Nitrogen Form Affects Growth, Mineral Nutrient Content, and Root Anatomy of Cotoneaster and Rudbeckia

Helen T. Kraus and Stuart L. Warren

Department of Horticultural Science, North Carolina State University, Raleigh, NC 27695-7609

Charles E. Anderson

Department of Botany, North Carolina State University, Raleigh, NC 27695-7612

Additional index words. root growth, *Cotoneaster dammeri* 'Skogholm', *Rudbeckia fulgida* 'Goldsturm', ammonium, nitrate, container-grown

Abstract. Five ratios of $\text{NH}_4^+ : \text{NO}_3^-$ (100:0, 75:25, 50:50, 25:75, and 0:100) were evaluated for impact on growth of *Cotoneaster dammeri* Schneid. 'Skogholm' (cotoneaster), a woody ornamental shrub, and *Rudbeckia fulgida* Ait. 'Goldsturm' (rudbeckia), an herbaceous perennial. Nitrate alone decreased dry weight and leaf area of cotoneaster and rudbeckia compared with mixtures of NH_4^+ and NO_3^- and NH_4^+ alone. Additionally, NO_3^- alone suppressed accumulation of cationic nutrients and N in cotoneaster, while mixes of NH_4^+ and NO_3^- enhanced accumulation of nutrients in roots and shoots of rudbeckia compared with solutions containing either NH_4^+ or NO_3^- alone. The steles of roots of cotoneaster and rudbeckia contained more secondary xylem with larger tracheary elements with a mix of 25 $\text{NH}_4^+ : 75 \text{NO}_3^-$ than with NO_3^- alone.

Developing a fertility program involves selecting fertilizer rates, and sources and ratios of nutrients, especially the form of N (NH_4^+ or NO_3^-). Nitrogen form affects mineral nutrient concentration of shoots and roots (Edwards and Horton, 1982; Rosen et al., 1990), growth rate and N uptake (Edwards and Horton, 1982), and root anatomy (Finn et al., 1990) of ornamental plants. Generally, increasing NO_3^- in fertilizer solutions stimulates organic anion synthesis and cation accumulation by the plant (Mengel and Kirkby, 1982). Active uptake of NO_3^- is believed to induce symport of cations; however, NO_3^- uptake may also occur in exchange for OH^- without cation symport (Mengel and Kirkby, 1982). In contrast, NH_4^+ often suppresses the absorption of cations and synthesis of organic anions produced by plants, whereas inorganic anion accumulation (SO_4^{2-} , PO_4^{3-} , and Cl^-) is increased (Mengel and Kirkby, 1982).

Growth of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], especially root growth, was reduced by NH_4^+ as the only N-source, while growth of lodgepole pine (*Pinus contorta* Dougl.) and Engelmann spruce (*Picea engelmannii* Parry) was reduced with NO_3^- as the only N-source when grown in sand and

perlite (Bigg and Daniel, 1978). Reports conflict on the effect of N form on growth of cotoneaster. Growth of cotoneaster 'Royal Beauty' was not affected when grown in sand that was supplied daily with nutrient solutions with different N forms (Gilliam et al., 1980). In contrast, when cotoneaster 'Royal Beauty' was grown in 4 pine bark : 1 sand (by volume) and supplied with weekly applications of nutrient solution, NO_3^- produced greater shoot growth than NH_4^+ , but root growth was not effected by N form (Gilliam et al., 1982/83). Frequency of nutrient solution application and pH of nutrient solution, along with differences in container substrates, may have contributed to the diversity of plant growth and nutrient accumulation results.

Root morphology and growth determine the ability of a plant to exploit the rooting volume for water and nutrients (Mengel and Kirkby, 1982) and may be altered by changes in the form of available N. Cultivars of peach [*Prunus persica* (L.) Batsch.] produced a greater volume of roots with 50:50 and 25:75 mixtures of NH_4^+ and NO_3^- than with NO_3^- alone (Edwards and Horton, 1982). Epidermal cells of roots from plants fertilized with NO_3^- had denser cytoplasm and were nearly isodia-

metric compared to roots of cranberry (*Vaccinium macrocarpon* Ait. 'Searles') fertilized with NH_4^+ that had rectangular epidermal cells (Finn et al., 1990). These differences in epidermal cell development were probably a result of less cell elongation with NO_3^- . Alterations in the phytohormone balance of the plant and differences in the assimilation pathways of NH_4^+ and NO_3^- in the root may account for the effect of N form on root morphology (Marschner, 1986).

