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Plant and soil natural abundance δ^{15}N: indicators of relative rates of nitrogen cycling in temperate forest ecosystems

**Pamela H. Templer · Mary A. Arthur ·
Gary M. Lovett · Kathleen C. Weathers**

Abstract Watersheds within the Catskill Mountains, New York, receive among the highest rates of nitrogen (N) deposition in the northeastern United States and are beginning to show signs of N saturation. Despite similar amounts of N deposition across watersheds within the Catskill Mountains, rates of soil N cycling and N retention vary significantly among stands of different tree species. We examined the potential use of δ^{15}N of plants and soils as an indicator of relative forest soil N cycling rates. We analyzed the δ^{15}N of foliage, litterfall, bole wood, surface litter layer, fine roots and organic soil from single-species stands of American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and sugar maple (*Acer saccharum*). Fine root and organic soil δ^{15}N values were highest within sugar maple stands, which correlated significantly with higher rates of net mineralization and nitrification. Results from this study suggest that fine root and organic soil δ^{15}N can be used as an indicator of relative rates of soil N cycling. Although not statistically significant, δ^{15}N was highest within foliage, wood and litterfall of beech stands, a tree species associated with intermediate levels of soil N cycling rates and forest N retention. Our results show that belowground δ^{15}N values are a better indicator of relative rates of soil N cycling than are aboveground δ^{15}N values.

Introduction

Human activities, such as fossil fuel combustion and industrial production of fertilizers, have increased the amount of nitrogen (N) deposited onto terrestrial ecosystems (Galloway et al. 1995, 2005). Nitrogen is an essential nutrient for plants, animals and soil microbes, but in large amounts can lead to N saturation of forest ecosystems. Nitrogen saturation is a process in which N accumulates in excess of biological demand, and thus "excess" N is lost from ecosystems via leaching or gaseous losses (Agren and Bosatta 1988; Aber et al. 1989; Stoddard 1994; Peterjohn et al. 1996). Knowing which ecosystems have inherently high rates of soil N cycling would enable scientists and land managers to focus their attention on forest stands or regions that may be most susceptible to saturation. Forests in the Catskill Mountains receive among the highest inputs of N deposition in the northeastern United States (Ollinger et al. 1993; Stoddard 1994; Weathers et al. 2000), but the fate of deposited N varies significantly among stands of different tree species (Templer et al. 2005). For example, the forest floor of red oak-dominated forests has greater N retention than the forest floor of sugar maple-dominated forests (Templer et al. 2005), which can be partially explained by differences in soil nitrification rates. Rates of net nitrification (Finzi et al. 1998; Lovett and Rueth 1999; Lawrence

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P. H. Templer (✉)
Department of Biology, Boston University,
5 Cummington Street, Boston, MA 02215, USA
e-mail: ptempler@bu.edu

M. A. Arthur
Department of Forestry, University of Kentucky,
Lexington, KY, USA

G. M. Lovett · K. C. Weathers
Institute of Ecosystem Studies, Millbrook, NY, USA

et al. 2000; Lovett et al. 2004; Templer et al. 2003) and N leaching (Templer et al. 2005) are significantly greater in sugar maple stands compared to stands of other tree species.

The goal of our study was to determine whether natural abundance ^{15}N of soil and plant pools could be used as indicators of relative rates of soil N cycling across stands of different tree species. Advantages of using natural abundance isotopes as tracers or proxies of ecological processes lie in their ease of measurement and relatively low cost compared to other techniques such as enriched ^{15}N isotopes. Numerous studies have shown a strong correlation between foliar δ^{15}N and soil N pool size and process rates. This correlation occurs because many soil microbial processes discriminate against ^{15}N, which is the heavier of the two stable N isotopes. For example, microbes discriminate against ^{15}N during decomposition, mineralization (Nadelhoffer and Fry 1994), nitrification (Nadelhoffer and Fry 1994; Högberg 1997; Handley and Raven 1992) and denitrification (Piccolo et al. 1996). Discrimination against ^{15}N causes the products of each of these processes to be relatively lighter in ^{15}N, or less enriched, while the substrate from which they were formed becomes heavier, or more enriched in ^{15}N (Peterson and Fry 1987; Yoneyama 1996). As N cycling rates increase, soil-available δ^{15}N can increase since ^{14}N can preferentially leave the ecosystem through either denitrification or leaching. As plants take up remaining—relatively enriched—N, they too can become relatively enriched in ^{15}N as they reflect the N that they take up. A positive relationship has been observed between enriched levels of ^{15}N in foliage and increased soil N concentration (Emmett et al. 1998; Meints et al. 1975; Högberg 1990; Gebauer and Schulze 1991), increased rates of N cycling (Garten 1993; Garten and Van Miegroet 1994; Pardo et al. 2002) and increased losses of N (Högberg and Johannisson 1993). This means that higher relative $^{15/14}$N ratios within foliage could indicate that a forest is closer to reaching N saturation (Högberg 1990). In fact, δ^{15}N signatures of bulk soil and needles of mixed conifer forests were significantly more enriched at more N-polluted sites within the San Bernardino Mountains of California compared to sites less polluted with N. This pattern was attributed to changes in soil N cycling rates (Korontzi et al. 2000).

