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SINKS FOR ^{15}N-ENRICHED ADDITIONS TO AN OAK FOREST AND A RED PINE PLANTATION

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Abstract. We added ^{15}N tracers to reference plots (receiving ambient N inputs) and to chronically fertilized plots (50 kg NH_4NO_3-N·ha^{-1}·yr^{-1} for 3 yr prior to and during tracer additions) in an oak-dominated deciduous forest and a red pine plantation in order to quantify sinks for N inputs to these forests. Plots (30 × 30 m) were located at the Harvard Forest Long-Term Ecological Research (LTER) site in central Massachusetts. Two forms of ^{15}N tracer were applied, with $^{15}NH_4$ and $^{15}NO_3$ added to separate halves of reference and chronically fertilized plots in each forest. Tracers were applied monthly during two growing seasons in order to simulate movements of background (8 kg·ha^{-1}·yr^{-1}) and chronically elevated (58 kg·ha^{-1}·yr^{-1}) N deposition. Forest floors and soils were the dominant sinks for N deposition in these forests, but the relative importance of trees as sinks for N inputs increased with N loading rate. Accumulations of ^{15}N in tree tissues after 2 yr of tracer additions showed that tree leaves, fine roots, bark, and recently formed wood assimilated <5% of the ^{15}N added to reference plots and 20–24% of the ^{15}N added to fertilized plots. The form of N input influenced its movement into ecosystem pools. Percent recoveries of ^{15}N in trees were typically greater after $^{15}NO_3$ additions than after $^{15}NH_4$ additions. Woody tissues (wood ≤5 yr old plus bark) accumulated small fractions of N inputs after 2 yr of tracer additions, with ^{15}N recoveries of <1% under ambient N deposition and <5% under chronic N fertilization. Regional and global assessments of the effects of N deposition on forest carbon balances should take into account observations suggesting that, although the proportion of N deposition assimilated by trees could increase with N input rate, most N deposition retained by temperate forests is likely to accumulate in soil pools with low C:N rather than in woody biomass with high C:N ratios.

Key words: ammonium and nitrate additions; chronic N deposition and saturation; C–N interactions, Harvard Forest, Massachusetts, USA; ^{15}N tracers; oak; Pinus resinosa; Quercus rubra; Quercus velutina; *red pine, temperate forests.*

INTRODUCTION

Chronically elevated N inputs (as ammonium and nitrate) to forests from the atmosphere can lead to changes in tree growth, mortality, and species composition, and to possible declines in soil fertility and drainage water quality (Nihlgård 1985, Van Breemen and Van Dijk 1988, Aber et al. 1989, Schulze 1989). Various studies have reported forest responses to N deposition ranging from changes in plant tissue chemistry, increased tree growth, and small N exports to tree tissue nutrient imbalances, growth declines, and large nitrate exports to drainage water (e.g., Aber et al. 1993, Kahl et al. 1993, Nilsson and Wiklund 1994, Boxman et al. 1995, Bredemeier et al. 1995, Emmett et al. 1995*a*, *b*, Gundersen and Rasmussen 1995, Moldan et al. 1995, Wright and Tietema 1995, Wright et al. 1995). Much of the variation in forest responses to N deposition is probably caused by variations in N deposition rates, land-use history, and soil properties (Aber et al. 1995, Dise and Wright 1995).

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Increased N deposition on forests also has implications for the global C cycle. For example, some studies have suggested that enhanced tree growth resulting from fertilization effects of N deposition over large regions could increase rates of atmospheric CO_2 sequestration by forests (Schindler and Bayley 1993, Townsend et al. 1996). In order to assess the implications of N deposition on forests for the global C cycle, however, it is necessary to determine how retention of N inputs is distributed among forest ecosystem components. For example, if N inputs are partitioned to components with high C:N ratios, such as wood, then the sink strength of N-enriched forests for CO_2 will be much greater than if N inputs are partitioned mainly to soils or other components with low C:N ratios (Rastetter et al. 1992, Townsend et al. 1996). Furthermore, because N deposition in north temperate regions ranges from <2 kg·ha^{-1}·yr^{-1} to >50 kg·ha^{-1}·yr^{-1} (Galloway et al. 1995), it is important to determine whether assimilation of N inputs into forest ecosystem pools varies with N input rates. Finally, because the ionic composition of N deposition varies among regions, it is important to determine whether

the fates of ammonium- and nitrate-N inputs to forests differ. Therefore, we used ^{15}N tracer additions to experimental plots in two temperate forests to address the following questions:

1) What are the dominant sinks for N deposition in forests?

2) Does the rate of N deposition affect the fate of N inputs to forests?

3) Does the ionic form of N deposition affect the fate of N inputs to forests?

