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Springtime ^{15}Nitrogen Uptake, Partitioning, and Leaching Losses from Young Bearing *Citrus* Trees of Differing Nitrogen Status

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Abstract. ^{15}Nitrogen uptake, allocation, and leaching losses from soil were quantified during spring, for 4-year-old bearing 'Redblush' grapefruit (*Citrus* × *paradisi* Macf.) trees on rootstocks that impart contrasting growth rates. Nine trees on either the fast-growing 'Volkamer' lemon (VL) (C. *volkameriana* Ten & Pasq.) or nine on the slower-growing sour orange (SO) (C. *aurantium* L.) rootstocks were established in drainage lysimeters filled with Candler fine sand and fertilized with 30 split applications of N, totaling 76, 140, or 336 g·year^{-1} per tree. A single application of double-labeled ammonium nitrate ($^{15}NH_4{}^{15}NO_3$, 20% enriched) was applied at each rate to replicate trees, in late April. Leaves, fibrous roots, soil, and leachates were intensively sampled from each treatment over the next 29 days, to determine the fate of the $^{15}NH_4{}^{15}NO_3$ application. Newly developing spring leaves and fruit formed dominant competitive sinks for ^{15}N, accounting for between 40% and 70% of the total ^{15}N taken up by the various treatments. Large fruit loads intercepted up to 20% of this ^{15}N, at the expense of spring flush development, to the detriment of overall tree N status in low-N trees. Nitrogen supply at less than the currently recommended yearly rate of 380 g/tree exceeded the requirements of 4-year-old grapefruit trees on SO rootstock; however, larger trees on VL rootstock took up the majority of ^{15}N from this rate over the 29-day period. Nitrogen-use efficiency declined with increasing N rate, irrespective of rootstock. The residual amounts of ^{15}N remaining in the soil profile under SO trees after this time represented a significant N leaching potential from these sandy soils. Therefore, under these conditions, present N recommendations appear adequate for rootstocks that impart relatively fast growth rates to *Citrus* trees, but seem excessive for trees on slower-growing rootstock species.

Foliar development in *Citrus* sp. can account for up to 25% of tree fresh weight (FW) (Jones and Steinacker, 1951) which can represent 30%–50% of the total N in a mature *Citrus* tree (Cameron and Compton, 1945). As most commercial *Citrus* cultivars are evergreen, leaves and structural components more than 1-year-old are a major source of N that supports spring and summer growth flushes (Wallace et al., 1954), since root uptake may not be able to fulfil immediate growth and fruit set requirements at this time (Kubota et al., 1976a, 1976b). *Citrus* leaves, therefore, constitute a major reserve of mobile N (Moreno and García-Martinez, 1984) and carbohydrates (Kriedemann and Barrs, 1981). Fertilization of *Citrus* trees is based on analysis of spring flush leaves sampled in early summer (Smith, 1966), as mineral nutrient concentrations at this time are a useful predictor of fertilizer requirements. Tree N reserves interact with N uptake by the tree, which can confound year-to-year studies of N requirements and allocation to tissues (Legaz and Primo-Millo, 1988; Proe and Millard, 1994). Manipulating the timing and amount of N fertilizer applied can maximize N uptake efficiency and minimize leaching losses below the root zone (Fiegenbaum et al., 1987; Syvertsen and Smith, 1996). Rootstock species that produce relatively fast-growing (vigorous) trees have larger N requirements than slower-growing trees (Syvertsen and Smith, 1996), especially during the critical spring period of flowering and fruit set (Moreno and García-Martinez, 1984).

Up to 57% of soil-applied ^{15}N was taken up by a N-deficient *Citrus* tree in comparison to only 40% taken up by a tree with sufficient N (Dasberg, 1987). Thus, whole tree N status can affect N uptake efficiency. The premise is that the efficiency with which trees take up N affects the residual N in the soil, which can represent a potential water quality problem when soils are susceptible to leaching. Therefore, the objective of this study was to quantify N uptake in *Citrus* trees of different N status on sandy soils, and to determine the subsequent allocation of N to fruit and vegetative sinks with varying N supply during a nutrient-dependent growth period. We also examined rootstock effects on tree growth, N allocation, N-use efficiency [dry weight (DW) per unit N] and N leaching losses below the root zone. We hypothesized that N uptake efficiency and N-use efficiency would be greatest in the lowest N trees, but that the total N taken up, and N leaching potential would be largely a function of tree growth and residual soil N.

Materials and Methods

General procedures

Lysimeter tanks and trees. This ^{15}N study was conducted during spring of the second year of a 4-year experiment (1992–95) that examined N uptake by young, bearing *Citrus* trees on two contrasting rootstock species under three fertilization regimes

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(Syvertsen and Smith, 1996). Nineteen polyethylene lysimeter tanks, ≈3.4 m in diameter and 0.9 m deep, were buried so that the top edge was ≈10 cm above the soil surface. These tanks were filled with ≈7.9 m^3 of a Candler fine sand (Typic quartzipsamments), having a pH of 5 to 6 and <0.8% organic matter (Alva and Syvertsen, 1991). A drainage system consisting of a 10 cm diameter perforated plastic pipe and a sump pump was placed at the bottom of each tank (Boman and Syvertsen, 1991) to collect the drainage water leachate, which was pumped out and measured volumetrically whenever it accumulated. Eighteen, 4-year-old 'Redblush' grapefruit (RGF) trees grown in large (25 L) containers were randomly transplanted into individual lysimeter tanks in March 1991, and designated as tank (T) trees. Nine of these RGF trees were budded on sour orange (SO) rootstock and nine were budded on 'Volkamer' lemon (VL) rootstock. A number of additional 4-year-old container-grown trees on each rootstock were transplanted into undisturbed soil in the rows without tanks (NT = no-tank trees). To estimate N leaching from soil without tree roots, a single lysimeter tank without a tree was established and designated as the no-tree tank. Trees in and out of tanks were in two rows at a spacing of 4.9 m in the row and 6.1 m between rows, such that final tree canopies did not interact. Soil surfaces were maintained weed-free year round with herbicide and hand cultivation. Trees were sprayed for pests when necessary. Trees were irrigated daily for 3 months to allow recovery from transplanting, and the low, medium, and high N treatments (described below) were randomly assigned to each rootstock in June 1991. The control (no-tree) tank and the no-tank trees were irrigated and fertilized exactly as the medium N treatment trees in tanks. At this time, four of the no-tank trees were randomly selected for a destructive whole-tree harvest at the end of the ^{15}N study in spring, 1992. In addition, three other no-tank trees on each rootstock were tagged and identified for the nondestructive growth analyses (see below).

All trees were irrigated at ≈0.6 of class A pan evaporation (Dasberg et al., 1991; Whitney et al., 1991) using 60 $L \cdot h^{-1}$ microsprinklers. The irrigation frequency was scheduled to minimize soil water deficits for the largest trees, but also to minimize leaching (Syvertsen and Smith, 1996), resulting in daily or irrigation every other day, depending upon season. Total annual rainfall in 1991 was 1422 mm; mean annual rainfall for this site is 1117 mm. When averaged across all treatments, total irrigation water applied in 1991 was ≈340 mm.

