Ammonium and Nitrate Uptake throughout Development in *Dendranthema ×grandiflorum*

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Additional index words. chrysanthemum, N nutrition, nutrient efficiency

Abstract. Ammonium and NO₃ uptake from hydroponic solutions containing 1 mM each of (NH₄)₂SO₄ and Ca(NO₃)₂ were measured during development of *Dendranthema ×grandiflorum* (Ramat.) Kitamura 'Iridon', 'Sequoia', and 'Sequest'. Nitrogen depletion from solutions approximated a 1 NH₄ : 1 NO₃ ratio throughout a 90-day growth cycle (r = 0.96). Although harvest date × cultivar interactions were significant for both forms of N, overall patterns of N uptake were similar among cultivars. Nitrogen removal from hydroponic solutions (milligrams per plant) was greatest from days 40 to 60; however, N removal (milligrams per gram of tissue dry weight) was greatest in the first month of development and decreased steadily until day 90. From day 40 to 60, new leaf development ceased while inflorescence buds developed to ≈1.0 cm in diameter. After this time, N uptake decreased rapidly as inflorescences expanded. Correlations between morphological changes and N demand could maximize the efficiency of applied N by matching form and application timing with plant needs.

Nitrogen requirements of potted *Dendranthema ×grandiflorum* are known to be highest during the first 7 weeks of growth, and during this time, deficiencies are difficult to correct in later stages of development (Lunt and Kofranek, 1958). Tissue N accumulation was rapid in median leaves of 'Bonnaffon Deluxe' chrysanthemum during weeks 1 to 4, after which N accumulation stabilized or decreased (Boodley and Meyer, 1965). The N accumulation rate in aboveground vegetative tissues of 'GT4 Indianapolis White' decreased after week 6 of growth, and N was lost from stems and petioles between weeks 6 and 9 (Woodson and Boodley, 1983). From week 1 through 7, a slight but steady decrease in relative N accumulation rate (grams N accumulated per gram N in plant per day) was observed in 'Fiesta' chrysanthemums (Willits et al., 1992). Nitrate accumulation in roots of 'GT4 Indianapolis White' occurred at nearly constant rates throughout plant development when NO₃ was supplied at 3.75 or 15.0 mM (Woodson et al., 1984).

To maximize the quality of chrysanthemum crops, reduction or termination of N applications is recommended when inflorescence bud diameters are 1.0 to 1.5 cm (Lunt and Kofranek, 1958). Continued fertilization after this stage caused distorted and brittle foliage (Kofranek, 1992) and diminished post-

harvest quality (Nell et al., 1989). Declining requirements for N after flower initiation are attributed to N remobilization from vegetative tissues supporting latter stages of inflorescence development (Woodson and Boodley, 1983).

Growth of chrysanthemum was improved with N supplied as combinations of NH₄ and NO₃, rather than as NO₃ alone (Elliott and Nelson, 1983). Some nutritional studies with chrysanthemum used flowing (Elliott and Nelson, 1983) or static (Willits et al., 1992) hydroponic solutions, but most researchers have used sand media with solutions of known concentration and volume added at regular intervals. The nature of the sand-media experiments prevented observation of forms and quantities of N removed from solutions during plant development. The purposes of our research were to 1) determine quantities of NH₄ and NO₃ removed from nutrient solutions during vegetative and reproductive stages of chrysanthemum development, 2) further examine if morphological changes could be used as indicators of changing N demands, and 3)

compare N requirements of three cultivars as a preliminary evaluation of genetic effects on N demands.