As N form affects growth and may alter root growth, thereby impacting establishment in landscape plantings, there is need for more research on the effects of N form on landscape plants. Additionally, results of N form impacts on cotoneaster growth were conflicting, and no reports of the effect of N form on rudbeckia growth were found, nor were any reports found describing the anatomy of cotoneaster and rudbeckia roots. Therefore, our objective was to evaluate the effects of N form and ratio on growth, mineral nutrient accumulation, and root anatomy of cotoneaster, a woody ornamental shrub, and rudbeckia, a popular herbaceous perennial.

Materials and Methods

An experiment was conducted for 12 weeks (14 Oct. 1994 to 4 Jan. 1995) in a glass greenhouse in Raleigh, N.C. The experiment used a randomized complete-block design with seven replications (seven plants per $\text{NH}_4^+ : \text{NO}_3^-$ treatment) and two species, cotoneaster 'Skogholm' and rudbeckia 'Goldsturm'. Nitrogen treatments included five $\text{NH}_4^+ : \text{NO}_3^-$ ratios (100:0, 75:25, 50:50, 25:75, and 0:100) (Table 1).

Cultural conditions. To facilitate complete recovery of root systems at harvest, rooted cotoneaster cuttings and rudbeckia seedlings were grown in 3.8-L containers filled with a substrate of arcillite (Turface, Aimcor Inc., Deerfield, Ill.), consisting of calcined montmorillite and illite clays. Arcillite was chosen as the container substrate because of its high moisture-holding capacity, good aeration, even retention of irrigation without channeling, and ease of removal from plant roots (Hiller and Koller, 1979). Temperatures were maintained at $24 \pm 3^\circ\text{C}$ day/ $13 \pm 3^\circ\text{C}$ night under natural irradiance. Plants were covered with black cloth at 5:00 PM and provided with a daily night interruption from 11:00 PM to 2:00 AM using incandescent bulbs (photosynthetic photon flux of $3.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ plus photomorphogenic radiation of $0.7 \text{ W}\cdot\text{m}^{-2}$) and uncovered at 8:00 AM.

Received for publication 27 Nov. 2000. Accepted for publication 6 June 2001. Research was funded in part by the North Carolina Agricultural Research Service (NCARS), Raleigh, NC 27695-7643. Use of trade names in this publication does not imply endorsement by the NCARS of products named nor criticism of similar ones not mentioned. The technical assistance of William Reece and Diane Mays, Analytical Service Laboratory, Dept. of Soil Science, and the statistical guidance of William Swallow are greatly appreciated.

Table 1. Nutrient solutions for each $\text{NH}_4^+ : \text{NO}_3^-$ ratio.

$\text{NH}_4^+ : \text{NO}_3^-$ ratio ^a	Nutrient source						
	NH_4NO_3	NH_4Cl	KNO_3	$\text{Ca}(\text{NO}_3)_2$	KH_2PO_4	$\text{K}_2(\text{SO}_4)$	CaSO_4
100:0		3.5			0.32	0.96	1.25
75:25	0.875	1.75			0.32	0.96	1.25
50:50	1.75				0.32	0.96	1.25
25:75	0.875		0.96	0.442	0.32		0.834
0:100			0.96	1.27	0.32		

^a1.03 mM MgSO_4 , 0.09 mM Fe DTPA, 0.05 mM H_3BO_3 , 0.0003 mM CuSO_4 , 0.009 mM MnCl , 0.001 mM $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$, and 0.0008 mM ZnSO_4 supplied to each $\text{NH}_4^+ : \text{NO}_3^-$ treatment.

