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Influence of Tree Species on Forest Nitrogen Retention in the Catskill Mountains, New York, USA

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Abstract

This study examines the effect of four tree species on nitrogen (N) retention within forested catchments of the Catskill Mountains, New York (NY). We conducted a 300-day ^{15}N field tracer experiment to determine how N moves through soil, microbial, and plant pools under different tree species and fertilization regimes. Samples were collected from single-species plots of American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* L.), red oak (*Quercus rubra* L.), and sugar maple (*Acer saccharum* Marsh). Using paired plots we compared the effects of ambient levels of N inputs (11 kg N/ha/y) to additions of 50 kg N/ha/y that began 1.5 years prior to and continued throughout this experiment. Total plot ^{15}N recovery (litter layer, organic and mineral soil to 12 cm, fine roots, and aboveground biomass) did not vary significantly among tree species, but the distribution of sinks for ^{15}N within the forest ecosystem did vary. Recovery in the forest floor was significantly lower in sugar maple stands compared to the other species. ^{15}Nitrogen recovery was 22% lower in the fertilized plots compared to the ambient plots and red oak stands had the largest drop in ^{15}N recovery as a result of N fertilization. Aboveground biomass became a significantly greater ^{15}N sink with fertilization, although it retained less than 1% of the tracer addition. These results indicate that different forest types vary in the amount of N retention in the forest floor, and that forest N retention may change depending upon N inputs.

Key words: northern hardwood forest; plant and microbial nitrogen uptake; forest floor; nitrogen cycling; stable isotopes.

Introduction

Human activity has increased the amount of nitrogen (N) deposited onto terrestrial ecosystems (Galloway and others 1995). Increased N deposition onto forests can lead to N saturation, the syndrome of responses in which excess N supply to forests leads to nitrate (NO_3^-) leaching into groundwater and streams and other alterations of forest nutrient cycling (Agren and Bosatta 1988; Aber and others 1989; Stoddard 1994; Peterjohn and others 1996). Symptoms of N saturation and excess N leaching have been observed in spruce forests of the Smoky Mountains (Johnson and others 1991), as well as hardwood forests of the Adirondack Mountains, NY (Driscoll and Van Dreason 1993) and Fernow, West Virginia (Gilliam and others 1996). Most temperate forests, even those showing signs of N saturation, still

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retain a large proportion of deposited N, some as much as 90% (Peterjohn and others 1996; Lovett and others 2000). Forest fertilization and tracer studies show that most of the N deposited onto forests is retained within the soil, while less is retained by the vegetation (Fenn and others 1998; Nadelhoffer and others 1999). Even if forests retain a large amount of deposited N, N leached in the form of NO_3^- can cause essential cations such as calcium (Ca) and potassium (K) to be leached out of the forest soil leading to nutrient imbalances within trees (Friedland and others 1988; Schulze 1989). Nitrogen leaching can also lead to acidification of stream water (Vitousek and others 1997) and eutrophication of estuaries and coastal areas (Howarth 1988).

The Catskill Mountains in southeastern NY State (Figure 1) receive among the highest inputs of N deposition in the northeastern United States (Ollinger and others 1993; Stoddard 1994) and have experienced increased stream NO_3^- concentrations over the last 25 years (Murdoch and Stoddard 1993). However, not all watersheds of the Catskill Mountains show the same pattern of N retention and loss. Nitrogen retention among watersheds ranges between 49% and 90% of atmospheric input and stream NO_3^- concentrations vary as much as 17-fold, even among watersheds that are completely forested and have similar rates of N deposition (Lovett and others 2000).

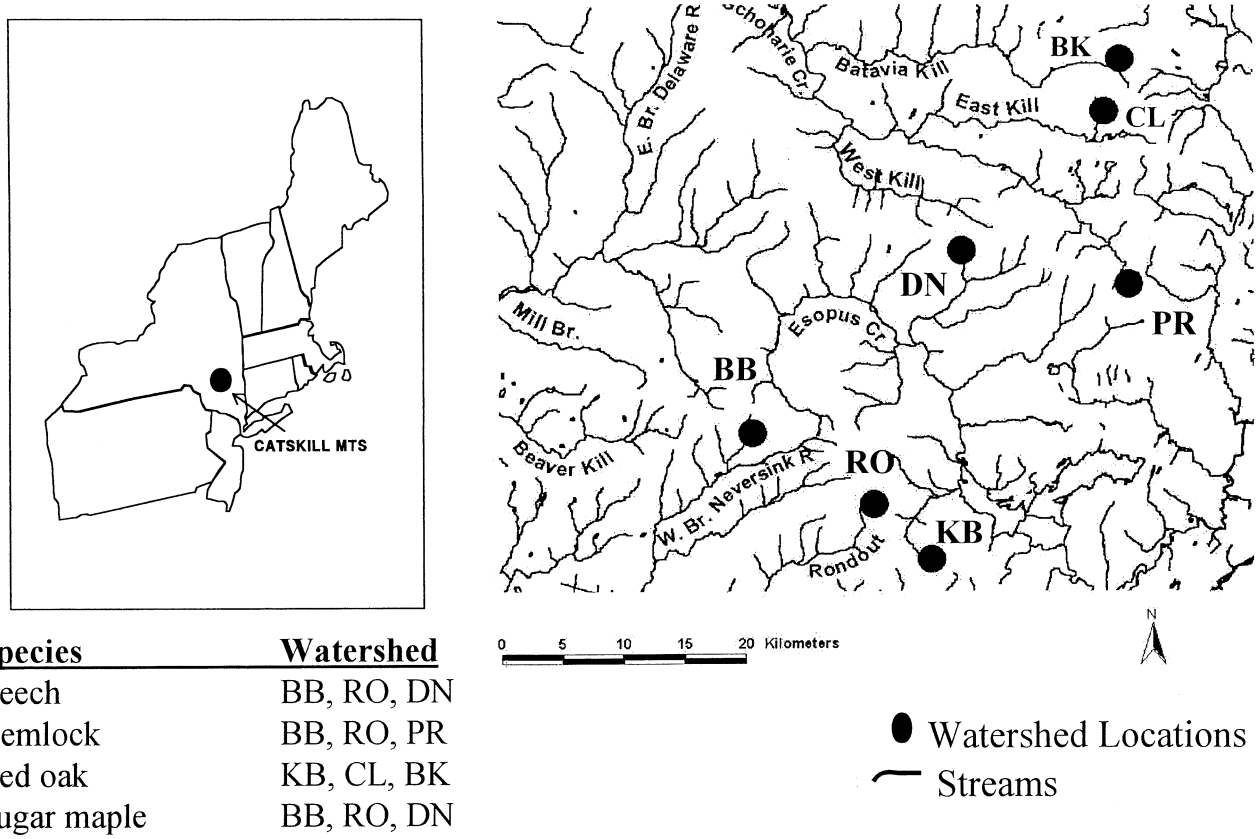
The definitive mechanism behind the variation in stream NO_3^- concentration remains elusive despite extensive research on possible controling factors such as hydrology (Burns and others 1998; West and others 2001), N deposition, and topography (Lovett and others 2000; Weathers and others 2000). Growing evidence suggests that some of the variation may be related to differences in tree species composition across watersheds. Watershed NO_3^- loss is inversely related to soil C:N ratio, which in turn is related to vegetation composition (Lovett and others 2002). In mixed-species stands, increasing dominance of sugar maple (*Acer saccharum* Marsh) is associated with lower soil C:N ratios, whereas increasing dominance of red oak (*Quercus rubra* L.) is associated with higher C:N ratios (Lovett and others 2002). These observations led to the hypothesis that tree species composition may influence N retention and thereby influence the amount of NO_3^- reaching streams (Lovett and others 2000, 2002).