Materials and Methods

We used unrooted cuttings of *Dendranthema ×grandiflorum* 'Iridon', 'Sequoia', and 'Sequest'. These cultivars are pot-type chrysanthemums with 'Iridon' in the 9-week flowering response group and 'Sequoia' and 'Sequest' in the 10-week group. 'Sequest' is a yellow-flowered sport of the bronze-flowered 'Sequoia'. Cuttings were stuck into sterile vermiculite and placed under a deionized-water misting system until adventitious roots were visible. Plants were transferred to round, black polyethylene greenhouse pots with drainage holes sealed with tape to eliminate light. Containers were lined with clear polyethylene bags, then filled with Hoagland's solution (Hoagland and Arnon, 1950) containing 1 mM each of (NH₄)₂SO₄ and Ca(NO₃)₂. Each container was covered with a square 2.5-cm-thick piece of extruded polystyrene insulation with a recessed circular groove cut to the diameter and wall thickness of the container. This arrangement allowed a tight seal between the container and lid to eliminate light penetration and moisture loss. One 4-cm hole bored into each lid allowed for placement of a rooted cutting into the nutrient solution. Pieces of foam sealed the holes around plant stems. Aeration was provided to the solution in each container. Solution pH was adjusted to 5.6 every 48 h, and deionized water was added to maintain solution volume throughout the experiment. Sixteen-liter stock containers held four plants for future sampling periods, one of each cultivar and one selected randomly from the cultivars. Four-liter sampling containers held single plants and were arranged in a randomized complete block, with four blocks and one plant per cultivar per block. Nutrient solution and plant samplings were from these 4-liter containers. In both container types, available N was 112 mg each of NH₄ and NO₃-N per plant. The experiment was conducted in a glasshouse where light levels were maintained at ≥550 μmol·m⁻²·s⁻¹ with 1000-W, high-pressure sodium lamps. From day 1 (22 Feb.), when rooted cuttings were placed into nutrient solutions, through day 17 (10 Mar.), the pho-

Table 1. Harvest date and cultivar effects on NH₄ and NO₃ removal from hydroponic solutions. Mean squares for linear, quadratic, and cubic polynomials are presented for harvest date only if the harvest date × cultivar interaction was not significant.

Source of variation	Mean squares			
	mg		mg/g dry wt	
	NH ₄	NO ₃	NH ₄	NO ₃
Block	639.9**	474.9**	30.5*	15.0*
Harvest date (D)	5208.1**	4923.0**	727.7**	486.7**
Linear	---	---	5463.8**	---
Quadratic	---	---	340.2**	---
Cubic	---	---	2.2 ^{NS}	---
Cultivar(C)	1137.9**	2468.1**	3.2 ^{NS}	3.6 ^{NS}
D × C	393.2**	377.4**	6.8 ^{NS}	10.3**
Linear	108.7 ^{NS}	92.8 ^{NS}	---	6.0 ^{NS}
Quadratic	1160.3**	1652.2**	---	42.1**
Cubic	909.6**	497.5**	---	12.7*

^{NS}, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Received for publication 2 Sept. 1994. Accepted for publication 29 Dec. 1995. Use of trade names does not imply endorsement of the products named nor criticism of similar ones not named. We gratefully acknowledge the gift of plant materials from Yoder Brothers, Barberton, Ohio. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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toperiod consisted of natural daylength plus one 4-h night interruption (2200 to 0200 HR). From day 17 to 90 (May 22), plants were grown under short days by covering with blackcloth from 1700 to 0800 HR. Plants were pinched and then disbudded to two inflorescences. Temperature settings were 17C minimum/24C maximum.

Plants were harvested from the 4-liter sampling containers every 10 days through day 90, and solutions were sampled at days 1, 5, and 10 of each cycle. Each new 10-day cycle was initiated by a change of polyethylene bags and solutions, and transferring 12 plants (three cultivars $\times$ four blocks) from 16-liter stock containers to 4-liter sampling containers.

Height and inflorescence diameter were measured and leaves were counted on harvested plants. Root and shoot portions were washed in deionized water, separated, and oven-dried at 60C for 5 days, after which dry weights were determined. Dried root and shoot tissues were ground in a Wiley mill to pass through a 0.425-mm (40-mesh) screen. Ammonium and NO_3 were extracted by treating 250 mg of dried tissue with 100 ml 2.0 M KCl for 30 min on a rotary shaker, then filtering through Whatman no. 1 filter paper. Blanks containing only KCl solutions were included for background levels of NH_4 and NO_3 . Ammonium and NO_3 concentrations of blanks, filtrates from extraction of dried tissues, and hydroponic solutions were determined by micro-Kjeldahl procedures (Keeney and Nelson, 1982), with magnesium oxide as the alkali and Devarda's alloy for NO_3 reduction to NH_4 . Samples were distilled into a boric acid-bromocresol green-methyl red indicator solution and titrated with 0.01 N H_2SO_4 to an endpoint determined by appearance of a light-pink pigment. Ammonium and NO_3 variables were expressed as milligrams removed from hydroponic solutions and as percentage of tissue dry weights.

