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Nitrate deposition in northern hardwood forests and the nitrogen metabolism of *Acer saccharum* marsh

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Abstract It is generally assumed that plant assimilation constitutes the major sink for anthropogenic Nitrate NO_3^- deposited in temperate forests because plant growth is usually limited by nitrogen (N) availability. Nevertheless, plants are known to vary widely in their capacity for NO_3^- uptake and assimilation, and few studies have directly measured these parameters for overstory trees. Using a combination of field and greenhouse experiments, we studied the N nutrition of *Acer saccharum* Marsh. in four northern hardwood forests receiving experimental NO_3^- additions equivalent to 30 kg N ha^{-1} $year^{-1}$. We measured leaf and fine-root nitrate reductase activity (NRA) of overstory trees using an in vivo assay and used ^{15}N to determine the kinetic parameters of NO_3^- uptake by excised fine roots. In two greenhouse experiments, we measured leaf and root NRA in *A. saccharum* seedlings fertilized with 0–3.5 g NO_3^-–N m^{-2} and determined the kinetic parameters of NO_3^- and NH_4^+ uptake in excised roots of seedlings. In both overstory trees and seedlings, rates of leaf and fine root NRA were substantially lower than previously reported rates for most woody plants and showed no response to NO_3^- fertilization (range = non-detectable to 33 nmol NO_2^- g^{-1} h^{-1}). Maximal rates of NO_3^- uptake in overstory trees also were low, ranging from 0.2 to 1.0 μmol g^{-1} h^{-1}. In seedlings, the mean V_{max} for NO_3^- uptake in fine roots (1 μmol g^{-1} h^{-1}) was approximately 30 times lower than the V_{max} for NH_4^+ uptake (33 μmol g^{-1} h^{-1}). Our results suggest that *A. saccharum* satisfies its N demand through rapid NH_4^+ uptake and may have a limited capacity to serve as a direct sink for atmospheric additions of NO_3^-.

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Introduction

Forests in northeastern United States currently receive substantial nitrogen (N) inputs from atmospheric deposition, much of which enters in the form of nitrate (NO_3^-; Galloway et al. 1984; Ollinger et al. 1993). Concerns have been raised that N deposition has the potential to alter patterns of carbon (C) and N cycling in forest ecosystems (Aber et al.. 1989; Ryan 1991; Schindler and Bayley 1993; Vitousek 1994). For example, Aber et al. (1989, 1991) have proposed that long-term N additions could lead to N saturation, a condition in which soil N availability exceeds the uptake capacity of biota. Most predictions of the consequences of N deposition assume that vegetation will directly take up anthropogenic N until plant growth is no longer N-limited (Aber et al. 1989, 1991; Rastetter et al. 1991). However, these predictions ignore variability in physiological processes of plants regulating the uptake of N by roots and its assimilation into biologically active compounds.

There is a great deal of variation among plant species in rates of NO_3^- uptake (Chapin et al. 1986), the ability to assimilate NO_3^- (Havill et al. 1974; Al Gharbi and Hipkin 1984), and the extent to which NO_3^- is assimilated in either roots or leaves (Smirnoff and Stewart 1985; Andrews 1986). Interspecific variation in NO_3^- uptake and assimilation suggests that ecosystem-level responses to atmospheric NO_3^- deposition will vary with the physiological characteristics of the dominant vegetation. The extent to which N additions influence plant and ecosystem C balance will depend on rates of NO_3^- assimilation as well as the primary location of NO_3^- assimilation, because assimilation in sun-lit leaves has a lower C cost than assimilation in roots (Smirnoff and Stewart 1985; Pate and Layzell 1990). Unfortunately, we know relatively little about the uptake and assimilation of NO_3^- by *Acer saccharum*

Marsh., a dominant overstory tree species throughout much of northeastern USA, where wet deposition of N ranges from 2 to 30 kg ha^{-1} $year^{-1}$ (Ollinger et al. 1993).