Biotic control of N retention, specifically inorganic N, has been suggested (Vitousek and Reiners 1975) and demonstrated in many forest ecosystems (Aber and others 1989; Goodale and others 2000). Plant species can affect the localized movement of N through an ecosystem via indirect effects on soil chemical properties and microbial activity (Vitousek and others 1982; Zak and others 1986; Finzi and others 1998) and through direct plant uptake of N (Gharbi and Hipkin 1984; Horsley 1988; Crabtree and Bazazz 1993; Nadelhoffer and others 1995). Trees can have an effect on how much N remains within a forest ecosystem by influencing the quality of the organic matter in the forest floor, generally the major repository of added N (Buchmann and others 1996; Tietema and others 1998; Nadelhoffer and others 1999). We hypothesized that N retention is low in stands dominated by sugar maple (*Acer saccharum* Marsh.), high in stands dominated by red oak (*Quercus rubra* L.), and intermediate in eastern hemlock (*Tsuga canadensis*, L.) and beech (*Fagus grandifolia* Ehrh.) stands. Our expectation is due to differences in litter quality and soil chemistry characteristics associated with these tree species. For example, both laboratory (Lovett and Rueth 1999; Templer and others 2003; Lovett and others forthcoming) and field rates (Finzi and others 1998; Lawrence and others 2000) of net nitrification are higher in stands of sugar maple compared to the other three tree species. This difference is partially explained by differences in soil C:N ratios (Lovett and others forthcoming). We expected the higher net nitrification rates in sugar maple stands to result in significantly greater NO_3^- leaching and lower forest N retention compared to forest stands dominated by other tree species. Lower rates of net nitrification in red oak and hemlock stands led us to predict N retention within these stands would be greater compared to other tree species.

Our objectives were to quantify the N retained within the forest floor and the microbial and plant biomass in stands of the dominant tree species, as well as to determine the impact of fertilization on forest N retention. We examined soil and plant pools to better understand actual routes of N movement through forests and retention times within various pools. If retention within different pools varies among tree species, changes in tree species composition in the future could alter the location and retention of N within forests. We used ^{15}N to trace the distribution of retained N among major N pools (forest floor, plant and microbial biomass) in plots dominated by different tree species in the Catskill Mountains of NY. A fertilization treatment was used to examine the potential effect of higher N inputs on N retention.

Site Description

The Catskill Mountains are a range of low, mostly flat-topped mountains in southeastern NY State



Species	Watershed
Beech	BB, RO, DN
Hemlock	BB, RO, PR
Red oak	KB, CL, BK
Sugar maple	BB, RO, DN

Figure 1. Map of the northeastern United States and Catskill Mountains showing watershed locations. The abbreviations for each watershed are as follows: BB: Biscuit Brook, RO: Rondout, DN: Diamond Notch, PR: Prediger, KB: Kanape Brook, CL: Colgate Lake, BK: Batavia Kill. The watersheds of this study are in an approximately 50-km × 60-km area in the central Catskill Mountains.

(Figure 1). The bedrock is composed mostly of sandstone, shale, and conglomerate (Stoddard and Murdoch 1991) and is covered by glacial till that ranges from 0 to more than 30 m (Kudish 2000). The soils are classified as Inceptisols, have moderate to high acidity (Stoddard and Murdoch 1991), and are well drained and moderately steep. Soils have on average 60% sand, 30% silt, and 10% clay content (Kudish 2000). Vegetation between 500-m and 1100-m elevation is dominated by northern hardwood forests common throughout the northeastern United States, including sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), red oak (*Quercus rubra* L.), and eastern hemlock (*Tsuga Canadensis* L.; Kudish 1971; McIntosh 1972). About 80%–90% of the original forest of the Catskill Mountains was subject to some level of harvesting by the end of the 19 century, although most of the cutting was selective harvest rather than clear-cutting. The Catskill Forest Preserve was created in 1885 with most of the land within its current borders added by the 1930s (Kudish 2000). Land within the forest preserve cannot be logged, farmed, or developed. Mean annual temperature is 4.3°C and mean annual precipitation is 153 cm at the 808-m-elevation weather station on Slide Mountain. Average N deposition in the Catskill Mountains is 11.2 kg N/ha/y (Lovett and Rueth 1999).

Methods

Experimental Design

In 1999–2000, we examined the fate of N in 6 sets of 12-m-diameter paired plots for sugar maple, American beech, red oak, and eastern hemlock (12 plots per species total). The plots were located within mixed-species forest and were composed of clusters of the target tree species. We chose the plots with the following criteria: (1) There were at least 3 dominant trees of the target species, (2) overstory canopy in plot was dominated (more than 80% estimated by observation) by foliage of

the target species, (3) visible litter on the forest floor was dominated by target species, and (4) there was no evidence of recent disturbance (for example, logging, fire). Our subsequent measurements showed that litter of the target tree species represented 67%–84% of the total litter at each plot (unpublished data), with nontarget litter resulting primarily from understory trees and trees outside the plot. The 6 paired plots were distributed across three watersheds for each of the tree species (Figure 1). Because of the distribution of tree species within the Catskill Mountains, we could not easily locate all four species within each watershed. One plot of each pair received only ambient levels of N deposition (approximately 11.2 kg N/ha/y), while the other had been fertilized with an additional 50 kg N/ha/y (as granular NH_4NO_3 in four doses per year—June, July, August, and November of each year) for the 1.5 years prior to and during this experiment. Thus, the total N enhancement in the fertilized plots by the end of this experiment was 112.5 kg N/ha. This enabled us to compare the movement of N within plots that received ambient levels of N to those that received a higher level of N. To each of the paired plots we added tracer amounts of 99 atom % enriched $^{15}NH_4Cl$ to the inner 8 m of each plot during July, August, and October 1999 (3 additions of 10 mg $^{15}NH_4Cl$-N/m^2 each; dissolved in 5 L deionized water for each plot). We added ^{15}N three times, including one dose in the fall after leaf drop, rather than as a single pulse, for a more natural simulation of N availability throughout the year. In July and August 1999, ^{15}N was added approximately 1.5 weeks following the N fertilization additions. We added the ^{15}N isotope as NH_4 to trace the large flux of N that is mineralized from organic matter as opposed to the smaller flux of N received from ambient deposition, which occurs primarily as NO_3. The tracer solution was applied to an 8-m-diameter subplot using a backpack sprayer to ensure even distribution. The experimental plots of this experiment were reduced to 8-m diameter because that area was adequate to detect ^{15}N tracer additions and because of the significant cost of ^{15}N addition.

Sampling

To determine natural abundance background ^{15}N, roots and soil (Oe and Oa horizons) samples were collected from each plot in June 1999. Surface litter layer (Oi) samples were collected from areas outside and directly adjacent to each plot during August 1999. Wood and bark samples were collected from areas outside and directly adjacent to each plot during May 2000.

To track the fate of the added ^{15}N in the soil, we collected four samples of the litter layer (Oi), organic (Oe and Oa horizons), and mineral soil and fine root samples from each plot on three dates. The first sampling occurred two days following the first ^{15}N addition in July 1999. The second sampling (day 90 after initial ^{15}N addition) occurred just prior to the third ^{15}N addition in October 1999. The third sampling (day 300) occurred during May 2000, prior to budbreak of the deciduous tree species. In the calculations of ^{15}N recovery percentages, we used only ^{15}N inputs that occurred before the sampling date. For each of the four samples per plot, the litter layer was removed under a 400-cm^2 template and a 6.5-cm diameter soil core was taken to a depth of 12 cm. Organic and mineral soil were kept separate and the four samples per plot were composited, resulting in one organic and one mineral soil sample for each plot. For each of the soil cores, all fine roots (diameter less than 2 mm) were removed to determine root uptake of ^{15}N. Fine roots were separated from bulk soil with forceps after being dried at 65°C. Adhered soil was removed from roots with forceps and careful wiping with tissue. We did not examine ^{15}N movement to greater soil depths than 12 cm because of the extremely rocky nature of Catskill Mountain forest soils. Surface litter layer, roots, and soil samples were dried at 65°C, ground (Kinetic Laboratory Equipment Company Model 4200 Pulverizer), and analyzed for N and ^{15}N.