In addition to soil processes influencing the δ^{15}N signature of available N for plants, within-plant processes (e.g., translocation and assimilation) can further alter the δ^{15}N signature of plant tissue following N uptake (Evans 2001; Dawson et al. 2002). In controlled pot studies, roots and foliage of the same plant have been shown to vary by as much as 7‰ (Yoneyama and Kaneko 1989; Evans et al. 1996). However, the sum of all within-plant fractionating processes could potentially lead to up to 12‰ variation (Handley and Raven 1992). We therefore considered the

possibility that root δ^{15}N would be a better indicator of changes in N pool size and process rates than foliar δ^{15}N. This is because there would be fewer within-plant processes that could lead to fractionation and ultimately to specific δ^{15}N values within root tissue compared to aboveground tissues following N uptake (Handley and Raven 1992).

Because forest stands dominated by different tree species of the Catskill Mountains vary in soil microbial processing of N and ecosystem N retention (Templer et al. 2003, 2005; Lovett et al. 2004), we sought to determine whether measurements of soil and plant natural abundance δ^{15}N could be used as indicators of relative rates of soil N cycling across different tree species. Alternatively, differences among species in N fractionation following N uptake by roots or foliage could suggest that straightforward interpretation of above- and belowground ^{15}N pools is not warranted. We compared foliar, litterfall, bole wood and fine root δ^{15}N values within plant samples collected from stands of four of the dominant tree species of the Catskill Mountains, NY. We also examined δ^{15}N of organic soil and the surface litter layer associated with each tree species and compared them to rates of N processing.

Materials and methods

This work was part of a larger project examining the effects of tree species on ecosystem nutrient cycling and N retention and loss in forests of the Catskill Mountains, NY (74.26° west, 41.94° north; annual rates of atmospheric deposition are approximately 11.2 kg N ha^{-1}; see Lovett et al. 2004 and Templer et al. 2005 for further details of our experimental design). Our stands were located within mixed-species forests and were composed of clusters of the target tree species. Each stand contained at least three individual trees of the target species, had at least 80% overstory canopy contained by the target tree species, visible litter on the forest floor dominated by the target tree species and no evidence of recent disturbance. The six stands were distributed across three watersheds for each of the tree species, making a total of 24 stands.

In 1999 and 2000, we collected three subsamples of foliage, bole wood and litterfall and four subsamples of the surface litter layer (Oi), organic soils (Oe and Oa horizons; maximum 12 cm depth) and fine roots (<2 mm diameter) from stands dominated by one of the following tree species: American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and sugar maple (*Acer saccharum*; $n = 6$ stands per tree species). All subsamples were bulked within each stand prior to ^{15}N analysis. Three samples of sun-lit foliage were dislodged with a shotgun from each stand during August 1999, the

peak growing season. We collected the outer 2 cm of bole wood (0.5-cm-diameter borer) from three individuals of the target tree species per stand during May 2000. We collected three litterfall subsamples per stand biweekly during leaf fall in 1999 (0.23 m^2 baskets). During July 1999, we sampled the surface litter layer (Oi) from beneath a 400 cm^2 template and then sampled the organic soil (6.5 cm soil corer) from the same location to a maximum depth of 12 cm. We excavated the fine roots from the soil cores and carefully removed the adhered soil using forceps and Kimwipes®. We did not separate the fine root samples by tree species. However, we collected fine roots from the center of each single-species stand, so we are confident that the majority of the fine roots sampled came from the target tree species.