Our objective was to determine the extent to which *A. saccharum* functions as a direct sink for anthropogenic NO_3^- in northern hardwood forests. We hypothesized that the uptake of added NO_3^- by *A. saccharum* should induce the synthesis of NO_3^- reductase (NR), the enzyme that catalyzes the first and rate-limiting step in the assimilation of NO_3^- (Beevers and Hageman 1969), and that NR activity (NRA) should be greater in leaves than roots. To test these hypotheses, we conducted field and greenhouse experiments to characterize the response of *A. saccharum* to added NO_3^- in four northern hardwoods stands distributed along an N-deposition gradient in Michigan, USA.

Materials and methods

Study sites and fertilization protocol

Our study sites consisted of four northern hardwood stands distributed along an existing NO_3^- deposition gradient in the Lake States (Fig. 1). These sites were selected to be similar in age, basal area, species composition, and soil development (Burton et al. 1991; MacDonald et al. 1991; Table 1). At each site, there were six 30 m × 30 m permanent plots each surrounded by a 10-m-wide buffer strip. Three plots, including buffer strips, were fertilized with NO_3^- and three served as controls. Fertilized plots received an equivalent of 30 kg NO_3^-–N ha^{-1} $year^{-1}$ applied as $NaNO_3$ in six equal applications at 5-week intervals from May to November 1994. All four sites were sampled and then fertilized (south to north) at 5-week intervals throughout the 1994 growing season. The initial fertilization was conducted 18 days before the first sampling date, and the sites were not fertilized on our last sampling date. We conducted all destructive sampling in the buffer strips around each plot.

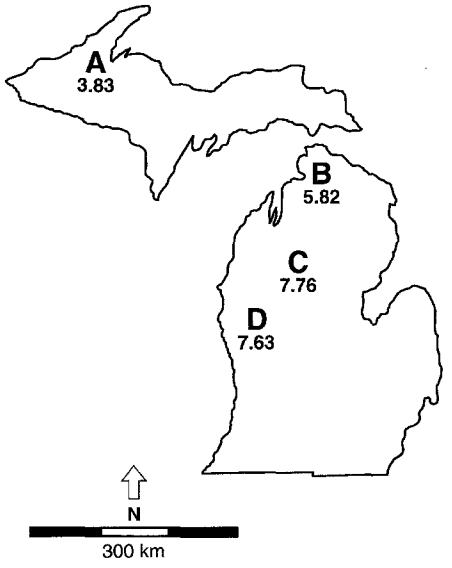

Fig. 1 Location of northern hardwood stands in Michigan, USA. Numbers represent mean annual wet + dry NO_3^- deposition (kg NO_3^- ha^{-1}) from 1987 to 1990 (MacDonald et al. 1992)

Field experiments

NRA in leaves and fine roots

Fine root and leaf NRA was measured using an in vivo assay based on NO_2^- production (Jaworski 1971; Al Gharbi and Hipkin 1984; Downs et al. 1993). Experiments to optimize enzyme activity in leaves and fine roots of *A. saccharum* were conducted in the summer of 1993, and the optimized assay medium consisted of 0.1 M NaH_2PO_4 (pH 7.5), 0.04 M KNO_3, 5% propanol, and 0.5 mg ml^{-1} chloramphenicol. To measure NRA, approximately 250 mg of leaf or root tissue were suspended in 7.5 ml of the assay medium in a glass screw-cap vial. The tissue was vacuum infiltrated and then incubated in the dark for 1 h at 25°C. Nitrite production was measured at 20-min intervals by removing 1-ml aliquots of the solution, which were analyzed colorimetrically on an Alpkem RFA 300 (Alpkem, Clackamas, Ore.). Simple linear regressions of NO_2^- production over time were used to calculate enzyme activity as nmoles of NO_2^- produced per gram of fresh tissue per hour (nmol NO_2^- g^{-1} h^{-1}).

To measure seasonal patterns of root NRA, soil cores (10 cm deep and 5 cm diameter) were collected from three random locations in the buffer strip of each plot. Cores were transported on ice to field laboratories, where all live woody-plant fine roots (≤1 mm diameter) were removed by hand and rinsed free of soil particles with deionized water. Roots from all three cores were pooled and then an approximately 250-mg subsample of fine roots was assayed for NRA. Subsamples were taken from all woody-plant roots in a core. We assumed that *A. saccharum* roots were predominant, because this species comprises approximately 80–90% of the stand basal area at each site (Table 1). These stands also lack a shrub layer.