Ammonium : nitrate ratio treatments were administered twice daily (9:00 AM and 1:00 PM) at 50 mg·L⁻¹ N and 450 mL per application (900 mL daily) via individual spray stake emitters (Spot-Spitter, Green 160°, Roberts Irrigation Products, San Marcos, Calif.) that dispersed nutrient solution treatments evenly over each container. A modified Hoagland solution was applied with the NH₄⁺ : NO₃⁻ treatments to provide other mineral nutrients necessary for plant growth (Table 1). Nutrient solutions in stock tanks were changed weekly, and pH of nutrient solutions was checked daily and adjusted as needed with NaOH or HCl to maintain a pH of 6.0. To monitor substrate pH, substrate solution displaced during the 1:00 PM irrigation with nutrient solution was collected on 25 Oct., 11 Nov., 23 Nov., 12 Dec., and 2 Jan. Substrate solution pH was measured for cotoneaster only with an Accumet pH meter (Fisher Scientific Co., Fairlawn, N.J.).

Plant growth and nutrient content. At harvest, roots were washed free of substrate. Stems, leaves, and roots were then washed with 0.1 N HCl, and rinsed with distilled water to remove any mineral nutrient residues. After washing, root length and root area were determined using an image analyzer (AgVision Monochrome System, Decagon Devices, Pullman, Wash.). Complete root systems of cotoneaster were measured. Due to their large size, root systems of rudbeckia were subsampled, measurements recorded, and data were adjusted following procedures developed by Thetford et al. (1995).

Stems, leaves, and roots were dried at 62 °C for 5 d, weighed, and ground in a Wiley mill to pass a 40-mesh (0.425-mm) screen. Each tissue sample [root or shoot (cotoneaster, leaves + stem; rudbeckia, leaves)] (1.25 g) was combusted at 490 °C for 6 h. The resulting ash was dissolved in 10 mL 6 N HCl and diluted to 50 mL with deionized distilled water. Phosphorus, K, Ca, Mg, Mn, and Fe tissue concentrations were determined by inductively coupled plasma emissions spectrophotometer (P-2000; Perkin Elmer, Norwalk, Conn.). Nitrogen concentration was determined using 10-mg

samples in a CHN elemental analyzer (Perkin Elmer 2400, Perkin Elmer). All tissue nutrient analyses were conducted at the Analytical Service Laboratory, Dept. of Soil Science. Leaf area of each species was determined at harvest with a leaf area meter (LI-3000; LI-COR, Lincoln, Nebr.). Dry weight and leaf area data were used to calculate root : shoot ratio [RSR (cotoneaster) = root dry weight ÷ shoot (leaf + stem) dry weight and RSR (rudbeckia) = root dry weight ÷ leaf dry weight] and specific leaf dry weight (SLW = leaf dry weight ÷ leaf area). Tissue nutrient content (mg) was based on percent concentration of the nutrient, multiplied by plant part (root or shoot) dry weight and divided by 100, and was utilized to show absolute differences in nutrient accumulation regardless of plant size.

Histological procedures. After washing, two root subsamples (1 cm long) from each species were collected from a primary root, 5 cm distally from the stem–root junction of the plant. Only roots of plants fertilized with 25:75 NH₄⁺ : NO₃⁻ and 0:100 NH₄⁺ : NO₃⁻ were sectioned (two plants per NH₄⁺ : NO₃⁻ treatment), based on conclusions drawn from root dry-weight analyses. Root tissue samples were fixed by vacuum infiltration with formalin acetic acid, dehydrated, infiltrated in a series of ethanol and tertiary butyl alcohol (Johansen, 1940), and embedded in TissuePrep (Fisher Scientific Co., Fairlawn, N.J.) using a Model 166 Histomatic Tissue Processor (Fisher Scientific Co.). Tissue samples were sectioned serially on a rotary microtome at 15-mm thickness, affixed to slides with Haupt's adhesive (Jensen, 1962), and stained with safranin, methyl violet, and fast green (Johansen, 1940). Root diameter (n = 20), diameter of the stele (n = 20), number of secondary tracheary elements (n = 10), size of secondary tracheary elements (n = 20), and number of cortical rows (n = 10, rudbeckia only) were determined by viewing cross sections of roots through a light microscope. Secondary tracheary elements were defined as secondary xylem >10 mm in diameter.

