	7.2 a	6.8 a	3.3 a	3.0 a
Fe (μg)	307.5 aA	305.7 aA	382.6 bB	273.4 aA	6.3 a	6.7 a	0.8 a	1.1 a
Mn (mg)	1.9 aA	2.5 aA	5.4 aC	4.7 aB	9.8 a	11.2 b	8.3 a	8.1 a
Zn (μg)	54.1 aA	59.1 aA	72.4 aA	60.1 aA	8.4 a	8.9 a	3.8 a	3.9 a
—2004 leaves[x]—								
P (mg)	9.3 aB	10.3 bB	4.8 aA	5.0 aA	7.6 a	11.3 b	8.2 a	8.5 a
K (mg)	39.9 bB	35.1 aA	40.5 bB	39.3 bB	44.8 a	45.8 a	11.5 a	11.5 a
S (mg)	7.2 aC	7.6 aC	3.2 aA	4.0 bB	29.6 a	30.7 a	5.8 a	6.9 b
Ca (mg)	42.4 aA	45.9 aA	67.6 aB	73.9 bB	45.9 a	47.6 b	18.1 a	19.3 a
Mg (mg)	12.0 aA	11.8 aA	12.6 aB	12.4 aB	40.8 a	40.5 a	11.8 a	13.0 b
Cu (μg)	48.6 aA	50.7 aA	41.0 aA	47.6 aA	26.9 a	24.4 a	8.0 a	9.5 a
Fe (μg)	1159.9 aB	1111.2 aB	1059.4 bB	894.6 aA	23.3 a	25.1 a	1.9 a	4.1 a
Mn (mg)	7.2 aA	9.0 bB	14.2 aC	13.7 aC	36.4 a	42.4 b	21.5 a	25.4 a
Zn (μg)	210.5 aA	218.1 aA	201.8 aA	176.8 aA	31.6 a	33.2 a	9.9 a	11.5 a

[z]Urea treatments: +U = sprayed with 3% urea, –U = sprayed with water.

[y]2004 content means adjusted for 2004 N uptake from N04 treatments and growth in 2004. 2004 partitioning means adjusted for 2004 N uptake from N04 treatments and biomass partitioning in 2004. 2005 content means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and growth in 2005. 2005 partitioning means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and biomass partitioning in 2005.

[x]Means followed by the same lower case letter within a row, year, and variable (content or partitioning) are not significantly different. Means followed by the same upper case letter within a row for content are not significantly different (Bonferroni's test, $P < 0.05$, 2004, n = 25; 2005, n = 50). For content in 2003 leaves and 2004 leaves in 2004, respectively, multivariate analysis of covariance (MANCOVA) partial eta-squared ($\acute{\eta}_p^2$) values for effects of growth: 0.96, 0.97; 2004 N uptake: 0.50, 0.62; urea treatment (U): 0.65, 0.64. For partitioning to 2003 leaves and 2004 leaves in 2004, respectively, MANCOVA $\acute{\eta}_p^2$ values for effects of biomass partitioning: 0.97, 0.95; 2004 N uptake: 0.81, 0.40; U: 0.65, 0.75. For content in 2003 leaves and 2004 leaves in 2005, respectively, MANCOVA partial eta-squared ($\acute{\eta}_p^2$) values for effects of growth: 0.87, 0.80; 2004 N uptake: 0.43, 0.40; 2005 N uptake: 0.42, 0.54; U: 0.34, 0.42. For partitioning to 2003 leaves and 2004 leaves in 2005, respectively, MANCOVA $\acute{\eta}_p^2$ values for effects of biomass partitioning: 0.83, 0.88; 2004 N uptake: 0.32, 0.57; 2005 N uptake: 0.37, 0.54; U: 0.34, 0.42.

stems but had no influence on allocation to these structures (Tables 5 and 6). Urea decreased P allocation to roots of rhododendron but had no influence on P content. Spraying azalea with urea increased net P, K, S, Mg, and Mn uptake (Table 4) and increased S, Mg, and Mn content and allocation to 2005 leaves (Tables 5 and 6). In general, urea increased P, K, S, and Mg content of 2004 and 2005 azalea stems but did not influence allocation to stems.

Urea sprays in 2004 decreased uptake of Fe and Mn in 2005 by rhododendron and net Cu and Fe uptake by azalea (Table 4), but significant decreases in both content and allocation of these nutrients were not detectable within any specific structure (Tables 3, 5, and 6). Urea decreased Fe content of 2003 leaves, 2004 leaves, and roots of rhododendron but not Fe allocation to these structures. Urea decreased Mn content of roots, 2004 stems, and 2005 leaves of rhododendron but not Mn allocation to these structures. Urea decreased Cu and Fe content in roots and 2005 stems of azalea but not allocation of these nutrients to these structures. In general, urea increased content of Cu and Fe in 2003 stems, 2004 stems, and 2005 leaves of azalea but not allocation of these nutrients to these structures.

Spraying rhododendron with urea had no influence on net Ca or Zn uptake (Table 4) in 2005 but increased Ca content of 2004 leaves, 2005 stems, and 2005 leaves and increased Zn content and allocation in 2005 leaves (Tables 5 and 6). Spraying azalea with urea had no influence on net Ca or Zn uptake but decreased Ca content and allocation to roots and increased Zn content in stems. Urea treatments in 2004 had the greatest effect on P ($\acute{\eta}^2 = 0.06$), K ($\acute{\eta}^2 = 0.07$), S ($\acute{\eta}^2 = 0.11$), and Ca ($\acute{\eta}^2 = 0.05$) allocation to 2005 leaves; Mg ($\acute{\eta}^2 = 0.07$), Mn ($\acute{\eta}^2 = 0.11$), and Zn ($\acute{\eta}^2 = 0.06$) allocation to 2005 stems; Cu ($\acute{\eta}^2 = 0.06$) to 2004 stems; and Fe ($\acute{\eta}^2 = 0.11$) allocation to 2003 stems.

Differences in nutrient uptake between cultivars in 2005 (Table 4) were reflected by differences in content and allocation of nutrients to roots, stems, and 2005 leaves (Tables 3, 5, and 6). Net uptake of K, Mg, Cu, and Zn by azalea in 2005 was greater than rhododendron and azalea content and allocation of these nutrients to roots (K, Cu, Zn), old stems (K, Cu, Zn), 2005 stems (K), and 2005 leaves (K, Mg) was greater than rhododendron. Net uptake of S and Ca by rhododendron in 2005 was greater than azalea and rhododendron content; and content and allocation of these nutrients to 2004 stems (Ca), 2005 stems (Ca), and 2005 leaves (S, Ca) was greater than azalea. Net uptake of P, Fe, and Mn by rhododendron in 2005 was greater than azalea; however, these differences in uptake were not reflected by both higher content and allocation of these nutrients to any specific plant structure. Differences between cultivars had the greatest effect on S ($\acute{\eta}^2 = 0.23$), Mg ($\acute{\eta}^2 = 0.51$), Cu ($\acute{\eta}^2 = 0.47$), and Zn ($\acute{\eta}^2 = 0.52$) allocation to 2005 leaves; P ($\acute{\eta}^2 = 0.11$), K ($\acute{\eta}^2 = 0.07$), and Mn ($\acute{\eta}^2 = 0.44$) allocation to 2005 stems; Ca ($\acute{\eta}^2 = 0.25$) allocation to 2004 stems; and Fe ($\acute{\eta}^2 = 0.07$) allocation to 2003 stems.