Foliage, litterfall, surface litter layer, wood, fine roots and soil samples were dried at 65 °C, ground (model 4200 pulverizer, Kinetic Laboratory Equipment Company, Visalia, CA, USA) and analyzed for N and $\delta^{15}N$. ^{15}N samples were analyzed on a Europa Scientific Ltd. (Crewe, UK) 20-20 mass spectrometer after combustion in a Europa ANCA-GSL combustion unit. Ammonium sulfate was used as the standard (1.35 ± 0.2‰ $\delta^{15}N$, mean ± standard deviation, respectively) and was calibrated against IAEA N1, an International Atomic Energy Agency standard. All isotope analyses were done at the Stable Isotope Facility at the University of California, Davis, CA.

To determine whether foliar %N values or plant and soil $\delta^{15}N$ values correlated with soil N cycling rates among dominant tree species of the Catskill Mountains, we examined the relationship between plant tissue and soil $\delta^{15}N$, as well as foliar %N values, and rates of net N mineralization and net nitrification measured in a 30-day laboratory incubation study using soils from the same stands. We collected and processed soil samples from each stand using methods identical to those described in Lovett et al. (2004). In brief, four soil cores (12 cm depth maximum) were taken from each stand during summer 2000. Soils were separated into organic (Oe + Oa) and mineral (A and/or B) horizons, but only values for the Oe + Oa horizons were included in this paper. Soils were sieved (8 mm sieve), homogenized and incubated for 28 days in plastic specimen cups. Net mineralization and net nitrification were calculated from the change in KCl extractable NH_4^+ plus NO_3^-, or NO_3^-, respectively. The average value for each stand was used in our correlation analyses.

Statistical analyses

To examine differences in $\delta^{15}N$ values among samples types (e.g., wood vs. fine root) and the stands of the four tree species, we conducted two-way analyses of variance (ANOVA) with sample type and tree species as the main effects. We used the Tukey's HSD procedure to make pairwise comparisons. We examined the potential correlations between $\delta^{15}N$ of belowground and aboveground pools and rates of net mineralization and nitrification. We also examined the potential correlation between foliar %N and rates of net mineralization and nitrification. We used SAS JMP software (Version 3.2.5, 1999) for all statistical analyses.

Results

There was a statistically significant effect of tree species ($P < 0.0001$) and sample type ($P < 0.0001$) on $\delta^{15}N$ values (Table 1). There was also a statistically significant interaction between the effects of tree species and sample type on $\delta^{15}N$ values ($P < 0.0001$; Table 1), with distinct patterns between the below- and aboveground ^{15}N pools. For example, $\delta^{15}N$ values were significantly greater within the fine roots ($P < 0.0001$) and organic soil ($P < 0.0001$) of sugar maple stands compared to the other tree species. While not statistically significant at the $\alpha = 0.05$ level, there was a trend for greater $\delta^{15}N$ values in the foliage and litterfall of beech trees compared to the other tree species ($P = 0.08$ and 0.096, respectively). There was also a trend for greater $\delta^{15}N$ values in the wood of beech and sugar maple trees compared to hemlock and red oak trees, but this pattern was also not statistically significant ($P = 0.14$).

Rates of net mineralization were positively correlated with both fine root $\delta^{15}N$ ($P = 0.003$; $r^2 = 0.59$; Fig. 1A) and organic soil $\delta^{15}N$ values ($P = 0.015$; $r^2 = 0.49$; Fig. 1B). There was no significant correlation between net mineralization and $\delta^{15}N$ of foliage, the surface litter layer or wood ($P = 0.39$, $r^2 = 0.18$ for foliage; $P = 0.13$, $r^2 = 0.31$ for surface litter layer; $P = 0.13$, $r^2 = 0.32$ for wood), but there was a significant relationship between net mineralization and $\delta^{15}N$ of litterfall ($P = 0.027$, $r^2 = 0.45$). The relationship between $\delta^{15}N$ values and net nitrification were stronger for the belowground than aboveground pools ($P < 0.0001$, $r^2 = 0.77$ for fine roots; $P = 0.0001$, $r^2 = 0.72$ for organic soil; Fig. 2). None of the relationships between net nitrification and $\delta^{15}N$ of the individual aboveground plant pools were significant ($P = 0.53$, $r^2 = 0.13$ for foliage; $P = 0.14$, $r^2 = 0.32$ for wood; $P = 0.12$, $r^2 = 0.32$ for litterfall).