Total N was determined for 'Sequoia' tissues by macro-Kjeldahl procedures (Bremner, 1965) with a permanganate-reduced Fe modification for recovery of NO_3 -N (Olsen, 1927). A single cultivar was sampled based on similarities of trends observed among the three cultivars for most characteristics studied.

Data were tested by analysis of variance (ANOVA), with blocks, harvest dates, and cultivars as independent variables affecting changes in N and growth attributes.

Results

In the ANOVA, harvest date $\times$ cultivar interactions significantly influenced the milligrams of NH_4 and NO_3 removed from hydroponic solutions, milligrams per gram dry weight of NO_3 removed from hydroponic solutions (Table 1), NO_3 concentration in roots, and NH_4 and NO_3 concentrations in shoots (Table 2). Harvest date significantly influenced all N variables tested (Tables 1 and 2). Cultivar significantly influenced all variables except milligrams per gram dry weight of NH_4 and NO_3 removed from solutions (Tables 1 and 2).

Table 2. Harvest date and cultivar effects on NH_4 and NO_3 concentration in root and shoot tissue of *Dendranthema $\times$ grandiflorum* grown in hydroponic solution. Mean squares for linear, quadratic, and cubic polynomials are presented for harvest date only if the harvest date $\times$ cultivar interaction was not significant.

Source of variation	Mean squares			
	Root		Shoot	
	NH_4	NO_3	NH_4	NO_3
Block	0.0001 ^{NS}	0.051 ^{**}	0.001 [*]	0.017 ^{NS}
Harvest date (D)	0.003 ^{**}	0.714 ^{**}	0.002 ^{**}	0.090 ^{**}
Linear	0.000 ^{NS}	---	---	---
Quadratic	0.013 ^{**}	---	---	---
Cubic	0.002 ^{**}	---	---	---
Cultivar (C)	0.012 ^{**}	0.287 ^{**}	0.023 ^{**}	0.553 ^{**}
D $\times$ C	0.0003 ^{NS}	0.031 ^{**}	0.0006 [*]	0.028 ^{**}
Linear	---	0.046 [*]	0.0005 ^{NS}	0.086 ^{**}
Quadratic	---	0.031 ^{NS}	0.0007 ^{NS}	0.069 ^{**}
Cubic	---	0.083 ^{**}	0.0014 [*]	0.032 [*]

NS, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Fig. 1. (A) Root and (B) shoot dry weights, (C) leaf number, (D) plant height, and (E) inflorescence diameter of *Dendranthema $\times$ grandiflorum* (□) 'Iridon', (○) 'Sequoia', and (Δ) 'Sequest' grown in hydroponic solution with 1 mM each of NH_4 and NO_3 -N. Vertical bars indicate least significant difference at $P \leq 0.05$.

Growth factors. Changes in root dry weight fit a cubic response for the harvest date $\times$ cultivar interaction (Fig. 1A). At the final harvest (day 90), root weights were 34 times greater than weights at day 1. Growth curves for all cultivars approximated sigmoid forms for shoot dry weight, leaf count, plant height, and inflorescence diameter (Fig. 1). For shoot dry weight, leaf count, and plant height (Fig. 1B–D), a lag phase of ≈ 20 days was followed by rapid growth until about day 50 for leaf count and day 70 for shoot dry weight and plant height. Inflorescence diameter (Fig. 1E) increased rapidly between days 30 and 70 for ‘Iridon’ and between days 40 and 80 for ‘Sequoia’ and ‘Sequest’.