Statistical analyses. All variables were

tested for differences using analysis of variance and regression analyses (SAS Institute, 1985) and were considered significant at *P* ≤ 0.05. Treatment comparisons were made by single degree of freedom linear contrast tests testing for differences between NH₄⁺ alone, NO₃⁻ alone, and the average response of NH₄⁺ : NO₃⁻ mixtures. No statistical analyses were conducted on the anatomical data and these data are included for comparison purposes only.

Results and Discussion

Although pH of the nutrient solutions in stock tanks was maintained at 6.0, substrate solution pH varied with sample date and NH₄⁺ : NO₃⁻ ratio, while the interaction between sample date and NH₄⁺ : NO₃⁻ ratio was nonsignificant (Table 2). Substrate solution pH increased quadratically over the course of the experiment with the substrate solution pH starting at 6.34 on 25 Oct. and the highest pH measured on 12 Dec (6.92). There was also a quadratic response in substrate pH as effected by NH₄⁺ : NO₃⁻ ratio, with the highest pH measured in the substrate solution of plants fertilized with the 50:50 NH₄⁺ : NO₃⁻ ratio.

Cotoneaster. Cotoneaster fertilized with NO₃⁻ alone had smaller leaf, stem, and root dry weights, less leaf area, and higher RSR than those fertilized with a combination of NH₄⁺ and NO₃⁻ or with NH₄⁺ alone (Table 3). Similarly, dry weights of cranberry (*Vaccinium macrocarpon* Ait.) (Rosen et al., 1990), lodgepole pine, and Engelmann spruce (Bigg and Daniel, 1978) were higher with NH₄⁺ and an equal mix of NH₄⁺ and NO₃⁻ (50:50) than with NO₃⁻ alone. In contrast, Gilliam et al. (1982–83) reported that NO₃⁻ increased shoot growth of cotoneaster 'Royal Beauty' compared to NH₄⁺ when applied weekly and grown in a substrate of 4 pine bark : 1 sand (by volume); however, N form did not impact root growth.

Nitrogen contents (mg) (Table 4) and concentrations (data not presented) in cotoneaster roots and shoots fertilized with NO₃⁻ were decreased an average of 54% and 26% for

Table 2. Effect of sample date and NH₄⁺ : NO₃⁻ ratio on substrate pH of cotoneaster.

Sample date	pH	NH ₄ ⁺ : NO ₃ ⁻ ratio	pH
25 Oct.	6.34	100:0	6.77
11 Nov.	6.56	75:25	6.89
23 Nov.	6.73	50:50	7.00
12 Dec.	6.92	25:75	6.74
2 Jan.	6.78	0:100	6.34
Regression[†]			
L	0.006		0.001
Q	0.005		0.001
Contrasts[‡]			
100:0 vs. mixes	---		NS
0:100 vs. mixes	---		0.001
100:0 vs. 0:100	---		0.001

[†]L = linear, Q = quadratic.

[‡]Treatment comparisons made by single degree of freedom linear contrast tests. Mixes = average of the 75:25, 50:50, and 25:75 NH₄⁺ : NO₃⁻ ratios.

NS = Nonsignificant at *P* > 0.05, *P* value stated otherwise. Sample date × NH₄⁺ : NO₃⁻ interaction was NS.

Table 3. Effect of N form and ratio on cotoneaster leaf, stem, and root dry weights, root : shoot ratio (RSR), and leaf area.

NH ₄ ⁺ : NO ₃ ⁻ ratio	Dry wt (g)				Leaf area (m ²)
	Leaf	Stem	Root	RSR [‡]	
100:0	1.84	1.34	0.54	0.172	0.0372
75:25	1.51	1.10	0.44	0.173	0.0296
50:50	1.86	1.21	0.52	0.171	0.0338
25:75	2.11	1.22	0.52	0.168	0.0315
0:100	1.04	0.71	0.37	0.221	0.0207
Regression[†]					
L	NS	0.02	NS	0.03	0.01
Q	NS	NS	NS	0.03	NS
Contrasts[‡]					
100:0 vs. mixes	NS	NS	NS	NS	NS
0:100 vs. mixes	0.006	0.004	0.04	0.002	0.006
100:0 vs. 0:100	0.02	0.002	0.02	0.002	0.001

[‡]Root dry weight ÷ shoot (leaf + stem) dry weight.

[†]L = linear, Q = quadratic.