We found no significant relationships between foliar %N values and soil N cycling rates ($P = 0.42$, $r^2 = 0.17$ for net mineralization and $P = 0.71$, $r^2 = -0.08$ for net nitrification).

Discussion

The range of values for natural abundance $\delta^{15}N$ found in this study is within the range found in other temperate forest studies (Fry 1991; Nadelhoffer and Fry 1994). However,

Table 1 $\delta^{15}N$ (‰) values (mean ± standard error; $n = 6$) of ecosystem pools across tree species

	Beech (B)	Hemlock (H)	Sugar maple (M)	Red oak (O)	P value
Wood	1.0 ± 0.2 [BC]	0.3 ± 0.34 [AB]	0.9 ± 0.3 [C]	0.4 ± 0.3 [BC]	0.14
Foliage	−0.5 ± 0.2 [A]	−0.6 ± 0.02 [AB]	−1.0 ± 0.4 [A]	−1.3 ± 0.2 [A]	0.08
Litterfall	0.1 ± 0.2 [AB]	−0.7 ± 0.09 [A]	−0.6 ± 0.3 [A]	−0.8 ± 0.2 [AC]	0.096
Surface litter layer	−0.5 ± 0.2 [A]	−0.7 ± 0.23 [A]	−0.4 ± 0.2 [AC]	−1.2 ± 0.2 [A]	0.14
Fine roots	1.0 ± 0.3 [aBC]	0.1 ± 0.42 [a AB]	2.7 ± 0.2 [b B]	0.6 ± 0.2 [a B]	<0.0001
Organic soil	1.4 ± 0.3 [a C]	0.7 ± 0.39 [a B]	2.9 ± 0.4 [b B]	1.1 ± 0.2 [a B]	<0.0001

Different lower-case letters within a row indicate a statistically significant difference ($P < 0.05$) across tree species for a given ecosystem pool. Different upper-case letters within a column indicate a statistically significant difference ($P < 0.05$) across ecosystem pools for a given tree species. P values shown are for comparisons across tree species within a sample type
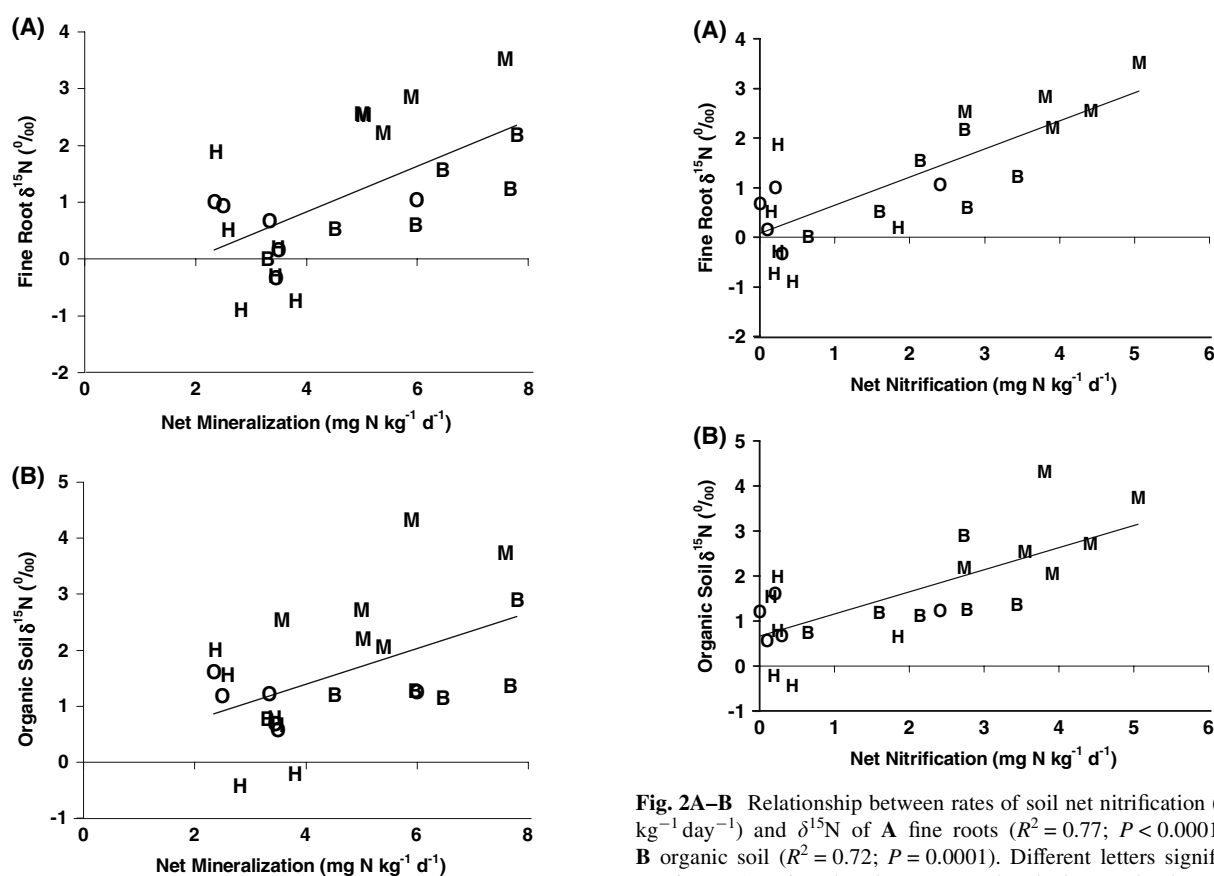

