

Rate of nitrogen application during the growing season alters the response of container-grown rhododendron and azalea to foliar application of urea in the Autumn

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SUMMARY

One-year-old rhododendron (*Rhododendron* ‘H-1 P.J.M.’) and azalea (*Rhododendron* ‘Cannon’s Double’) plants grown at different nitrogen (N) fertilisation rates were used to assess the influence of soil N applications during the growing season, and foliar applications of urea in the Autumn, on N uptake and accumulation, and plant growth in the following Spring. N uptake efficiency declined linearly during the first growing season with an increasing rate of N fertilisation. For both cultivars, foliar urea application in the Autumn significantly increased plant N content without affecting plant size, regardless of plant N status. Leaves of rhododendron accumulated more N than other plant structures. Plants sprayed with foliar urea in the Autumn had more new growth the following Spring than plants receiving no urea, regardless of whether the plants received fertiliser in the Spring. For azalea, N uptake in the Spring was, in general, not affected by applications of urea during the previous year. For rhododendron, urea application in the Autumn decreased N uptake the following Spring. For both cultivars, increasing N availability during the growing season increased the ratio of above-ground to below-ground dry weight. Our results suggest that combining optimum N applications during the growing season with foliar application of urea in the Autumn can improve N uptake efficiency, increase N storage, and optimise growth in *Rhododendron*.

Environmental concerns about N run-off from container nursery production have increased the need for improved fertilisation practices that increase the efficiency of fertiliser use and decrease the potential for environmental contamination, without impacting crop productivity or quality (Yeager *et al.*, 1993). Low recovery of N from fertiliser is common with bareroot and container-grown nursery stock (Cabrera, 2003; Catanzaro, 1998; Colangelo and Brand, 2001; Juntunen *et al.*, 2003). Low N uptake efficiency suggests fertilisation practices can be improved by taking into account when plants take up available N most efficiently, and what method of N application is most effective for promoting plant growth (Alt, 1998; Salifu and Timmer, 2003). In woody plants, early growth relies on remobilisation of N reserves before substantial root uptake occurs, which results in a strong relationship between plant growth and N reserves (Cheng *et al.*, 2001; Henry *et al.*, 1992; Millard, 1996).

The method of N application also greatly influences plant quality, through effects on growth and storage of N (Habib, 1993). Liquid application of N, or incorporation of N-containing fertilisers in the substrate, are traditional methods to supply N to plants in container production. With bareroot nursery trees, N application to soil usually

has a high risk of losses due to leaching, while foliar N application can have a higher recovery rate (Klein and Weinbaum, 1984; Rosecrance *et al.*, 1998; Shim *et al.*, 1972; Tagliavini *et al.*, 1998). Foliar fertilisation in the Autumn is a common strategy used with fruit tree nursery stock to decrease the potential for N-leaching and problems with hardiness sometimes associated with high soil N in the Autumn, and to improve plant performance the following Spring (Bi *et al.*, 2003; Dong *et al.*, 2005; Rikala *et al.*, 2004).

Deciduous perennial species store N in stems and roots (Millard, 1995) while N storage in evergreen species may also occur in over-wintering leaves (Stephens *et al.*, 2001). Both deciduous and evergreen plant species store N during the Winter and remobilise the stored N for new growth in the following Spring (Grelet *et al.*, 2001; Millard, 1995). 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 available nutrients. The ability of foliar N applications to increase N storage, and improve the quality of container-grown ornamental nursery stock, has not been investigated. Comparing the responses of deciduous and evergreen plants to Autumn applications of foliar urea could be useful for optimising N-fertilisation strategies based on plant growth habit.

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The genus *Rhododendron* consists of evergreen and deciduous species and hybrids commonly known as rhododendrons and azaleas. Improper fertilisation of *Rhododendron* during production can decrease stock quality and productivity. Excessive soil fertilisation can damage fine roots near the surface of the soil, and soil fertilisation in late Summer promotes tender growth and slows the development of hardiness, resulting in the death of buds for next year's flowers or shoots (Reiley, 1992). While high N promotes foliage growth, it can also inhibit flower bud production and increase whitefly infestation. In contrast, too little N can cause premature leaf loss (Reiley, 1992). There is little published literature on N-use in nursery production of *Rhododendron* (Witt, 1994). Knowledge of N uptake and use by *Rhododendron* is available from natural ecosystems (Lamaze *et al.*, 2003; Pasche *et al.*, 2002); however, this information may not be applicable to the environmental conditions of container nursery production. The different growth habits (e.g., deciduous *vs.* evergreen) found within this genus could alter resource-use in plants (Grelet *et al.*, 2001; Kloeppel *et al.*, 2000; Takashima *et al.*, 2004). Information on how *Rhododendron* responds to Autumn application of foliar urea will aid in the development of fertiliser management strategies.

Using deciduous and evergreen cultivars of container-grown *Rhododendron*, the objectives of this study were to determine: (i) whether N application rate during the growing season influenced plant response to foliar urea application in the Autumn; and (ii) whether plant N-status in the Winter influenced plant reliance on fertiliser for growth the following Spring.

MATERIALS AND METHODS

Plant culture and treatments

Year 1 (2004): One-year-old plants of *Rhododendron* 'H-1 P.J.M.' (rhododendron - evergreen) and *Rhododendron* 'Cannon's Double' (azalea - deciduous) were transplanted into 7.6 l polyethylene pots (1 plant/pot) containing a 2:1:1 (v/v/v) mix of peat moss:pumice:sandy loam soil in late May 2004 and grown outdoors in a lathe house (40% shading) at Corvallis, OR, USA (45° 59' 04" N; 123° 27' 22" W). The substrate for this study was chosen to minimise N availability to plants. Thirty plants of each cultivar were assigned at random to one of five groups and fertilised two-times a week for 5 weeks, starting on 10 June, then once a week for 5 weeks (referred to as 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 from NH₄NO₃). All the plants were hand-watered, as needed, throughout the growing season. After terminal bud set, half of the plants in each N fertigation treatment were randomly selected and leaves were sprayed twice (20 and 29 October) with 3% urea (+U treatment), and the remaining plants in each treatment were sprayed with water (-U treatment). Plants were sprayed to the point of run-off.

Year 2 (2005): In Spring 2005, after budbreak, half of the plants in each N04 and +U or -U treatment combination were assigned at random to one of two

groups and fertilised 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 from NH₄NO₃ (+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).

Measurements

Year 1 (2004): Before transplanting, five plants of each cultivar were selected at random and divided into roots, stems, and leaves. All samples were washed in doubled-distilled (DD) water, placed in an -80°C freezer and freeze-dried. The dry weight (DW) of each plant structure was recorded. In December 2004, five randomly selected plants from each N04 and +U or -U treatment combination were harvested and divided into roots, stems, and leaves, and the samples were processed as described above. For both cultivars, stems were further separated by growing season and, for rhododendron, the leaves were also separated by growing season (e.g., 2003 and 2004). Samples for nutrient analyses were analysed as reported previously (Bi *et al.*, 2003).

Total N content was calculated from the sum of the total N in each structure based on the DW and nutrient concentrations of each structure. Uptake of N from fertiliser in the N04 treatment was estimated by subtracting the average N uptake (mg) of plants in the 0 mM N treatment from the N uptake (mg) of plants in the other N04 treatments (i.e., N04 treatments with 5, 10, 15, or 20 mM). The uptake efficiencies of N from fertiliser in the N04 treatments were calculated as the proportion of the total N applied accounted for by N uptake of plants in the 5, 10, 15, and 20 mM N04 treatments. N uptake from foliar applications of urea in the Autumn was estimated by subtracting the average N content of plants in the -U treatment from the N content of plants in the +U treatment, for each N04 treatment. The amount of N in the different plant structures was used to characterise the primary locations of N use and storage.