Discussion

Effects of urea sprays in the fall on net nutrient uptake in 2004. Spraying rhododendron with urea in the fall alters the uptake of nutrients other than N although fertilizer application with other nutrients stopped before plants were sprayed with urea. Across a wide range of plant sizes and N status, urea sprays in the fall increased net P, Cu, and Mn uptake and decreased net K and Mg uptake during the year of urea application. Spraying rhododendron with urea in the fall had no influence on total plant biomass (Bi et al., 2007); therefore, differences in net nutrient uptake between plants sprayed with urea and plants that were not sprayed with urea were a result of physiological changes resulting from urea application.

Spraying plants with urea in the fall can increase the N content of several plant species (Bi et al., 2003; Klein and Weinbaum, 1984; Millard, 1996; Tagliavini et al., 1998), including *Rhododendron* (Bi et al., 2007). There is little published information describing the influence of fall urea sprays on the uptake of nutrients other than N (Fallahi et al., 2002; Yildirim et al., 2007). Lack of information on this subject may be result of the systems in which fall sprays with urea have been tested. Most studies have assessed the effects of urea sprays on bareroot, deciduous nursery plants where fall root uptake has generally been assumed to be minimal. Using different *Rhododendron* cultivars, Scagel et al. (2007) estimated that between 13% and 18% of the N uptake from soil that occurred over 9 months happened after N fertilizer applications stopped in September. Using ^{15}N ammonium nitrate, Grelet et al. (2001) reported N uptake by *V. myrtillus* and *V. vitis-idaea* occurred as late as November, and uptake between September and November accounted for ≈25% of total plant uptake. Andersen and Michelsen (2005) reported N uptake occurred after November in *Calluna*, even when soil temperatures were ≈0 °C. If roots are capable of taking up N in the fall and early winter, it stands to reason that late-season uptake of other nutrients may also occur.

Table 4. Net nutrient uptake of two *Rhododendron* cultivars between Dec. 2004 and June 2005 after leaves were sprayed (+U) or not (–U) with urea in the fall of 2004.

	Net uptake from June to Dec. 2004[z]									
	Rhododendron		Azalea		$\acute{\eta}^{2}$[w]					
Nutrient	–U	+U	–U	+U	G05	N04	N05	C	U	C*U
	—Unadjusted means[y]—									
P (mg)	28.0 a	34.1 b	27.1 a	36.4 b						
K (mg)	225.1 a	300.9 b	323.7 b	419.1 c						
S (mg)	25.7 a	41.8 b	25.1 a	40.6 b						
Ca (mg)	262.1 c	309.1 d	179.0 a	218.9 b						
Mg (mg)	68.9 a	75.7 a	86.8 b	118.8 c						
Cu (µg)	266.1 a	261.0 a	700.9 b	683.1 b						
Fe (mg)	44.1 b	30.9 a	38.3 b	33.7 a						
Mn (mg)	43.3 c	33.6 b	24.7 a	35.4 b						
Zn (µg)	1062 a	1039 a	1664 b	1980 c						
	—Adjusted means[x]—									
P (mg)	31.8 b	36.6 c	27.3 a	29.9 b	0.06	0.07	0.70	0.05	0.02	NS
K (mg)	250.3 a	300.7 b	333.7 c	383.3 d	0.28	0.08	0.16	0.22	0.09	NS
S (mg)	28.8 b	44.7 d	25.3 a	34.3 c	0.02	0.02	0.60	0.05	0.15	0.02
Ca (mg)	284.2 b	300.0 c	193.6 a	191.7 a	0.29	0.02	0.03	0.38	0.04	0.03
Mg (mg)	78.0 a	73.9 a	91.2 b	107.4 c	0.37	0.03	0.05	0.21	0.04	0.05
Cu (µg)	311.4 a	260.2 a	717.3 c	622.2 b	0.04	0.19	0.03	0.35	0.03	0.03
Fe (mg)	49.3 c	29.5 a	40.1 b	28.1 a	0.23	0.18	0.10	0.02	0.12	0.02
Mn (mg)	45.2 c	30.5 ab	27.9 a	33.4 b	0.24	0.28	0.02	0.07	0.03	0.16
Zn (µg)	1205 a	1029 a	1715 b	1796 b	0.12	0.03	0.04	0.27	0.02	0.02

[z]Cultivars: Rhododendron = *Rhododendron* 'H-1 P.J.M', Azalea = *Rhododendron* 'Cannon's Double'. Urea treatments: +U = sprayed with 3% urea, –U = sprayed with water.

[y]Unadjusted means. Means followed by the same letter within a row are not significantly different (Bonferroni's test, $P < 0.05$, n = 50).

[x]Means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and growth in 2005. Means followed by the same letter within a row are not significantly different (Bonferroni's test, $P < 0.05$, n = 50).

[w]Eta-squared ($\acute{\eta}^2$) values for effects from univariate results. C = cultivar, U = urea treatment, C*U = cultivar by urea treatment interaction, NS = nonsignificant effect. Multivariate analysis of covariance partial eta-squared ($\acute{\eta}_p{}^2$) values for effects of growth: 0.63; 2004 N uptake: 0.26; 2005 N uptake: 0.91, C: 0.81; U: 0.66; C*U: 0.51.

Foliar uptake, metabolism, and translocation of urea are rapid (Klein and Weinbaum, 1984; Nicoulaud and Bloom, 1996; Oland, 1963). Spraying leaves with urea increases activity of urease, a nickel-dependent metaolloenzyme, and results in increased accumulation of ammonium in leaves (Witte et al., 2002). The ammonium released may be assimilated in the leaves by Gln synthetase and transported to other plant structures (Lam et al., 1996) or foliar-applied urea can be directly transported into other plant structures (Nicouland and Bloom, 1996). The uptake of N by leaves may increase plant metabolic demand for other nutrients required to assimilate and translocate the N within the plant, thus causing increased uptake or altered allocation of other nutrients.

Urea sprays caused a 70% increase in plant N (Bi et al., 2007) and plants sprayed with urea took up 12% more Mn and 44% (azalea) more Cu (azalea) than plants that were not sprayed with urea. Both Cu and Mn are known to play integral roles in plant N metabolism (Dhillon et al., 1983). Increased Mn and Cu uptake by plants sprayed with urea may be a result of increased plant demand for these nutrients to assimilate and translocate N from urea. Copper and Mn also play roles in protection from oxidative stress [Mn superoxide dismutase (SOD) and Cu-SOD] (Van Camp et al., 1994). Urea can cause damage to plant cells and potentially release superoxide radicals (Witte et al., 2002). It is possible that increased Mn and Cu uptake may be a response to oxidative stress caused by urea sprays.

Plants sprayed with urea took up 10% more P than plants that were not sprayed with urea. Phosphorous is necessary for photosynthesis, protein formation, and almost all aspects of growth and metabolism in plants (Marschner, 1995). In our study, spraying *Rhododendron* with urea had no effects on plant growth; therefore, the resulting influence of urea sprays on P uptake was not related to growth. Increased P uptake may have been stimulated by metabolic demands associated with urea application or may be a result of other effects on plant activity. For example, foliar N applications are thought to increase higher root exudation that in turn stimulate uptake of nutrients from the soil through promotion of microbial processes (Yildirim et al., 2007). Storage of N in the fall is also linked to increased protein formation (Cook and Weih, 2005). Increased P uptake by plants sprayed with urea may be a result of increased P demand required for its role in energy cycling and protein formation. Storage of P in the fall has also been correlated with cold-hardiness (Chapin and Kedrowski, 1983) and increased plant N status has been associated with decreased cold tolerance in some species (Raese, 1997). It is possible that increased P uptake may also be a protective metabolic response to the increased N status.