Fig. 1A–B Relationship between rates of soil net mineralization (mg N kg^{-1} day^{-1}) and $\delta^{15}N$ of **A** fine roots ($R^2 = 0.59$; $P = 0.003$) and **B** organic soil ($R^2 = 0.49$; $P = 0.01$). Different letters signify tree species: *B* American beech; *H* eastern hemlock; *O* red oak; *M* sugar maple. Correlation coefficients and P values for each relationship are shown

Fig. 2A–B Relationship between rates of soil net nitrification (mg N kg^{-1} day^{-1}) and $\delta^{15}N$ of **A** fine roots ($R^2 = 0.77$; $P < 0.0001$) and **B** organic soil ($R^2 = 0.72$; $P = 0.0001$). Different letters signify tree species: *B* American beech; *H* eastern hemlock; *O* red oak; *M* sugar maple. Correlation coefficients and P values for each relationship are shown

this is the first study that we are aware of that has examined a variety of forest ^{15}N pools across single-species stands. Our experimental design allows us to examine the direct relationship between plant ^{15}N pools and rates of soil N-cycling within forested stands of individual tree species. Our results show that natural abundance $\delta^{15}N$ values varied significantly among stands of the four tree species, but the

pattern for belowground pools was different from that of aboveground pools, suggesting that different processes are leading to below- versus aboveground $\delta^{15}N$ values. For example, $\delta^{15}N$ values of organic soil and fine roots were significantly higher in the sugar maple stands compared to the other tree species, while foliage, litterfall and wood tissues were all higher in ^{15}N within beech trees compared to the other tree species, although the aboveground patterns were not statistically significant. The patterns of $\delta^{15}N$ variation can potentially be explained by considering how

below- and aboveground processes vary among these species.

Patterns across tree species for δ^{15}N: belowground pools

Differences in soil N cycling rates at least partially explain the greater δ^{15}N values observed in the organic soil and fine roots of sugar maple stands compared to the other tree species. For example, net mineralization explained a significant amount of the variation in δ^{15}N values of fine roots and organic soil, respectively ($r^2 = 0.59$ and 0.49; Fig. 1A,B). Net nitrification explained even more of the variation in δ^{15}N values ($r^2 = 0.77$ and 0.72 for the relationships between δ^{15}N values of the fine roots and organic soil, respectively; Fig. 2A,B). It is not surprising that rates of net nitrification were more strongly correlated with belowground δ^{15}N values than the correlation with net mineralization since nitrification is a more strongly fractionating process than mineralization (Högberg 1997).

Species differences appear to drive some of the variation in soil N cycling and δ^{15}N values. Compared to the other tree species, sugar maple stands have significantly greater rates of net nitrification (Table 2; see also Finzi et al. 1998; Lovett and Rueth 1999; Templer et al. 2003; Lovett et al. 2004), greater NO_3^- leaching and lower net retention of deposited N (Templer et al. 2005). Since microbes discriminate against the heavier ^{15}N isotope, microbial processes such as nitrification cause the residual pool of N (e.g., NH_4^+ during nitrification) to become relatively enriched over time (Mariotti 1981). In this way, the greater rates of N cycling in sugar maple stands could have led to greater δ^{15}N of soil NH_4^+ that is available for plant uptake. Individuals of sugar maple have been shown to take up more of their N as NH_4^+ than NO_3 (Rothstein et al. 1996; BassiriRad et al. 1999; Templer and Dawson 2004), thus their roots may become enriched because they take up a relatively enriched N pool. Furthermore, the fact that rates of net nitrification and N leaching are greater in sugar maple stands suggests that the relatively depleted NO_3^- has been lost to a greater degree from the soil compared to stands of the other tree species.