Sun-lit canopy leaves were harvested using a 12-gauge shotgun. Canopy leaves that offered a clear shot were taken from the tree nearest to one random location within the buffer strip of each

Table 1 Climate, soil, and vegetation characteristics of four northern hardwood forest stands

	Site A	Site B	Site C	Site D
Climate				
Longitude (W)	88°53′	84°52′	85°50′	86°09′
Latitude (N)	46°52′	45°33′	44°23′	43°40′
Mean annual temperature (°C)	4.2	5.2	5.8	7.6
Mean annual precipitation (cm)	87	83	81	85
Soil[a]				
Silt+clay (%)				
A+E	14.8	10.6	10.6	12.7
B	13.7	13.4	11.1	11.0
pH (1:1 soil-H_2O)				
A+E	4.83	5.03	4.47	4.66
B	5.24	5.30	5.49	5.26
Bulk density (mg m^{-3})				
A+E	11.1	17.9	21.8	17.6
B	49.6	71.6	64.0	73.7
Vegetation				
Overstory age (years)	83	77	78	82
Total basal area (m^2 ha^{-1})	32	30	30	30
Acer saccharum Basal area (%)	87	87	83	77

[a] A+E and B horizon soil properties calculated for 10 cm sampling increments from soil data of MacDonald et al. (1991)

plot. Leaves were transported on ice to field laboratories, where they were cut into 5-mm-diameter discs. Approximately 250 mg leaf tissue was used to measure NRA.

To determine if NO_3^- fertilization resulted in an immediate induction of root NRA, a short-term fertilization experiment was performed on the July sampling date. Three 1-m^2 plots within the buffer of each fertilized plot were fertilized with 3.3 g of $NaNO_3$ dissolved in 1 l of deionized water (equivalent to 5 kg NO_3^-–N ha^{-1}). Three plots of the same size were located in the buffer strip of each control plot and were treated with 1 l of deionized water. One soil core was collected from the center of each 1-m^2 plot within 12–18 h of treatment and root NRA was determined as described above.

Nitrate uptake in fine roots

Nitrate uptake rate in fine roots was measured on the June sampling date using $^{15}NO_3^-$. Soil cores were collected and processed as described above, except that four 100-mg subsamples were collected from the composite root samples from each plot. The harvested roots were rinsed with 0.5 mM $CaSO_4$ (3 approx. 25-ml rinses) and the 100-mg subsamples were suspended in 25 ml of 1, 10, 100, or 1000 µmol $K^{15}NO_3$ (99 atom% excess), 0.5 mM $CaSO_4$, and 1% sucrose at 25°C (sensu Bassirirad et al. 1993). After 0.5 h of incubation, the roots were rinsed three times in 5 mM $CaSO_4$ and then oven dried for 24 h at 75°C. Roots were ground using a mortar and pestle, and ^{15}N abundance was determined using a Europa Scientific Roboprep and Tracermass (Europa Scientific, Franklin, Ohio). Nitrate uptake rates were reported as µmol $^{15}NO_3^-$ per gram tissue dry weight per hour, and the Michaelis-Menten kinetic parameters (V_{max} and K_m) were calculated using a Hane's plot transformation of the $^{15}NO_3^-$ uptake rates (Wood et al. 1981).

Greenhouse experiments

NRA in leaves and fine roots

Fifty *A. saccharum* seedlings were collected from site D on 12 August 1994 and transplanted into 2.5-l plastic pots along with their native soil. The seedlings were then grown at the University of Michigan Matthai Botanical Gardens under 16-h days maintained by supplemental light. Soils were watered to saturation every other day. All plants were fertilized on 16 August 1994 with 0.5 g NO_3^-–N m^{-2} in order to minimize transplant shock. Three randomly selected seedlings were assigned to each of five fertilization treatments (0, 0.5, 0.9, 1.7, and 3.5 g NO_3^-–N m^{-2}). The 0.5 g NO_3^-–N m^{-2} treatment was equivalent to the 5 kg NO_3^-–N ha^{-1} applied in the field. The N was applied as $NaNO_3$ dissolved in 30 ml of deionized water. Nitrate treatments were applied following the normal watering on 27 September 1994. Plants were harvested 24 h after fertilization; roots and leaves were prepared and analyzed for NRA as described above.