Year 2 (2005): Eight weeks after budbreak, plants were harvested as described above. Stems of both cultivars, and rhododendron leaves, were separated by growing season (i.e., 2003, 2004, and 2005). The DW of each plant structure was recorded and samples were analysed for total N as described above. Uptake of N from the Spring fertiliser application (N05 treatment) was estimated by subtracting the average N uptake (mg) by plants in the -N treatment from the N uptake (mg) of plants in the +N treatment for each urea and N04 treatment. The amount of N in different plant structures was used to characterise the primary locations of N remobilisation and use.

Experimental design and statistical analyses

The experiment was set-up in a completely randomised design, with each treatment unit (pot) replicated five times for each N04 treatment (0, 5, 10, 15, or 20 mM N), Autumn foliar urea treatment (+U, -U), N05 treatment (+N, -N), and cultivar (rhododendron, azalea). Biomass and N content data from December 2004 were analysed in a complete factorial design using ANOVA, with cultivar, N04 treatment, and foliar urea treatment as main effects.

N-uptake data from December 2004 were analysed in a complete factorial design using ANOVA, with cultivar and N04 treatment as main effects. Biomass and N content data from June 2005 were analysed in a complete factorial design using ANOVA, with cultivar, N04 treatment, foliar urea treatment, and N05 treatment as main effects. N-uptake data from June 2005 were analysed in a complete factorial design using ANOVA, with cultivar, N04 treatment, and foliar urea treatment as main effects. Means of interactions are presented only when significant ($P \leq 0.05$). Estimates of N-uptake efficiency and biomass, and N partitioning were square-root transformed prior to analysis to correct for unequal variance, and to achieve the best-fit model. Back-transformed least squares means of actual data are reported in Table and Figures. Where indicated by ANOVA, means were separated using

Tukey's Honestly Significant Difference at $P = 0.05$ (THSD_{0.05}). Plant response to N04 treatments was evaluated using linear and quadratic polynomial contrasts based on the total amount of N applied to the soil in 2004. The relationships between plant growth in 2005, plant N content in 2004, N uptake from foliar urea in 2004, and N uptake from fertiliser in 2005 were assessed using Spearman R at $P < 0.05$. All analyses were performed using Statistica® (Statsoft, Inc., Tulsa, OK, USA; 1996).

RESULTS AND DISCUSSION

Plant growth

In our study, we used five N fertigation rates to investigate the optimum amount of N required for plant growth during the 2004 growing season. Our results

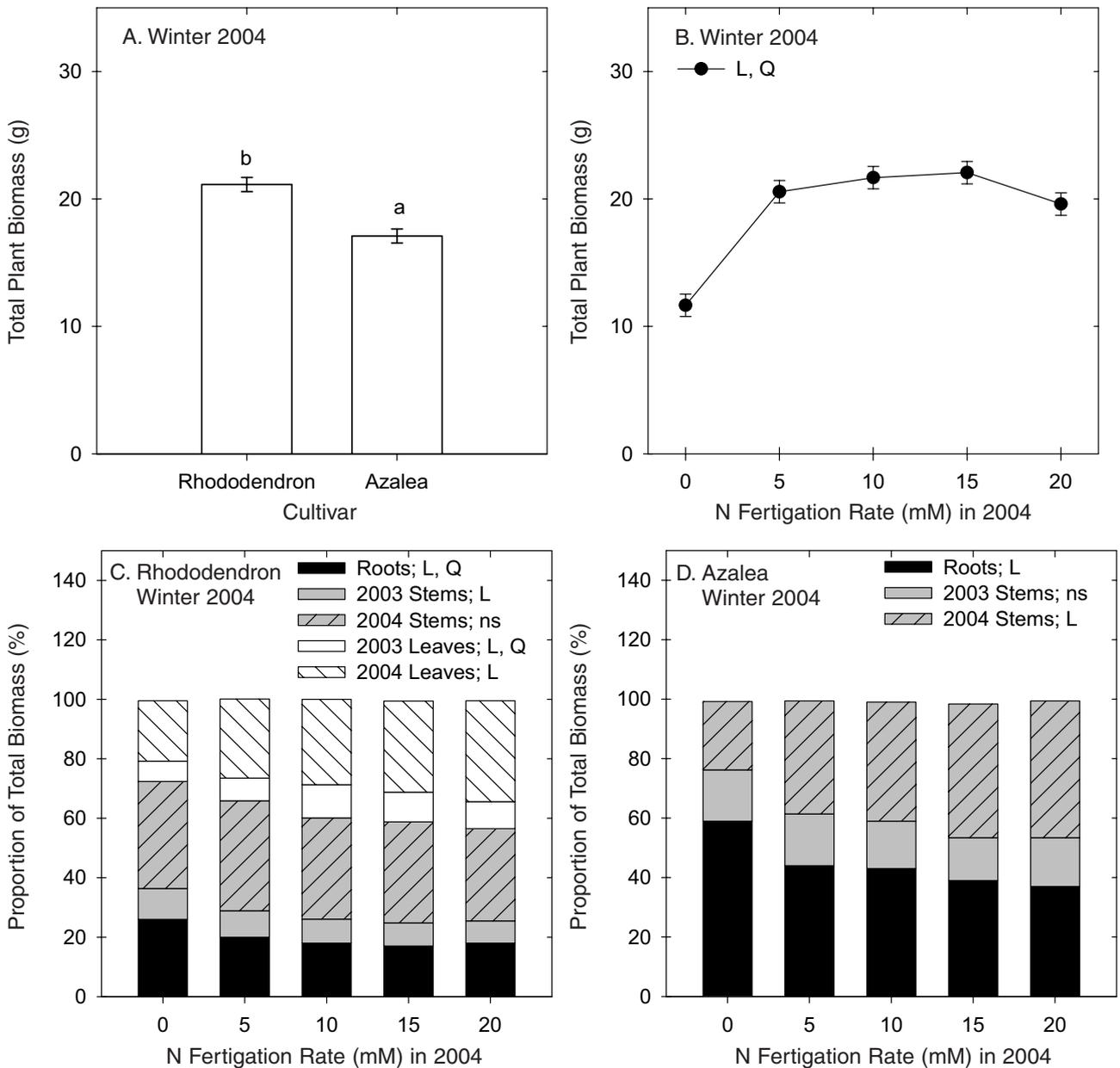


FIG. 1

Influence of nitrogen (N) fertigation rate in 2004 (N04) on total plant biomass and biomass partitioning by two *Rhododendron* cultivars in Winter 2004. Rhododendron = *Rhododendron* 'H-1 P.J.M.'; Azalea = *Rhododendron* 'Cannon's Double'. L and Q = significant linear and quadratic responses to N04; ns = no significant polynomial response to N04. Data points and columns represent means and error bars represent standard errors (Panel A, n = 20; Panel B, n = 50; Panel C and Panel D, n = 10). Data points (Panel A) with a different letter are significantly different (THSD_{0.05}, n = 50).

showed that, by December 2004, the biomass of rhododendron was greater than that of azalea (Figure 1A). The total biomass of both cultivars increased with increasing N availability from N04 fertiliser applications, and plant growth (biomass) was greatest for plants that received 10 mM or 15 mM N (Figure 1B), even when plants in the 0 mM N treatment were excluded from the data set. Plants exhibited an asymptotic growth response to increasing N supply (Figure 1B) which was similar to that observed in other species (Barnett and Ormrod, 1985; Cabrera, 2003; Henry *et al.*, 1992) and suggests that the N supply ≥ 10 mM used in our study may be unnecessary and decreases the efficiency of fertiliser use. Application of foliar urea in the Autumn had no influence on plant size in 2004 ($P > 0.05$) measured as biomass, leaf area, or stem length (data not shown).