Spraying plants with urea may also result in anatomical changes that influence uptake and allocation of other nutrients. Depending on the urea concentration, foliar sprays of urea can damage leaves (Bremner, 1995). Urea-induced phytotoxicity can cause marginal scorch or premature leaf abscission. This is generally a result of accumulation of urea (or low urease activity) rather than the accumulation of ammonia (the product of urease action) (Krogmeier et al., 1989). Even a low level of damage to leaf surfaces can result in nutrient losses from leaves. For example, nutrients such as potassium can be leached from leaves and stems by aqueous solutions, including rain, dew, and mist (Tukey and Mecklenburg, 1964). Although we did not see visible damage to leaves on plants sprayed with urea, it is possible that decreased K and Mg content (decreased net uptake) of plants sprayed with urea is a result of a low level of damage from the urea, making leaves more susceptible to leaching. Magnesium plays a significant role in chlorophyll synthesis and structure and K is essential for many metabolic processes, including phloem translocation, nitrate reduction, photosynthesis, respiration, and regulation of water balance and is an activator for several enzymes (Marschner, 1995). It is possible that decreased K and Mg status of plants sprayed with urea in the fall may result in an increased demand for these nutrients during the following growing season.

Effects of urea sprays in the fall on nutrient allocation in 2004. Spraying *Rhododendron* with urea in the fall alters nutrient content and allocation to different plant structures in the winter. Urea sprays had no influence on biomass allocation in either cultivar during the winter of 2004 or allocation of N to different structures in azalea (Bi et al., 2007). This suggests the influence of urea on allocation of nutrients other than N in azalea were independent of biomass or N allocation. In comparison, spraying rhododendron with urea decreased N allocation to 2003 leaves and increased N allocation to 2004 stems (Bi et al., 2007). This suggests the influence of urea on allocation of nutrients other than N in rhododendron may be dependant, in part, on the effects of urea on N allocation. Urea sprays influenced nutrient allocation in several ways, depending on the nutrient and the cultivar.

We hypothesized that if urea increased uptake of a nutrient, then content and allocation of that nutrient in the winter would increase in the primary storage structure for that nutrient. This hypothesis was supported for some nutrients. For example, spraying azalea with urea increased net P uptake; azalea roots contained the greatest proportion of total plant P. Urea sprays increased content and allocation of P to roots but not the content in stems. This suggests urea sprays influence storage or use of P primarily in roots of azalea. Similarly, urea sprays influence both the storage and use of Mn in 2004 stems of azalea and 2004 leaves of rhododendron, and these structures have increased demand or sink strength in response to urea. In comparison, spraying azalea with urea increased net Cu uptake; roots of azalea contained the greatest proportion of total plant Cu, but urea

Table 5. Nutrient content and nutrient partitioning of roots, 2003 stems and 2004 stems on two *Rhododendron* cultivars in June 2005 after leaves were sprayed (+U) or not (–U) with urea in the fall of 2004.

	Content and proportion of total plant content[z]							
	Content (mg or µg)[y]				Proportion of total plant content (%)[y]			
	Rhododendron		Azalea		Rhododendron		Azalea	
Nutrient	–U	+U	–U	+U	–U	+U	–U	+U
				—Roots—				
P (mg)	12.9 a[x]	12.3 a	15.8 b	16.0 b	26.4 b	23.6 a	26.3 b	27.5 b
K (mg)	32.3 a	33.5 a	60.1 b	63.8 b	11.6 a	11.7 a	13.3 b	14.4 c
S (mg)	16.4 a	18.0 ab	20.2 c	19.1 bc	35.1 ab	32.8 a	40.5 c	36.5 b
Ca (mg)	51.1 a	47.5 a	59.0 b	51.3 a	15.6 a	15.9 a	24.4 c	21.7 b
Mg (mg)	26.3 ab	22.2 a	29.9 b	27.5 ab	26.6 c	25.2 bc	23.1 ab	21.0 a
Cu (µg)	215.7 a	208.3 a	569.5 c	494.9 b	42.0 a	43.6 a	57.3 b	54.2 b
Fe (mg)	47.1 c	33.3 b	35.6 b	28.3 a	87.9 a	86.6 a	84.6 a	85.1 a
Mn (mg)	6.0 b	4.6 a	7.1 c	6.8 bc	11.3 a	11.8 a	15.3 b	18.7 c
Zn (µg)	697.4 b	558.5 a	1282.0 c	1290.2 c	39.0 b	36.1 a	50.6 b	52.7 b
				—2003 stems—				
P (mg)	1.5 a	1.6 a	1.7 ab	1.8 b	2.7 a	2.7 a	3.1 b	3.2 b
K (mg)	7.5 a	8.1 a	9.4 b	10.6 c	2.3 a	2.3 a	2.4 ab	2.6 b
S (mg)	1.0 a	1.1 a	0.8 a	1.0 a	2.1 a	1.9 a	1.9 a	2.2 a
Ca (mg)	5.5 a	5.4 a	5.1 a	5.1 a	1.7 a	1.8 a	2.4 b	2.3 b
Mg (mg)	1.4 a	1.3 a	1.2 a	1.4 a	1.4 b	1.4 b	1.1 a	1.2 a
Cu (µg)	22.1 a	22.2 a	30.1 b	40.0 c	3.5 a	3.9 a	3.2 a	4.5 a
Fe (µg)	263.2 b	270.3 b	184.5 a	242.7 b	0.7 a	1.1 a	0.4 a	0.8 a
Mn (mg)	1.8 a	1.4 a	1.3 a	1.3 a	3.2 a	3.2 a	3.3 a	4.0 a
Zn (µg)	69.4 a	62.2 a	70.0 a	90.1 b	3.2 a	3.5 a	3.0 a	3.7 a
				—2004 stems—				
P (mg)	7.5 a	8.0 a	7.9 a	8.7 b	12.9 a	12.7 a	14.4 b	14.9 b
K (mg)	37.2 a	40.0 b	46.1 c	51.9 d	10.9 a	10.8 a	11.7 b	12.0 b
S (mg)	5.4 bc	5.8 c	4.2 a	4.9 b	9.9 a	8.9 a	9.2 a	9.8 a
Ca (mg)	28.5 b	27.5 ab	25.7 a	25.0 a	7.6 a	7.0 a	11.3 b	10.6 b
Mg (mg)	7.0 a	6.3 a	6.4 a	7.1 a	6.6 b	6.3 b	5.7 a	5.6 a
Cu (µg)	81.1 a	88.5 a	148.0 b	204.1 c	16.3 a	18.2 a	15.8 a	18.5 a
Fe (µg)	1285.5 a	1355.7 a	1002.6 a	1180.1 a	3.1 a	5.0 a	2.7 a	3.8 a
Mn (mg)	9.4 b	7.1 a	6.9 a	6.5 a	14.8 a	13.8 a	15.3 a	18.6 b
Zn (µg)	257.0 a	252.0 a	357.2 b	458.5 c	14.2 a	15.0 a	15.3 a	16.9 a

[z]Cultivars: Rhododendron = *Rhododendron* 'H-1 P.J.M', Azalea = *Rhododendron* 'Cannon's Double'. Urea treatments: +U = sprayed with 3% urea, –U = sprayed with water.

[y]Content means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and growth in 2005. Partitioning means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and biomass partitioning in 2005.