Fertilizer treatments. Microelements N, P, K, and Mg were applied on average, every 10 d, by injecting a liquid 6%–0.9%–5.0%–0.3% (N–P–K–Mg) fertilizer into the irrigation system (fertigation) at concentrations of 200 mg N, 23 mg P, 167 mg K, and 19 mg Mg/L for the first 4 months after transplanting (March to June 1991). From July 1991, N rates of 76, 140 and 336 g per year per tree were imposed on the treatments, using 2–0.9–5.0–0.3, 6–0.9–5.0–0.3 and 12–0.9–5.0–0.3 (N–P–K–Mg) fertilizer formulations, respectively. Hereafter, these rates will also be denoted as low, medium, and high N application rates. These rates were ≈0.2, 0.4, and 0.9 times the recommended annual per tree N rate of 380 $g \cdot year^{-1}$ for 4-year-old grapefruit trees (Koo et al., 1984; Tucker et al., 1995). The fertilizer was applied to each treatment in 30 (approximately weekly) split applications over the growing season (mid-March through September) to minimize the potential for nutrient leaching (Willis et al., 1990). The no-tank trees on each rootstock (plus the no-tree tank) received N at the 140 $g \cdot year^{-1}$ rate, providing a tank/no-tank comparison at the medium N rate. The N rates were increased in August 1992 (after this study was completed) according to currently recommended rates for typical 5-year-old trees (Tucker et al., 1995).

Growth analysis

Fall flush. Eight representative branches that had been initiated in the Fall (October) were tagged on the nine tank and three no-tank trees of each rootstock, just prior to any spring growth in February 1992. One branch was tagged in the upper and one in the lower half of each quadrant of the canopy (n = 8 branches per tree). The basal stem diameter of each branch was measured 0.5 cm above the terminal scar where the previous summer flush had ceased in the fall, together with stem length and leaf number. The total number of equivalent fall shoot units were counted for each tree and their basal stem diameters measured. Twenty-four fall branches of varying basal stem diameters were harvested from the three additional no-tank trees on each rootstock (n = 8 per tree). Basal stem diameter, leaf area, and leaf number on these branches was measured, together with the DW of leaves and stems after oven drying at 60 °C (until a constant DW was obtained). Regression equations to predict the fall stem and leaf DW from basal stem cross-sectional area were calculated for each rootstock species (Lea-Cox, 1993). These equations (R^2 = 0.56–0.92; P < 0.05–0.001) were then used to predict the fall stem and leaf DW from the stem diameters of the eight branches on each tank tree. The total fall stem and leaf DW per tree (Lea-Cox, 1993) was calculated by summing all individual fall branch diameter regression estimates.

Spring flush. In March, the five most distal spring shoots on each of the eight tagged fall branches per tree were chosen to monitor the spring flush development of all 24 trees in a similar fashion to that described for the fall flush. These shoots were identified as being floral (more than four flowers per shoot) or vegetative (less than four flowers per shoot). Two nontagged spring shoots per tree (one floral and one vegetative) were harvested from the 24 study trees each week for 8 weeks, to calculate stem length and basal stem diameter regressions versus stem and leaf DW (R^2 = 0.77–0.82; P < 0.01–0.001). The total spring DW per tree was then estimated by multiplying the mean spring flush DW from each tagged shoot (n = 8) by the total number of fall shoots on each tree (Lea-Cox, 1993). Fruit diameters were measured on all the spring and fall shoots on 23 Apr., and again on 26 May after the 'May/June drop' fruit abscission period. On 26 May, two representative fruit per tree were sampled for ^{15}N analysis. Regression equations (R^2 = 0.69–0.91; P < 0.01–0.001) were used to predict total fruit DW from the diameter of all fruit on each tree (Lea-Cox, 1993).

Nitrogen experiment

Nitrogen application. The ^{15}N was applied to the 24 experimental trees 5 days after the spring growth analysis was completed. The ^{15}N applications were calculated (Cabrera and Kissel, 1989) to provide 2.59, 5.12, or 11.56 g total N for the N rates of 76, 140, and 336 g, respectively. Approximately 20% of this total N was as ^{15}N (19.97, 19.80, and 19.76 ^{15}N excess for the three rates, respectively) applying a total of 0.52, 1.01, and 2.29 g ^{15}N per tree. The four no-tank trees (two on each rootstock) destined for whole-tree harvest and the no-tree tank were also labeled with 1.01 g ^{15}N.

The ^{15}N was uniformly applied to a 90 cm diameter (2.55 m^2) of soil around the trunk of each tree in 5 L of water. This N application substituted for a normal fertigation through the microsprinklers. An additional 20 L of water per tree was imme-

diately applied through the microsprinklers to ensure that the ^{15}N moved into the rooting zone. All trees were irrigated 4 d later without leaching. Normal ^{14}N fertigations were applied 9, 17, and 23 d after the ^{15}N application and continued approximately weekly thereafter.

Soil, nondestructive plant tissue, and leachate sampling. Soil profiles were sampled throughout May as part of the ^{15}N study. A 30 cm deep × 1.8 cm diameter soil core sample (76 cm^3) was taken from each of four cardinal directions under each tree canopy, at distances of 45, 90, and 135 cm from the trunk and at depths of 0–30, 31–60, and 61–90 cm trees (along with similar soil samples taken from the no-tree tank). Fibrous root samples were sieved from the soil cores taken from each of the cardinal directions and pooled from each of the three depths sampled on days 1, 3, 8, 15, 22, and 29 after ^{15}N application. A well-mixed sample (±100 g) of the soil from each depth was then frozen until analyzed.

Leaves were also sampled from each of the 24 tank trees on days 1, 3, 8, 15, 22, and 29, with a final sampling 77 d after ^{15}N application. Eight fall and eight spring flush leaves were sampled from each tree, care being taken to avoid the tagged fall branches used in the growth analyses. One spring and one fall leaf were sampled from the upper and the lower half of the canopy in each quadrant (n = 8 per flush). Fibrous root and leaf samples were dried at 60 ºC until constant weight was attained, then weighed, and milled (Cyclotec 1093, Tecator, Sweden). Total leaf and fibrous root material harvested each day was <3 and 0.5 g, respectively; thus the effect on the total ^{15}N budget was inconsequential. The calculation of total fibrous DW and densities ($mg \cdot cm^{-3}$) are described in detail by Syvertsen et al. (1993).

A 750-mL sample of drainage water was collected 8 d after ^{15}N application, and again on days 16, 31, and 77 (after rainfall). Water leached from the control tank was sampled on days 7, 23, and 29 after ^{15}N application. Subsamples were immediately frozen on these dates until N and ^{15}N analyses were performed.