The fumigation–extraction method was used to determine soil microbial biomass N (Vance and others 1987) with the following modification. We used KCl rather than K_2SO_4 as a soil extractant. We conducted a laboratory experiment that demonstrated that there was no difference in the recovery of digested total dissolved nitrogen (TDN) standards or samples when using either of these extractants (unpublished data). Ten grams of each fresh organic soil sample (Oe and Oa horizons) were fumigated with chloroform for 24 h to kill and lyse microbial cells in the sample. Both the fumigated and nonfumigated soil samples were extracted with 60 mL of 2 N KCl, shaken for 1 h at 125 rpm, and filtered through a Whatman 42 filter. Total dissolved N was determined for fumigated and nonfumigated soils by digesting 2 mL soil extract sample with 4 mL persulfate (Cabrera and Beare 1993). After autoclaving the samples at 240°C for 3 h, we added 0.2 mL (0.88 g/L) ascorbic acid to break apart precipitates (Williams and others 1995). Microbial biomass N was calculated as the

difference in N mass between the fumigated and nonfumigated soils (Vance and others 1987). The ^{15}N content of each soil extract was determined using the diffusion technique (Stark and Hart 1996). We determined the amount of net microbial uptake by calculating how much of the added ^{15}N was incorporated into microbial biomass.

Ion-exchange resin bags were placed in the mineral soil during the growing and dormant seasons to provide a relative index of N leaching from the sites (Giblin and others 1994). Bags were placed in the soil by pounding in a flat pry bar at an angle to create a slit extending into the mineral soil. The resin bags were inserted into this slit to a depth of 8–12 cm, which was below the zone of high fine-root density. Four anion and four cation resin bags were placed within two plots of each tree species from July to November 1999 (red oak in the Kanape Brook watershed and beech, hemlock, and sugar maple in the Rondout Creek watershed), and new resin bags were placed within each plot (all watersheds) from November 1999 to early May 2000. Before deployment in the field, the cation resin bags were charged with 0.5 M HCl overnight, whereas the anion resin bags were charged with 0.5 M NaOH. Each resin bag was extracted two times with 100 mL of 2 N KCl upon retrieval from the field. The four 200-mL cation and anion resin bag extracts for each plot were combined (cation and anion extractions kept separate) and diffused onto acid traps to determine ^{15}N content (Stark and Hart 1996). The amount of NH_4^+, NO_3^-, and ^{15}N collected by resin bags from each plot was calculated from the difference between the amount of N extracted from bags left in the soil and the amount of N extracted from bags not placed in the field (used as resin bag blanks).

We determined soil water content by drying 10 g of each organic horizon soil sample at 65°C until they reached a constant weight (approximately 48 h) and calculated water loss. On the same samples, we determined organic matter by calculating loss on ignition after combustion at 450°C for 4 h.

We collected the outer 2 cm of wood and bark from three individuals of the target tree species within each plot during May 2000 (prior to budbreak) to examine how much of the N was moved to long-term sinks within the trees. The three samples per plot were combined prior to ^{15}N analysis yielding one sample per plot. We report data on the outer 2 cm of trees (bark + wood) because analysis to 15 cm into trees indicated undetectable ^{15}N translocation to inner rings. The diameter at breast height (dbh, cm) of each live tree within the 12-m-diameter plot was determined in 1997. We used allometric equations for each of the tree species (Tritton and Hornbeck 1982) to calculate total aboveground tree biomass (kg) of each plot (4-m radius). We also calculated the aboveground biomass for each plot based on the dbh minus 4 cm of each tree (2 cm on each side of tree). We used the difference in aboveground biomass between the two measurements (total tree dbh and dbh minus outer 2 cm) to calculate the amount of ^{15}N recovered within the outer 2 cm of wood and bark of each tree.

Litterfall samples were collected biweekly in three baskets per plot during leaf fall of 1998 and 1999 (0.226-m^2 baskets) and were composited within each plot prior to ^{15}N analysis. Three samples of sunlit foliage were dislodged with a shotgun from each plot during the peak growing season (August) of 1998, 1999, and 2000 and were composited by plot and year prior to ^{15}N analysis. Leaf area was determined on a Li-Cor Model 3100 Leaf Area Meter. Litterfall mass and N data presented included all litter that fell into the plot, regardless of tree species. Foliar mass and N data included the target tree species only. Foliage mass for beech, oak, and sugar maple was determined by the following calculation:

$$F_m = \mathrm{LF} * R_{fl} \quad (1)$$

where F_m is foliage mass per unit ground area (kg/ha), LF is litterfall mass per unit ground area (kg/ha), and R_{fl} is the ratio of mass per unit area leaf of 10 fresh foliage leaves to 10 litterfall leaves (kg/ha). This allowed us to convert the known litterfall mass per unit ground area to foliage mass per unit ground area. Foliage mass for hemlock plots was determined by multiplying annual litterfall mass by 3 because the average needle longevity of eastern hemlock needle is approximately 3 years (Barnes and Wagner 1981). ^{15}Nitrogen values from foliage collected during summer 2000 were not used in the day 300 calculations of total biomass recovery of ^{15}N for the deciduous tree species' stands because the day 300 sampling date was prior to budbreak. We included the 2000 summer foliage ^{15}N values within the day 300 calculations for total recovery of ^{15}N within hemlock stands because those trees had foliage at the time of the day 300 sampling. This results in an overestimation of ^{15}N recovery within hemlock plots at day 300, but is quite small as evidenced by the small amount of ^{15}N in hemlock foliage during August 2000 relative to the other ecosystem pools at day 300.

Sample Analyses

All solid samples were analyzed using a Carlo-Erba NA-1500 Autoanalyzer for total N using acetanilide

as a reference standard in the Institute of Ecosystem Studies (IES) Analytical Laboratory. All soil solutions were analyzed using an Alpkem Flow Solution III Autoanalyzer for NH_4^+, NO_3^-, and TDN, also at the IES Analytical Laboratory. Natural-abundance ^{15}N samples were analyzed on a Europa 20–20 mass spectrometer after combustion in a Europa ANCA-GSL combustion unit. Enriched ^{15}N samples were run on a Europa Integra, which is a combined sample combustion unit and isotope ratio mass spectrometer. The standard used was 0.36679 atom % ^{15}N 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.

^{15}N Recovery Calculations

We calculated ^{15}N recovery using N mass, the amount of ^{15}N added, and the atom % ^{15}N enrichment of the various ecosystem pools. The following equation (based on the calculations described by Buchmann and others, 1996) used to determine % ^{15}N recovery within each ecosystem pool:

$$\%^{15}N_{rec} = 100 * \frac{m_{pool} * (\text{atom } \%^{15}N_{pool} - \text{atom } \%^{15}N_{ref})/100}{^{15}N_{tracer}} \quad (1)$$

where % $^{15}N_{rec}$ = percent of ^{15}N tracer recovered in the labeled N pool, m_{pool} = N mass of the labeled pool, atom % $^{15}N_{pool}$ = atom percent ^{15}N in the labeled pool, atom % $^{15}N_{ref}$ = atom percent ^{15}N of the reference (nonlabeled) plots, and $^{15}N_{tracer}$ = amount of ^{15}N added to each plot prior to sample collection. We used ^{15}N recovery as an estimate of net retention of N in a given pool at a given point in time.