[x]Means followed by the same letter within a row and variable (content or partitioning) are not significantly different (Bonferroni's test, $P < 0.05$, n = 50). For content in roots, 2003 stems, and 2004 stems, respectively, multivariate analysis of covariance (MANCOVA) partial eta-squared ($\acute{\eta}_p^2$) values for effects of growth: 0.12, 0.73, 0.92; 2004 N uptake: 0.50, 0.16, 0.33; 2005 N uptake: 0.76, 0.49, 0.63; cultivar (C): 0.66, 0.48, 0.69; urea treatment (U): 0.35, 0.43, 0.47; C*U: 0.30, 0.36, 0.35. For partitioning to roots, 2003 stems, and 2004 stems, respectively, MANCOVA $\acute{\eta}_p^2$ values for effects of biomass partitioning: 0.70, 0.87, 0.91; 2004 N uptake: 0.50, 0.36, 0.38; 2005 N uptake: 0.42, 0.38, 0.40; C: 0.76, 0.73, 0.84; U: 0.26, 0.32, 0.34; C*U: 0.30, 0.26, 0.25.

sprays increased content and allocation of Cu to stems. Urea sprays caused similar effects on content and allocation of P in 2003 stems and 2004 leaves of rhododendron. This suggests urea sprays influenced the demand for Cu in stems of azalea and P in 2003 stems and 2004 leaves of rhododendron. Increased demand for P, Mn, and Cu in specific structures may be a result of the role these nutrients play in N metabolism and transport (Dhillon et al., 1983; Marschner, 1995).

We also hypothesized that if urea decreased the net uptake of a nutrient, then content (but not allocation) of that nutrient in the winter would decrease in the primary storage structures for that nutrient. This hypothesis was partially supported. For example, spraying azalea with urea decreased net K uptake and azalea roots and 2004 stems contained the greatest proportion of total plant K. Urea sprays decreased K content of roots and 2004 stems but not K allocation to these structures. Urea sprays caused similar effects on content of K in 2004 leaves of rhododendron and Mg content in roots of azalea. This suggests urea sprays influence storage of K in *Rhododendron* and Mg in azalea but probably not the demand. In contrast, spraying rhododendron with urea decreased net Mg uptake and 2004 leaves contained the greatest proportion of total plan Mg. Urea sprays decreased Mg content of roots and 2003 leaves but not 2004 leaves. This suggests urea sprays influence both storage and demand for Mg in 2004 leaves.

Finally, we hypothesized that if urea had no influence on the uptake of a nutrient but altered demand for that nutrient in a specific structure, then content and allocation of that nutrient in the winter to that structure would also change. This hypothesis was supported for a few nutrients. For example, spraying azalea had no influence on net Fe uptake; however, urea decreased Fe content and allocation to roots and increased content and allocation to stems. Roots of azalea contained the greatest proportion of total plant Fe, suggesting that urea sprays influence the mobilization of Fe from storage as well as demand for Fe in stems. Urea sprays also decreased allocation to roots of rhododendron and increased allocation to 2003 stems. Translocation of Fe from roots occurs through active transporters that load Fe from the root cortical cells to the xylem (Briat and Lobréaux, 1997). Fe is necessary for many enzyme functions, a catalyst for the synthesis of chlorophyll, and a cofactor in several hormone interactions. It is also an important component of free radical protection in the form of Fe-SOD. It is possible that, similar to the effects of urea on Cu and Mn uptake and allocation, increased Fe allocation may be a result of increased requirements for protection from oxidative stress.

Urea sprays caused similar effects on content and allocation of Ca and Zn in *Rhododendron*. Spraying plants had no influence on net Zn uptake; however, urea decreased Zn allocation to roots and increased Zn content and allocation to stems. Spraying plants had no influence on net Ca uptake; however, urea increased Ca allocation to 2003 stems and decreased Ca allocation to 2004 stems. The extent to which N derived from urea metabolism is distributed into different organs appears to be regulated by their sink strength (Klein and Weinbaum, 1984). Our results on nutrient allocation, as a whole, support the hypothesis that urea sprays alter plant demand for certain nutrients other than required to metabolize, transport, or respond to urea sprays.

Differences between cultivars in nutrient status and allocation in 2004. In general, nutrient uptake by rhododendron in 2004 was greater than azalea; however, N uptake ratios for azalea were generally greater than those of rhododendron. This suggests that rhododendron was more efficient at using most nutrients for growth than azalea. There is little available information on the relationship between N-availability and uptake of nutrients other than N in container production of *Rhododendron*. Ristvey et al., (2007) showed that N influences the total growth of *Rhododendron* (azalea) and P uptake was a function of P fertilizer rate and growth as influenced by N rate. Dependence of P uptake on N availability is commonly linked to the growth effects from N availability. Most reported research on use of urea sprays to increase plant N status has been done with deciduous plants. Interestingly, in our study, net N uptake from urea was similar between the two cultivars (Bi et al., 2007) and the influence of urea on net uptake of most other nutrients was similar (except K and Cu).

Using the same cultivars grown at N rates similar to those in the 10 mM N04 treatment, Scagel et al. (2008) reported an average rate of P uptake between May and September was $\approx$0.10 mg·d^{-1} for rhododendron and 0.19 mg·d^{-1} for azalea. By comparison, between May and December in the present study, the P

Table 6. Nutrient content and nutrient partitioning of 2005 stems and 2005 leaves on two *Rhododendron* cultivars in June 2005 after leaves were sprayed (+U) or not (–U) with urea in the fall of 2004.

	Content and proportion of total plant content[z]							
	Content (mg or µg)[y]				Proportion of total plant content (%)[y]			
	Rhododendron		Azalea		Rhododendron		Azalea	
Nutrient	–U	+U	–U	+U	–U	+U	–U	+U
——2005 stems——								
P (mg)	7.0 a[x]	8.6 b	6.7 a	7.0 b	12.6 b	13.4 c	11.5 a	11.3 a
K (mg)	47.8 a	53.9 b	66.6 c	71.8 d	13.7 a	14.4 a	16.0 b	15.7 b
S (mg)	5.3 a	6.3 b	5.3 a	5.2 a	9.7 ab	9.3 a	10.8 b	9.8 ab
Ca (mg)	35.6 b	42.9 c	20.5 a	18.2 a	9.7 b	10.9 b	8.3 a	8.0 a
Mg (mg)	11.6 a	12.2 ab	11.3 a	13.2 b	10.7 b	12.1 c	9.4 a	9.8 a
Cu (µg)	33.8 a	36.9 a	53.0 c	45.9 b	7.1 b	8.0 b	5.1 a	5.2 a
Fe (µg)	326.2 a	232.5 a	603.9 b	384.7 a	0.7 a	1.1 a	1.5 a	1.2 a
Mn (mg)	7.2 a	6.5 a	6.6 a	7.8 a	11.9 a	12.9 a	17.4 b	17.7 b
Zn (µg)	119.8 a	138.1 a	183.2 b	206.6 c	6.9 a	8.4 b	7.7 ab	7.7 ab
——2005 leaves——								
P (mg)	21.0 a	27.1 c	22.4 ab	23.8 b	38.0 a	41.0 b	40.3 a	38.3 a
K (mg)	172.6 a	181.0 a	223.9 b	220.6 b	48.3 a	49.6 ab	53.8 c	50.5 b
S (mg)	19.0 b	31.9 d	15.2 a	22.9 c	40.2 c	44.3 d	30.8 a	36.8 b
Ca (mg)	165.9 c	177.4 c	114.8 a	129.2 b	43.7 a	45.8 a	48.6 b	51.6 c
Mg (mg)	47.9 a	44.3 a	63.77 b	75.4 c	41.9 a	44.8 a	54.6 b	57.4 c
Cu (µg)	98.4 a	106.8 a	104.5 a	130.1 b	22.9 b	22.0 b	10.9 a	11.5 a
Fe (µg)	1903.6 a	2177.8 a	1986.4 a	2712.2 b	6.7 b	7.4 b	4.7 a	6.9 a
Mn (mg)	19.2 b	15.3 a	15.0 a	19.2 b	31.2 a	30.1 a	38.6 b	43.2 c
Zn (µg)	429.4 a	524.0 b	370.9 a	424.2 a	27.4 b	31.0 c	14.8 a	14.0 a

[z]Cultivars: Rhododendron = *Rhododendron* 'H-1 P.J.M', Azalea = *Rhododendron* 'Cannon's Double'. Urea treatments: +U = sprayed with 3% urea, –U = sprayed with water.