A similar combination of plant and soil microbial processes may explain why the roots of beech trees are less enriched in ^{15}N compared to sugar maple. Individuals of beech tend to take up most of their N as NO_3^- (Templer and Dawson 2004). Because NO_3^- tends to be more depleted in the soil relative to NH_4^+ (Mariotti et al. 1981; Binkley et. al. 1985; Emmett et al. 1998), the roots of beech may become more depleted than those of sugar maple. It is not possible to compare patterns of inorganic N uptake to soil N availability in hemlock and red oak stands, since previous studies have not found significant differences in NH_4^+ versus NO_3^- uptake for either of these tree species (Templer and Dawson 2004).

Because rates of net nitrification were close to zero for most of the red oak and hemlock stands (Table 2; Fig. 2), we also evaluated the correlation between δ^{15}N values of forest pools and net nitrification in sugar maple and beech stands only. We found that the correlation between net nitrification and fine root and organic soil ^{15}N values became stronger when red oak and hemlock stands were omitted from our analyses. For example, within the smaller dataset, net nitrification explained 84% ($N = 12$, $P = 0.001$) and 74% ($N = 12$, $P = 0.006$) of the variation in δ^{15}N values of the fine roots and organic soil, respectively. These analyses show that the δ^{15}N values of belowground pools such as fine roots and organic soil can be especially strong indicators of relative rates of net nitrification when net nitrification is significantly greater than zero.

Differences in mycorrhizal associations could also influence the patterns we observed in belowground δ^{15}N values. Fractionation during uptake by mycorrhizae and subsequent transfer of N could result in differential patterns of δ^{15}N among species with different mycorrhizal associations. Ectomycorrhizae tend to fractionate against ^{15}N during N uptake more than arbuscular mycorrhizae (Högberg 1997). Sugar maple is associated with arbuscular mycorrhizae, whereas the other species in this study are predominantly associated with ectomycorrhizae. Therefore, it is possible that greater δ^{15}N values of sugar maple fine roots could be explained at least partially by smaller fractionation upon uptake by its fungal symbiont compared to the three other tree species.

Table 2 Rates of soil net mineralization and nitrification (both µg N g soil^{-1} day^{-1}), soil C:N, soil %N, and foliar %N values (mean ± standard error) across stands of four tree species ($n = 6$ per tree species)

	Beech (B)	Hemlock (H)	Sugar maple (M)	Red oak (O)
Potential net mineralization	5.9 ± 0.7^C	3.1 ± 0.2^A	5.4 ± 0.5^{BC}	3.5 ± 0.5^{AB}
Potential net nitrification	2.2 ± 0.4^A	0.5 ± 0.3^B	3.9 ± 0.3^C	0.5 ± 0.4^B
Soil C:N	19.8 ± 0.6^A	22.8 ± 0.5^B	17.2 ± 0.9^A	18.8 ± 0.7^A
Soil %N	1.6 ± 0.09^{AB}	1.9 ± 0.02^A	1.5 ± 0.1^{AB}	1.4 ± 0.1^B
Foliar %N	2.1 ± 0.1^A	1.4 ± 0.02^B	1.7 ± 0.1^C	2.4 ± 0.1^D

Different letters within a row indicate a statistically significant difference ($P < 0.05$) across tree species for a given ecosystem trait. Data for foliar %N values from Templer et al. (2005)

Regardless of the mechanism explaining greater $\delta^{15}N$ values in belowground pools of sugar maple forests, these results show that organic soil and fine root $\delta^{15}N$ could be used as an indicator of relative rates of soil N cycling in forests of the Catskill Mountains.