Statistical Analyses

For each plot, we averaged the mass and N pool size for soil and plant samples over time. For these properties, we conducted two-way analyses of variance (ANOVA) using SAS JMP software (Version 3.2.5, 1999, SAS Institute, Cary, NC) with tree species and N treatment (ambient versus fertilized) as the main effects. Plot was nested within tree species because of the paired-plot design. Data that were not normally distributed were log-transformed prior to statistical analysis. Among the ambient and fertilized plots, we conducted separate linear contrasts of the means with Tukey–Kramer *post hoc* tests to test the hypothesis that tree species have different effects on soil and plant N within forests of the Catskill Mountains.

To examine the effect of tree species on forest floor ^{15}N recovery over time, we conducted a repeated-measures ANOVA using SAS software (Version 8.01, 1999) using tree, N treatment, and date as main effects. Plot was nested within tree species because of the paired-plot design. We conducted linear contrasts of the means using Tukey–Kramer *post hoc* tests to compare each sampling date (day 2, 90, and 300) for those samples that were collected repeatedly (surface litter layer, roots, and soil), to compare ambient and fertilized plots, and to examine the effect of tree species on forest ^{15}N recovery. For the latter two tests, we present results from day 300 (May 2000) only.

We calculated statistical power for those relationships that were found to be insignificant to determine if lack of sufficient sample size could explain some of our results. Statistical power refers to the odds of concluding that there is a relationship between two factors when in fact there is one. It is related to the Type II error, which is the probability of failing to detect a true difference among populations. A greater power value is related to a greater chance of coming to the correct conclusion given the sample size and difference among populations of one's study. Values of power range between zero and 1. A relatively high value for a statistical test that has an alpha value = 0.05 is 0.8 (Cohen 1992).

Results

Ambient N Deposition Plots

Nitrogen Pools, Soil Moisture, and Organic Matter. Soil NO_3^- pools were more than twice as large in sugar maple stands compared to the other tree species ($P < 0.05$; Table 1). Hemlock had a significantly greater amount of organic soil N per unit area compared to beech and red oak ($P = 0.016$; Table 2). However, fine root, litterfall, and aboveground biomass N were significantly lower in hemlock plots ($P < 0.05$; Table 2). Hemlock organic horizon samples had approximately 1.35 times the amount of soil organic matter as the other three tree species ($P = 0.01$), whereas soil water content did not vary across tree species ($P > 0.05$).

Differences in ^{15}N Recovery Among Tree Species. Total plot ^{15}N recovery (sum of surface litter layer, fine roots, total soil to 12 cm depth, and aboveground biomass) did not vary among tree species ($P = 0.68$) but was greater in the ambient

Table 1. Soil (Oe and Oa horizons) NH_4^+, NO_3^-, Dissolved Inorganic Nitrogen, Total Dissolved Nitrogen, and Microbial Biomass Nitrogen (μg N/g dry soil) at Day 300 (May 2000)

	Beech		Hemlock		Red Oak		Sugar Maple	
	Ambient	Fertilized	Ambient	Fertilized	Ambient	Fertilized	Ambient	Fertilized
NH_4–N	*17.9 ± 3.9	*37.0 ± 6.5	*21.2 ± 2.2	*32.2 ± 4.0	16.9 ± 4.7	30.1 ± 4.7	*28.4 ± 10.7	*35.4 ± 10.0
NO_3–N	8.4^{a} ± 1.2	6.2^{A} ± 1.8	1.2^{b} ± 0.5	1.5^{A} ± 0.6	2.1^{ab} ± 2.0	0.4^{A} ± 0.1	16.5^{c} ± 3.8	20.3^{B} ± 5.9
DIN (NH_4–N + NO_3–N)	*26.3 ± 4.0	*43.2 ± 7.1	*22.4 ± 2.0	*33.7 ± 4.5	19.0 ± 6.5	30.5 ± 4.8	*44.9 ± 12.5	*55.7 ± 13.1
TDN	119.6 ± 11.2	152.2 ± 28.6	185.0 ± 29.6	170.5 ± 21.5	122.0 ± 20.2	127.2 ± 18.4	135.4 ± 31.7	136.9 ± 22.2
Microbial biomass N	*180.1 ± 22.6	*123.4 ± 25.4	182.9 ± 37.6	211.2 ± 41.3	227.7 ± 43.3	237.1 ± 48.1	219.2 ± 43.9	229.5 ± 45.0

DIN, dissolved inorganic nitrogen (NH_4^+ plus NO_3^-); TDN, total dissolved nitrogen.
*Data are means with one standard error (n = 6). Different lower- and upper-case letters above values represent statistically significant differences among tree species within ambient or fertilized plots, respectively (P < 0.05). Within a tree species, significant differences among ambient and fertilized plots are denoted by the following: *P < 0.05, **P < 0.01, and **P < 0 005.*

than fertilized plots ($P = 0.019$; Figure 2). It ranged between 62% and 75% in the ambient plots and between 48% and 61% in the fertilized plots.

The forest floor, including the surface litter layer (Oi), organic soil (Oe and Oa horizon), and fine roots, was the dominant sink for ^{15}N in all forest plots, and forest floor ^{15}N recovery varied significantly among plots occupied by different tree species ($P = 0.0052$; repeated-measures ANOVA; Figure 3). Sugar maple plots had significantly lower forest floor ^{15}N recovery compared to beech, hemlock, and red oak plots. This pattern is due to differences in ^{15}N concentration and not due to differences in forest floor mass. For example, the difference in leaf litter atom % ^{15}N, the largest component of the forest floor in terms of mass, varied significantly ($P = 0.0049$), with red oak stands having the greatest atom % ^{15}N value and sugar maple stands the least. There was no significant difference in litter mass between these two tree species' stands ($P > 0.05$; Table 2).

At day 300 (May 2000), ^{15}N recovery within aboveground woody biomass varied among tree species ($P = 0.056$; Table 3). Aboveground biomass within beech and sugar maple plots had significantly greater ^{15}N recovery compared to hemlock, whereas red oak plots did not differ from any of the other tree species. There was no significant difference among tree species in the amount of ^{15}N recovered within microbial biomass ($P = 0.16$).

Summer (July–November) ^{15}N concentrations within the resin bags did not vary significantly among plots occupied by different tree species, although resin bags within sugar maple plots had more than 7 times the recovery of $^{15}NO_3$ compared to the other tree species (Table 4). The statistical power of this comparison was low (power = 0.18) because $n = 2$. Resin bags within beech and sugar maple plots recovered more ^{15}N in the winter (November–May) than hemlock and red oak plots ($P = 0.0019$). The large amount of ^{15}N in winter resin bays of sugar maple plots corresponded to larger soil NO_3^- pools than other tree species' plots. For example, soil NO_3 was 8–10 times higher in sugar maple plots compared to red oak plots ($P < 0.05$; Table 1).