[‡]Treatment comparisons made by single degree of freedom linear contrast tests. Mixes = average of the 75:25, 50:50, and 25:75 NH₄⁺ : NO₃⁻ ratios.

NS = Nonsignificant at *P* > 0.05, *P* value stated otherwise.

Table 4. Nitrogen form and ratio effects on cotoneaster root and shoot tissue nutrient contents.

NH ₄ ⁺ : NO ₃ ⁻ ratio	Root					Shoot				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
	mg									
100:0	15.2	1.4	10.4	1.6	1.2	102.5	8.5	70.3	32.7	11.5
75:25	12.0	1.3	9.4	1.5	1.1	83.2	7.0	57.8	29.2	9.8
50:50	14.3	1.8	10.8	1.8	1.3	90.3	8.5	59.9	37.3	12.1
25:75	12.2	1.9	11.6	2.3	1.6	96.9	9.4	63.7	44.0	13.3
0:100	7.2	1.2	7.8	2.0	1.1	45.2	4.9	35.2	22.1	7.3
Regression^z										
L	0.007	NS	NS	0.004	NS	0.005	NS	0.002	NS	NS
Q	NS	0.02	NS	NS	NS	NS	NS	NS	0.02	0.03
Contrasts^y										
100:0										
vs. mixes	0.01	0.03	NS	0.03	NS	0.04	NS	0.004	0.02	NS
0:100										
vs. mixes	0.001	0.001	0.006	NS	0.001	0.001	0.001	0.001	0.001	0.001
100:0										
vs. 0:100	0.001	NS	0.003	0.01	NS	0.001	0.001	0.001	0.003	0.001

^zL = linear, Q = quadratic.

^yTreatment comparisons made by single degree of freedom linear contrast test. Mixes = average of the 75:25, 50:50, and 25:75 NH₄⁺ : NO₃⁻ ratios.

^{ns}Nonsignificant at $P > 0.05$, P value stated otherwise.

content and concentration, respectively, compared to N supplied as NH₄⁺ alone, and 47% and 20% for content and concentration, respectively, compared to mixes of NH₄⁺ and NO₃⁻. In contrast, Gilliam et al. (1982–83) reported higher shoot N concentrations (percent dry weight) with weekly NO₃⁻ applica-

tions to *Cotoneaster dammeri* 'Royal Beauty' grown in a substrate of 4 pine bark : 1 sand (by volume) than with weekly NH₄⁺ applications. Mixtures of NH₄⁺ and NO₃⁻ increased P, K, and Mg contents in cotoneaster roots and shoots compared to NO₃⁻ alone; whereas NO₃⁻ lowered root K and Ca contents and shoot P,

K, Ca, and Mg contents compared to NH₄⁺ alone (Table 4). Cotoneaster root and shoot Fe contents were not changed by N form, but mixtures of NH₄⁺ and NO₃⁻, and NH₄⁺ alone increased root and shoot Mn contents (data not presented).

Root diameter of cotoneaster was greater when fertilized with a mix of NH₄⁺ and NO₃⁻ compared to NO₃⁻ alone (Table 5). Diameter of the stele of cotoneaster roots was also larger with a mix of NH₄⁺ and NO₃⁻ than with NO₃⁻ alone. Furthermore, roots fertilized with a mix of NH₄⁺ and NO₃⁻ had a higher number of secondary tracheary elements that were slightly larger than with NO₃⁻ alone. Increased root dry weight when fertilized with mixtures of NH₄⁺ and NO₃⁻ may have resulted from increased root diameter, since root length and area were unaffected by N form (Table 5). Root anatomy may be affected by the environment (Fahn, 1990), so the larger, more developed vascular system of cotoneaster roots fertilized with the mix of NH₄⁺ and NO₃⁻ may relate to the more favorable nutrient supply, resulting in a larger plant.

Rudbeckia. Similar to cotoneaster, NO₃⁻ as the sole N source produced lower leaf and root dry weights and smaller leaf area than rudbeckia fertilized with NH₄⁺ or with mixes of NH₄⁺ and NO₃⁻ (Table 6). Furthermore, plants in all treatments had equivalent specific leaf

Table 5. Total root area, total root length, and relative comparisons of the presence and diameter of root tissues and tissue systems (mean ± standard error). Based on results of root dry weight analysis, only roots from 25:75 NH₄⁺ : NO₃⁻ and 0:100 NH₄⁺ : NO₃⁻ ratios were sectioned for root diameter, diameter of stele, number of secondary tracheary elements, and number of cortical rows determinations.