[y]Content means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and growth in 2005. Partitioning means adjusted for 2004 N uptake from N04 treatments, 2005 N uptake from N05 treatments, and biomass partitioning in 2005.

[x]Means followed by the same letter within a row and variable (content or partitioning) are not significantly different (Bonferroni's test, $P < 0.05$, n = 50). For content in 2005 stems and 2005 leaves, respectively, multivariate analysis of covariance (MANCOVA) partial eta-squared ($\acute{\eta}_p^2$) values for effects of growth: 0.75, 0.67; 2004 N uptake: 0.42, 0.26; 2005 N uptake: 0.73, 0.78; cultivar (C): 0.82, 0.86; urea treatment (U): 0.26, 0.50; C*U: 0.33, 0.43. For partitioning to 2005 stems and 2005 leaves, respectively, MANCOVA $\acute{\eta}_p^2$ values for effects of biomass partitioning: 0.83, 0.74; 2004 N uptake: 0.21, 0.33; 2005 N uptake: 0.44, 0.47; C: 0.87, 0.93; U: 0.22, 0.30; C*U: 0.09, 0.39.

uptake by rhododendron and azalea was, respectively, ≈0.12 $mg \cdot d^{-1}$ and ≈0.13 $mg \cdot d^{-1}$. The slightly higher rate of P uptake by rhododendron in this study compared with Scagel et al. (2008) suggests that appreciable P uptake by this cultivar may occur in the fall and early winter, similar to the late season N uptake reported for evergreen *Rhododendron* cultivars by Scagel et al. (2007). The lower rate of P uptake for azalea, and most other macronutrients for both cultivars in this study compared with Scagel et al. (2008), may be a result of lower rates of nutrient uptake in the fall and early winter compared with in the summer; however, for azalea, it is also possible that this cultivar may lose nutrients resulting from leaf abscission or possibly root turnover. Root biomass of container-grown *Rhododendron* can also decrease during the early winter (Scagel et al., 2007). Since roots contain a large amount of most macronutrients during the winter, it is possible that root turnover during the winter may account for the lower average net nutrient uptake.

Interestingly, the rate of N uptake by azalea in Ristvey et al. (2007) was similar to the average rate of N uptake of azalea in our experiment at the 10 mM N04 rate (Bi et al., 2007); however, the rate of P uptake was higher than the rate we calculated for azalea from May through December (≈0.13 $mg \cdot d^{-1}$). These differences in P uptake could be the result of differences in cultivar and seasonal differences in photosynthesis, temperature, and moisture (Carrara et al., 2004), but there is also a possibility that uptake of P may be higher earlier in the growing season and that leaf abscission by azalea in our experiment resulted in some P loss.

The evergreen and deciduous cultivars used in this study stored nutrients differently. In general, azalea stored the greatest proportion of most nutrients in roots and 2004 stems and rhododendron tended to store more in 2004 leaves. For example, leaves on rhododendron accounted for more than 50% of total plant K, Ca, Mg, and Mn; between 30% and 40% of total plant S, Fe, and Zn; and less than 20% of total plant P. Deciduous and evergreen plants have different strategies for nutrient storage (Jonasson, 1989). Both deciduous and evergreen plant species store N during winter and remobilize the stored N for new growth in the following spring (Grelet et al., 2001; Millard, 1996). For perennial plants, recycled N may contribute a large proportion of the annual nutrient supply required to support new growth and allow plants to make the most efficient use of the available nutrients. Deciduous perennial species generally store N in stems and roots, whereas N storage in evergreen species may also occur in overwintering leaves (Bi et al., 2007; Millard, 1996; Stephens et al., 2001). Our results indicate that regardless of differences in N and biomass allocation between evergreen and deciduous cultivars, differences in allocation of nutrients other than N also exist.

Effects of urea sprays in the fall of 2004 on net nutrient uptake in 2005. Spraying *Rhododendron* with urea in the fall alters the uptake or demand for nutrients other than N during the following growing season and in both cultivars, plant growth in 2005 was positively correlated with N content of all plant structures in the winter of 2004 (Bi et al., 2007). This indicates that stored N is important for initial growth and development in *Rhododendron* similar to many other plant species (Millard, 1996). The positive correlations between uptake of nutrients other than N in the spring of 2005 with N status in 2004 or resulting plant growth in 2005 suggests that increased growth resulting from spraying plants with urea increases uptake and potentially demand for other nutrients. Nutrient uptake and demand are separate but related concepts. Nutrient uptake is driven by external abiotic and biotic factors, whereas nutrient demand is primarily driven by plant growth and metabolism. In our study, we realize that nutrient uptake and demand cannot be completely separated; differences in uptake could be a result of scaling effects of plant size on nutrient content (Righetti et al., 2007a, 2007b). One way to eliminate the influence of scaling on comparisons of content between individuals in which scaling is an issue is to use covariance models to account for these differences.

Even after accounting for differences in plant size and N status, urea sprays increased uptake of P, K, and S for both cultivars during the following spring; increased spring uptake of Ca by rhododendron; and increased spring uptake of Mg and Mn by azalea. This indicates that although the plant N status plays a significant role in growth and uptake of nutrients other than N during the spring, there are other factors that also influence nutrient uptake or demand during this time. From an applied perspective, this also indicates that when growers spray plants with urea in the fall, spring fertilizer practices may need to be modified to account for increased uptake or demand of certain nutrients.

There numerous speculative reasons why spraying plants with urea may alter nutrient uptake and allocation in the fall and early winter; however, one important result of this increased uptake or altered nutrient allocation is to determine whether it influences plant growth or performance during the following growing season. Increased nutrient uptake in the fall after urea sprays have the potential to decrease plant uptake or demand for these nutrients during the following growing season. For example, spraying rhododendron with urea in the fall increased net uptake of Mn in 2004 and decreased Mn uptake in the spring of 2005, and spraying azalea with urea in the fall increased net uptake of Cu in 2004 and decreased Cu uptake in the spring of 2005. One reason urea sprays may decrease uptake of Mn and Cu during the following growing season may be decreased demand; however, urea sprays may also alter root exudation processes (Yildirim et al., 2007) that influence rhizosphere pH and availability of certain nutrients. For example, spraying plants with urea decreased uptake of Fe and Mn by rhododendron during spring of the following year and decreased spring uptake of Cu and Fe. Availability of Cu, Fe, and Mn for plant uptake is commonly limited by the pH of the medium surrounding the roots. Optimum availability of these nutrients is at pH 4.5 to 5.5. Foliar sprays of urea have been shown to increase soil pH (Smith et al., 1991). It is possible that decreased uptake of Cu, Fe, and Mn during the spring are a result of the influence of urea on growing substrate pH and that urea sprays may actually result in deficiencies of these nutrients during spring growth. Further research is needed to understand how urea sprays may have a potential negative impact on uptake of certain nutrients during the next growing season.