Sinks for ^{15}N Tracer. The majority of the added ^{15}N was recovered in the surface litter layer (Oi) across all four tree species and sampling dates ($P < 0.001$; Figure 3). The relative size of the fine-root and microbial biomass ^{15}N sink depended on the sampling date. Microbial biomass had approximately 1.25 and 1.13 times the amount of ^{15}N recovered in roots on days 2 (P = 0.037) and 90, respectively (P = 0.13). The relationship between microbes and roots changed by day 300, with fine-

Table 2. Dry Mass, % Nitrogen and kg N/ha of Organic Soil (Oe and Oa horizons), Total Soil to 12 cm Depth, Roots, Litter layer, Litterfall, Foliage, and Aboveground Woody Biomass

	Kg/Ha		% Nitrogen		Kg N/Ha	
	Ambient	Fertilized	Ambient	Fertilized	Ambient	Fertilized
Organic Soil (Oe and Oa Horizons)						
Beech	64400 ± 10247.2	64400^{A} ± 6227	1.21^{a} ± 0.06	1.24^{A} ± 0.07	770^{a} ± 105	790^{A} ± 86
Hemlock	82500 ± 9822.3	104400^{B} ± 13946	1.53^{b} ± 0.08	1.73^{B} ± 0.04	1250^{b} ± 136	1810^{B} ± 264
Red oak	59100 ± 7211.2	49800^{A} ± 6730	1.06^{a} ± 0.06	1.18^{A} ± 0.08	610^{a} ± 53	580^{A} ± 74
Sugar Maple	77800 ± 12243.3	60600^{A} ± 11844	1.24^{a} ± 0.09	1.54^{AB} ± 0.12	950^{ab} ± 199	850^{a} ± 134
Organic and mineral soil to 12-cm depth						
Beech	151590 ± 26228	165625 ± 36383	0.78 ± 0.11	0.74^{AB} ± 0.09	1070 ± 86	1070^{A} ± 135
Hemlock	186800 ± 41353	184258 ± 6145	1.04 ± 0.20	1.12^{AB} ± 0.13	1590 ± 135	2060^{B} ± 236
Red oak	251630 ± 32224	194782 ± 33178	0.52 ± 0.04	0.61^{A} ± 0.09	1280 ± 147	1070^{A} ± 89
Sugar Maple	191280 ± 33435	125488 ± 42877	0.74 ± 0.12	1.19^{B} ± 0.22	1350 ± 237	1100^{A} ± 172
Fine roots						
Beech	1600^{ac} ± 183	1300^{A} ± 37	1.61^{a} ± 0.05	1.52^{AD} ± 0.05	25.7^{a} ± 3.2	19.9^{A} ± 1.1
Hemlock	1200^{a} ± 92	800^{B} ± 37	1.23^{b} ± 0.06	1.37^{ABC} ± 0.05	14.4^{b} ± 1.5	11.0^{B} ± 0.5
Red oak	3100^{b} ± 712	2200^{c} ± 165	1.27^{b} ± 0.06	1.29^{BC} ± 0.05	38.4^{a} ± 8.5	28.0^{A} ± 2.6
Sugar Maple	2200^{bc} ± 56	900^{B} ± 165	1.60^{a} ± 0.05	1.66^{D} ± 0.06	34.5^{a} ± 1.6	14.1^{B} ± 2.5
Surface litter layer						
Beech	7870^{a} ± 503.1	7429^{A} ± 488	1.74^{a} ± 0.05	1.71^{A} ± 0.04	140 ± 6	127 ± 7
Hemlock	10850^{b} ± 941.4	11054^{B} ± 950	1.51^{b} ± 0.05	1.47^{B} ± 0.04	170 ± 20	163 ± 19
Red oak	7760^{a} ± 643.7	6837^{A} ± 520	1.62^{ab} ± 0.05	1.62^{AB} ± 0.06	130 ± 9	111 ± 12
Sugar Maple	7130^{a} ± 538.1	7575^{A} ± 569	1.74^{a} ± 0.07	1.75^{A} ± 0.06	120 ± 8	133 ± 9.7
Litterfall						
Beech	2700^{ac} ± 161	2486^{A} ± 138	1.35^{a} ± 0.10	1.38^{A} ± 0.09	36.2^{a} ± 2.95	33.8^{AD} ± 1.89
Hemlock	1670^{b} ± 149	1643^{B} ± 80	0.77^{b} ± 0.08	0.67^{B} ± 0.06	12.8^{b} ± 1.92	11.0^{B} ± 1.46
Red oak	2650^{a} ± 205	2603^{A} ± 142	1.06^{c} ± 0.12	1.10^{C} ± 0.12	27.7^{a} ± 3.29	28.0^{AC} ± 1.63
Sugar Maple	3230^{c} ± 134	3520^{C} ± 231	1.05^{ac} ± 0.06	1.04^{C} ± 0.06	34.0^{a} ± 1.79	36.3^{D} ± 1.84
Foliage						
Beech	2052 ± 260	2267^{A} ± 369	2.08^{a} ± 0.09	2.10^{A} ± 0.08	42.2 ± 4.2	47.0 ± 6.8
Hemlock	1987 ± 181	2350^{A} ± 257	1.39^{b} ± 0.02	1.53^{B} ± 0.04	28.0 ± 2.8	35.7 ± 3.6
Red oak	1433 ± 156	1425^{B} ± 182	2.40^{c} ± 0.10	2.34^{C} ± 0.11	34.7 ± 4.4	33.0 ± 4.1
Sugar Maple	1667 ± 196	1962^{AB} ± 144	1.72^{d} ± 0.05	1.78^{D} ± 0.04	28.5 ± 3.4	35.2 ± 2.7
Aboveground woody biomass (outer 2 cm only)						
Beech	81800 ± 8299	61767^{A} ± 4721	0.17^{ab} ± 0.02	0.16^{AB} ± 0.03	147.7^{a} ± 28.5	102.5^{A} ± 23.2
Hemlock	55283 ± 4592	48400^{A} ± 6597	0.13^{a} ± 0.01	0.14^{AB} ± 0.01	69.8^{b} ± 8.6	67.2^{A} ± 7.0
Red oak	72083 ± 5771	84750^{B} ± 6247	0.19^{b} ± 0.02	0.19^{A} ± 0.01	730^{A} ± 587	159.8^{B} ± 15.3
Sugar Maple	80100 ± 10545	91940^{B} ± 6454	0.13^{a} ± 0.02	0.12^{B} ± 0.01	94.4^{ab} ± 14.1	102.6^{A} ± 14.5
Aboveground woody biomass						
Beech	346617 ± 36561	244700^{A} ± 23899				
Hemlock	243217 ± 30469	204000^{A} ± 21271				
Red oak	327500 ± 32500	446800^{B} ± 46567				
Sugar Maple	385540 ± 73278	452200^{B} ± 33411				

Data are means with one standard error (n = 6). Data for soil, roots, and litter layer represent the means of days 2, 90, 300; foliage collected August 1999 and litterfall collected autumn 1999. Tree cores collected at day 300 (May 2000). Different lower- and upper-case letters above values represent statistically significant differences among tree species within ambient or fertilized plots respectively (P < 0.05).

root biomass containing more than twice the amount of ^{15}N compared to the microbial biomass ($P = 0.043$).

^{15}Nitrogen recovery at day 300 was significantly higher in plant biomass ($P = 0.004$; 2.11 ± 0.50% ^{15}N recovered in fine roots + aboveground woody biomass) compared to microbial biomass (0.87 ± 0.20% ^{15}N recovered) in the beech ($P = 0.02$), red oak ($P = 0.06$), and sugar maple plots (P = 0.002). In hemlock plots, ^{15}N recovery within microbial biomass was not different from recovery in plant biomass ($P = 0.10$).

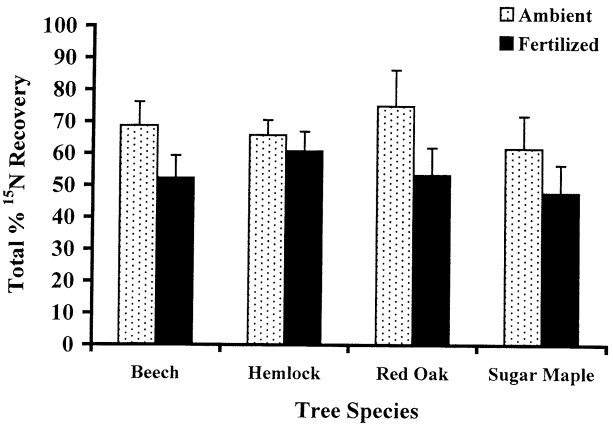


Figure 2. Total forest % ^{15}N retention at day 300. Includes surface litter layer, fine roots and total soil to 12 cm depth and aboveground biomass. Values are means with standard error ($n = 6$). Fertilization significantly reduced total % ^{15}N retention ($P = 0.019$).