Ammonium and nitrate uptake in seedlings

Seven seedlings were randomly selected from the remaining pool to compare uptake rates of NO_3^- and NH_4^+. These seedlings were harvested on 10 October 1994 and their fine roots were collected as described above. Uptake of NO_3^- and NH_4^+ was determined using the same methods as the field $^{15}NO_3^-$ uptake experiment, except that additional subsamples of fine roots from each plant were incubated in a series of $^{15}NH_4^+$ solutions. The concentrations of NO_3^- and NH_4^+ were identical: 1, 10, 100, 250, 500, and 1000 µmol $K^{15}NO_3^-$ or $^{15}NH_4Cl$. Michaelis-Menten kinetic parameters for NO_3^- and NH_4^+ uptake were calculated for each seedling as described above. Seedlings showed no signs of autumnal senescence during either experiment.

Statistical analysis

Field experiments

Field NRAs were compared among sampling dates, sites, and treatments using a three-way analysis of variance (ANOVA). Values were log transformed to meet the assumptions of normality and homogeneity of variances. Sampling dates and sites were fixed effects, whereas treatment was a random effect in the ANOVA model. Differences in field NRA between leaves and roots also were compared using a three-way ANOVA. Differences in NRA within 18 h of fertilization and field-based measurements of the kinetic parameters of NO_3^- uptake were compared among sites and treatments using two-way ANOVA.

Greenhouse experiments

The relationship between seedling NRA and fertilization level was examined using simple linear regression. Differences in leaf and root NRA in seedlings and the kinetic parameters of NO_3^- and NH_4^+ uptake by seedlings were compared using *t*-tests for paired observations. All statistical analyses were performed using SYSTAT (Wilkinson 1990). Treatment means were compared using Fisher's LSD procedure, and significance for all statistical analyses was accepted at $\alpha = 0.05$.

Results

Field experiments

NRA in *A. saccharum* leaves and fine roots showed no significant response to NO_3^- fertilization throughout the growing season (Fig. 2 A–H). Mean leaf NRA was 8 nmol NO_2^- g^{-1} h^{-1} (SE = 1.8) and ranged from 3 to 25 nmol NO_2^- g^{-1} h^{-1}, while mean root NRA was 3 nmol NO_2^- g^{-1} h^{-1} (SE = 0.3) and ranged from non-detectable to 5 nmol NO_2^- g^{-1} h^{-1}. Rates of root NRA were generally very low and there was no clear temporal trend. In contrast, leaf NRA reached a seasonal maximum in June (12 nmol NO_2^- g^{-1} h^{-1}); rates prior to and following this date were significantly lower. Leaf NRA was significantly greater than root NRA throughout the growing season (Fig. 2).

Eighteen hours after fertilization, root NRA significantly increased at site C, but rates were still very low (10 nmol NO_2^- g^{-1} h^{-1}). Nitrate fertilization did not have a significant short-term effect on root NRA at any of the other sites (Table 2). Nitrate uptake rates in excised roots were not significantly different between control and fertilized plots across all sites (Table 3). There were no significant differences in V_{max} of NO_3^- uptake between sites A, B, and C, whereas V_{max} at site D was significantly higher than at all other sites (Table 3). There were no significant differences in K_m for $^{15}NO_3^-$ uptake between sites or treatments.