Spraying plants with urea in the fall has been reported to improve plant growth and performance during the next growing season (Bi et al., 2003; Klein and Weinbaum, 1984; Millard, 1996; Tagliavini et al., 1998). However, there are some reports that fall foliar sprays of urea have a variable effect on plant growth the next year. Timing of application, urea concentration, and environmental conditions are known to influence plant response to foliar sprays of urea (Bi et al., 2004; Bremner, 1995; Xia and Cheng, 2004). It is possible that part of this variation in response to urea sprays may be a result of the effect of urea on other plant nutrients. For example, spraying rhododendron with urea in the fall increased uptake of specific nutrients and allocation to storage; however, spraying azalea with urea actually cause losses of specific nutrients (e.g., K). Potassium is an essential element for plants. Fertilizer application rates are often based on optimal N rate and not plant K requirements, which can lead to excesses or shortages of K depending on the plant species (Öborn et al., 2005). Plants deficient in K can be more susceptible to drought, pathogen, and low-temperature damage. A better understanding of the physiological changes that occur in response to urea sprays beyond just N metabolism might be useful in explaining some of the variation in response to this practice.

Effects of urea sprays in the fall of 2004 on nutrient allocation in 2005. Spraying *Rhododendron* with urea in the fall of 2004 altered nutrient content and allocation to different plant structures during the next spring. Urea sprays in 2004 caused similar decreases in biomass and N allocation to roots and 2003 stems of both cultivars in the spring of 2005, similar increases in biomass and N allocation to new growth, and had no influence on biomass and N allocation to 2004 stems (Bi et al., 2007). Spraying rhododendron with urea in 2004 also decreased biomass and N allocation to old leaves in 2005 (Bi et al., 2007). This suggests the influence of urea on allocation of nutrients other than N may be dependent, in part, on the effects of urea on biomass and N allocation. Urea sprays influenced nutrient allocation in several ways, depending on the nutrient and the cultivar.

We hypothesized that if urea increased uptake and demand for a nutrient, then content and allocation of that nutrient in the spring would increase primarily in the structures with the greatest requirements for that nutrient (highest sink strength). This hypothesis was supported for some nutrients. For example, spraying rhododendron with urea in the fall increased S uptake in the spring, and plants allocated more S to old leaves and 2005 stems and leaves. This suggests urea sprays increase the demand for S in these structures. This is not surprising because we can predict that new growth (2005 stems and leaves) should be strong sinks for S and photosynthetically active structures such as old leaves may have an increased S demand because of the essential role of S in several enzymes and the production chlorophyll (Marschner, 1995). Urea sprays caused similar effects on demand for P by new growth of rhododendron; for Ca by new stems and old leaves on rhododendron; and for S, Mg, and Mn by new leaves of azalea. In comparison, spraying *Rhododendron* with urea increased K uptake and increased K content in stems but had no influence on K allocation to stems. This suggests that although K uptake was increased by urea sprays, this increase in uptake was not the result of an increase in plant demand. Demand for K in stems was high regardless of urea sprays. These results indicate that when growers spray plant in the fall, they may need to consider new nutrient management strategies during the spring to ensure that the increased demands by new growth for nutrients other than N are met.

We also hypothesized that if urea decreased uptake and demand for a nutrient, then allocation but not content of that nutrient in the spring would decrease in the structures with the lowered requirements for that nutrient. This hypothesis was not supported by our data. Instead, we found that decreased uptake was only associated with decreased content. For example, spraying rhododendron with urea in 2004 decreased uptake of Mn in the spring of 2005 and decreased Mn content in roots, old leaves, 2004 stems, and 2005 leaves. The 2005 leaves of rhododendron contained the greatest proportion of total plant Mn. Urea sprays caused similar decreases in content of Fe and Cu in roots and new stems of azalea. Roots of azalea contained the greatest proportion of total plant Fe and Cu. These results suggest that spraying rhododendron may either increase the efficiency of Mn, Fe, and Cu use or, more likely, that urea sprays in the fall may result in deficiency. Further research is needed to understand whether urea sprays actually increase the efficiency at which certain nutrients are used or whether they result in deficiency of these nutrients.

Finally, we hypothesized that if urea had no influence on the uptake of a nutrient but altered demand for that nutrient in a specific structure, then content and allocation of the nutrient to that structure would also change. This hypothesis was supported for a few nutrients. For example, spraying rhododendron with urea had no influence on Zn uptake in the spring; however, urea increased Zn content and allocation to new leaves and decreased Zn content and allocation to roots. Roots of rhododendron contained the greatest proportion of total plant Zn, suggesting that urea sprays influence the mobilization of Zn from storage in roots to meet an increased demand for Zn in new leaves. Urea sprays caused similar effects of mobilization of Ca from roots to new leaves in azalea. Our results on nutrient allocation, as a whole, support the hypothesis that urea sprays alter plant demand for certain nutrients as a result of increased growth or metabolism; however, urea sprays may also result in the deficiency of certain nutrients.

Differences between cultivars in nutrient status and allocation in 2005. In general, rhododendron took up more P, S, Ca, Fe, and Mn than azalea during the spring and azalea took up more K, Mg, Cu, and Zn than rhododendron. The N uptake ratios for P and Ca were lower for rhododendron than azalea and N uptake ratios for most other nutrients were higher for rhododendron than azalea. This suggests that in the spring, rhododendron was more efficient at P and Ca uptake than azalea and azalea was generally more efficient at uptake of other nutrients. Nutrient allocation between structures in June was very similar between cultivars, with 2005 leaves and roots accounting for the greatest proportion of total plant nutrient content. In evergreen plants, the overwintering leaves are considered a reservoir of resources that can support early spring growth (Chapin et al., 1990; Millard, 1996). Interestingly, between Dec. 2003 and June 2004, there appeared to be both nutrient import as well as export from 2003 and 2004 leaves of the evergreen *Rhododendron* cultivar we used. The S content of 2003 and 2004 leaves and P content in 2004 leaves decreased between Dec. 2003 and June 2004, suggesting S and P were exported to other structures in the plant. The K content of 2003 leaves and Ca, Mg, and Mn content of 2003 and 2004 leaves decreased between Dec. 2003 and June 2005, suggesting these nutrients were imported into old leaves. Leaf retention on evergreen *Rhododendron* can vary with cultivar, species, and environmental conditions. Carbon fixation by old leaves on evergreen *Rhododendron* is known to contribute significantly to growth of both vegetative and reproductive structures during the spring (Karlsson, 1994a, 1994b; Pasche et al., 2002); therefore, nutrient import into old leaves may be required for carbon metabolism. Our results indicate that regardless of differences in N and biomass allocation between evergreen and deciduous cultivars, differences in allocation of nutrients other than N also exist.

Pulses of nutrient availability characterize many seasonal environments and can result in a strong asynchrony between nutrient uptake and demand by plants (Chapin et al., 1990). Others have reported seasonal changes in the rate of N uptake, loss, and remobilization by *Rhododendron* but not for other nutrients (Karlsson, 1994a; Lamaze et al., 2003; Pasche et al., 2002). In most of these reports, the nutrient uptake rates were probably a response to the seasonality of nutrient availability that occurs in natural ecosystems in response to the multitude of abiotic and biotic factors. Compared with natural ecosystems, during nursery production of container-grown *Rhododendron* there is probably a lower variation in the seasonality of nutrient availability and nutrient uptake; therefore, extrapolation of uptake rates from natural ecosystem data are probably not appropriate for nutrient management in container production systems.