The partitioning of biomass between roots, stems, and leaves responded differently to the rate of N fertiliser application, depending on the cultivar. As a result of the differential responses of the top (stems and leaves) and root biomass to N supply, increasing the availability of N increased the ratio of top:root growth for both cultivars (Figure 1C, D), resulting in a relatively small root system to support the large top biomass. Similar results have been reported for other species (Millard and Neilsen, 1989). This response in dry matter partitioning is a mechanism that plants use to optimise available resources (Millard and Neilsen, 1989). Under high N availability, a relatively small root system is sufficient to take up enough N and other nutrients. Reduced development of root systems in relation to the top portion of the plant may, however, cause problems after transplanting plants into the landscape. Plants with large top:root ratios can be more susceptible to transplant shock, moisture and temperature stress, and may show poor establishment (Andersen and Bentsen, 2003; Fitter and Hay, 2002; van den Driessche,

1991). Therefore, determining the optimum N rates for growth of *Rhododendron* is important, not only for improving N-uptake efficiency, but also for aspects of transplant quality.

By June 2005, the total biomass increased with increasing N availability from N04 fertiliser applications (Figure 2A) and the response to N04 fertigation rate varied between cultivars (i.e., the quadratic response to N04 varied between cultivars; $P < 0.05$). Rhododendron growth (biomass) was greatest for plants grown at the 10 mM N-fertigation rate, and growth in azalea was greatest for plants grown at 10–20 mM N. For both cultivars, the growth (as total biomass) response to N04 treatments was not influenced by foliar urea or N05 treatment (data not shown).

Applications of foliar urea in Autumn 2004 increased the total plant biomass of both cultivars in June 2005 (Figure 2B). Plants that received foliar urea applications accumulated 14% more total biomass than plants that received no urea. Fertigation with N in the Spring (N05 treatment) increased the total plant biomass of both cultivars in June 2005, but only when plants received no foliar urea in the Autumn of 2004 (Figure 2B). Plants that received N05 fertigation accumulated 9% more total biomass than plants that received no N in the Spring.

N content

By December 2004, the total N content of both cultivars increased with increasing N availability from N04 fertiliser applications (Figure 3A). Plants grown at the 10 mM and 20 mM N fertigation rates contained most N, but the N contents of roots, stems, and leaves responded differently to the rate of N fertigation, depending on the cultivar. For rhododendron, increasing N availability decreased the proportion of total N in roots and preferentially increased the N content in 2004

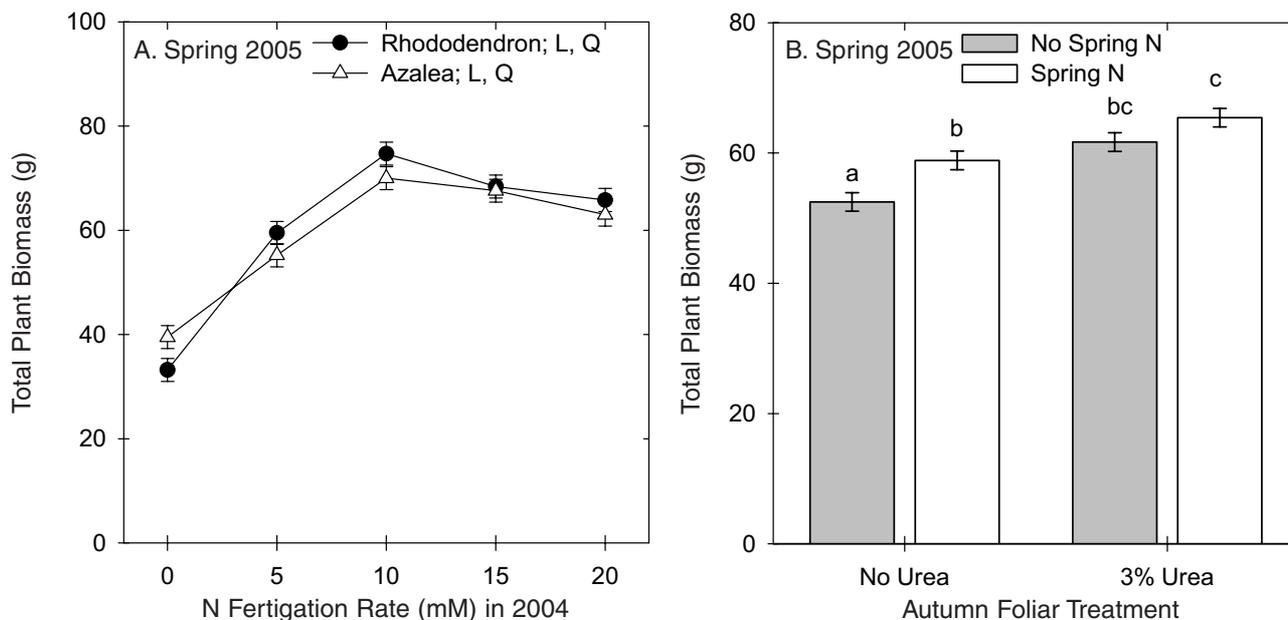


FIG. 2

Influence of (Panel A) nitrogen (N) fertigation rate in 2004 (N04) and (Panel B) foliar urea application in Autumn 2004 with or without N fertigation in Spring 2005 (N05) on total plant biomass of two *Rhododendron* cultivars in Spring 2005. Rhododendron = *Rhododendron* 'H-1 P.J.M'; Azalea = *Rhododendron* 'Cannon's Double'. L and Q = significant linear and quadratic responses to N04. 3% Urea = plants received foliar urea applications in Autumn 2004. No Urea = no foliar N application in Autumn 2004. Spring N = plants receiving N fertigation in 2005; No Spring N = no N in 2005. Data points and columns represent means and error bars represent standard errors (Panel A, $n = 10$; Panel B, $n = 50$). Columns (Panel B) with the same letter are not significantly different (THSD_{0.05}, $n = 50$).