Greenhouse experiments

Root NRA in seedlings averaged 19 nmol NO_2^- g^{-1} h^{-1} (SE = 2.4) and ranged from 7 to 33 nmol NO_2^- g^{-1} h^{-1}, while leaf NRA averaged 5 nmol NO_2^- g^{-1} h^{-1} (SE = 0.7)

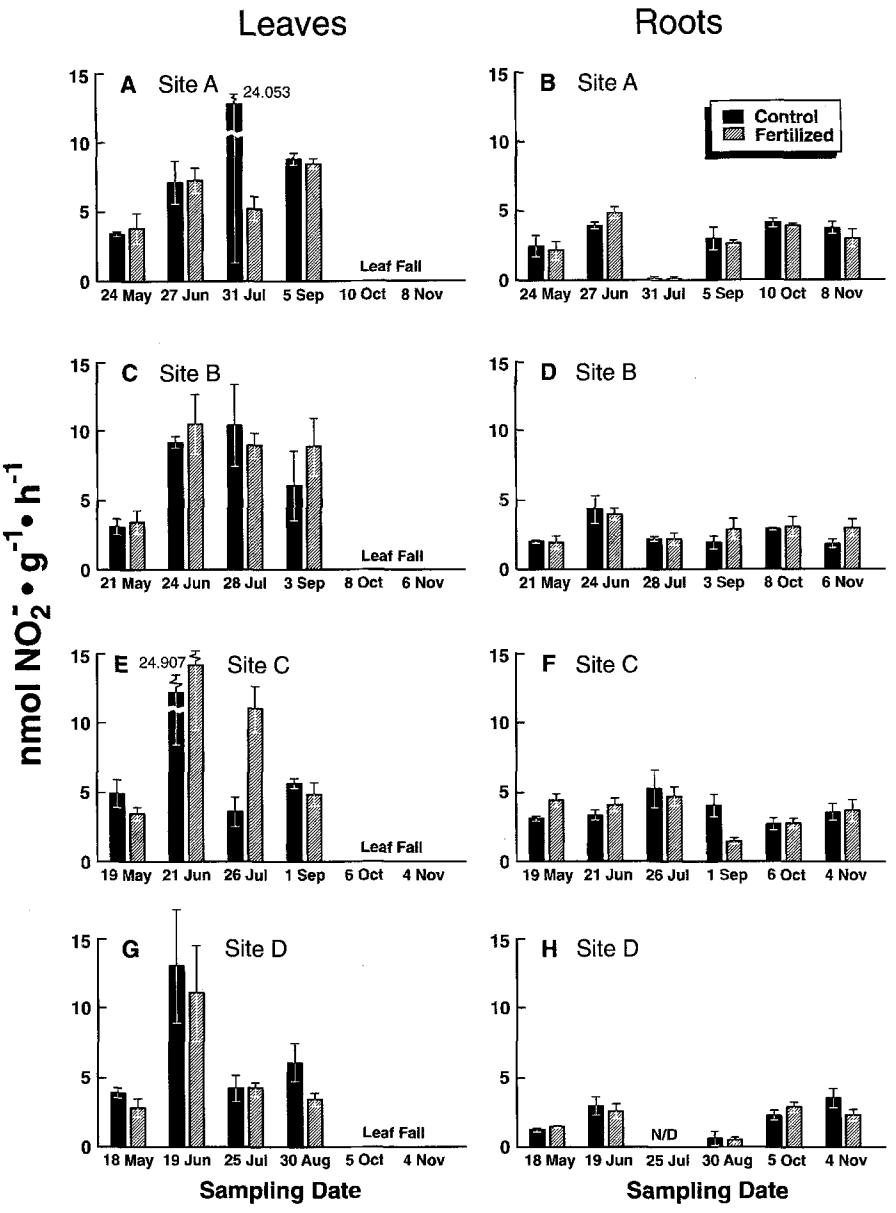

Fig. 2 Seasonal patterns of leaf and fine-root NO_3^- reductase activity in field-grown trees. Values represent treatment means and the bars indicate standard errors of the mean. (*N/D* = not detectable)

Table 2 Mean root nitrate reductase activity (nmol NO_2^- g^{-1} h^{-1}) 18 h after NO_3^- fertilization. Numbers in parentheses represent standard error of the mean. Means with the same letter in a row or column are not significantly different