Rates of P uptake between Dec. 2004 and June 2005 by rhododendron and azalea were $\approx$0.07 $mg \cdot d^{-1}$. This rate is lower than the rates of P uptake report by Scagel et al. (2008) from May to September and the rates reported by Ristvey et al. (2007) from March to August. Our average P uptake for the first 6 months of 2005 is probably a lower rate of P uptake compared with these studies because it is a reflection of the lower rates of P uptake that occur during the cool winter months. To develop a more complete understanding of the dynamics of nutrient uptake, loss, and remobilization during the fall and early winter, sequential harvests of plants during the fall and winter are required. In the current study, estimated uptake rates were calculated based on the change in nutrients over an extended amount of time (e.g., several months) and although this can give a general indication of nutrient uptake rates, it lacks the sensitivity required for developing nutrient management guidelines.

Effects of urea sprays in the fall on relationships between nutrients. There were positive relationships between net uptake of nutrients in 2004, and uptake ratios between N and other nutrients in 2004 were increased by spraying *Rhododendron* with urea. In contrast, there were positive relationships between net uptake of nutrients in 2005, and uptake ratios between N and other nutrients 2005 were decreased by spraying *Rhododendron* with urea. The balance between different nutrients can play an important role in development of nutritional problems that limit crop productivity or quality (Ingestad, 1991). The ratio of N:P has been suggested as a tool for analyzing nutrient limitations and determining fertilizer requirements in agriculture and forestry (Güsewell et al., 2003; Koerselman and Meuleman, 1996;Tessier and Raynal, 2003). Other nutrient ratios indicating nutrient covariation have also been proposed for use in plant production (Sinclair et al., 1997).

Scagel et al. (2008) reported N ratios for container-grown 1-year-old *Rhododendron* in the fall of greater than 14:1 (N:P), 1.5:1 (N:K), 10:1 (N:S), 3:1 (N:Ca), and 6:1 (N:Mg) when plants were grown without N limitation and less than 9:1 (N:P), 1:1 (N:K), 8:1 (N:S), 2:1 (N:Ca), and 4:1 (N:Mg) when plants were N-deficient. The N uptake ratios we calculated from our study in Dec. 2004 were similar or greater than those reported for by Scagel et al. (2008). When plants were sprayed with urea, the N:K, N:S, N:Ca, and N:Mg ratios in Dec. 2004 were much greater than those reported by Scagel et al. (2008) suggesting that the influence of urea on N uptake has the potential to result in a nutrient balance that shifts cause plants to be deficient in K, S, Ca, and Mg and increase demand for these nutrients during the next growing season. These same ratios in June 2005 were generally much lower than those in Dec. 2004 and those reported by Scagel et al. (2008) indicating the dynamic aspect of nutrient ratios. Lower N uptake ratios in 2005 for plants sprayed with urea in 2004 supports others (Bi et al., 2003, 2007; Xia and Cheng, 2004; Tagliavini et al., 1998) who report that urea sprays decrease reliance of plants on N from soil uptake in the spring.

The influence of urea sprays on fall uptake of nutrients by *Rhododendron* is not solely driven by the N status of the plant. Increased N availability from N04 fertilizer application increased the uptake of most nutrients by container-grown *Rhododendron* in 2004 (data not shown). This is not surprising because increased N availability from N04 fertilizer applications increased biomass accumulation (Bi et al., 2007), thus driving demand for increased uptake of other nutrients. The rate of biomass accumulation (C accumulation) is a reflection of photosynthetic rate, and N has been shown to influence the photosynthetic capacity and nutrient use efficiency of *Rhododendron* (Karlsson, 1994b). The lack of interaction between N04 rate and urea treatment suggests that spraying plants with urea must alter other aspects of plant physiology beyond just N metabolism.

In conclusion, our results indicate spraying *Rhododendron* with urea in the fall can increase net uptake of P, Cu, and Mn during the year of application and decrease net uptake of K and Mg. Plants sprayed with urea in the fall can have an increased demand for several nutrients the next spring; therefore, when using urea sprays in the fall as a N management technique during nursery production, spring fertilizer practices may require adjustment to ensure optimal growth. A better understanding of the physiological changes induced by urea sprays is required for predicting plant response to this practice.

Literature Cited

Andersen, L.C. and A. Michelsen. 2005. Off-season uptake of nitrogen in temperate heath vegetation. Oecologia 144:585–597.

Bi, G., C.F. Scagel, L. Cheng, S. Dong, and L.H. Fuchigami. 2003. Spring growth of almond nursery trees depends upon both nitrogen reserves and spring nitrogen application. J. Hort. Sci. Biotechnol. 78:853–858.

Bi, G., C.F. Scagel, L. Cheng, S. Dong, and L.H. Fuchigami. 2004. Soil and foliar nitrogen supply affects the composition of nitrogen and carbohydrates in young almond trees. J. Hort. Sci. Biotechnol. 79:175–181.

Bi, G., C.F. Scagel, L.H. Fuchigami, and R.P. Regan. 2007. Rate of nitrogen application during the growing season alters response of container-grown rhododendron and azalea to foliar urea application in the autumn. J. Hort. Sci. Biotechnol. 82:753–763.

Bremner, J.M. 1995. Recent research on problems in the use of urea as a nitrogen fertilizer. Fert. Res. 42:321–329.

Briat, J.-F. and S. Lobréaux. 1997. Iron transport and storage in plants. Trends Plant Sci. 2:187–193.

Cabrera, R.I., R.Y. Evans, and J.L. Paul. 1993. Leaching losses of N from container-grown roses. Sci. Hort. 53:333–345.

Carrara, A., I.A. Janssens, J.C. Yuste, and R. Ceulemans. 2004. Seasonal changes in photosynthesis, respiration, and NEE of a mixed temperature forest. Agr. For. Meterol. 126: 15–31.

Chapin F.S. III and R.A. Kedrowski. 193. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecol. 64:376–391.

Chapin F.S. III, E. Schulze, and H.A. Mooney. 1990. The ecology and economics of storage in plants. Ann. Rev. Ecol. System. 21:423–447.

Cheng, L., S. Dong, S. Guak, and L.H. Fuchigami. 2001. Effects of nitrogen fertigation on reserve nitrogen and carbohydrate status and regrowth performance of pear nursery plants. Acta Hort. 564:51–62.

Cook, J.E.K. and M. Weih. 2005. Nitrogen storage and seasonal nitrogen cycling in Populus: Bridging molecular physiology and ecophysiology. New Phytol. 167:19–30.

del Amor, F.M., S. Molina, M.F. Espinosa, P. Varó, and M.C. Gómez. 2007. Foliar applications of urea as at tool to reduce nitrate contamination in greenhouse crops. Acta Hort. 761: 403–408.

Dhillon, K.S., B.A. Yagodeen, and A.C. Pleshkov. 1983. Micronutrients and nitrogen metabolism. I. Effects of different levels of micronutrients on nitrogen constituents in maize plants. Plant Soil 73:355–363.

Dong, S., D. Neilsen, G.H. Neilsen, and L.H. Fuchigami. 2004. Foliar N application reduces soil NO_3^--N loss in apple orchards. Plant Soil 268:357–366.

Fallahi, E., H. Khemira, T.L. Righetti, and A.N. Azarenko. 2002. Influence of foliar application of urea on tree growth, fruit quality, leaf minerals, and distribution of urea-derived nitrogen in apples. Acta Hort. 594:603–610.

Grelet, G., I.J. Alexander, and M.F. Proe. 2001. Leaf habit influences nitrogen remobilization in *Vaccinium* species. J. Expt. Bot. 52:993–1002.

Güsewell, S., U. Bollens, P. Ryser, and F. Klötzli. 2003. Contrasting effects of nitrogen, phosphorus and water regime on first-year and second-years growth of 16 wetland plant species. Funct. Ecol. 11:754–765.