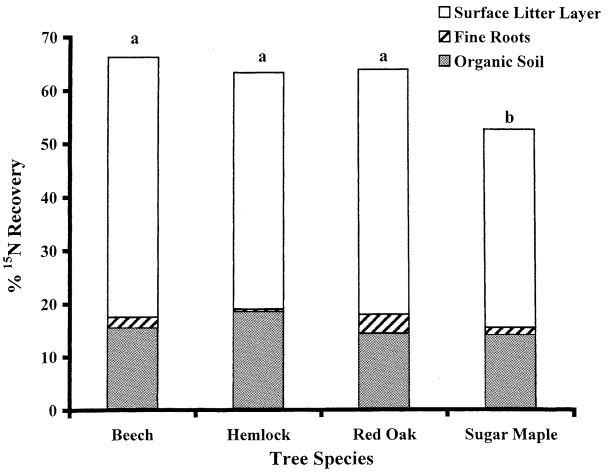


Figure 3. Percent ^{15}N recovery within the forest floor (surface litter layer, fine roots, and organic soil) of ambient plots (no N fertilizer) at day 300 (May 2000). Values are means ($n = 6$). Different letters above values represent statistically significant differences among tree species at $P < 0.05$.

Effect of N Fertilization

Total dissolved inorganic N in soil increased significantly with fertilization among all species plots, demonstrating that the fertilization treatment increased N availability. Fertilization increased soil pools of NH_4^+ and total dissolved inorganic pools of N (NH_4^+ plus NO_3^-) at all days (Table 1), but soil NO_3^- pools increased only on day 2 ($P = 0.0078$). Fertilization significantly decreased root biomass and total root N, but not % N of roots (Table 2; $P = 0.0003$ and $P = 0.0005$).

Examining all tree species together ($n = 48$ plots) shows that the fertilized plots, relative to the unfertilized plots, had significantly lower total forest floor recovery of ^{15}N ($P = 0.026$ at day 300; $P = 0.068$ repeated-measures ANOVA; Table 3) and total ^{15}N recovery (forest floor and soil to 12–cm depth, plus aboveground biomass; $P = 0.0076$; Figure 2). Fertilization had no effect on root ^{15}N recovery ($P > 0.05$; repeated-measures ANOVA), although it significantly increased ^{15}N recovery within aboveground biomass ($P = 0.025$; Table 3). However, the species-averaged difference in recovery in aboveground biomass between ambient and fertilized plots was only 0.091% of total ^{15}N recovery. There was no significant effect of fertilization on ^{15}N recovery within microbial biomass or TDN nor on the amount of ^{15}N in resin bags ($P > 0.05$; Table 4).

The data indicate a trend for fertilization to reduce forest floor ^{15}N recovery (Table 3) in stands of each species. Despite the fact that there was no significant interaction between tree species and fertilization effects ($P > 0.05$), red oak was the only tree species to have a significant drop in total forest floor ^{15}N recovery with fertilization ($P = 0.011$; repeated-measures ANOVA). Although the forest floor of the ambient plots of red oak recovered more ^{15}N than sugar maple ($P = 0.046$; repeated-measures ANOVA), the difference between the two tree species disappeared with fertilization ($P = 0.87$; repeated-measures ANOVA). Fertilization also changed the ^{15}N recovery by red oak stands relative to the other tree species. Forest floor recovery in the ambient plots of red oak was similar to that of beech ($P = 0.85$) and hemlock ($P = 0.59$), but with fertilization, red oak and sugar maple plots had significantly lower forest floor ^{15}N recovery than hemlock and beech ($P = 0.012$; repeated-measures ANOVA; Table 3).

Discussion

Three important general results emerge from this experiment. First, there was no significant difference in total ^{15}N recovery among plots dominated by different species. However, although the differences among species were not statistically significant, they could well be ecologically significant in terms of their effect on the N budgets of the sites. Second, there were significant species differences in the distribution of the ^{15}N recovery among ecosystems pools, particularly in the amount of recovery in the forest floor, which was the dominant sink for ^{15}N in all plots. Third, the N fertilization resulted in a significant reduction in N retention across all species. We focus the discussion below on these three points.

Table 3. Percent ^{15}N Recovery within Microbial Biomass, Organic Soil (Oe and Oa Horizons), Total Soil to 12 cm depth, Fine Roots, Surface Litter Layer, Forest Floor (includes Organic Soil, Fine Roots, and Surface Litter Layer), and Aboveground Woody Biomass at Day 300 (May 2000)

	Beech		Hemlock		Red Oak		Sugar Maple	
	Ambient	Fertilized	Ambient	Fertilized	Ambient	Fertilized	Ambient	Fertilized
Microbial biomass N	0.69 ± 0.53	0.11 ± 0.05	1.16 ± 0.31	1.65 ± 0.65	1.05 ± 0.30	0.62 ± 0.18	0.59 ± 0.11	-1.52 ± 2.12
Organic Soil	15.40 ± 5.79	9.43^{A} ± 1.37	18.49 ± 2.92	21.18^{B} ± 4.24	14.37 ± 3.41	9.85^{A} ± 2.20	14.00 ± 2.39	13.67^{AB} ± 4.58
Organic and mineral soil to 12-cm depth	17.53 ± 6.23	12.34 ± 1.40	20.36 ± 3.13	22.09 ± 4.07	25.31 ± 5.12	15.21 ± 2.85	19.01 ± 3.07	15.18 ± 4.50
Fine roots	$^{**}2.06^{a}$ ± 0.49	$^{**}0.87^{AB}$ ± 0.06	0.48^{b} ± 0.08	0.63^{A} ± 0.28	3.56^{a} ± 1.71	1.64^{B} ± 0.41	$^{*}1.43^{a}$ ± 0.20	$^{*}0.61^{A}$ ± 0.16
Surface litter layer	48.69^{a} ± 4.92	38.73 ± 6.88	44.32^{a} ± 2.72	36.82 ± 3.46	45.90^{a} ± 8.63	36.21 ± 6.85	37.11^{b} ± 6.70	34.45 ± 4.17
Forest floor	66.15^{a} ± 6.94	48.89^{A} ± 6.90	63.28^{a} ± 4.96	58.64^{A} ± 6.40	$^{*}63.82^{a}$ ± 10.28	$^{*}47.69^{B}$ ± 7.97	52.54^{b} ± 8.24	48.73^{B} ± 7.38
Aboveground Woody biomass	0.41 ± 0.136	0.431 ± 0.11	$^{***}0.12^{b}$ ± 0.03	$^{***}0.290$ ± 0.07	0.181^{ab} ± 0.09	0.25 ± 0.11	0.31^{a} ± 0.126	0.39 ± 0.12
Foliage 1999	1.51 ± 1.55	0.04 ± 0.11	-0.03 ± 0.03	0.01 ± 0.08	-0.07 ± 0.04	−0.04 ± 0.03	0.03 ± 0.04	0.10 ± 0.07
Foliage 2000	0.77 ± 0.13	0.81 ± 0.19	0.49 ± 0.15	0.92 ± 0.28	$^{**}0.65$ ± 0.15	$^{**}0.56$ ± 0.13	0.43 ± 0.05	$^{*}0.63$ ± 0.12
Litterfall 1999	0.76^{a} ± 0.43	0.28^{A} ± 0.17	0.045^{b} ± 0.02	0.045^{B} ± 0.02	0.52^{ab} ± 0.34	0.17^{AB} ± 0.04	0.28^{ab} ± 0.16	0.30^{A} ± 0.11

Table also shows % ^{15}N recovery within foliage and litterfall. Values are means with standard error (n = 6). Different lower- and upper-case letters above values represent statistically significant differences among tree species within ambient or fertilized plots, respectively (ANOVA; $P < 0.05$). Statistical analyses for forest floor are based on repeated-measures ANOVA. Within a tree species, significant differences among ambient and fertilized plots are denoted by the following: $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.005$.