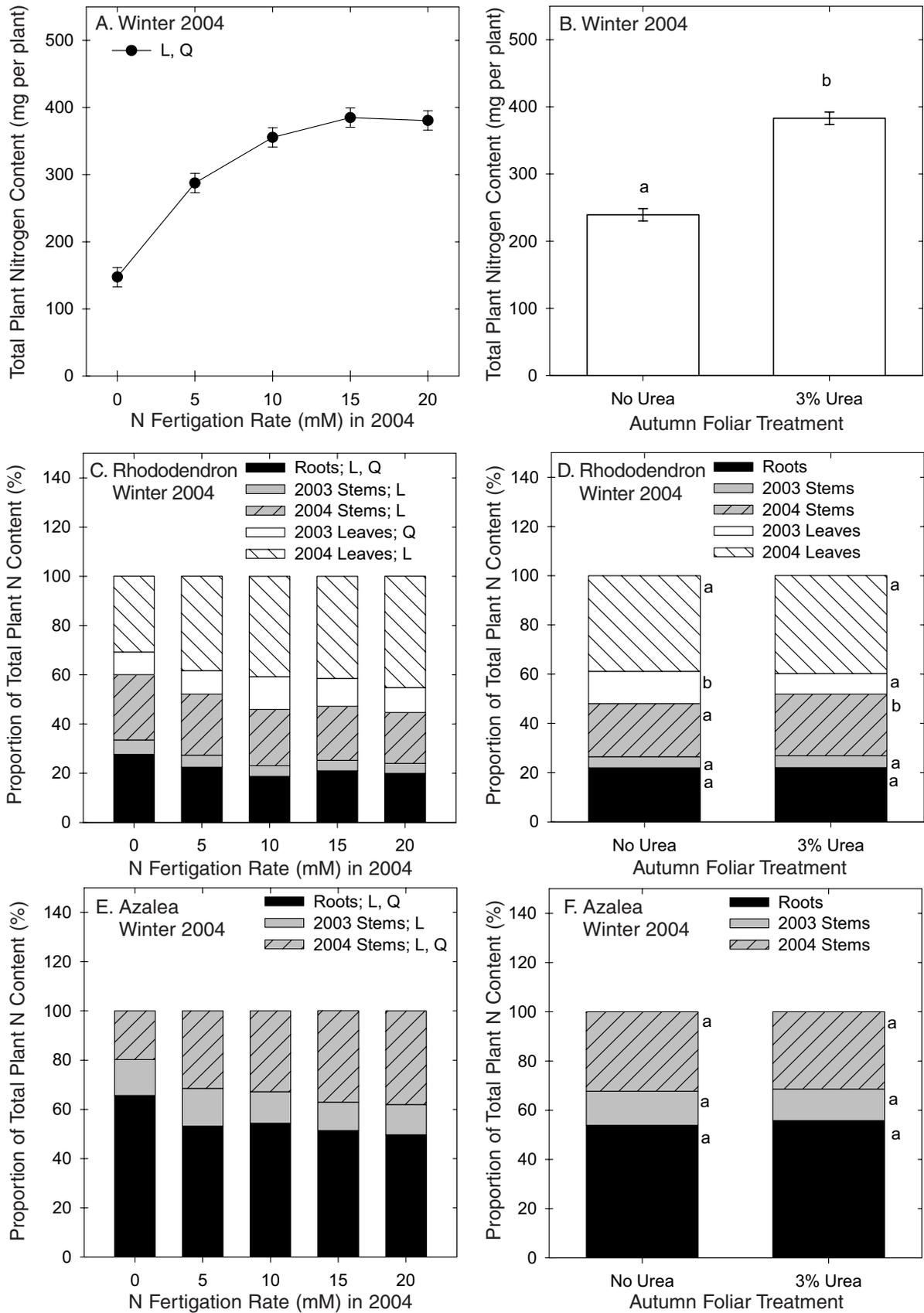


FIG. 3

Influence of nitrogen (N) fertilization rate in 2004 (N04) and application of foliar urea in Autumn 2004 on total plant N content and N partitioning by two *Rhododendron* cultivars in Winter 2004. *Rhododendron* = *Rhododendron* 'H-1 P.J.M'; Azalea = *Rhododendron* 'Cannon's Double'. 3% Urea = plants received foliar urea applications in Autumn 2004. No Urea = no foliar N application in Autumn 2004. L and Q = significant linear and quadratic responses to N04. Data points and columns represent means and error bars represent standard errors (Panel A, n = 20; Panel B, n = 50). Data points (Panel B) with a different letter are significantly different (THSD_{0.05}; B, n = 50). Column segments within a plant structure (Panels D, F) with the same letter are not significantly different (THSD_{0.05}; Panels D, F, n = 25).

leaves (Figure 3C). For azalea, increasing N availability decreased the proportion of total N in roots and 2003 stems, and preferentially increased the N content in 2004 stems (Figure 3E).

Applications of foliar urea in the Autumn increased the total plant N content of both cultivars (Figure 3B). Results from ANOVA of the total N content data from December 2004 indicated no significant interaction between N04 treatment and foliar urea treatment. N contents in roots, stems, and leaves responded differently to foliar urea application, depending on the cultivar. Azalea roots contained more than 50% of total plant N, and foliar urea application increased N contents in stems and roots (data not shown), but had no influence on the partitioning of N between different plant structures (Figure 3F). Nitrogen accumulation in roots and stems of azalea was similar to that described for many other deciduous woody plants (Millard, 1995). Rhododendron leaves contained 40–50% of total plant N, and foliar urea application increased the N content in all structures, except 2003 leaves (data not shown), and preferentially increased N partitioning to 2004 stems (Figure 3D).

Evergreen plants have been reported to use alternative methods for storing N, depending on leaf phenology and developmental stage (Karlsson, 1994). In young evergreen *Rhododendron ferrugineum* L., older leaves stored N, and the N was remobilised slowly throughout the growing season, regardless of current-season N availability (Lamaze *et al.*, 2003). Older needles on coniferous tree seedlings (Millard and Proe, 1993; Nambiar and Fife, 1987) have also been shown to contribute a high proportion of N to current-year above-ground growth. In our study, the foliar application of urea increased the N contents of stems, roots, and 2004 leaves in rhododendron without affecting biomass, indicating that rhododendron utilised not only woody tissues (stems and roots), but also leaves for storing N, and that leaves acted as a primary location for N storage. Nitrogen in 2004 stems and 2004 leaves of rhododendron accounted for approx. 63% of total plant N, suggesting it is important to maintain these structures at the end of the year. If these structures were lost or damaged through shearing or handling, the loss of N reserves could be substantial and potentially negatively influence new plant growth in the following Spring.

For many species, stored N is important for initial growth and development (Henry *et al.*, 1992; Millard, 1996). It has been shown that N storage can be altered either by N fertilisation during the growing season, or foliar urea application after plants have set their terminal buds (Cheng and Xia, 2004). However, plants receiving high amounts of N fertiliser from the soil throughout late Summer and Autumn tend to continue growing late into the season; therefore, late applications or high rates of N fertiliser during this time may delay dormancy, and increase the susceptibility of plants to environmental stresses such as freezing (Bramlage *et al.*, 1980; Millard, 1995). In contrast, decreasing the availability of soil N fertilisation in late Summer or early Autumn, followed by foliar urea application after terminal bud set, can increase N reserves without stimulating growth, and therefore improve early acclimation to environmental stresses. Our results demonstrate that foliar urea applications in the

Autumn, after terminal bud set, significantly increased the total plant N content in *Rhododendron* without affecting plant size, and have the potential to decrease applications of soil N fertiliser to container-grown plants in the Autumn.

By June 2005, the total plant N content of both cultivars increased with increasing N04 fertiliser application rate, and plants grown at 10 mM N contained most N (Figure 4A). The response of total N content to N04 fertiliser rate in June 2005 was not influenced by foliar urea or N05 treatment (data not shown).

Applications of foliar urea in Autumn 2004 increased the total plant N contents of both cultivars in June 2005, and the response to foliar urea was dependent on whether or not plants received N fertigation in Spring 2005 (Figure 4B,C). Plants that received no N in Spring 2005 were more responsive to foliar urea than plants that received N05 fertigation ($P < 0.05$). Urea increased total plant N by 27% when plants received N05 fertigation, and by 49% when plants received no N05 fertigation. Fertigation with N in the Spring (N05 treatment) increased the total plant N content of both cultivars in June 2005, and the magnitude of the response varied between cultivars (Figure 4B,C). Azalea was more responsive to N05 fertigation than rhododendron ($P < 0.05$). Compared to plants that received no N in Spring 2005, fertigation with N in the Spring increased the total plant N of rhododendron by 62%, and azalea by 74%.