Whole-tree harvest. Four ^{15}N-labeled no-tank trees were destructively harvested on 28 May to obtain DW estimates for comparable trees on SO and VL rootstocks and provide mean N and ^{15}N concentrations for the respective tissues (Lea-Cox, 1993). At harvest, trunks were cut at the bud union and the shoot components classified into spring shoots (with and without fruit), fall shoots, shoots > 9-months-old, wood + stems > 1-year-old, and trunk. The taproot and all roots from each tree were excavated from a radius of 0.5 m from the trunk (0.79 m^2) and 1.5 m in depth. In addition, a 2.4 m^2 quadrant (to the midpoint within and between trees in the rows, with alternate quadrants harvested on each of the four trees) was excavated to a depth of 30 cm. Roots were removed by sieving, to give a representative DW estimate for each rootstock species. Thus, ≈55% [40% from the core (totally excavated) + 15% from the alternate quadrants excavated] of the total root system was harvested by this method. Roots were classified into fibrous roots (<2 mm diameter), and two classes of woody roots (2–10 mm and >10 mm diameter). All tree parts were weighed after drying at 60 ºC until there was no further weight change. Trunk diameter of all the trees was also measured on 26 May and the harvest trunk measurements were then used to estimate the DW of the trunk (trunk + wood > 1-year-old; R^2 = 0.91, $P < 0.01$) and woody root (taproot + roots >2 mm diameter; $R^2 = 0.60$, $P < 0.05$) DW of all treatments by regression (Lea-Cox, 1993).

Nitrogen and ^{15}N analyses. A well-mixed sample of each tissue from the whole tree and nondestructive growth analysis harvests were analyzed for N and ^{15}N concentration using a Carlo Elba (NA 1500; Fison Instruments, Paramus, N.J.) carbon–nitrogen analyzer, connected in series to a VG602E (Vacuum Generators, Winsford, United Kingdom) mass spectrometer, as described by Lea-Cox and Syvertsen (1996). The day 29 fall leaf N concentrations and ^{15}N:^{14}N ratios for each treatment were used

Table 1. Predicted dry weight of various tissues from 4-year-old 'Redblush' grapefruit (RGF) on sour orange (SO) or 'Volkamer' lemon (VL) rootstocks (cultivar = C, rootstock = R), growing in lysimeter tanks (T) at N rates of 76, 140, and 336 $g \cdot year^{-1}$, with a no tank (NT) comparison at the N rate of 140 $g \cdot year^{-1}$.

Treatment		Fruit	Spring flush	Fall flush	Trunk + wood	Woody roots	Fibrous roots	Total
C/R	N rate	Dry wt (g)						
RGF/SO	76 T	348	1373	480	1813	2367	569	6950
	140 T	380	2478	695	1947	2522	960	8982
	336 T	359	1497	497	2320	2954	546	8173
	140 NT	1371	838	509	1875	2439	455	7487
Linear			NS	NS			NS	NS
Quadratic			NS	NS			NS	NS
RGF/VL	76 T	811	1392	708	3417	4222	1243	11793
	140 T	673	1612	708	3358	4154	1341	11846
	336 T	416	3038	1186	4077	4986	1010	14713
	140 NT	215	1987	784	3878	4576	1571	13011
Linear			***	***			*	**
Quadratic			***	***			*	**
ANOVA (*P* values)								
Rootstock		0.22	0.37	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Rate		0.75	**0.04**	**0.05**	0.12	0.12	**0.03**	**0.06**
Rootstock × rate		0.73	**<0.01**	**<0.01**	0.84	0.84	0.46	0.10
Rootstock		0.22	0.62	0.30	**<0.001**	**<0.001**	**0.02**	**<0.01**
Tank		0.45	**0.06**	0.68	0.44	0.44	0.49	0.92
Rootstock × tank		**0.06**	**<0.01**	0.34	0.31	0.31	0.18	0.17

*,**,***Significant (boldface) at $P < 0.10$, 0.05, or 0.01, respectively. Where significant, effect of rate within tank treatments separated by regression analysis.

to estimate the relative ^{15}N:^{14}N concentrations of the trunk, woody root, fall stem, and spring stem tissues for the respective low, medium, and high rates on each rootstock. Total tree ^{15}N concentrations were then corrected for each tissue and treatment by multiplying the total ^{15}N recovered (mg) by the reciprocal of the %^{15}N enrichment, which corrected for the small differences in isotopic enrichment between rates. Total tree tissue DW from the whole tree harvest were then used to calculate the ^{15}N recovered from the respective N treatments, as a percentage of the original amount of ^{15}N applied [i.e., DW of each tissue (at each rate) x

Table 2. Nitrogen concentrations (n = 3) from fibrous roots, fall leaves, spring leaves, and fruit (n = 6), sampled 29 d after ^{15}N application, from 4-year-old 'Redblush' grapefruit (RGF) on sour orange (SO) 'Volkamer' lemon (VL) or rootstocks (cultivar = C, rootstock = R), growing in lysimeter tanks (T) at N rates of 76, 140, and 336 g·year^{-1}, with a no tank (NT) comparison at the N rate of 140 g·year^{-1}.

Treatment		Fibrous roots	Fall leaves	Spring leaves	Fruit
C/R	N Rate	(N, mg·g^{-1} dry wt)			
RGF/SO	76 T	12.2	18.2	19.9	9.1
	140 T	12.7	17.7	19.2	9.3
	336 T	20.5	24.1	25.1	15.0
	140 NT	15.5	21.4	25.7	12.5
Linear		*	*	NS	NS
Quadratic		*	*	NS	*
RGF/VL	76 T	10.0	17.4	19.0	9.8
	140 T	11.5	18.3	21.1	10.7
	336 T	18.9	19.4	25.6	12.7
	140 NT	12.5	19.9	20.2	9.2
Linear		***	***	**	**
Quadratic		***	***	**	**
ANOVA (*P* values)					
Rootstock		0.10	0.24	0.56	0.96
Rate		**<0.001**	**0.04**	**<0.001**	**<0.01**
Rootstock × rate		0.89	0.24	0.41	0.19
Rootstock		0.14	0.75	0.24	**0.09**
Tank		0.16	0.11	0.25	**0.02**
Rootstock × tank		0.49	0.50	**0.02**	**<0.01**

*,**,***Significant (boldface) at $P < 0.10$, 0.05, or 0.01, respectively. Where significant, effect of rate within tank treatments separated by regression analysis.

Table 3. Predicted N contents (N concentration ×dry weight) of various tissues from 4-year-old 'Redblush' grapefruit (RGF) on sour orange (SO) 'Volkamer' lemon (VL) or rootstocks (cultivar = C, rootstock = R), growing in lysimeter tanks (T) at N rates of 76, 140, and 336 g·year^{-1}, with a no tank (NT) comparison at the N rate of 140 g·year^{-1}.

Treatment		Fruit	Spring flush	Fall flush	Trunk + wood	Woody roots	Fibrous roots	Total
C/R	N rate	Dry wt (g)						
RGF/SO	76 T	3.2	24.6	7.3	7.4	14.2	6.9	63.6
	140 T	3.5	42.8	10.3	7.8	14.9	12.2	91.5
	336 T	5.4	33.8	10.1	12.5	23.6	11.2	96.6
	140 NT	16.5	18.1	9.1	9.0	17.3	7.0	77.0
Linear			NS	**	**	**	**	**
Quadratic			NS	***	***	***	***	***
RGF/VL	76 T	8.0	24.0	10.0	15.0	19.4	12.4	88.8
	140 T	7.2	30.9	10.5	15.8	20.4	15.4	100.2
	336 T	5.3	70.5	18.6	20.4	25.9	19.1	159.8
	140 NT	2.0	36.4	12.7	19.8	25.2	19.7	115.8
Linear			***	**	**	**	**	***
Quadratic			***	***	***	***	***	***
ANOVA (*P* values)								
Rootstock		0.25	0.14	**<0.01**	**<0.001**	**0.03**	**<0.001**	**<0.001**
Rate		0.99	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.001**	**<0.001**
Rootstock × rate		0.67	**<0.01**	**0.03**	0.99	0.68	0.34	**0.02**
Rootstock		0.18	0.63	0.42	**<0.001**	**0.03**	**0.05**	**0.07**
Tank		0.18	**0.07**	0.86	0.10	0.15	0.76	0.93
Rootstock × tank		**0.03**	**0.03**	0.41	0.31	0.59	0.17	0.20

*,**,***Significant (boldface) at $P < 0.10$, 0.05, or 0.01, respectively. Where significant, effect of rate within tank treatments separated by regression analysis.

concentration of ^{15}N = total ^{15}N content per tissue at each rate]. The final results therefore reflect the real proportion of ^{15}N taken up at each N rate.