	Site A	Site B	Site C	Site D
Control	0.5 (0.3)[a]	1.3 (0.5)[a]	5.2 (0.5)[b]	0.0 (0.0)[a]
Fertilized	0.1 (0.1)[a]	1.3 (0.6)[a]	10.4 (1.5)[c]	1.6 (0.9)[a]

and ranged from 2 to 12 nmol NO_2^- g^{-1} h^{-1}. There was no relationship between leaf or root NRA and fertilization level, but root NRA was significantly greater than leaf NRA. The mean V_{max} for NH_4^+ and NO_3^- uptake by excised roots of *A. saccharum* seedlings were 33 µmol g^{-1} h^{-1} (SE = 3) and 1 µmol g^{-1} h^{-1} (SE = 0.1) respectively. The mean K_m for NH_4^+ uptake was 125 µM (SE = 16), an order of magnitude greater than the K_m for

Table 3 Mean V_{max} and K_m for $^{15}NO_3^-$ uptake by excised roots collected in the field. Numbers in parentheses represent standard error of the mean. Means for the same kinetic parameter in a column or row with the same letter are not significantly different

	Site A	Site B	Site C	Site D
V_{max} (mmol g^{-1} h^{-1})				
Control	0.56 (0.29)[a]	0.65 (0.24)[a]	0.45 (0.03)[a]	1.02 (0.04)[b]
Fertilized	0.23 (0.04)[a]	0.70 (0.18)[a]	0.43 (0.07)[a]	1.24 (0.15)[b]
K_m (mM NO_3^-)				
Control	8.30 (5.08)[a]	11.43 (5.94)[a]	8.86 (1.36)[a]	4.19 (0.387)[a]
Fertilized	1.50 (0.63)[a]	9.43 (3.68)[a]	5.62 (1.66)[a]	4.83 (1.11)[a]

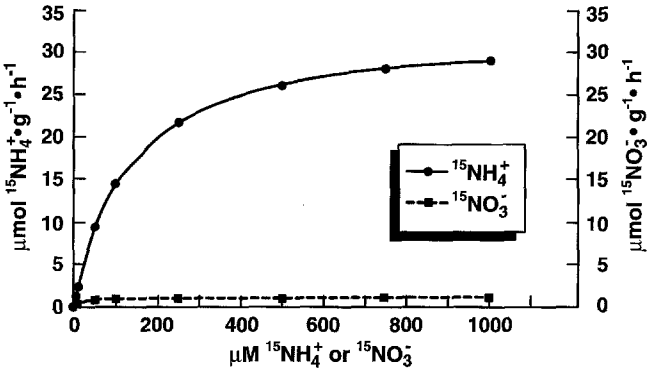

Fig. 3 Nitrate and NH_4^+ uptake rates of excised fine roots of *Acer saccharum* seedlings as a function of solution NO_3^- or NH_4^+ concentrations. Mean values of V_{max} and K_m were used to calculate uptake curves

NO_3^- uptake (12 μM; SE = 4). Both mean V_{max} and K_m for NH_4^+ uptake were significantly greater than mean V_{max} and K_m for NO_3^- uptake (Fig. 3).

Discussion

Anthropogenic NO_3^- deposition in northern temperate forests has the potential to alter ecosystem C and N cycling, and over the long term, may result in N saturation of some ecosystems. However, the extent to which N deposition influences ecosystem-level C and N dynamics will be modified by the N metabolism of the dominant vegetation. In particular, the capacity for NO_3^- uptake and reduction, and the ratio of root:shoot NO_3^- reduction will strongly influence ecosystem NO_3^- retention and the effects of increasing N availability on plant and ecosystem C balance. If NO_3^- reduction takes place in roots this cost must be borne by oxidation of C fixed aboveground, while reduction in light-saturated leaves can be subsidized by excess reductant generated in the light reactions of photosynthesis (Smirnoff and Stewart 1985; Pate and Layzell 1990). Our results suggest that *A. saccharum*, a dominant overstory species throughout much of northeastern United States, has a limited capacity for uptake and assimilation of anthropogenic NO_3^-.

Rates of NO_3^- reduction were consistently very low, so that differences in rates between leaves and roots are unlikely to affect plant C balance. In addition, *A. saccharum* appears to be adapted for rapid NH_4^+ uptake, and as a consequence, direct uptake of soil NO_3^- is unlikely to serve as a substantial sink for anthropogenic N in northern hardwood forests.