N-uptake

By December 2004, plants that had received no additional N as N04 fertiliser or foliar urea applications accumulated 60–90 mg N from the substrate, or from residual fertiliser in the initial liner substrate. Increasing the N availability increased N uptake from N04 fertiliser applications by 116–247 mg, depending on N fertigation rate and cultivar (Figure 5A). For rhododendron, the uptake of N from N04 fertigation was greatest at the 15 mM N rate and, for azalea, N uptake was similar for plants given 10–20 mM N. The estimated N uptake from fertigation in 2004 may not account for N losses that occur in *Rhododendron* in the Autumn. Our estimates of N-uptake from fertigation were similar for rhododendron and azalea at the end of 2004. However, the total amount of N taken up from the soil could be underestimated for azalea because some of the N from fertigation may have been lost when the leaves abscised at the end of the year. The commonly cited value for N resorption from senescing leaves is 50% of total leaf N content (Niederholzer *et al.*, 2001). Scagel *et al.* (unpublished data) found that container-grown azalea (*Rhododendron* 'Gibraltar') reabsorbed approx. 38% of the total N from leaves in the Autumn prior to abscission. Thus the amount of N-uptake for growth of azalea may be greater than our estimated values, due to N losses from leaf abscission.

N-uptake efficiency from the 2004 fertigation declined with increasing N fertiliser rate (Figure 5A). N-uptake efficiency was lowest (~18%) for plants that received 20 mM N, and greatest (~43%) for plants that received 5 mM N. This is consistent with results reported for bearing *Citrus* trees, where N-uptake efficiency ranged from 14.9% when trees were given 336 g N year⁻¹ tree⁻¹ to 42.2% when trees were given 140 g N year⁻¹ tree⁻¹

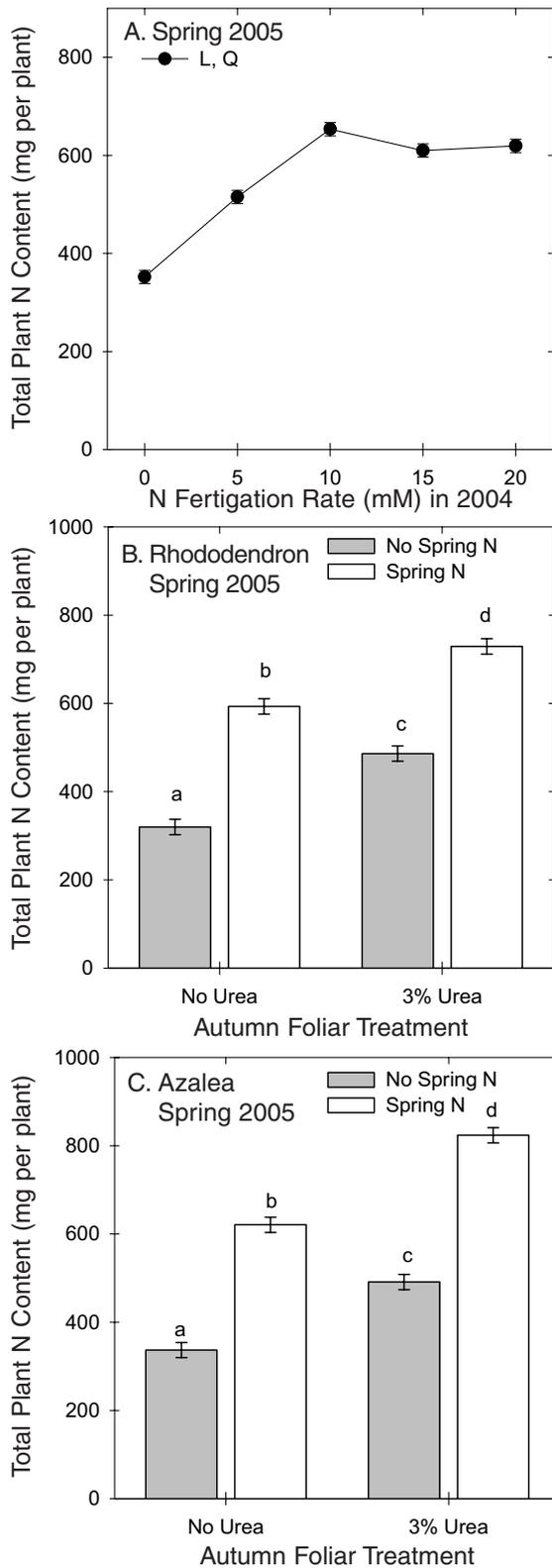


FIG. 4

Influence of (Panel A) nitrogen (N) fertilization rate in 2004 (N04) and (Panels B, C) foliar urea application in Autumn 2004 and N fertilization in Spring 2005 (N05) on N content of two *Rhododendron* cultivars in the spring of 2005. *Rhododendron* = *Rhododendron* 'H-1 P.J.M.'; *Azalea* = *Rhododendron* 'Cannon's Double'. 3% Urea = plants receiving foliar urea applications in Autumn; No Urea = no foliar N application in Autumn. Spring N = plants receiving N fertilization in 2005; No Spring N = no N in 2005. L and Q = significant linear and quadratic responses to N04. Data points and columns represent means and error bars represent standard errors (Panel A, $n=40$). Columns (Panels B, C) with a different letter are significantly different (THSD_{0.05}, $n = 25$).

(Lea-Cox *et al.*, 2001). Reported N-uptake efficiencies vary widely for different crops, and can be affected by many factors including plant age, fertiliser application time, level of applied N, fertiliser type, fertiliser application method (e.g., soil vs. foliar), soil texture, cultural practices (e.g., irrigation), and environmental conditions such as temperature and precipitation (Dong *et al.*, 2001; Neilsen *et al.*, 2001; Weinbaum *et al.*, 1984).

Fertiliser rates with the highest N-uptake efficiency in container-grown *Rhododendron* may not result in the best growth. Under our experimental conditions, plants grown at the lowest N rate (5 mM N) had the highest N-uptake efficiency, but reduced top biomass in comparison to plants grown at the higher N rates. Our previous study, with container-grown 1-year-old *Rhododendron*, also found that the rate of N-uptake was correlated with the rate of plant growth, and maximum uptake occurred during the period of rapid plant growth in Summer (Bi *et al.*, 2007). These results highlight the importance of selecting N fertiliser rates and application times that optimise both uptake efficiency and plant growth to minimise potential N losses and maintain plant productivity.

N-uptake from foliar applications of urea ranged from 56–216 mg, depending on the cultivar and the rate of N04 fertiliser application (Figure 5B). *Rhododendrons* that received 10 mM or 15 mM N accumulated the highest amount of N from urea (approx. 213 mg N). *Azalea* that received no N fertiliser during the growing season accumulated less than 50% of the N from foliar urea compared to plants that received 5–20 mM N (approx. 135 mg N).

By June 2005, plants that had received N fertilization in the Spring (N05 treatment) accumulated 130–350 mg N (*rhododendron*), or 250–350 mg N (*azalea*) depending on the rate of N fertilization in 2004 (N04 treatment), and whether or not the plants received foliar urea in the Autumn of 2004 (Figure 5C, D). For both cultivars, foliar urea application in the Autumn increased N uptake from N05 fertilization when plants were grown with 0 mM N from N04 fertilization. For *rhododendron*, increasing N04 fertilization rate decreased the uptake of N from N05 fertilization when plants received foliar urea, and plants that received foliar urea generally had a lower uptake of N from N05 fertilization compared to plants that received no foliar urea. For *azalea*, plants grown with 10–15 mM N from N04 fertilization had the lowest N uptake from the N05 fertilization, and the application of foliar urea had little influence on N-uptake from N05 fertilization.