Nitrogen removal from solutions. Ammonium and NO_3 removal from solutions approximated a 1 NH_4 : 1 NO_3 ratio ($r=0.96$) for all cultivars throughout the crop cycle (Fig. 2). There was a significant cubic response for the harvest date $\times$ cultivar interactions for these variables. The period of greatest N uptake was between days 30 and 60 (Fig. 2 A and B). Uptake was greatest around day 40 for ‘Iridon’ and ‘Sequest’ and day 50 for ‘Sequoia’. On a tissue dry-weight basis, removal of NH_4 and NO_3 from solutions was greatest during the first 10 days of the experiment, then declined to nearly zero by day 90 (Fig. 2 C and D). Ammonium removal fit a quadratic pattern over harvest dates, and NO_3 removal fit a cubic pattern for harvest date $\times$ cultivar.

Amounts of NH_4 and NO_3 removed from solutions during the first and second 5 days of each 10-day cycle were compared to determine if preferential depletion of one form between days 1 and 5 lead to compensatory depletion of the other form between days 5 and 10. This partitioning revealed no preferential uptake of either form of N at any time during this period (Table 3).

Nitrogen assimilation. Percent NH_4 in roots for all cultivars declined between days 10 and 30 then increased from days 30 to 90 (Fig. 3A). Percent NO_3 in roots was variable by cultivar at day 10, but values for all cultivars were equal at day 20 and then followed similar patterns through day 90 (Fig. 3B). From day 30 to 60, root NO_3 levels declined two- to five-fold, depending on cultivar. From day 60 through day 90, root NO_3 levels tended to increase slightly in ‘Sequoia’ and ‘Sequest’ but remained constant in ‘Iridon’. The greatest similarities among cultivars for root NO_3 occurred on days 30 and 90; however, on day 30 the level was 2.5 times that on day 90. Shoot NH_4 tended to increase slowly throughout development in ‘Sequoia’ and ‘Sequest’ but remained unchanged in ‘Iridon’, except for an increase by day 90 (Fig. 3C). In ‘Sequoia’ and ‘Sequest’, shoot NO_3 increased from days 10 to 30, then decreased until day 60, and remained mostly unchanged through day 90 (Fig. 3D). Shoot NO_3 in ‘Iridon’ was nearly constant from days 10 through 50, then declined by day 60 to a level that was maintained through day 90. Ammonium and NO_3 concentrations in roots tended to be higher in ‘Iridon’ than in ‘Sequoia’ and ‘Sequest’ (Fig. 3 A and B), whereas NH_4 and NO_3 concentrations in

shoots tended to be lower in ‘Iridon’ than in ‘Sequoia’ and ‘Sequest’ (Fig. 3 C and D).

Total N. Tissue N in ‘Sequoia’ (Fig. 4) was initially 1.3% of shoot dry weight and 6.4% of root dry weight. At day 30, shoot N had increased to 5.2%, and root N had decreased to 5.5%. Thereafter, root and shoot total N levels were similar, tending to decline slightly, with final levels (day 90) of 4.3% and 4.8% for shoot and root tissue, respectively.

Discussion

Ammonium and NO_3 removal from hydroponic solutions (on a whole-plant basis) was greatest between days 40 and 50, with rapid reductions in N requirements after inflorescence buds had reached 1.0 cm in diameter (Fig. 2 A and B). Ammonium and NO_3 removal (in milligrams per gram dry weight) was greatest on day 10, then decreased by 20- to 25-fold during the 90 days of plant growth in this experiment (Fig. 2 C and D). This decline suggests a high cellular requirement (in milligrams per gram dry weight) for N early in development. Total N was about 6 times less in shoots than in roots at the outset, but shoot N increased rapidly to a level similar to that in roots and remained mostly unchanged from days 30 through 90 (Fig. 4). Perhaps the physiological need for N was greatest early in the plant’s growth cycle due to N deficiencies in cuttings that were rooted under a deionized-water mist, requirements associated with ad-

ventitious root formation, or N loading in advance for rapid shoot growth.

Total shoot N levels stabilized between days 20 and 30, a time that corresponded to initiation of rapid shoot growth (Fig. 1B–D). The apparent steady-state level for total N ($\approx 5\%$) found in this study agrees with the 3% to 6% found by Willits et al. (1992) and suggested by Dole and Wilkins (1988) for chrysanthemum. The fact that cellular demand for N (milligram per gram of dry weight) under nonlimiting conditions was greatest at planting and declined throughout development supports recommendations that N application be maximized in the first 7 weeks of growth and reduced thereafter. The requirement for early N applications also could be inflated by restricted uptake of N by small root systems of young plants.