Patterns across tree species for $\delta^{15}N$: aboveground pools

The pattern of greater $\delta^{15}N$ values within the foliage and litterfall of beech trees compared to the other tree species is different from what we would expect if there is a strong relationship with patterns of soil net nitrification, N uptake or mycorrhizal associations. It is possible that either differences among species in within-plant fractionation, caused by such processes as NO_3^- reduction or N assimilation, or differences in canopy uptake of N among tree species could have driven the observed patterns of aboveground $\delta^{15}N$ values. Within-plant processes can cause within-plant variations of 7–12‰ (Evans 2001; Handley and Raven 1992). This is more than enough to explain the discrepancy we observed between below- and aboveground patterns in plant tissue $\delta^{15}N$ values, which varied at most by 2‰ (Table 1). Differences in canopy uptake of N could also influence within-plant variation in $\delta^{15}N$ values. For example, foliage of epiphytes in a rainforest in Costa Rica were shown to vary by as much as 2‰, which was attributed to differences in canopy uptake of N and subsequent fractionation during assimilation (Wanie et al. 2002). We are not aware of any published studies, to date, that have examined the effect of canopy N uptake on $\delta^{15}N$ values of trees in temperate forests.

We are aware of two other published studies that separated beech and sugar maple forest $\delta^{15}N$ values by tree species in northeastern United States forests. One study is from Harvard Forest in central Massachusetts (Nadelhoffer et al. 1999) and the other is from Hubbard Brook, New Hampshire (Pardo et al. 2002). Both studies used mixed species stands and foliage was the only pool that was distinguished by tree species. It is therefore not possible in those studies to characterize the direct connection between the below- and aboveground ^{15}N values of a forest caused by a particular species. In both studies, foliar $\delta^{15}N$ values of beech trees were relatively more enriched compared to the other tree species, including oak, birch and maple species in Harvard Forest and sugar maple and yellow birch at Hubbard Brook.

Consistent patterns among ecosystem pools

We observed some consistent patterns in $\delta^{15}N$ among the different ecosystem pools. The significant increase in ^{15}N enrichment from the litterfall and surface litter layer to the organic soil is consistent with other studies (Nadelhoffer and Fry 1994; Nadelhoffer et al. 1999) and may be caused

by the release of N that is depleted in ^{15}N at each stage of microbial decomposition and the release of inorganic N. Although not statistically significant, the plant tissue of all tree species was depleted in ^{15}N relative to the soil. This pattern may be due to the fact that plants take up the products of decomposition and mineralization, which produce relatively depleted pools of N (see Nadelhoffer and Fry 1994).

Conclusions

Organic soil and fine root $\delta^{15}N$ values were significantly positively correlated with mineralization and nitrification rates, with greater $\delta^{15}N$ in sugar maple stands compared to the other tree species. Part of this may be explained by species differences in mycorrhizal association and the form of N uptake. Because of the significant correlation with soil net nitrification, we conclude that organic soil or fine root $\delta^{15}N$ measurements could be used as an indicator of relative rates of forest NO_3^- production. Despite the fact that many previous studies have used foliar $\delta^{15}N$ as an indicator of relative rates of N cycling or progression toward N saturation (e.g., Meints et al. 1975; Högberg 1990; Gebauer and Schulze 1991; Garten 1993; Högberg and Johannisson 1993; Garten and Van Miegroet 1994; Emmett et al. 1998; Pardo et al. 2002), we found foliar $\delta^{15}N$ values to be poorly correlated with soil N cycling rates. While examining foliage alone may be adequate under certain conditions and for some questions, this study indicates that if multiple tree species are considered, a better understanding of the differences between below and aboveground forest $\delta^{15}N$ values is necessary. In fact, a regional study across an N deposition gradient, which included data from our study, compared the relationship between fine root $\delta^{15}N$ and soil N cycling rates with foliar $\delta^{15}N$ values and N cycling rates (Pardo et al. 2006). The regional study found that fine root $\delta^{15}N$ values were a stronger indicator of soil N cycling rates than foliar $\delta^{15}N$ values, suggesting that in general belowground plant ^{15}N pools may provide a stronger proxy for relative rates of soil N cycling.

Previous work has shown that tree species can vary in their effects on N cycling (Lovett and Rueth 1999; Lovett et al. 2004; Finzi et al. 1998), retention and loss (Templer et al. 2005). Many external factors such as climate change, selective harvest, introduced pests and changing land use are all producing changes in temperate forest tree species composition. Therefore, further work is needed to investigate the relationship between below and aboveground forest ^{15}N pools of dominant tree species if we want to use plant $\delta^{15}N$ values as an indicator of relative rates of N cycling and to predict how these relationships may change in the future.

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