Relationships between N content in 2004 and growth in 2005

In both cultivars, total plant biomass, stem biomass, and biomass of 2005 leaves (in 2005) were positively correlated with the N content of all plant structures in the Winter of 2004 (Table I). Root growth in 2005 was positively correlated with leaf N content in 2004 (*rhododendron*), and 2004 stem N content in the Winter of 2004 (*azalea*). Growth of 2003 and 2004 leaves in 2005 was positively correlated with 2003 leaf N content in the Winter of 2004. N-uptake from urea was positively correlated with the growth of all plant structures in 2005, while N-uptake from fertilization in the Spring of 2005 was correlated only with 2005 leaf and stem growth.

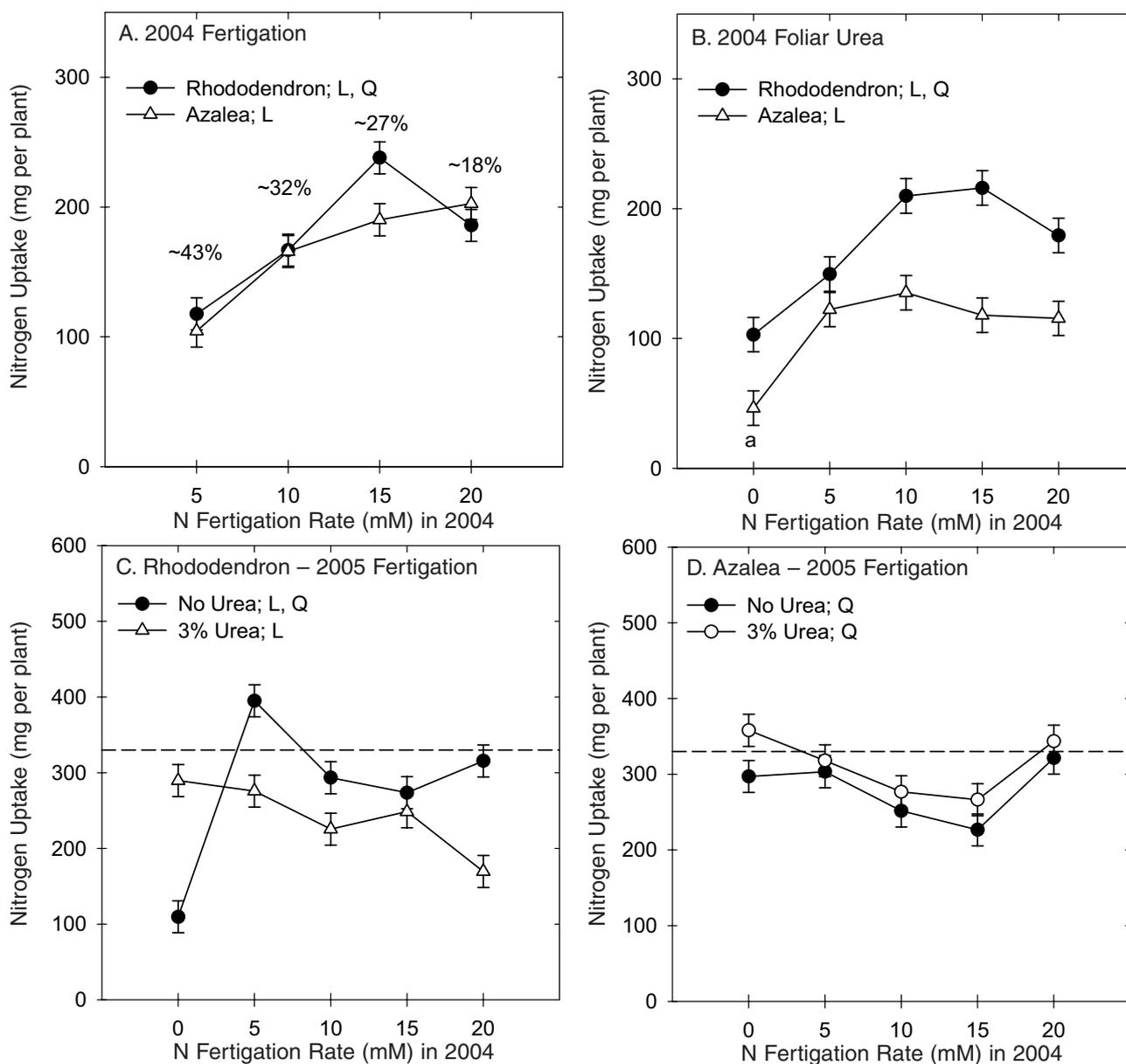


FIG. 5

Influence of nitrogen (N) fertigation rate in 2004 (N04), foliar urea application in Autumn 2004, and N fertigation in 2005 (N05) on N uptake by two *Rhododendron* cultivars. N uptake from 2004 fertigation in Winter 2004 (Panel A), 2004 foliar urea application in Winter 2004 (Panel B), and 2005 fertigation in Spring 2005 (Panels C, D). Rhododendron = *Rhododendron* 'H-1 P.J.M.'; Azalea = *Rhododendron* 'Cannon's Double'. No Urea = plants received no foliar N application in Autumn 2004. 3% Urea = plants receiving foliar urea applications in Autumn 2004. L and Q = significant linear and quadratic responses to N04. Data points represent means and error bars represent standard errors ($n = 5$). Numbers above data points (Panel A) are estimates of N uptake efficiency (% of N applied) averaged across both cultivars at each N04 fertigation rate. Horizontal line (Panels C, D) represents an N uptake efficiency of 50%.

Foliar applications of urea in the Autumn have been reported to be an effective way to increase N reserves and, consequently, to improve plant growth and development in the following Spring in several plant species (Bi *et al.*, 2003; Cheng and Xia, 2004; O'Kennedy *et al.*, 1975). The level of N reserves in perennial plants has been correlated not only with growth, but also depends on N fertiliser during the following Spring (Bi *et al.*, 2003; Cheng and Xia, 2004; Feigenbaum *et al.*, 1987). In our study, N uptake from fertigation in Spring 2005 was correlated with 2005 leaf and stem growth, but the effect of urea application on the dependence on fertiliser in the Spring varied between cultivars. For azalea, N-uptake in the Spring was not affected by foliar

applications of urea during the previous year. This is similar to the response of young 'Concord' grapevines (*Vitis labruscana* Bailey) to urea application (Cheng and Xia, 2004). For rhododendron, N-uptake in the Spring was lower in plants sprayed with foliar urea during the previous year. This is similar to the response of young almond trees [*Prunus dulcis* (Mill) D. A. Webb] to urea application (Bi *et al.*, 2003).