A 50 g subsample from each soil sample was extracted with 2 mol·L^{-1} KCl, distilled into boric acid, and analyzed for N and ^{15}N concentration, using the same mass spectrometer described above, using the analytical protocol described by Lea-Cox and Syvertsen (1996). After KCl extraction, the residual soil samples were air-dried, milled, and analyzed for any remaining organic ^{15}N using the mass spectrometer. Soil ^{15}N recoveries were calculated by multiplying the soil volume within the 45 cm radius with the KCl extract N and ^{15}N concentration (Lea-Cox, 1993). Leachate samples were distilled and analyzed as described previously (Lea-Cox and Syvertsen, 1996). Recoveries of ^{15}N in the drainage water were similarly normalized, i.e., by multiplying the volume of leachate (liters) collected by the total N and ^{15}N concentrations (mg·L^{-1}) of the solution (= N and ^{15}N content in milligrams).

Statistical analysis

Data for trees within tanks were analyzed using a 2 rootstock × 3 N rate generalized linear model (PROC GLM) factorial analysis of variance (ANOVA) with three single-tree replications in a completely randomized design (SAS Inst. Inc., Cary, N.C.). The effects of lysimeter tanks were tested using a 2 rootstock × 2 treatment (tank vs. no tank) factorial ANOVA within the 140 g N treatment. Growth analysis and ^{15}N uptake data were analyzed by tissue type, using a repeated measures through time analysis (Littell, 1989).

Results

Dry weight partitioning. Tank trees of the same age on VL were considerably larger than trees on SO, irrespective of N rate, as evidenced by total DW (Table 1). Few significant DW differences were noted between N treatments for the fall flush, trunk and wood or woody roots on either rootstock. However, VL trees at the 336 g N rate had significantly higher tissue and total DW compared to any other treatment. Spring flush DW totals (those expected to show the most differences to N rate over a year) were significantly increased at the highest N rate for VL but not for SO. Fibrous root DW showed a tendency to decrease with increasing N rate, with proportionate increases in woody root DW (Table 1).

There was a significant decrease in spring flush DW for the 140-NT vs. 140-T trees on SO, which did not occur with the VL-140 treatments. One obvious difference was that fruit DW was significantly higher for the SO no-tank trees and significantly lower for the VL no-tank trees (Table 1). The DW of fall and spring flushes tended to show an inverse relationship with fruit load, irrespective of rootstock. If the percentage DW partitioning is calculated between treatments (using the data from Table 1), the competitive effect of fruit load on the DW allocation to the spring flush becomes very clear.

Nitrogen partitioning. Nitrogen concentrations generally increased with N application rate in all tissues sampled over time (data not presented) and at day 29 (Table 2). The fall and spring leaf N concentrations for the low and intermediate treatments of both rootstock species could be considered to be low to deficient, but it is notable that the intermediate rate also produced the largest total DW for SO (Table 1). The interaction between N concentration and total DW is why total N content (N concentration × DW) data are presented as normalized data (Table 3). These total N content data therefore account for differences in tree size, particu-

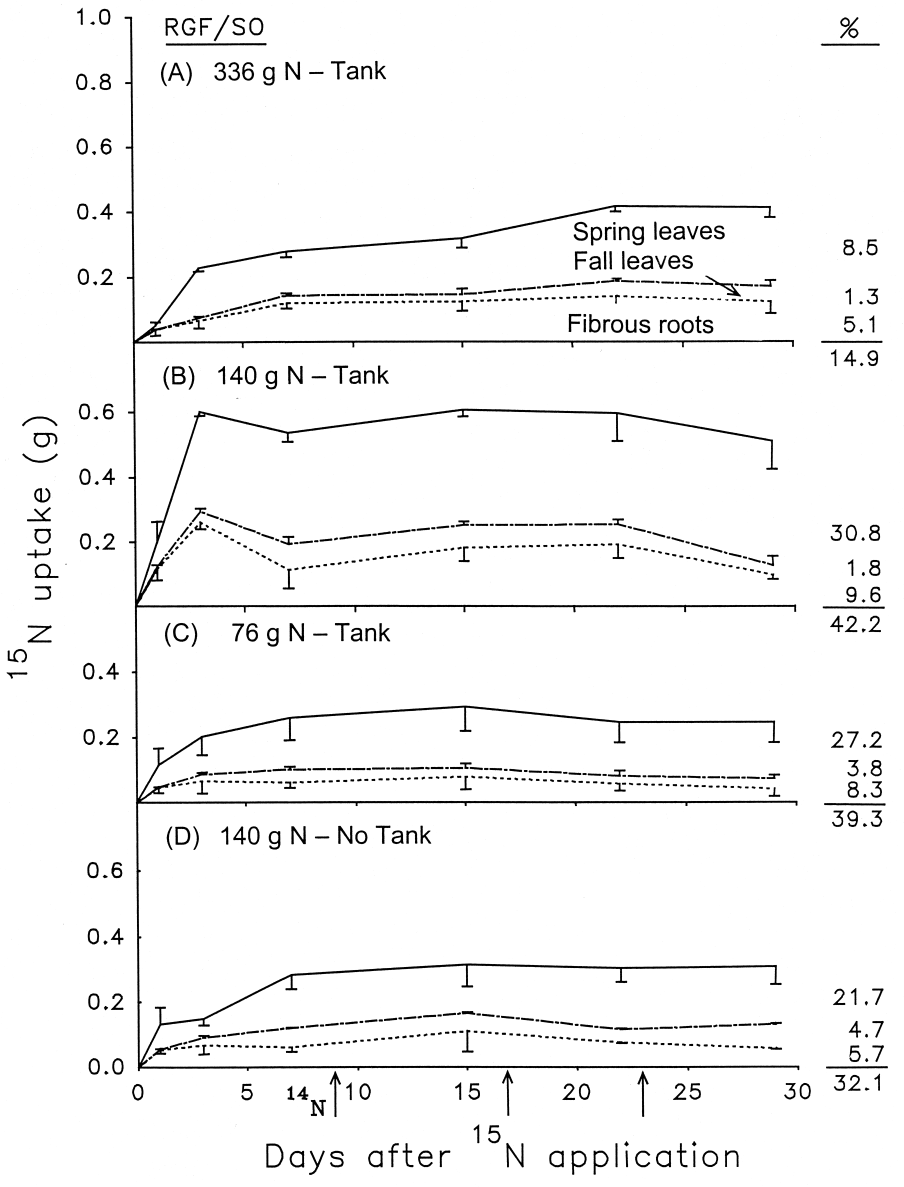

Fig. 1. Mean (n = 3) ^{15}N uptake (mg) into fibrous roots, fall, and spring leaves of 'Redblush' grapefruit (RGF) trees on sour orange (SO) rootstock, from 0 to 29 d after ^{15}N application. Trees were grown in lysimeter tanks (T) at N rates of (A) 336, (B) 140, and (C) 76 g·year^{-1}, with a (D) no tank (NT) comparison at the N rate of 140 g·year^{-1}. Vertical bars represent SE. Percentages refer to the fraction of applied ^{15}N recovered in each tissue after 29 d. Further ^{14}N applications (arrows) were made at 9, 17, and 23 d after the ^{15}N application, as per standard fertilization practice.