Contrary to our hypothesis that fertilization would induce NRA in *A. saccharum*, measurements of leaf and fine-root NRA showed no response to NO_3^- fertilization. In addition, rates of leaf and fine-root NRA were extremely low compared to activities reported for other species. In vivo NRA typically ranges from 2000 to 9000 nmol NO_2^- g^{-1} h^{-1} for ruderal species (Havill et al. 1974; Smith and Rice 1983; Al Gharbi and Hipkin 1984), and from 100 to 4000 nmol NO_2^- g^{-1} h^{-1} for woody perennials (Al Gharbi and Hipkin 1984; Downs et al. 1993; Knoepp et al. 1993; Truax et al. 1994). The rates we measured for *A. saccharum* are low, comparable to those for ericaceous species restricted to acid soils with low NO_3^- availability (non-detectable to 220 nmol NO_2^- g^{-1} h^{-1}; Townsend and Blatt 1966; Havill et al. 1974). Although NO_3^- availability has been shown to be positively correlated with NRA in other plants (Hogberg et al. 1986; Zak and Pregitzer 1988; Downs et al. 1993; Widmann et al. 1993), *A. saccharum* showed no response to NO_3^- fertilization. Because NRA was extremely low in all instances, the statistically significant differences in NRA between sites and sampling dates are probably not of ecological importance.

Because the NO_3^- reductase enzyme can turn over rapidly (Oaks et al. 1972; Remmler and Campbell 1986), it could be argued that uptake of added NO_3^-, induction of NRA, and return to pre-fertilization levels of NRA, all took place within the 5-week periods between fertilization and sampling. The results of our short-term fertilization experiment confirm that induction of NRA was minimal to non-existent following NO_3^- additions in the field. Although rates of fine-root NRA significantly increased 18 h after fertilization at site C, all values are still extremely low.

Fertilizing *A. saccharum* seedlings with high levels of NO_3^- in the greenhouse indicates that an activity of approximately 30 nmol NO_2^- g^{-1} h^{-1} may represent their maximum attainable rate of NO_3^- reduction. The fact that there were no significant differences in NRA between seedlings in the control treatment and all other fertilization levels is probably a result of increased NO_3^- availability due to repotting of seedlings in their native soil. Johnson et al. (1995) recently measured an increase in soil solution NO_3^- concentration of two orders of magnitude after sieving and repotting native soil. In our greenhouse experiment, all of the seedlings were most likely at their maximal NRA before fertilization so that the added NO_3^- had no significant effect.

Although the difference between field-measured leaf and root NRA was statistically significant, these low rates probably have little influence on plant C metabolism. The fact that seedlings demonstrated the opposite relationship of root to shoot NRA when compared to overstory trees may represent a developmental difference. This is consistent with the observation that leaf NO_3^- reduction is less expensive energetically only when photosynthesis is light saturated (Smirnoff and Stewart 1985). Therefore, leaf NO_3^- reduction would offer little advantage to a seedling growing in the shade of overstory trees.

The V_{max} for NO_3^- uptake in fine roots from all four sites was low compared to those reported for other plant species and was consistent with the extremely low levels of NRA. Maximal rates of NO_3^- uptake reported in the literature range from 1 to 12 μmol g^{-1} h^{-1} for herbaceous species (Goyal and Huffaker 1986; Bassirirad et al. 1993), and 1–38 μmol g^{-1} h^{-1} for tree species (Chapin et

al. 1986; Rygiewicz and Bledsoe 1986; Kamminga-van Wijk and Prins 1993; Lathja 1994). There is no readily apparent explanation for the higher V_{max} at site D, but estimates from field-collected roots at this site (Table 3) are consistent with estimates of V_{max} for roots from seedlings collected from the same site (Fig. 3). Although measurements of V_{max} for NO_3^- uptake are low, they are approximately one order of magnitude greater than rates of NO_3^- reduction. However, rates of uptake under field conditions are certainly much lower than our estimates of V_{max}. Soil solution NO_3^- concentration at 10 cm, averaged over all sites and sampling dates, was 21 μM (Govindarajalu 1995) which, given optimum uptake kinetics, would lead to uptake rates approximately 75% of maximal rates. In addition, inhibition of NO_3^- uptake in the presence of NH_4^+ has been shown for numerous plant species (Pilbeam and Kirkby 1990), suggesting that field uptake rates are lower than the maximum velocity calculated from the Michaelis-Menten equation.