Compared to azalea, the greater influence of foliar urea on N-uptake by rhododendron in the following Spring may have been due to a combination of factors: (1) foliar urea application may not be as effective at increasing N reserves in azalea compared to rhododendron; (2) the methods of N storage in

TABLE I

Correlations (Spearman's R ; $n = 20$) between growth of two *Rhododendron* cultivars and plant nitrogen (N) content in 2004, N uptake from foliar urea applications in 2004 (U04 uptake) and N uptake from fertiliser in 2005 (N05 uptake)

| Cultivar ^z | Response Variable | Plant Growth in 2005 | | | | | | | |
|-----------------------|-------------------|----------------------|-------|-------|-------|-------|--------|-------|-------|
| | | Total | | Stems | | | Leaves | | |
| | | Plant | Roots | 2003 | 2004 | 2005 | 2003 | 2004 | 2005 |
| Rhododendron | Total Plant N | 0.797 | 0.517 | 0.651 | 0.781 | 0.825 | ns | ns | 0.837 |
| | Root N | 0.697 | ns | 0.526 | 0.700 | 0.779 | ns | ns | 0.793 |
| | 2003 Stem N | 0.689 | ns | 0.540 | 0.675 | 0.788 | ns | ns | 0.796 |
| | 2004 Stem N | 0.702 | ns | 0.562 | 0.674 | 0.795 | ns | ns | 0.801 |
| | 2003 Leaf N | 0.857 | 0.742 | 0.725 | 0.822 | 0.747 | 0.499 | 0.698 | 0.736 |
| | 2004 Leaf N | 0.802 | 0.541 | 0.673 | 0.791 | 0.798 | ns | ns | 0.817 |
| | U04 Uptake | 0.778 | 0.789 | 0.677 | 0.715 | 0.610 | 0.585 | 0.678 | 0.623 |
| | N05 Uptake | ns ^y | ns | ns | ns | 0.497 | ns | ns | 0.499 |
| Azalea | Total Plant N | 0.843 | 0.521 | 0.627 | 0.856 | 0.697 | – | – | 0.772 |
| | Root N | 0.812 | ns | 0.513 | 0.795 | 0.730 | – | – | 0.772 |
| | 2003 Stem N | 0.796 | ns | 0.709 | 0.746 | 0.651 | – | – | 0.700 |
| | 2004 Stem N | 0.840 | 0.467 | 0.696 | 0.786 | 0.629 | – | – | 0.746 |
| | U04 Uptake | 0.708 | 0.580 | 0.807 | 0.784 | 0.497 | – | – | 0.488 |
| | N05 Uptake | ns | ns | ns | ns | 0.679 | – | – | 0.643 |

^zRhododendron = *Rhododendron* 'H-1 P.J.M'; Azalea = *Rhododendron* 'Cannon's Double'.

^yns, non-significant ($P > 0.05$)

rhododendron may be more efficient than those in azalea; and/or (3) new growth in azalea may be more rapid than in rhododendron. Our data showed that foliar urea application caused a greater increase in the N content of rhododendron (164 mg per plant) compared to azalea (123 mg per plant), and this difference could account for differences in the dependence of cultivars on N availability in the Spring. There have been no previous reports on the response of *Rhododendron* to foliar applications of urea, so the rates and timing of applications used in this study were based on prior research with almond (Bi *et al.*, 2003). It is possible that modifying the rates and timing of urea applications could increase N storage in azalea, and thereby decrease plant dependence on N availability in the Spring.

Our results also indicate that rhododendron and azalea accumulated N in different structures, and that this difference could account for differences in the dependence of the cultivars on N availability in the Spring. For example, in azalea, some of the N absorbed from urea may have been lost when the leaves abscised at the end of the year. In contrast, in rhododendron, leaves that were retained on the plant were the primary location for N. The greater above-ground growth of new structures (leaves and stems; approx. 3 g per plant) in azalea compared to rhododendron could also account for the differences in the dependence of the cultivars on N availability in the Spring. Our previous study, with container-grown 1-year-old *Rhododendron*, also found that deciduous azalea accumulated biomass at a faster rate than evergreen rhododendron, and the effects of increased availability of soil N on total biomass were observed at least 2 weeks earlier in azalea than in rhododendron (Bi *et al.*, 2007).

In conclusion, our results show that foliar applications

of urea to container-grown *Rhododendron* in the Autumn have the potential to improve N storage during Winter, and plant performance in the following Spring. Foliar urea applications may also decrease plant dependence on N fertiliser in the following Spring for new growth in some *Rhododendron* cultivars; however the influence of foliar urea applications on a wider range of cultivars needs to be assessed, as well as the optimum rates and timing of applications. We also found that the increased N availability to container-grown *Rhododendron* decreased N-uptake efficiency, and the relationships between N fertiliser rate, N-uptake efficiency, and growth need to be considered when selecting optimum rates for N fertilisation. A combination of optimum soil fertilisation during the growing season, with foliar applications of urea in the Autumn after terminal bud set, could be a useful management strategy to improve N-uptake efficiency, increase N storage, and optimise growth in container-grown *Rhododendron*.