larly with respect to the total N in the trunk, woody root, and fibrous root (large DW) components. However, structural N content was largely unaffected by N treatments at this time, with the exception of the high rate VL trees. Most notable was the fact that the spring flush alone contained up to 50% of the total N content of many treatments at the end of May (Table 3). The largest competitive effects on existing N (and DW) partitioning were seen where trees had heavy fruit loads (e.g., compare SO-140T vs. SO-140NT treatments; Tables 1 and 3). Final fruit DW in November averaged 1299 g/tree vs. 3349 g/tree for these two treatments, respectively (Lea-Cox, 1993), indicating that these fruit load effects persisted throughout the growing season. Similar November fruit load effects were seen for the 140-VL treatments, i.e., 6215 g/tree (T) vs. 3975 g/tree (NT), although the competitive effect of fruit load was compensated by more equitable spring vegetative flush between these treatments (Table 1).

The flowering of low-N trees was enhanced, despite adequate cold induction for flowering that year (Lea-Cox, 1993). Fruit set (Table 1) persisted through this study period (April/May) despite the low N contents of these trees (Table 3). However a marked June-drop fruit abscission occurred with these low N treatments (data not presented) and final yield was significantly reduced by low-N status (Tables 2 and 3). Final fruit yield was 964 g/tree for the SO-76 and 2953 g/tree for the VL-76 treatments (Lea-Cox, 1993). Thus, this high fruit set and large June-drop competed for, and reduced the N content of the spring flush. In contrast, high N supply enhanced vegetative growth of trees on both rootstocks without significantly improving early (Table 1) or final fruit yield (Lea-Cox, 1993).

^{15}N UPTAKE AND PARTITIONING. From the fibrous roots, fall and spring leaf samples analyzed over the 29-d period, ^{15}N uptake was generally rapid and efficient at the higher rates for trees on both SO (Fig. 1) and VL (Fig. 2) rootstocks. The uptake of ^{15}N into fruit was not measured during the 29-d period, so these results do not show the interactive competition for immediate N by the spring flush and fruit (as reported above). By calculating the relative proportion of ^{15}N taken up into each of these tissues from the predicted ^{15}N content data (Table 4) and the actual ^{15}N uptake percentages (Figs. 1 and 2), a direct comparison can be made between these two datasets. If we add the predicted fruit N content to spring leaf N content (Table 4) and calculate the proportion of ^{15}N uptake into each tissue (as above), there is a remarkable correlation between predicted and measured uptake ratios for all tissues and treatments on both SO and VL. This provides an important validation of this modeling approach, particularly since these tissue types account for 67% to 75% and 77% to 89% of the total ^{15}N taken up by the SO and VL treatments, respectively (by calculation, Table 4).

Overall, N availability appeared to limit the uptake of ^{15}N by SO at the lowest rate (Fig. 1C). However, it was apparent that the low and intermediate N rates limited ^{15}N uptake on VL tank trees, as evidenced by the lower percent recoveries after 29 d (Fig. 2B and C) and the large uptake into the VL-336 spring flush over the month. Higher ^{15}N uptake for the no-tank VL trees (Fig. 2D) may have been influenced by the greater total root and spring flush DW of these trees (Table 1). When soil N availability was high, ^{15}N uptake continued past day 23 for SO, (Fig. 1A) and day 15 for VL (Fig. 2A). The uptake efficiency from this single N application was greatest over the first 15 d for VL-336 trees, but was reduced for the SO-336 trees, perhaps indicating an interaction between uptake and sink demand.