Throughout the crop cycle, about equal NH_4 and NO_3 removal from solutions might have been due to their 1:1 concentration ratio in solutions, or it may indicate that preferential uptake of one N form does not occur at any growth stage in chrysanthemum. However, evidence for a possible preferential assimilation of NH_4 early in development was apparent in this study. Between days 10 and 30, the NH_4 and NO_3 (milligrams per gram dry weight) removed from solutions were high relative to later samplings, with NH_4 uptake being slightly greater than NO_3 uptake (Fig. 2 C and D). During this period, the percentage of NH_4 in roots (Fig. 3A) declined steadily, but the per-

Fig. 2. (A and C) Ammonium and (B and D) NO_3 removal from hydroponic solutions containing 1 mM (112 mg) each of NH_4 and NO_3 -N expressed in (A and B) milligrams and (C and D) milligrams per gram of tissue dry weight of *Dendranthema $\times$ grandiflorum* ($\square$) ‘Iridon’, ($\circ$) ‘Sequoia’, and (Δ) ‘Sequest’. Vertical bars indicate least significant difference at $P \leq 0.05$.

centage of NO_3 (Fig. 3B) either increased or was stable, depending on cultivar. Also, between days 10 and 30, shoot NH_4 (Fig. 3C) remained nearly constant in all cultivars, but shoot NO_3 accumulated in 'Sequoia' and 'Sequest' and was stable in 'Iridon' (Fig. 3D). During this period, total N increased in shoots and decreased in roots of 'Sequoia' (Fig. 4).

Nitrate assimilation requires reduced ferredoxin and, therefore, can compete with CO_2 for light-derived chemical energy; NH_4 assimilation is carbohydrate dependent (Hageman, 1984). During the first 30 days of development, photosynthetic shoot tissue was limited (Fig. 1B). Therefore, decreasing NO_3 reduction and favoring NH_4 as a N source may have been more energy efficient and provided a means of keeping NH_4 concentrations below toxic levels. An alternative to this possibility is presented by Elliott and Nelson (1983), who calculated that the energy saved by restricted NO_3 reduction would be insignificant and that under adequate light intensities, NO_3 reduction likely would not compete with CO_2 reduction. They hypothesized that assimilation of NH_4 may satisfy a critical need for organic N in young, rapidly growing meristems that lack carbon skeletons and reductant for NO_3 assimilation.

Nitrate accumulation suggests low NO_3 reductase activity in the first 30 days of growth. We did not assay NO_3 reductase activity, but our data are difficult to reconcile with previous reports of high NO_3 reductase activity during this period (Woodson et al., 1984). High NO_3 reductase activity might be expected if previous findings were based on plants supplied with only NO_3 -N.

On a whole-plant basis, the period of greatest N demand [days 30 to 60 (Fig. 2 A and B)] corresponded to a time of rapid shoot growth and early inflorescence development. Comparing inflorescence diameter (Fig. 1E) with N uptake shows that rapid declines in uptake began when the diameter was 1.0 cm. These events occurred near day 40 for 'Iridon' and day 50 for 'Sequoia' and 'Sequest': an expression of genotypic differences of the 9- and 10-week response groups, respectively. Our data support Lunt and Kofranek (1958), who suggested terminating N applications when inflorescence buds are 1.0 to 1.5 cm wide.

Patterns of N removal from solutions (Fig. 2) and N assimilation (Fig. 3) for the three cultivars were similar; however, cultivars differed in their magnitudes of assimilation. For root NH_4 , shoot NH_4 , and shoot NO_3 , 'Iridon' was distinct from 'Sequoia' and 'Sequest' (Fig. 3 A, C, and D). Generally, 'Iridon' tended to partition more of NH_4 and NO_3 into root tissue, whereas 'Sequoia' and 'Sequest' tended to partition these into shoot tissue. Clustering of data points for 'Sequoia' and 'Sequest' reflects their close genetic relationship, because 'Sequest' was selected as a sport from 'Sequoia'. Our data suggest that, in chrysanthemum, a genotypic effect in assimilating and partitioning N exists that could be manifested phenotypically as N efficiency. Nitrogen uptake per milligram of plant dry weight was similar for the three cultivars tested (Table