We applied $^{15}NH_4$ or $^{15}NO_3$ separately for two consecutive growing seasons to forest floors in reference (nonfertilized) and chronically fertilized plots in an oak-dominated deciduous forest and in a red pine plantation at the Harvard Forest Long-Term Ecological Research (LTER) site in central Massachusetts (USA). These plots have been used to study the effects of chronic N additions on forest N cycling, plant tissue chemistry, primary production, and soil solution chemistry (Aber et al. 1993, Magill et al. 1997), and on trace gas fluxes from forest soils (Bowden et al. 1990, 1991). We report here on the fates of ^{15}N tracers which were applied in fertilization years 4 and 5 in order to estimate N fluxes into plant tissues and soils under ambient and chronically elevated (fertilizer) N deposition. A companion paper (Currie et al. 1999) compares the movements of ^{15}N tracers in these plots to model-based predictions of tracer movements in order to characterize controls on N dynamics and C–N interactions in these forests.

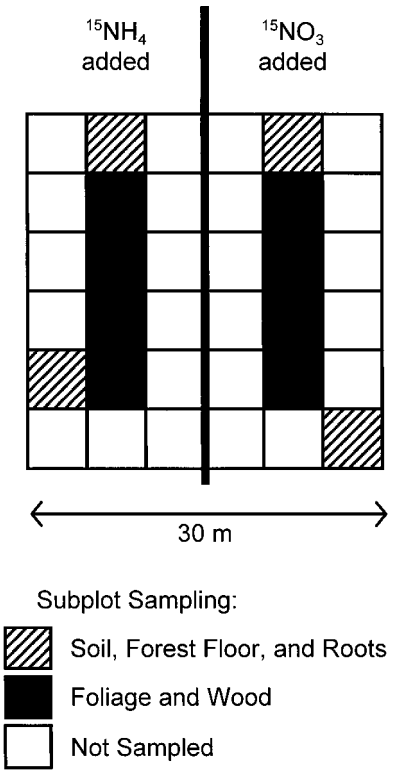

FIG. 1. Schematic map of ^{15}N tracer additions and sampling on one of the N addition plots at Harvard Forest (hardwood plot with ambient N inputs). $^{15}NH_4$ and $^{15}NO_3$ ions were applied to separate halves of 30 × 30 m plots in chronically fertilized and ambient (nonfertilized) plots in an oak-dominated forest and a red pine plantation. No samples were taken from subplots abutting other subplots labeled with a different N ion. Foliage, wood, and bark were sampled from trees in subplots located 5 m from the plot edges. Forest floor, mineral soil, and fine root samples were taken from two subplots in each plot half. Forest floor and soil samples were always taken at least 1 m from outer plot boundaries.

METHODS

Study site

The two forests are located in the Prospect Hill tract of Harvard Forest (42°30′ N, 72°10′ W) in Petersham, Massachusetts (USA). One is a hardwood forest that developed after clearcutting in the mid 1940s, and the other is a red pine (*Pinus resinosa* Ait.) plantation established in 1926. The hardwood forest is dominated by oaks (*Quercus velutina* Lam.; *Q. rubra* L.) with admixtures of red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), paper birch (*Betula paperifera* L.), and beech (*Fagus grandifolia* Ehrh.). Soils are Inceptisols (Typic Dystrochrepts) on stony till with sandy-loam textures. Detailed descriptions of the site, plots, and treatments are provided in Bowden et al. (1990), Aber et al. (1993), and Magill et al. (1997).

Chronic N additions

Four treated plots were established in each forest in 1988: control (hereafter referred to as ''ambient'' because these plots receive only atmospheric N inputs), low N, low N plus sulfur (N + S) and high N. We used only the ambient and low N plots for our ^{15}N tracer study. Plots are 30 × 30 m (0.09 ha) each and are divided into 36 5 × 5 m subplots for sampling (Fig. 1). Low N plots (hereafter referred to as ''fertilized'') have received 50 kg $N \cdot ha^{-1} \cdot yr^{-1}$ as NH_4NO_3 (applied in solution with backpack sprayers, equivalent to 0.012 cm water/yr) in six equal monthly applications from April through September since 1988. A regional model predicted 8 kg $N \cdot ha^{-1} \cdot yr^{-1}$ deposition at the site with equal inputs of ammonium- and nitrate-N (Ollinger et al. 1993). N inputs in bulk throughfall to forest floors at the site for 1 yr were 3.5 and 5.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ for NH_4-N and NO_3-N, respectively (Currie et al. 1996).