Han, Z., X. Zeng, and F. Wang. 1989. Effects of autumn foliar application of 15N-urea on nitrogen storage and resuse in apple. J. Plant Nutr. 12:675–685.

Henry, P.H., F.A. Blazich, L.E. Henesley, and R.D. Wright. 1992. Nitrogen nutrition of containerized Eastern red cedar. I. Growth, mineral nutrient concentrations, and carbohydrate status. J. Amer. Soc. Hort. Sci. 117:563–567.

Hoagland, D.R. and D.I. Arnon. 1950. The water-culture method for growing plants without soil. Calif. Agr. Exper. Stat. Circ. 347:1–32.

Ingetstad, T. 1991. The influence of plant nutrition on biomass allocation. Ecol. Appl. 1:168–174.

Jonasson, S. 1989. Implications of leaf longevity, leaf nutrient re-absorption and translocation for the resource economy of five evergreen plant species. Oikos 56:121–131.

Karlsson, P.S. 1994a. The significance of internal nutrient cycling in branches for growth and reproduction of *Rhododendron lapponicum*. Oikos 70:191–200.

Karlsson, P.S. 1994b. Photosynthetic capacity and photosynthetic nutrient use efficiency of *Rhododendron lapponicum* leaves as related to leaf nutrient status, leaf age and branch reproductive status. Funct. Ecol. 8:694–700.

Klein, I. and S.A. Weinbaum. 1984. Foliar application of urea to olive: Translocation of urea nitrogen as influenced by sink demand and nitrogen deficiency. J. Amer. Soc. Hort. Sci. 109:356–360.

Koerselman, W. and A.F.M. Meuleman. 1996. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33:1441–1450.

Krogmeier, M.J., G.W. McCarty, and J.M. Bremner. 1989. Phytotoxicity of foliar-applied urea. Proc. Natl. Acad. Sci. USA 86:8189–8191.

Lam, H.-M., K.T. Coschigano, I.C. Oliveira, R. Melo-Oliveira, and G.M. Coruzzi. 1996. The molecular-genetics of nitrogen assimilation into amino acids in higher plants. Plant Physiol. Mol. Biol. 47:569–593.

Lamaze, T., F. Pashe, and A. Pornon. 2003. Uncoupling nitrogen requirements for spring growth from root uptake in a young evergreen shrub (*Rhododendron ferrugineum*). New Phytol. 159:637–644.

Marschner, H. 1995. Mineral nutrition of higher plants. 2nd Ed. Academic Press, San Diego, CA.

Millard, P. 1996. Ecophysiology of the internal cycling of nitrogen for tree growth. J. Plant Nutr. Soil Sci. 159:1–10.

Nicoulaud, B.A.L. and A.J. Bloom. 1996. Absorption and assimilation of foliarly applied urea in tomato. J. Amer. Soc. Hort. Sci. 121:1117–1121.

Öborn, I., Y. Andrist-Rangel, M. Askekaard, C.A. Grant, C.A. Watson, and A.C. Edwards. 2005. Critical aspects of potassium management in agricultural systems. Soil Use Mgt. 21:102–111.

Oland, K. 1963. Responses of cropping apple trees to post-harvest urea sprays. Nature 198:1282–1283.

Pasche, F., A. Pornon, and T. Lamaze. 2002. Source-sink nitrogen relationships between the different leaf generations and the growing shoots in the evergreen shrub *Rhododendron ferrugineum* L.: A 15N study. New Phytol. 154:99–105.

Pierce, C.A., R.A. Block, and H. Aguinis. 2004. Cautionary not on reporting eta-squared values from multifactor ANOVA designs. Educ. Psycholog. Measurement 64:916–924.

Raese, J.T. 1997. Cold tolerance, yield, and fruit quality of ‘d’Anjou’ pears influence by nitrogen fertilizer rates and time of application. Plant Nutrition 20:1007–1025.

Righetti, T.L., D. Dalthorp, D.R. Sandrock, B. Strik, and P. Banados. 2007a. Slope-based and ratio-based approaches to determine fertilizer-derived N in plant tissues for established perennial plants. J. Hort. Sci. Biotechnol. 82:641–647.

Righetti, T.L., D.R. Sandrock, G. Strik, and C. Vasconcellos. 2007b. Analysis of ratio-based responses. J. Amer. Soc. Hort. Sci. 132:3–13.

Rikala, R., J. Heiskanen, and M. Lahti. 2004. Autumn fertilization in the nursery affects growth of *Picea abies* container seedlings after transplanting. Scand. J. For. Res. 19:409–414.

Ristvey, A.G., J.D. Lea-Cox, and D.S. Ross. 2007. Nitrogen and phosphorus uptake efficiency and partitioning of container-grown azalea during spring growth. J. Amer. Soc. Hort. Sci. 132:563–571.

Scagel, C.F., G. Bi, L.H. Fuchigami, and R.P. Regan. 2007. Seasonal variation in growth, nitrogen uptake and allocation by container-grown evergreen and deciduous *Rhododendron* cultivars. HortScience 42:1440–1449.

Scagel, C.F., G. Bi, L.H. Fuchigami, and R.P. Regan. 2008. Nitrogen availability alters nutrient uptake and demand in deciduous and evergreen container-grown *Rhododendron*. J. Environ. Hort. (in press).

Sinclair, A.G., J.D. Morrison, C. Smith, and K.G. Dodds. 1997. Determination of optimum nutrient element ratios in plant tissue. J. Plant Nutr. 20:1069–1083.

Smith, C.J., J.R. Freney, R.R. Sherlock, and I.E. Galbally. 1991. The fate of urea nitrogen applied in a foliar spray to wheat at heading. Nutrient Cycling Agroecosystems 28:129–138.

Stephens, D.W., P. Millard, M.H. Turnbull, and D. Whitehead. 2001. The influence of nitrogen supply on growth and internal recycling of nitrogen in young *Nothofagus fusca* trees. Aust. J. Plant Physiol. 28:249–255.

Tagliavini, M., P. Millard, and M. Quartieri. 1998. Storage of foliar absorbed nitrogen and remobilization for spring growth in young nectarine (*Prunus persica* var. *nectarina*) trees. Tree Physiol. 18:203–207.

Tessier, J.T. and D.Y. Raynal. 2003. Use of nitrogen and phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. J. Appl. Ecol. 40:523–534.

Tukey, H.B. and R.A. Mecklenburg. 1964. Leaching of metabolites from foliage and subsequent reabsorption and redistribution of the leachate in plants. Amer. J. Bot. 51:737–742.

Van Camp, W., H. Willekens, C. Bowler, M. Van Montagu, D. Inzé, P. Reupold-Popp, H. Sandermann, Jr., and C. Langebartels. 1994. Elevated levels of superoxide dismutase protect transgenic plants against ozone damage. Nat. Biotechnol. 12:165–168.

Witte, C.-P., S.A. Tiller, M.A. Taylor, and H.V. Davies. 2002. Leaf urea metabolism in potato. Urease activity profile and patterns of recovery and redistribution of 15N after foliar urea application in wild-type and urease-antisense trangenics. Plant Physiol. 128:1129–1136.

Xia, G.H. and L. Cheng. 2004. Foliar urea application in the fall affects both nitrogen and carbon storage in young ‘Concord’ grapevines grown under a wide range of nitrogen supply. J. Amer. Soc. Hort. Sci. 129:653–659.

Yildirim, E., I. Guvenc, M. Turan, and A. Karatas. 2007. Effect of foliar urea application on quality, growth, and mineral uptake and yield of broccoli (*Brassica oleraceae* L., var. *italica*). Plant Soil Environ. 53:120–128.