1), suggesting equal requirements at a cellular level. However, because 'Iridon' is an earlier genotype, it required less total N to complete its life cycle, therefore attaining N efficiency temporally. Genotypes with increased efficiency of N use have been described in *Zea mays* L. (Harvey, 1939) and in *Lycopersicon esculentum* Mill. (O'Sullivan, et al., 1974), where the trait is controlled by relatively few major genes with dominance and additive $\times$ additive gene actions. Although not expressed as efficiency of N use, large differences in uptake of NH_4 and NO_3 occurred throughout development among four cultivars of *Antirrhinum majus* L. (Hood et al., 1993). These findings suggest the possibility of finding more extreme variation for N requirements by screening wider ranges of chrysanthemum germplasm than we used.

In this experiment, the plants demonstrated dramatic developmental changes around day 30. This was the first harvest day on which flower buds were visible (Fig. 1E). Also at this time, total N in 'Sequoia' roots and shoots

achieved 5.5% and 5.2%, respectively (Fig. 4). After day 30, total N levels changed only slightly through day 90. At day 30, other observations included initiation of large increases in N removal from solutions (Fig. 2 A and B), lowest root NH_4 (Fig. 3A), highest root NO_3 (Fig. 3B), and highest shoot NO_3 concentrations for 'Sequoia' and 'Sequest' (Fig. 3D). These landmarks in N relations may be due to the transition from floral induction to floral development or a requirement for total N equilibrium between roots and shoots. Until this equilibrium is achieved (in this case, $\approx 5\%$ N for both tissue types), the plant might be held in a physiological lag phase. Causes of the apparent physiological flux at about day 30 may be more discernible by extending vegetative growth beyond achievement of N equilibrium and then beginning floral induction.

Our results extend the conclusions of previous research (Boodley and Meyer, 1965; Elliott and Nelson, 1983; Willits et al., 1992; Woodson and Boodley, 1983; Woodson et al., 1984) by integrating the role of genotype with

Table 3. Ammonium or NO_3 -N removed from solutions by *Dendranthema $\times$ grandiflorum* 'Iridon', 'Sequoia', and 'Sequest' during the first 5 and second 5 days of 10-day harvest cycles. Values are means $\pm$ SE of nine harvest cycles.

Cultivar	Uptake for days 1 to 5 (mg)		Uptake for days 6 to 10 (mg)	
	NH_4	NO_3	NH_4	NO_3
Iridon	23.4 $\pm$ 2.8	19.2 $\pm$ 2.6	24.7 $\pm$ 3.3	20.7 $\pm$ 6.3
Sequoia	28.3 $\pm$ 3.8	26.6 $\pm$ 4.5	34.2 $\pm$ 5.7	31.6 $\pm$ 5.3
Sequest	24.5 $\pm$ 3.3	23.0 $\pm$ 3.5	30.8 $\pm$ 4.9	27.5 $\pm$ 4.2

Fig. 3. Percentage of (A and C) NH_4 and (B and D) NO_3 in (A and B) roots and (C and D) shoots of *Dendranthema $\times$ grandiflorum* (□) 'Iridon', (○) 'Sequoia', and (Δ) 'Sequest' grown in hydroponic solution with 1 mM each of NH_4 and NO_3 -N. Vertical bars indicate least significant difference at $P \leq 0.05$.

Fig. 4. Total N in (●) roots and (■) shoots of *Dendranthema x grandiflorum* 'Sequoia' grown in hydroponic solution containing 1 mM each of NH_4 and $\text{NO}_3\text{-N}$. Vertical bars indicate $\pm$ SE.

uptake and tissue levels of NH_4 and $\text{NO}_3\text{-N}$ during all stages of growth from newly rooted cuttings to plants with fully developed inflorescences. This information should assist growers in matching N applications with a crop's developmentally dependent requirements and apprise plant breeders of genetic variation available in chrysanthemum to develop more N-efficient cultivars.

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