NH ₄ ⁺ : NO ₃ ⁻ ratio	Root area ^z (m ²)	Root length (m)	Root diam (mm)	Diam of stele (mm)	No. of secondary trach. elem. ^y	Diam of secondary trach. elem. (mm)	No. of cortical rows
Cotoneaster							
25:75	0.01 ± 0.01	0.09 ± 0.01	1.13 ± 0.13	1.00 ± 0.12	59 ± 9.1	0.030 ± 0.002	---
0:100	0.01 ± 0.01	0.08 ± 0.01	0.69 ± 0.01	0.58 ± 0.01	30 ± 2.2	0.027 ± 0.001	---
Rudbeckia							
25:75	0.19 ± 0.07	1.82 ± 0.63	1.04 ± 0.09	0.15 ± 0.01	24 ± 0.6	0.042 ± 0.001	11 ± 0.6
0:100	0.08 ± 0.05	0.78 ± 0.43	1.11 ± 0.08	0.12 ± 0.04	18 ± 0.6	0.025 ± 0.001	11 ± 0.3

^zRoot area and root length were not affected by NH₄⁺ : NO₃⁻ ratio ($P > 0.05$). No statistical analyses were conducted on root diameter ($n = 20$), diameter of the stele ($n = 20$), number of secondary tracheary elements ($n = 10$), size of secondary tracheary elements ($n = 20$), and number of cortical rows ($n = 10$, rudbeckia only) data. These data are included for comparisons only.

^ySecondary tracheary elements were defined as secondary xylem ≥ 10 mm in diameter.

Table 6. Effect of N form and ratio on rudbeckia leaf and root dry weights, root : shoot ratio (RSR), and leaf area.

NH ₄ ⁺ : NO ₃ ⁻ ratio	Dry weight (g)			Leaf area (m ²)
	Leaf	Root	RSR ^z	
100:0	6.21	1.87	0.304	0.102
75:25	6.66	2.15	0.341	0.114
50:50	6.74	2.53	0.366	0.110
25:75	6.19	2.38	0.417	0.105
0:100	2.61	1.03	0.404	0.046
Regression^y				
L	0.04	NS	0.004	0.05
Q	0.03	0.004	NS	0.03
Contrasts^x				
100:0 vs. mixes	NS	NS	0.05	NS
0:100 vs. mixes	0.001	0.002	NS	0.001
100:0 vs. 0:100	0.009	0.03	0.03	0.02

^zRoot dry weight ÷ leaf dry weight.

^yL = linear, Q = quadratic.

^xTreatment comparisons made by single degree of freedom linear contrast tests. Mixes = average of 75:25, 50:50, and 25:75 NH₄⁺ : NO₃⁻ ratios.

^{ns}Nonsignificant at $P > 0.05$, P value stated otherwise.

Table 7. Nitrogen form and ratio effects on rudbeckia root and shoot tissue nutrient contents.

NH ₄ ⁺ : NO ₃ ⁻ ratio	Root					Shoot				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
	mg									
100:0	101.2	19.6	114.9	6.1	9.1	220.3	27.1	239.7	190.3	84.9
75:25	101.7	24.4	135.2	6.5	10.3	254.0	39.5	317.5	190.7	72.2
50:50	106.6	29.8	156.4	8.8	12.2	255.7	35.3	332.5	184.5	72.1
25:75	95.4	26.2	153.6	7.5	13.2	254.4	47.0	273.4	177.7	65.8
0:100	43.7	10.1	70.6	3.6	5.7	104.0	28.0	99.6	81.5	28.4
Regression^a										
L	0.003	NS	NS	NS	NS	0.03	NS	0.04	0.001	0.001
Q	0.001	0.001	0.001	0.001	0.002	0.001	0.03	0.001	0.003	0.02
Contrasts^b										
100:0 vs. mixes	NS	0.004	0.001	0.007	0.001	0.007	0.03	0.002	NS	0.01
0:100 vs. mixes	0.001	0.001	0.001	0.001	0.001	0.001	0.04	0.001	0.001	0.001
100:0 vs. 0:100	0.001	0.002	0.001	0.005	0.001	0.001	NS	0.001	0.001	0.001