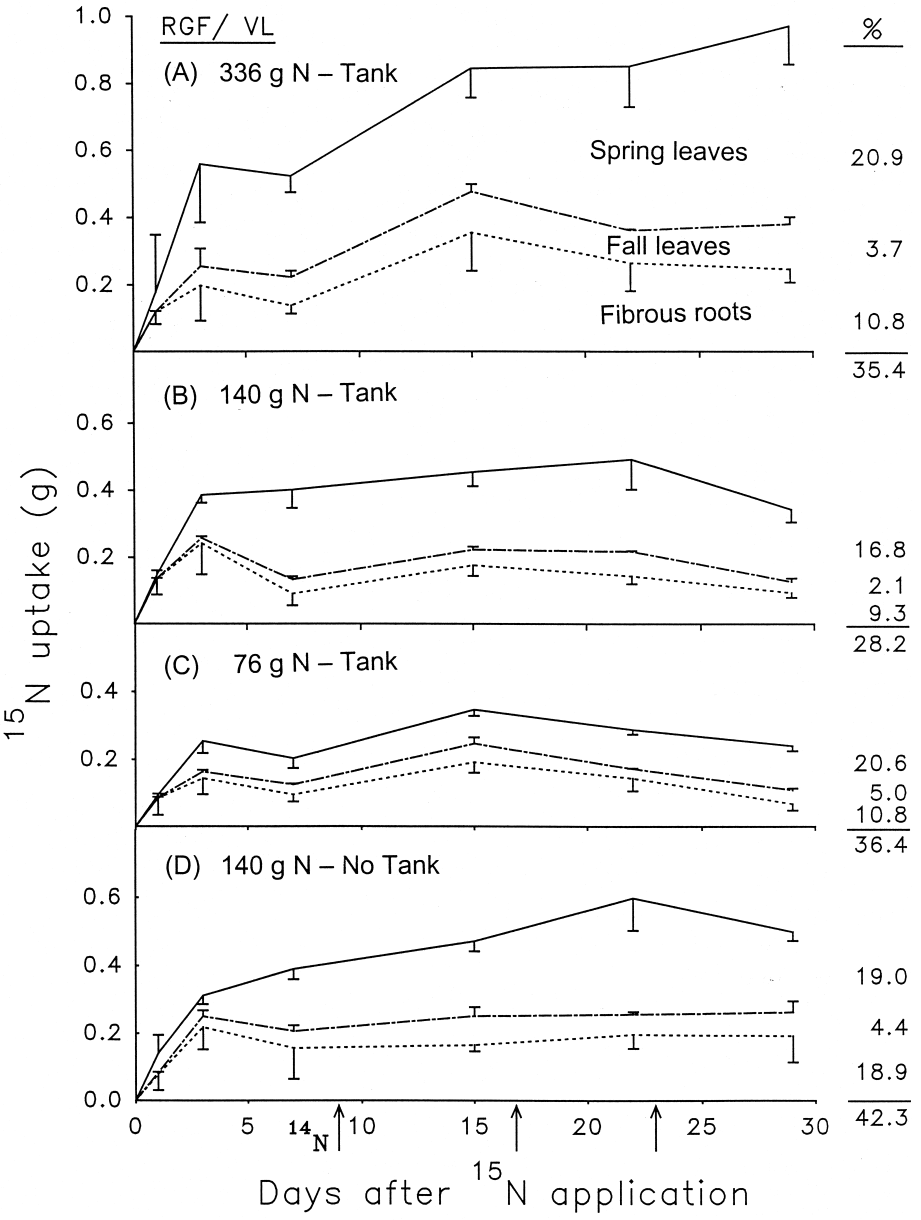

Fig. 2. Mean (n=3) ^{15}N uptake (mg) into fibrous roots, fall, and spring leaves of 'Redblush' grapefruit (RGF) trees on 'Volkamer' lemon (VL) rootstock, from 0 to 29 d after ^{15}N application. Trees were grown in lysimeter tanks (T) at N rates of (A) 336, (B) 140, and (C) 76 g·year^{-1}, with a (D) no tank (NT) comparison at the N rate of 140 g·year^{-1}. Vertical bars represent SE. Percentages refer to the fraction of applied ^{15}N recovered in each tissue after 29 d. Further ^{14}N applications (arrows) were made at 9, 17, and 23 d after the ^{15}N application, as per standard fertilization practice.

RESIDUAL SOIL ^{15}N AND ^{15}N LEACHING. Increasing proportions of soil $^{15}NO_3$ generally were recovered with increasing N supply on all sampling days (Table 5). Ammoniacal-^{15}N was only recovered in the samples taken 1 d after ^{15}N application to these sandy aerobic soils. Thereafter, only NO_3-N was recovered; thus, rapid nitrification appeared to be occurring in all treatments. The soil samples were analyzed by depth on day 8 to determine the movement of ^{15}N through the soil profile (Table 5). Nitrate-N was

Table 4. Predicted ^{15}N uptake (mg) by various tissues of 4-year-old 'Redblush' grapefruit (RGF) on sour orange (SO) 'Volkamer' lemon (VL) or rootstocks (cultivar = C, rootstock = R), growing in lysimeter tanks (T) at N rates of 76, 140, and 336 g·year^{-1}, with a no tank (NT) comparison at the N rate of 140 g·year^{-1}.

Treatment		Fruit	Spring flush	Fall flush	Trunk + wood	Woody roots	Fibrous roots	Total
C/R	N rate				Dry wt (g)			
RGF/SO	76 T	190	783	236	73	286	214	1782
	140 T	205	1745	156	50	257	491	2904
	336 T	275	1095	245	94	576	585	2870
	140 NT	1259	749	407	115	388	289	3207
Linear			NS	NS		**	***	
Quadratic			NS	NS		***	***	
RGF/VL	76 T	437	593	216	394	370	279	2289
	140 T	410	868	188	449	408	474	2797
	336 T	329	2697	712	741	912	1251	6642
	140 NT	486	1081	368	514	489	969	3907
Linear			***	***		***	***	
Quadratic			***	***		***	***	
ANOVA (*P* values)								
Rootstock		0.28	0.39	**0.03**	**<0.001**	**<0.001**	**0.03**	
Rate		0.99	**<0.01**	**<0.01**	0.24	**<0.001**	**<0.001**	
Rootstock × rate		0.86	**<0.001**	**0.02**	0.35	**0.09**	**0.02**	
Rootstock		0.31	0.22	0.83	**<0.001**	**0.04**	**0.09**	
Tank		**0.06**	**0.08**	**0.05**	**<0.001**	**0.05**	0.48	
Rootstock × tank		0.11	**0.03**	0.72	0.98	0.61	**0.05**	

*,**,***Significant (boldface) at $P < 0.10$, 0.05, or 0.01, respectively. Where significant, effect of rate within tank treatments separated by regression analysis.

Table 5. Mean (n = 3) percentage residual soil ^{15}N recovery as NH_4 and NO_3 (day 1) and as NO_3 thereafter, from pooled soil samples (n = 4 per tree from each cardinal direction) at 1, 8, 29, and 77 d after ^{15}N application, to 'Redblush' grapefruit (RGF) on sour orange (SO) or 'Volkamer' lemon (VL) rootstocks (cultivar = C, rootstock = R), growing in lysimeter tanks (T) at N rates of 76, 140, and 336 g·year^{-1}, with a no tank (NT) comparison at the N rate of 140 g·year^{-1}.

Treatment		Day 1			Day 8 (NO_3)			Day 29	Day 77
C/R	N Rate	NH_4	NO_3	Total	30 cm	60 cm	90 cm	(NO_3)	(NO_3)
RGF/SO	76 T	0	70.2	35.1	9.7	0.3	0.1	4.5	0
	140 T	22.3	83.1	52.7	8.1	0.1	0.1	0.7	1.6
	336 T	45.7	79.1	62.4	21.2	19.7	10.4	38.7	3.6
	140 NT	4.9	140.1	75.5	17.9	0.5	0	2.9	0
Linear					**	**	***	***	**
Quadratic					**	**	***	***	**
RGF/VL	76 T	0	12.0	6.0	4.8	0	0.1	0.1	0
	140 T	13.5	128.0	70.7	1.5	0	0.2	4.2	0
	336 T	70.8	169.2	120.0	13.2	11.1	4.4	12.2	2.2
	140 NT	6.5	51.5	29.0	23.6	0.2	0.1	4.1	0
Linear					**	**	***	**	***
Quadratic					**	**	***	**	***
Control tank		41.0	90.3	65.6	5.5	6.9	35.5	40.5	6.5
ANOVA (*P* values)									
Rootstock		0.61	**0.03**	0.83	**0.02**	0.24	**<0.01**	**0.09**	**0.03**
Rate		**0.02**	0.35	**0.07**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
Rootstock × rate		0.41	0.38	**0.05**	0.79	0.72	0.53	**0.03**	0.15
Rootstock		0.76	0.71	0.68	0.47	**0.02**	0.72	0.23	**<0.01**
Tank		0.21	0.58	0.66	**<0.01**	**<0.01**	**<0.01**	0.37	**<0.01**
Rootstock × tank		0.68	0.42	**0.07**	0.20	0.67	0.78	0.35	**<0.01**

*,**,***Significant (boldface) at $P < 0.10$, 0.05, or 0.01, respectively. Where significant, effect of rate within tank treatments separated by regression analysis.

Table 6. Mean (n = 3) percentage ^{15}N recovery after 29 d of the total ^{15}N applied to 'Redblush' grapefruit (RGF) on sour orange (SO) or 'Volkamer' lemon (VL) rootstocks (cultivar = C, rootstock = R), growing in lysimeter tanks (T) at N rates of 76, 140 and 336 g·year^{-1}, with a no tank (NT) comparison at the N rate of 140 g·year^{-1}.