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REFERENCES

- ALT, D. (1998). N-fertilization of nursery crops in the field – a review. Part 1. *Gartenbauwissenschaft*, **63**, 165–170.
- ANDERSEN, L. and BENTSEN, N. S. (2003). Survival and growth of *Abies nordmanniana* in forest and field in relation to stock type and root pruning prior to transplanting. *Annals of Forest Science*, **60**, 757–762.
- BARNETT, C. E. and ORMROD, D. P. (1985). Responses of *Tilia cordata* and *Acer platanoides* in pots to nitrogen levels. *HortScience*, **20**, 283–285.
- BI, G., SCAGEL, C. F., CHENG, L., DONG, S. and FUCHIGAMI, L. H. (2003). Spring growth of almond nursery trees depends upon both nitrogen reserves and spring nitrogen application. *Journal of Horticultural Science & Biotechnology*, **78**, 853–858.
- BI, G., SCAGEL, C. F., FUCHIGAMI, L. H. and REGAN, R. P. (2007). Differences in growth, nitrogen uptake, and storage between two container-grown *Rhododendron* cultivars. *Journal of Environmental Horticulture*, **25**, 13–20.
- BRAMLAGE, W. J., DRAKE, M. and LORD, W. J. (1980). The influence of mineral nutrition on the quality and storage performance of pome fruits grown in North America. In: *Mineral Nutrition of Fruit Trees*. (Atkinson, D., Jackson, J. E., Sharples, R. O. and Waller, W. N., Eds.). Butterworths, London, UK. 29–39.
- CABRERA, R. I. (2003). Nitrogen balance for two contain-grown woody ornamental plants. *Scientia Horticulturae*, **97**, 297–308.
- CATANZARO, C. J., WILLIAMS, K. A. and SAUVE, R. J. (1998). Slow release versus water soluble fertilization affects nutrient leaching and growth of potted chrysanthemum. *Journal of Plant Nutrition*, **21**, 1025–1036.
- CHENG, L. and XIA, G. (2004). Growth and fruiting of young 'Concord' grapevines in relation to reserve nitrogen and carbohydrates. *Journal of the American Society for Horticultural Science*, **129**, 660–666.
- CHENG, L., DONG, S., GUAQ, S. and FUCHIGAMI, L. H. (2001). Effects of nitrogen fertilization on reserve nitrogen and carbohydrate status and regrowth performance of pear nursery plants. *Acta Horticulturae*, **564**, 51–62.
- COLANGELO, D. J. and BRAND, M. H. (2001). Nitrate leaching beneath a containerized nursery crop receiving trickle or overhead irrigation. *Journal of Environmental Quality*, **30**, 1564–1574.
- DONG, S., SCAGEL, C. F., CHENG, L., FUCHIGAMI, L. H. and RYGIWICZ, P. T. (2001). Soil temperature and plant growth stage influence nitrogen uptake and amino acid concentration of apple during early spring growth. *Tree Physiology*, **21**, 541–547.
- DONG, S., CHENG, L., SCAGEL, C. F. and FUCHIGAMI, L. H. (2005). Method of N application in the summer affects plant growth and N uptake in autumn in young 'Fuji'/M26 apple trees. *Communications in Soil Science and Plant Analysis*, **36**, 1465–1477.
- FEIGENBAUM, S., BIELORAI, H., ERNER, X. and DASBERG, S. (1987). The fate of ¹⁵N labeled nitrogen applied to mature citrus trees. *Plant and Soil*, **97**, 179–187.
- FITTER, A. and HAY, R. (2002). *Environmental Physiology of Plants*. Academic Press, San Francisco, CA, USA. 367 pp.
- GRELET, G., ALEXANDER, I. J. and PROE, M. F. (2001). Leaf habit influences nitrogen remobilization in *Vaccinium* species. *Journal of Experimental Botany*, **52**, 993–1002.
- HABIB, R., MILLARD, P. and PROE, M. F. (1993). Modeling the seasonal nitrogen partitioning in young sycamore (*Acer pseudo-platanus*) trees in relation to nitrogen supply. *Annals of Botany*, **71**, 453–459.
- HENRY, P. H., BLAZICH, F. A., HENESLEY, L. E. and WRIGHT, R. D. (1992). Nitrogen nutrition of containerized Eastern red cedar. I. Growth, mineral nutrient concentrations, and carbohydrate status. *Journal of the American Society for Horticultural Science*, **117**, 563–567.
- HOAGLAND, D. R. and ARNON, D. I. (1950). The water-culture method for growing plants without soil. *California Agricultural Experiment Station Circular*, **347**, 1–32.
- JUNTUNEN, M. L., HAMMAR, T. and RIKALA, R. (2003). Nitrogen and phosphorus leaching and uptake by container birch seedlings (*Betula pendula* Roth) grown in three different fertilizations. *New Forests*, **25**, 133–147.
- KARLSSON, P. S. (1994). The significant of internal nutrient cycling in branches for growth and reproduction of *Rhododendron lapponicum*. *Okios*, **70**, 1191–1200.
- KLEIN, I. and WEINBAUM, S. A. (1984). Foliar application of urea to olive: translocation of urea nitrogen as influenced by sink demand and nitrogen deficiency. *Journal of the American Society for Horticultural Science*, **109**, 356–360.
- KLOEPEL, B. D., GOWER, S. T., VOGEL, J. G. and REICH, P. B. (2000). Leaf-level resource use for evergreen and deciduous conifers along a resource availability gradient. *Functional Ecology*, **14**, 281–292.
- LAMAZE, T., PASCHE, F. and PORNON, A. (2003). Uncoupling nitrogen requirements for spring growth from root uptake in a young evergreen shrub (*Rhododendron ferrugineum*). *New Phytologist*, **159**, 637–644.
- LEA-COX, J. D., SYVERTSEN, J. P. and GRAETZ, D. A. (2001). Springtime ¹⁵N nitrogen uptake, partitioning, and leaching losses from young bearing *Citrus* trees of differing nitrogen status. *Journal of the American Society for Horticultural Science*, **126**, 242–251.
- MILLARD, P. (1995). Internal cycling of nitrogen in trees. *Acta Horticulturae*, **383**, 3–13.
- MILLARD, P. (1996). Ecophysiology of the internal cycling of nitrogen for tree growth. *Journal of Plant Nutrition and Soil Science*, **159**, 1–10.
- MILLARD, P. and NEILSEN, G. H. (1989). The influence of nitrogen supply on the uptake and remobilization of stored N for the seasonal growth of apple trees. *Annals of Botany*, **63**, 301–309.
- MILLARD, P. and PROE, M. F. (1993). Nitrogen uptake, partitioning and internal cycling in *Picea sitchensis* (bong) Carr. as influenced by nitrogen supply. *New Phytologist*, **125**, 113–119.
- NAMBIAR, S. E. K. and FIFE, D. N. (1987). Nutrient retranslocation in temperate conifers. *Tree Physiology*, **9**, 185–207.
- NEILSEN, D., MILLARD, P., HERBERT, L. C., NEILSEN, G. H., HOGUE, E. J., PARCHOMCHUK, P. and ZEBARTH, B. J. (2001). Remobilization and uptake of N by newly planted apple (*Malus domestica*) trees in response to irrigation method and timing of N application. *Tree Physiology*, **21**, 513–521.
- NIEDERHOLZER, F. J. A., DEJONG, T. M., SAENZ, J. L., MURAOKA, T. T. and WEINBAUM, S. A. (2001). Effectiveness of fall versus spring soil fertilization of field-grown peach trees. *Journal of the American Society for Horticultural Science*, **125**, 644–648.
- O'KENNEY, B. T., HENNERTY, M. J. and TITUS, J. S. (1975). Changes in the nitrogen reserves of apple shoots during the dormant season. *Journal of Horticultural Science*, **50**, 321–329.
- PASCHE, F., PORNON, A. and LAMAZE, T. (2002). Do mature leaves provide a net source of nitrogen supporting shoot growth in *Rhododendron ferrugineum*? *New Phytologist*, **154**, 99–105.
- REILEY, H. E. (1992). *Success with Rhododendrons and Azaleas*. Timber Press, Portland, OR, USA. 285 pp.
- RIKALA, R., HEISKANEN, J. and LAHTI, M. (2004). Autumn fertilization in the nursery affects growth of *Picea abies* container seedlings after transplanting. *Scandinavian Journal of Forest Research*, **19**, 409–414.
- ROSECRANCE, R. C., JOHNSON, R. S. and WEINBAUM, S. A. (1998). The effect of timing of post-harvest foliar urea sprays on nitrogen absorption and partitioning in peach and nectarine trees. *Journal of Horticultural Science & Biotechnology*, **73**, 856–861.
- SALIFU, K. T. and TIMMER, V. R. (2003). Optimizing nitrogen loading of *Picea mariana* seedlings during nursery culture. *Canadian Journal of Forest Research*, **33**, 1287–1294.
- SHIM, K. K., TITUS, J. S. and SPLITTSTOESSER, W. E. (1972). The utilization of post-harvest urea sprays by senescencing apple leaves. *Journal of the American Society for Horticultural Science*, **97**, 592–596.
- STEPHENS, D. W., MILLARD, P., TURNBULL, M. H. and WHITEHEAD, D. (2001). The influence of nitrogen supply on growth and internal recycling of nitrogen in young *Nothofagus fusca* trees. *Australian Journal of Plant Physiology*, **28**, 249–255.
- TAGLIAVINI, M., MILLARD, P. and QUARTIERI, M. (1998). Storage of foliar absorbed nitrogen and remobilization for spring growth in young nectarine (*Prunus persica* var. nectarina) trees. *Tree Physiology*, **18**, 203–207.

- TAKASHIMA, T., HIKOSAKA, K. and HIROSE, T. (2004). Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. *Plant, Cell and Environment*, **27**, 1047–1054.
- VAN DEN DRIESSCHE, R. (1991). Influence of container nursery regimes on drought resistance of seedlings following planting. I. Survival and growth. *Canadian Journal of Forest Research*, **21**, 555–565.
- WEINBAUM, S. A., KLEIN, I., BROADBENT, F. E., MICKE, W. C. and MURAOKA, T. T. (1984). Use of isotope nitrogen to demonstrate dependence of mature almond trees on annual uptake of soil nitrogen. *Journal of Plant Nutrition*, **7**, 975–990.
- WITT, H. H. (1994). Regulation of nitrogen supply of *Rhododendron* hybrids. *Acta Horticulturae*, **364**, 79–87.
- YEAGER, T. H., WRIGHT, R. D., FARE, D., GILLIAM, C. H., JOHNSON, J. R., BILDERBACK, T. and ZONDAG, R. (1993). Six state survey of container nursery nitrate nitrogen runoff. *Journal of Environmental Horticulture*, **11**, 206–208.