Differences in Total ^{15}N Recovery Among Tree Species

The lack of a significant effect of tree species on total ^{15}N recovery in the plots was surprising, given the known differences in N cycling associated with these species (see for example, Finzi and others 1998; Templer and others 2003; Lovett and others forthcoming). This result contradicts our hypothesis that significant differences would occur, although we note that the mean values of ^{15}N recovery are in the order we predicted: red oak greater than sugar maple plots, with beech and hemlock plots intermediate.

There are several possible reasons for this result. One is that the statistical power of this experiment was low, despite having 6 replicate plots of each species, because of the high variability among plots. For our current sample size, our statistical power was only 0.14. To increase our power to 0.8, we would have needed a sample size approximately 5 times the current one. The least significant value for the number of plots needed was 258, while we had only 48 in our study. A second possible reason for the lack of differences among species is that ^{15}N experiments such as this trace the short-term (in this case, 300 days) fate of added N in the system. The dominant fate of that N in the short term is retention in the litter and forest floor, especially when NH_4 is added (as in this case) and is subject to cation exchange in the litter and organic soil. This process of N retention may in fact differ only slightly among species, as long as a forest floor is present. Interesting differences among species may emerge as we continue to follow this ^{15}N as it moves from the forest floor into other ecosystem pools or is lost from the system. Although variability among our plots was too high to detect a statistically verifiable difference in N retention among tree species' plots without a much larger number of samples, the difference could be extremely important in predicting the role of species in regulating N losses from forested watersheds.

After 300 days, there was a 13% difference in total % ^{15}N recovery between plots of red oak and sugar maple, the species with the highest and lowest ^{15}N recovery, respectively (Figure 2). If we assume 70 kg N/ha/y of N mineralization (rate for a northern hardwood forest at Hubbard Brook; Likens and Bormann 1995), the 13% difference in retention of this cycling N could represent about 9 kg N/ha/y, a large number compared to the 1–5 kg N/ha/y that is lost from these watersheds annually in stream water (Lovett and others 2000). Therefore, even relatively small differences among

Table 4. Resin Bags placed in Field Summer and Winter

	Ambient	Fertilized	Ambient	Fertilized
Summer resin bags	μg NO_3–N/g res/day		μg NH_4–N/g res/day	
Beech	18.10 ± 15.35	11.57 ± 2.35	0.76 ± 0.15	9.24 ± 1.24
Hemlock	6.80 ± 4.98	38.82 ± 20.39	1.76 ± 1.62	7.09 ± 1.37
Red Oak	0.51 ± 0.24	8.63 ± 2.69	1.25 ± 0.96	4.83 ± 2.67
Sugar Maple	39.70 ± 12.64	26.88 ± S	2.00 ± 0.06	7.11 ± 3.79
	μg $^{15}NO_3$–N/g res/day		μg $^{15}NH_4$–N/g res/day	
Beech	0.0039 ± 0.0027	0.0010^{A} ± 0.0001	0.0007 ± 0.0007	0.0131^{AD} ± 0.0000
Hemlock	0.0005 ± 0.0005	0.0015^{AC} ± 0.0000	0.0019 ± 0.0019	0.0121^{BC} ± 0.0015
Red Oak	0.0007 ± 0.0007	0.0003^{B} ± 0.0001	0.0172 ± 0.0164	0.0180^{A} ± 0.0000
Sugar Maple	0.0543 ± 0.0320	0.0022^{C} ± 0.0028	0.0042 ± 0.0016	0.0079^{CD} ± 0.0009
Winter resin bags	μg NO_3–N/g res/day		μg NH_4–N/g res/day	
Beech	4.68^{a} ± 1.95	4.38^{A} ± 0.77	*0.44 ± 0.12	*1.63 ± 0.35
Hemlock	2.59^{a} ± 0.79	4.31^{A} ± 1.25	0.40 ± 0.08	1.10 ± 0.49
Red Oak	1.40^{a} ± 0.86	1.98^{A} ± 0.48	*0.46 ± 0.06	*2.00 ± 0.42
Sugar Maple	12.80^{b} ± 5.58	8.18^{B} ± 1.51	0.49 ± 0.07	1.24 ± 0.63
	μg $^{15}NO_3$–N/g res/day		μg $^{15}NH_4$–N/g res/day	
Beech	0.00074^{ac} ± 0.00014	0.00089^{AB} ± 0.00043	*0.00026 ± 0.00005	*0.00054 ± 0.00008
Hemlock	0.00022^{ab} ± 0.00015	0.00071^{AB} ± 0.00047	0.00051 ± 0.00025	0.00302 ± 0.00225
Red Oak	0.00007^{b} ± 0.00005	0.00002^{A} ± 0.00003	0.00032 ± 0.00012	0.00072 ± 0.00014
Sugar Maple	0.00079^{c} ± 0.00028	0.00129^{B} ± 0.00057	0.00024 ± 0.00006	0.00033 ± 0.00015

*Values are means with one standard error (n = 2 for summer and n = 6 for winter). Different lower and upper-case letters above values represent statistically significant differences among tree species within ambient or fertilized plots, respectively (P < 0.05). Within a tree species, significant differences among ambient and fertilized plots are denoted by the following: *P < 0.05, **P < 0.01, and ***P < 0.005.*

species in retention of mineralized N are large enough to account for the variation in stream N export observed in Catskill watersheds (Lovett and others 2000, 2002).

^{15}N Retention in the Forest Floor

Despite the lack of significant difference in total ^{15}N retention in the stands, recovery in the forest floor (including litter layer, organic horizons, and fine roots) did differ significantly among species, with sugar maple having lower retention than the other three species. This lower N retention in sugar maple forest floors was obviously not compensated by higher retention in other pools to produce the lack of difference in total ^{15}N recovery discussed above (Table 3). Rather it seems that the variability among plots obscured differences in total plot retention but did not obscure differences in forest floor retention.

Because the aboveground biomass in sugar maple plots did not retain higher amounts of ^{15}N than other species, we suspect that the significantly lower forest floor ^{15}N recovery in sugar maple plots compared to the other tree species results from greater hydrologic or gaseous N losses from the plots. Under ambient N conditions, sugar maple plots had the highest levels of extractable soil NO_3 (Table 1) and resin bag NO_3 (Table 4), both of which indicate the potential for high N leaching losses. ^{15}Nitrogen losses could also occur as leaching of dissolved organic N (DON), which is not retained by resin bags, or by evolution of N-containing gases. Preliminary data from these plots suggest that sugar maple plots do in fact have higher rates of evolution of NO than do the plots of beech or red oak (R. Venterea personal communication). The differences we observed among species in forest floor N retention are consistent with studies elsewhere in the eastern US which have shown that sugar maple forests are associated with greater nitrification rates and NO_3^- leaching than beech, oak, and conifer forests (Ollinger and others 2002; Venterea and others 2003; Christ and others 2002, Lewis and Likens 2000; Lovett and others 2002). In conjunction with greater nitrification rates, the lack of significant NO_3^- uptake by sugar maple trees (Templer 2001) could also contribute to NO_3^- losses. This leaching might be enhanced by the ability of sugar maple to mobilize nutrients more efficiently than other tree species via hydraulic lift (for example, water loss from roots; Dawson 1993, 1996, 1998).