Treatment		Plant ^{15}N	Soil ^{15}N	Leached ^{15}N	Total ^{15}N
C/R	N rate	(%)[z]	(%)[z]	(%)	(%)
RGF/SO	76 T	63.1	4.5	1.1	68.7
	140 T	54.8	0.8	0.1	55.7
	336 T	23.5	38.7	2.9	65.1
	140 NT	62.7	2.9	---	65.6
Linear		***	***		
Quadratic		***	***		
RGF/VL	76 T	84.0	0.1	0	84.1
	140 T	50.2	4.2	0.5	54.9
	336 T	54.8	12.2	0.9	67.9
	140 NT	76.3	4.1	---	80.4
Linear		NS	***		
Quadratic		NS	***		
Control tank		---	40.5	16.8[y]	57.3
ANOVA (*P* values)					
Rootstock		**<0.01**	**0.09**	0.18	
Rate		**<0.001**	**<0.001**	0.22	
Rootstock × rate		**0.05**	**0.03**	0.81	
Rootstock		0.47	0.23	---	
Tank		0.11	0.37	---	
Rootstock × tank		0.34	0.35	---	

[z]All percentages represent percent ^{15}N recovery of the total applied (which varied per treatment).
[y]Control tank total includes additional leached N on days 23, 29, and 30.
*,**,***Significant (boldface) at $P < 0.10$, 0.05, or 0.01, respectively. Where significant, effect of rate within tank treatments separated by regression analysis.

only seen at depths below 30 cm in any appreciable amounts at the highest (336-T) rates, and were insignificant below 30 cm for the low and intermediate N treatments (Table 5), despite all treatments having received two 61-L irrigations in the week after the ^{15}N was applied. Less than 30% of the total ^{15}N applied was recovered at day 8 from the soil profile for the VL-336 trees, compared to over 50% recovery for SO-336 trees. Over 30% of the ^{15}N applied to the SO-336 trees was in the soil profile below 30 cm depth, below the zone in which the largest proportion of fibrous roots was found (data not presented). In contrast, a large amount of N appeared to have been taken up by the VL-336 trees during the first week (Table 5) and the various proportions of N found in the first 30 cm of soil tended to reflect the amount of N taken up by the various treatments in this time (Table 1, Figs. 1 and 2). A substantial proportion (39%) of the ^{15}N applied still remained in the soil profile after 29 d for the SO-336 treatment, whereas little more than 12% was recovered from VL at the same rate (Table 5). These were the only treatments from which ^{15}N was recovered at the final soil sampling on day 77. Therefore, the potential for leaching was highest at this rate, particularly for trees on SO rootstock (Table 6).

Total soil N recoveries from the control tank (with no tree), fertilized at the medium rate were comparable to the totals recovered from the SO-336 trees on days 29 and 77 (Table 5). The recovery of N from the control tank at day 1 was comparable to that recovered from the plant treatments at the same yearly N rate of 140 g (Table 6). Thus, it appears that a considerable proportion of ^{15}N was lost from all treatments within 1 d. Residual soil ^{15}N after extraction with 2 mol·L^{-1} KCl was very low and averaged <0.02% of the N applied to all treatments after 29 d (Lea-Cox, 1993).

The percentage N recoveries in leached water were very low (Table 6), and highly variable within treatments (data not presented). Thus, only cumulative leached totals from each treatment over the 29 d are presented, together with plant and soil N recoveries at day 29 (Table 6). Total recovery of ^{15}N leached from the control tank over this period included 2.9% leached after 21 mm of rainfall on day 15, 6.6% leached after 45 mm of rain on day 29, together with 5.8% and 1.4% ^{15}N leached after irrigation on day 23 and 28, respectively (Table 6).

Total ^{15}N recovery from the control tank (fertilized at the N rate of 140 g·year^{-1}) at day 29 was almost equal to the total ^{15}N recovery from both the medium N rate SO and VL tank trees, where tree uptake accounted for nearly the entire amount of ^{15}N recovered, compared to this ^{15}N remaining in the soil profile of the control tank (Table 6). The percentage ^{15}N uptake efficiency (= ^{15}N taken up/total ^{15}N applied) of trees at the lowest N rate (63% and 84% for SO and VL, respectively) was significantly higher than the uptake efficiencies at higher rates. However, the N uptake of low N trees only represented 60% and 34% of the total N taken up by SO and VL at the highest rate, respectively (Table 6), indicating that these treatments were N-limited. Interestingly, the high rate SO trees had the lowest ^{15}N uptake over the 29 d (24%), which represented less total N than that taken up by the medium rate SO trees (Table 4).

Nitrogen-use efficiency. Whole-tree nitrogen-use efficiency (NUE = g DW/mg N) decreased significantly with increasing N rate (Fig. 3). No further decrease in NUE occurred between the medium rate and the high rate SO trees, which also did not put on any more growth than the trees fertilized at the intermediate rate. The negative relationship was stronger ($R^2 = 0.67$) for the trees on VL, since tree growth was highest and NUE lowest for the high N trees. The no-tank trees were not included in the fitting of the

regression lines, even though the R^2-value for VL was not significantly reduced when the VL no-tank data were included.

Discussion

Under the springtime growth conditions of this study, N supply at the highest N rate clearly exceeded the requirements for growth and development of 4-year-old 'Redblush' grapefruit trees on SO rootstock. Trees on VL rootstock effectively took up most of the ^{15}N provided at the high N rate, with a relatively low proportion (12%) of the single ^{15}N application remaining in the soil after 29 d. However, large residual amounts of ^{15}N were still present in the soil profile of high N trees on SO after 29 d, representing a significant N leaching or denitrifying potential from these sandy soils. It should be noted that this single ^{15}N application represented only ≈3.3% of the annual recommended N application for these age trees (Tucker et al., 1995). The rationale of splitting annual N applications into small, frequent applications has obvious implications for minimizing residual soil N that is susceptible to leaching (Willis et al., 1990).

It has been shown that *Citrus* trees take up proportionately more N during the spring period (Kubota et al., 1976a, 1976b) when N requirements are higher than in autumn (Kato and Kubota, 1982). The uptake of ^{15}N for both rootstock species is, therefore, likely to be more efficient in spring than at times of the year when trees are not actively growing. Given this, and the fact that the study period encapsulated (in large part) the fruit set, leaf and fruit expansion phase, the N demand by the trees during the study period was almost certainly high. Thus, these results may represent values that are close to the maximum uptake from a single N application in this climate, and so the apparent over fertilization of trees on SO is probably a conservative estimate. It also seems reasonable to assume that percentages of N recovered in the soil and leached water are likely to be higher at other times of the year when N demand by trees on these rootstock species is lower.

Total uptake of N from the single ^{15}N fertilization in the month after spring flush development appeared to be influenced by the immediate growth of the tree. Interestingly, N uptake from this single fertilization accounted for a relatively consistent 2.5% of the total N content of most trees on either rootstock. Overall percentage N allocations were similar to those reported by Cameron and Compton (1945), and the spring flush and developing fruit formed the dominant sinks for N during the spring growth period, similar to that reported for 4-year-old 'Valencia' (*C. sinensis* L.) trees supplied with ^{15}N during the fruit set period (Legaz at al., 1982). The total ^{15}N uptake efficiencies (60%–80%) in this study were very similar to those reported previously for mature *Citrus* trees (Dasberg et al., 1984; Fiegenbaum et al., 1987), pistachio (*Pistacia vera* L.) trees (Weinbaum at al., 1994) and *Citrus* rootstock seedlings (Lea-Cox and Syvertsen, 1996).