The low rates of NO_3^- uptake for *A. saccharum* fine roots indicate that this species is unlikely to serve as a direct sink for anthropogenic NO_3^-. However, in order to demonstrate this conclusively it will be necessary to quantify soil solution NO_3^- concentrations in the zone of maximum fine-root proliferation, and to determine if plant uptake rates are sufficient to serve as an important sink. If soil solution NO_3^- concentrations are greater than 50–100 μM, then *A. saccharum* fine roots will be at or above their maximal velocity for NO_3^- uptake, and will not be able to respond to increases in NO_3^- availability by increasing their rates of uptake. It is possible that with a large fine-root biomass, plants could take up substantial amounts of NO_3^- even with very low uptake rates. To test this contention, it will be necessary to combine measurements of fine-root uptake kinetics, fine-root biomass, soil solution NO_3^- concentrations, and rates of nitrification and NO_3^- deposition.

The approximately 30-fold difference in NH_4^+ versus NO_3^- uptake by seedlings is consistent with the low rates of NO_3^- uptake and assimilation we measured in the field; similar results have been observed in several coniferous (Ingestad 1979; Rygiewicz and Bledsoe 1986; Kamminga-van Wijk and Prins 1993; Knoepp et al. 1993; Buchman et al. 1995) and broadleaved trees (Chapin et al. 1986; Finlay et al. 1989). Few studies demonstrate such a pronounced difference in maximal uptake rates for NH_4^+ versus NO_3^-, most report rates of NH_4^+ uptake 2–4 times those of NO_3^- uptake. However, Chapin et al. (1986) found that NH_4^+ uptake was 10–20 times that of NO_3^- uptake in the roots of four broadleaved taiga trees (*Populus balsamifera, P. tremuloides, Betula papyrifera,* and *Alnus crispa*). Maximal rates of NH_4^+ uptake range from 30–50 μmol g^{-1} h^{-1}, consistent with those we measured in *A. saccharum* seedlings.

The pattern of very high rates of NH_4^+ uptake and very low rates of NO_3^- uptake and assimilation is surprising for a species like *A. saccharum* which is characteristic of N-rich sites, often with apparently high rates of nitrification (Pastor et al. 1984; Zak and Pregitzer 1990). Ecological studies of N metabolism often have focused on correlating NO_3^- uptake and assimilation with differences in NO_3^- availability, either through succession or across edaphic gradients (Havill et al. 1974; Haines 1977; Smith and Rice 1983; Al Gharbi and Hipkin 1984; Lee et al. 1986). Because nitrification is an important process in many northern hardwood forests in the Lake States (Zak et al. 1989; Zak and Pregitzer 1990), our results suggest that NO_3^- availability alone is not a good predictor of N metabolism in *A. saccharum*. This species appears to satisfy its N requirements through rapid NH_4^+ uptake, which may represent a "short circuiting" of the N cycle, or an adaptation of an extremely shade-tolerant species to minimize its C cost for N nutrition.

In conclusion, it appears that *A. saccharum* has a limited potential to serve as a direct sink for anthropogenic NO_3^- in northern hardwood forests. Because of its capacity for rapid NH_4^+ uptake, *A. saccharum* may represent a substantial indirect sink if added NO_3^- is first immobilized by soil microorganisms and later released as NH_4^+ during mineralization. Unless anthropogenic NO_3^- is retained in these ecosystems by the microbial community it is unlikely to have any significant effect on plant or ecosystem C balance, and has the potential to be lost to groundwater or denitrification (Durka et al. 1994). These results are quite unexpected. If *Acer saccharum* dominated forests do not directly assimilate atmospheric NO_3^-, we need to re-evaluate the mechanisms regulating N saturation.

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