^aL = linear, Q = quadratic.^bTreatment comparisons made by single degree of freedom linear contrast tests. Mixes = average of the 75:25, 50:50, and 25:75 NH₄⁺ : NO₃⁻ ratios.NS Nonsignificant $P > 0.05$, P value stated otherwise.

dry weights (60 g·m⁻²), indicating that differences in leaf area were due to changes in leaf expansion or number, not leaf thickness. There were no differences in leaf and root dry weights of plants fertilized with NH₄⁺ and plants fertilized with mixes of NH₄⁺ and NO₃⁻, suggesting that any addition of NH₄⁺ to fertilizer solutions improved growth. The RSR was lower with NH₄⁺ than if N was supplied as mixes of NH₄⁺ and NO₃⁻, or as NO₃⁻ alone, indicating that energy was allocated to shoot growth at the expense of root growth. Similarly, Klett and Gartner (1975) reported that growth of *Chrysanthemum morifolium* Ramat. 'Bright Golden Anne' in hardwood bark was higher with an equal mix of NH₄⁺ and NO₃⁻ than with N supplied as NH₄⁺ or NO₃⁻ alone.

Roots and shoots of rudbeckia fertilized with 100% NO₃⁻ had lower contents of N, K, Ca, and Mg than plants fertilized with NH₄⁺ alone and mixes of NH₄⁺ and NO₃⁻ (Table 7). Similarly, NH₄⁺ resulted in higher N contents in shoots of *Chrysanthemum morifolium* 'Bright Golden Anne' than NO₃⁻ (Klett and Gartner, 1975). Phosphorus contents in roots and shoots fertilized with mixes of NH₄⁺ and NO₃⁻ were 20% to 75% higher than those fertilized with NH₄⁺ or NO₃⁻ alone (Table 7). Such dramatic reductions in tissue nutrient content and growth reiterate the need for proper N form selection. Maximum nutrient content was generally found with the 50:50 NH₄⁺ : NO₃⁻ ratio, which also corresponds to maximum leaf and root dry weights (Table 6). Shoot Fe contents were higher in plants fertilized with mixtures of NH₄⁺ and NO₃⁻ than in those fertilized with NH₄⁺ or NO₃⁻ alone, but NH₄⁺ resulted in the greatest Mn contents in shoots and roots (data not presented).

Root diameter of rudbeckia fertilized with a mix of NH₄⁺ and NO₃⁻ was similar to those grown with NO₃⁻ alone (Table 5) even though root dry weight was higher with the mixes of NH₄⁺ and NO₃⁻ than with NO₃⁻ alone (Table 6). This result suggests that increased root dry weight with a mix of NH₄⁺ and NO₃⁻ might be due to increased root length and/or root number instead of increased diameter. Root length was not changed by N form (Table 5), so a greater number of roots with a mix of NH₄⁺ and

NO₃⁻ may have resulted in increased dry weight. Diameter of the stele of rudbeckia roots and number of rows of cortical layers did not differ with N form (Table 5). However, stele of roots exposed to a mix of NH₄⁺ and NO₃⁻ had more secondary xylem with larger tracheary elements than stele of roots exposed to NO₃⁻ alone. A mixture of NH₄⁺ and NO₃⁻ resulted in a larger rudbeckia plant and a larger, more developed vascular system in rudbeckia roots.