What was more apparent from these results was the strong competitive effects between these two dominant sinks for N at this time. Nitrogen supply at the lowest rate in this study clearly limited tree growth, and final yield of the trees on both rootstocks. Total immediate N uptake (from ^{15}N) was highest for the trees that showed strong vegetative growth and/or had a large fruit load, which in turn was determined by total soil N availability. Both the SO no-tank trees with a large fruit load and the highly vegetative, high N rate trees on VL took up a total of 4.2% of the total tree N content from this single fertilization. Trees with a large fruit set appeared to exert an overriding influence on immediate (^{15}N) uptake, to the detriment of the requirements of the spring flush. This effect was most pronounced on the low-N trees, which experienced a relatively high loss of N to fruit set, since trees initially set large amounts of fruit, apparently in response to low tree N status, (Lovatt et al., 1988), and then lost that N through a large June-drop fruit abscission. Thus, fruit set under these conditions apparently not only outcompeted and reduced the N content (and size) of the spring flush, but also reduced remobilization of N for further use by the tree. In contrast, high N supply enhanced vegetative growth of trees on both rootstocks without significantly improving early or final fruit yield.

Nitrogen reserves (largely from older leaves) are an important resource for immediate growth of *Citrus* trees (Moreno and

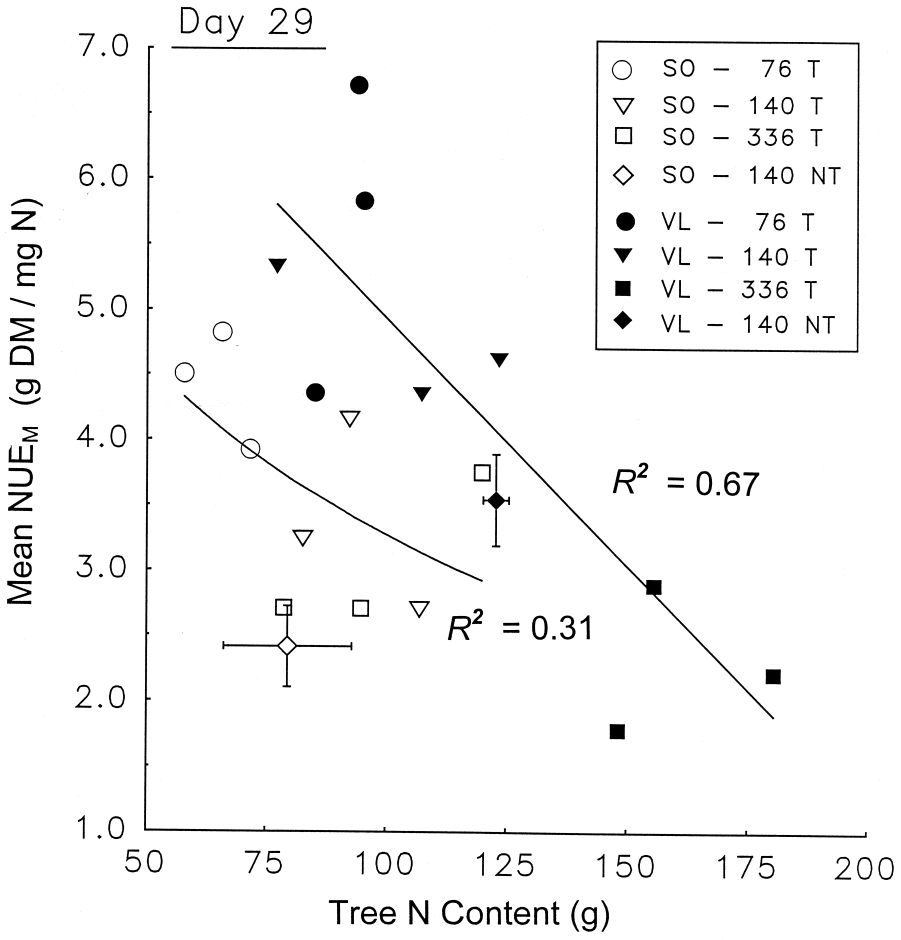

Fig. 3. Mean (n = 3) nitrogen-use efficiency (NUE_w, g dry weight/mg N) calculated from total ^{15}N uptake by 4-year-old 'Redblush' grapefruit (RGF) trees on sour orange (SO) and 'Volkamer' lemon (VL) rootstock after 29 d, growing in lysimeter tanks (T) at N rates of 76, 140, and 336 g·year^{-1}, with a no tank (NT) comparison at the N rate of 140 g·year^{-1}, for 29 d after ^{15}N application. Regression lines fitted through the tank treatments only, VL NUE_w = 26.1 – 4.61(log N); SO NUE_w = 12.1 – 1.91(log N).

García-Martinez, 1984), and the efficiency of N use increases as N supply becomes limiting to plant growth (Dasberg, 1987). In this study, total tree NUE decreased with increasing N rate for trees on 'Volkamer' lemon up to the highest rate, but did not decrease for trees on sour orange above the yearly medium N rate of 140 g·year^{-1}. This supports our conclusion about the over fertilization of SO at the high N rate, as it is apparent that N supply above this rate provided no growth or yield benefit to the SO trees.

The sandy soil type in this study undoubtedly influenced the results. Weinbaum et al. (1987) estimated that the annual percentage ^{15}N depletion from sandy soils, attributed mostly to leaching losses, was up to 10 times greater than that from heavier textured soils. The interaction of soil type and water application (from rainfall and irrigation) therefore becomes a significant factor for the retention of NO_3-N in the root zone to maximize the potential for N uptake by the tree (Willis et al, 1990). Since the leached volumes from the tanks were continuously monitored (Syvertsen et al., 1993), precise water application rates minimized leaching from the treatments in this study. Only one significant leaching event occurred during the 29-d period, with 21 mm of rain on day 15. It was not possible to distinguish whether trees preferentially took up NH_4 or NO_3, but the results suggest that the NH_4-N fraction was either nitrified or incorporated very rapidly by microbial populations (Lea-Cox and Syvertsen, 1996), absorbed rapidly by roots, or volatilized. It was unlikely that much N was lost to volatilization, since the double-labeled $^{15}NH_4{}^{15}NO_3$ was immediately watered into the root zone after application. The day 8 soil results indicate that NO_3 moves relatively quickly through the profile of these sandy soils. The leaching potential of NO_3 applied at the high rate was greater than at the lower rates since 39% of the high rate ^{15}N was still present in the soil of SO after 29 d. The slower-growing, less vigorous SO rootstock did not take up as much N as VL in this time, which resulted in higher residual soil N, and hence, a higher leaching potential.

In summary, distinct differences in N requirement exist for same-age 'Redblush' grapefruit trees, grafted on rootstocks that impart different vegetative and fruit development characteristics. The uptake of available N is heavily influenced by the strength of newly developing (spring flush and fruit) sinks in the spring. The differences in uptake (combined with a reduction in tree N-use efficiency with increasing N availability) are reflected in the residual amounts of N left in the soil profile, which may be easily leached from sandy soils with low nutrient-retention capabilities. Present N fertilizer recommendations may be adequate for rootstocks that impart relatively fast growth rates to *Citrus* trees, but appear excessive for trees on slower-growing rootstock species.

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