Across all tree species, the ^{15}N recovered within the forest floor 2 days after the initial tracer addition was significantly greater than after 90 and 300 days. This suggests that after 2 days, some ^{15}N moved out of the forest floor into aboveground tree biomass, to deeper soil pools that we did not measure, or out of the forest through leaching or gaseous losses. The majority of added ^{15}N was recovered in the surface litter layer across all sampling dates in plots of all tree species, a finding that is consistent with studies of other northeastern forests (Nadelhoffer and others 1999). After the litter layer, organic soil was the largest ^{15}N sink, whereas microbial biomass accounted for less than 3% of the recovery of ^{15}N. Although most of the ^{15}N was found in nonliving SOM, the mechanism of incorporation of N in SOM is not well understood. Microbial processes may well be involved because several studies suggest that some of the N immobilized into microbial biomass is fairly rapidly transferred to a pool within the SOM (Emmett and Quarmby 1991; Seely and Lajtha 1997; Zogg and others 2000). However, it appears there could also be substantial direct incorporation of inorganic N into SOM via abiotic reactions (Johnson 1992; Magill and others 1997; Aber and others 1998; Berntson and Aber 2000; Dail and others 2000; Johnson and others 2000; Fitzhugh and others 2003, forthcoming).

Microbial ^{15}N uptake was significantly higher than root ^{15}N uptake on day 2, suggesting that soil microbes are strong competitors for N compared to roots on this short time scale. This is consistent with results of similar studies in Chile (Perakis and Hedin 2001) and Michigan (Zogg and others 2000). By day 300 in our study, ^{15}N retention in microbial biomass was less than ^{15}N retention in roots for all species except hemlock, which presumably has lower N uptake rates than the deciduous species (Cole and Rapp 1981). Likewise, at day 300, total plant biomass (aboveground and fine roots) ^{15}N recovery was higher than microbial ^{15}N recovery for all species except hemlock, but plant biomass was still a small sink for ^{15}N relative to the forest floor. ^{15}Nitrogen addition studies elsewhere have also shown this pattern (Nadelhoffer and others 1999). Our measurements probably resulted in an underestimate of plant biomass ^{15}N recovery for several reasons: (1) Some of the ^{15}N could have been removed via uptake to biomass outside the plot through roots extending into the plot, (2) we did not measure ^{15}N in coarse roots, and (3) our calculations assume ^{15}N retention per unit biomass production is the same in stems as in branches.

Effects of N Fertilization

The decrease in total plot ^{15}N retention with fertilization is important and indicates that further increases in N availability, for example, from higher rates of N deposition, could cause more N to be lost from forested watersheds in the Catskill Mountains. The decrease is primarily due to lower retention in the forest floor, and the ^{15}N sink in tree biomass is not large enough to compensate. Averaged across tree species, fertilization reduced forest floor ^{15}N recovery by approximately 10% at all sampling dates. The increase in aboveground retention between the ambient and fertilized plots was a very small proportion of the total recovery (0.091%). Although this does not balance the decline in forest floor retention, it could represent a significant amount of N if the increased uptake is sustained for a long period of time. Our estimates of ^{15}N recovery within aboveground woody biomass in our ambient plots are similar to those found in the ambient plots of a study at Harvard Forest in Massachusetts. However, our estimates of ^{15}N recovery are lower than the 3% recovery found in their fertilized plots (Nadelhoffer and others 1999). Nitrogen fertilization rates and the form of ^{15}N addition were similar for the comparisons made between our two studies (50 kg NH_4NO_3–N/ha/y and $^{15}NH_4Cl$, respectively). However, Nadelhoffer and others (1999) examined ^{15}N recovery two years after addition, whereas this study examined ^{15}N recovery only within the first 300 days of tracer addition. Perhaps with time, more ^{15}N will move into the aboveground tree biomass as additional N becomes available from the decomposition of the litter layer and other organic material.

Fertilization reduced total forest ^{15}N recovery in plots of all tree species, with the most pronounced effect (22% decline) in red oak plots. Although ambient plots of red oak had significantly greater forest floor ^{15}N recovery than sugar maple, there was no difference between the two species in the fertilized plots. This convergence is attributable to the decreased percent recovery of ^{15}N found in the forest floor of red oak plots. The fact that red oak had the largest drop in forest floor ^{15}N recovery as a result of fertilization, but still had the lowest indicators of N leaching (extractable NO_3 and NO_3 on resin bags), suggests that added N could cause ^{15}N to move to a sink we did not measure. One possible sink is leaching DON, which was not sampled by our resin bags. Another possible pathway for N loss from red oak plots is through evolution of N-containing gases during denitrification and nitrification.

However, current work in these plots (R. Venterea personal communication) suggests that gaseous losses are not large enough to explain differences in forest floor ^{15}N recovery between the ambient and fertilized plots of red oak. Whatever the mechanism is for decreased ^{15}N recovery with fertilization in red oak plots, these results demonstrate that N retention could decline in red oak forests if N deposition or availability increases in the future.

The decrease in forest floor ^{15}N recovery with fertilization is in contrast to the results of Nadelhoffer and others (1999). In their study, the forest floor recovered 1.7 times more ^{15}N in the fertilized plots of a hardwood forest and 1.5 times more in a pine plantation than the ambient plots. Even though the forest floor became a stronger sink for ^{15}N with fertilization in their study, the authors explain that the larger tree uptake with fertilization means that soils become proportionately less important as a sink as N supply increased. Similarly, results from our study suggest that although the forest floor is currently the dominant sink for added N, increases in N availability could decrease its role in forest retention over relatively short time scales.

Species Effect or Site Effect?

In the absence of a mature-tree ''common garden'' experiment, it is necessary to infer species effects from comparison among plots growing naturally. In this experiment, we could not find acceptable single-species plots of all species in the same set of watersheds. This situation creates the potential for confounding species effects with watershed or site effects. Although species and site effects are difficult to distinguish conclusively in this type of experiment, we believe that the differences among species that we observed are in fact species effects for the following reasons: First, it is well known that different tree species produce litter of very different qualities, and these litter quality differences can influence N cycling (Melillo and others 1982; Aber and Melillo 2001). Second, each species was represented by 6 pairs of plots in three separate watersheds distributed across the Catskill Mountains, so any possible confounding site effect would have to be widespread and consistently associated with the species. Soil texture is one possible confounding site effect, but soil texture does not vary significantly among species in these plots (Lovett and others forthcoming). Third, land-use history is another possible confounding effect, in particular because Catskill oak forests tend to be associated with areas with a history of repeated harvesting or burning (Kudish 2000). Analysis of 145 mixed species plots showed that the C:N ratio, which is a good indicator of potential for NO_3^- leaching, is correlated with species composition but not with forest history (Lovett and others 2002). Although not conclusive, these factors lead us to believe that the patterns in ^{15}N retention observed here are most likely the results of a species effect rather than a site effect.

Conclusions and Implications

This study showed that forest floor retention, which was the largest sink for added N on the time scale of this study (300 days), varied among tree species, although total plot N retention did not vary among tree species in the Catskill Mountain forest plots. With current levels of N deposition and availability, N is more likely to be lost from the forest floor of sugar maple plots than any of the other tree species we studied. However, the fertilizer treatment of this study showed that if N availability increases, N retention in red oak plots is likely to decrease, possibly to levels of N retention as low as sugar maple plots. Species composition in the northeastern United States has changed dramatically over the past 100 years and further changes in tree species composition could have the potential to alter the N cycling of this ecosystem. For instance, beech bark disease is now leading to beech tree mortality throughout the Catskill Mountains (Houston and others 1979; Griffin and others forthcoming). Furthermore, the hemlock woolly adelgid (*Adelges tsugae* Annand), an introduced aphidlike insect from Asia, threatens hemlock stands throughout the northeastern United States. This insect is responsible for up to 95% of tree mortality in some forest stands of southern New England (Orwig and Foster 1998). The resulting change in tree species composition caused by tree mortality could lead to an increase in N loss from forests because the forest floor of beech and hemlock currently take up and retain a larger amount of N than the sugar maple stands that could replace them. This study demonstrates the need to consider tree species composition when thinking about the ability of forests to retain N.

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