In summary, growth and mineral nutrient accumulation of cotoneaster, a woody plant, and rudbeckia, an herbaceous plant, were generally higher with NH₄⁺, or if NH₄⁺ was mixed with NO₃⁻, than with NO₃⁻ alone. Nutrient solutions containing NH₄⁺ resulted in a marked increase in shoot and root growth of both species. A similar response was found if NH₄⁺ was applied to a broad range of plants already being grown with NO₃⁻ (Kirkby, 1981; Mengel and Kirkby, 1982). Root diameter of the woody roots of cotoneaster was higher with a mix of NH₄⁺ and NO₃⁻ than with NO₃⁻ alone, whereas diameter of the herbaceous roots of rudbeckia was not impacted by N form. Nutrient solutions with a mixture of NH₄⁺ and NO₃⁻ appeared to increase root diameter of the woody roots of cotoneaster and to result in a greater number of roots with the herbaceous rudbeckia. Steles of both plants contained more secondary xylem with larger tracheary elements with a mix of NH₄⁺ and NO₃⁻ than with nutrient solutions containing NO₃⁻ alone. Increased number and size of secondary tracheary elements may relate to increased dry weight and leaf area of both cotoneaster and rudbeckia fertilized with mixes of NH₄⁺ and NO₃⁻ rather than with NO₃⁻ alone. The surface area of the root system correlates to leaf surface area, so there may also be some correlation between size of the water-conducting system and the leaf area supplied by it (Kramer, 1983). Adaptations in the anatomical features of xylem are related to moisture availability, transpiration, and requirements for mechanical strength (Fahn, 1990). As utilization of N compounds is regulated by hormonal activity (Kirkby, 1981), higher transpirational demand may induce a hormonal signal for increased secondary tracheary differentiation.

Literature Cited

- Bigg, W.L. and T.W. Daniel. 1978. Effects of nitrate, ammonium, and pH on the growth of conifer seedlings and their production of nitrate reductase. *Plant Soil* 50:371-385.
- Edwards, J.H. and B.D. Horton. 1982. Interaction of peach seedlings to NO₃⁻ : NH₄⁺ ratios in nutrient solutions. *J. Amer. Soc. Hort. Sci.* 107:142-147.
- Fahn, A. 1990. *Plant anatomy*. Pergamon Press, Elmsford, N.Y.
- Finn, C.E., C.J. Rosen, and J.J. Luby. 1990. Nitrogen and solution pH effects on root anatomy of cranberry. *HortScience* 25:1419-1421.
- Gilliam, C.H., T.A. Fretz, and W.J. Sheppard. 1980. Effect of nitrogen form and rate on elemental content and growth of pyracantha, cotoneaster, and weigela. *Scientia Hort.* 13:173-179.
- Gilliam, C.H., M.E. Watson, and W.J. Sheppard. 1982/83. Fertilization of cotoneaster in a pine bark medium. *Scientia Hort.* 18:185-190.
- Hiller, L.K. and D.C. Koller. 1979. Potato growth responses in arcillite and sand. *HortScience* 14:534-536.
- Jensen, W.A. 1962. *Botanical histochemistry*. W.H. Freeman, San Francisco.
- Johansen, D.A. 1940. *Plant microtechnique*. McGraw-Hill, New York.
- Kirkby, E.A. 1981. Plant growth in relation to nitrogen supply, p. 249-267. In: F.E. Clark and T. Rosswall (eds.). *Terrestrial nitrogen cycles, processes, ecosystem strategies and management impacts*. *Ecol. Bul.* 33:249-267.
- Klett, J.E. and J.B. Gartner. 1975. Growth of chrysanthemums in hardwood bark as affected by nitrogen source. *J. Amer. Soc. Hort. Sci.* 100:440-442.
- Kramer, P.J. 1983. *Water relations of plants*. Academic, San Diego.
- Marschner, H. 1986. *Mineral nutrition of higher plants*. Academic, London.
- Mengel, K. and E.A. Kirkby. 1982. *Principles of plant nutrition*. Intl. Potash Inst., Worblaufen-Bern, Switzerland.
- Rosen, C.J., D.L. Allen, and J.J. Luby. 1990. Nitrogen form and solution pH influence growth and nutrition of two *Vaccinium* clones. *J. Amer. Soc. Hort. Sci.* 115:83-89.
- SAS Institute. 1985. *SAS user's guide: Statistics*. Version 5 ed. SAS Inst., Cary, N.C.
- Thetford, M., S.L. Warren, and F.B. Blazich. 1995. Response of *Forsythia × intermedia* 'Spectabilis' to uniconazole. I. Growth; dry-matter distribution; and mineral nutrient content, concentration, and partitioning. *J. Amer. Soc. Hort. Sci.* 120:977-982.