^{15}N tracer additions

The isotopic composition of the nitrogen normally applied to the fertilized plots was similar to that of the atmospheric N_2 standard (0.3663 atom% ^{15}N, or, $\delta^{15}N = 0‰$); the mean of four nonlabeled ammonium nitrate fertilizer batches was $\delta^{15}N = 0.0‰$ (range −1.3 to +0.8‰). (We follow the convention of expressing ^{15}N contents of natural materials using $\delta^{15}N$ notation where units are expressed as parts per thousand deviations from the atmospheric standard of 0.3663 atom% ^{15}N

and are calculated; $\delta^{15}N = [(\text{atom\% } ^{15}N \text{ sample}/0.3663) - 1] \times 1000$). We applied ^{15}N tracers to the plots during the 1991 and 1992 growing seasons (fertilization years 4 and 5). The NH_4NO_3 fertilizer added to half of each low N plot in these years was labeled with enough $^{15}NH_4Cl$ to increase the ammonium $\delta^{15}N$ value from 0 to 965‰ (or from 0.3663 to 0.7173 atom% ^{15}N). Fertilizer applied to the remaining half of each low N plot was labeled with enough $K^{15}NO_3$ to increase the nitrate $\delta^{15}N$ to 761‰ (from 0.3663 to 0.6433 atom% ^{15}N). Although our target value was 1000‰ for each form, incomplete dissolution of $K^{15}NO_3$ in our stock solution resulted in lower $\delta^{15}N$ values than expected in the nitrate-labeled fertilizer. Ambient plots received the same amounts of ^{15}N excess as were applied to low N plots: 17.9 mg $^{15}N \cdot m^{-2} \cdot yr^{-1}$ applied as dissolved $^{15}NH_4Cl$ (99.1 atom% ^{15}N) and 16.2 mg $^{15}N \cdot m^{-2} \cdot yr^{-1}$ applied as dissolved $K^{15}NO_3$ (98.6 atom% ^{15}N) to separate halves (15×30 m) of each nonfertilized 30×30 m plot. Tracers were applied to the ambient plots six times during the 1991 and 1992 growing seasons on the same days as ^{15}N-labeled fertilizers were applied to the low N plots using backpack sprayers and the same amounts of water as on fertilized plots.

Sampling

Plant tissues.—Tree foliage, bark, and bolewood were sampled exclusively from the three central subplots in each 15×30 m half plot in order to minimize edge effects (Fig. 1). Foliage was sampled in mid-August 1990 (before applying ^{15}N to plots) and annually in mid-August from 1991 through 1995. Bolewood and bark samples were collected ~1.3 m above the soil surface using a 1.9 cm inside diameter hole saw in November 1990 (before labeling) and again in November 1992 after ^{15}N additions were completed. For samples collected in 1990, wood formed from 1988 through 1990 was analyzed for ^{15}N and total N. For samples collected in 1992, we analyzed wood formed from 1988 through 1990 and from 1991 through 1992 separately. We also analyzed bark (all bark, not just recently formed) associated with each increment core collected in 1992. Live fine roots (intact and fibrous) were separated from forest floor (Oa horizon) and mineral soil (0–10 cm layer) samples collected from labeled plots in October or November from 1991 through 1993. The ^{15}N content of nonlabeled roots in both soil strata was estimated using fine roots collected in 1993 along 30-m transects located at least 15 m from the labeled plots in each forest.

Soils.—Forest floor (Oa horizon) and mineral soil (0–10 cm) samples were collected from two 5×5 m subplots in each 15×30 m half plot (Fig. 1) before labeling and again each fall from 1991 through 1993. Forest floors were sampled using a 10×10 cm template, and mineral soils were sampled to 10 cm using a 5.5 cm inside diameter corer. Forest floor Oe horizons (2–5 yr old litter) and deeper mineral soils (10–20 cm layer) were sampled from nonlabeled reference areas and from labeled plots in 1992 after all labels were applied. The 10–20 cm soils were sampled with a 1.5 cm inside diameter corer. Forest floor masses (Oe and Oa horizons) were calculated as dry masses (50°C) per unit area corrected for coarse fragments (>2 mm). Bulk densities (dry masses corrected for fragments >2 mm) were determined for each 0–10 cm soil sample. Because 10–20 cm soils were collected with a narrow corer, we estimated bulk densities in this lower mineral soil layer as 0.8 g/cm^3 in the oak and 0.9 g/cm^3 in the pine forest based on separate bulk density sampling.

Elemental and ^{15}N analysis

Samples subjected to elemental and ^{15}N analysis were ground to a fine powder and dried (50°C) prior to analysis. Total C and N contents of plant tissues were measured using either Perkin-Elmer 240C or 2400 elemental analyzers with acetanilide as a reference standard. Forest floor and soil N concentrations were determined using mass spectrometry on the same samples as were analyzed for ^{15}N. Plant tissue and soil sample ^{15}N contents were determined by combusting finely powdered subsamples to N_2, cryogenic purification, and analysis using either a trapping box or a continuous flow system and a Finnegan MAT Delta S isotope ratio mass spectrometer (Fry et al. 1992). Analytical precision of this method is typically better than 0.2‰ $\delta^{15}N$.

Ecosystem C and N pools

We estimated dry masses and element contents of ecosystem pools on each plot using values from Magill et al. (1997) and our own measurements. These estimates were derived using the largest numbers of samples available in order to increase the reliability of pool size estimates.

Species foliar masses were estimated using 1991 and 1992 litterfall measurements, summarized in Magill et al. (1997), multiplied by 1.1 to correct for leaching, retranslocation, and herbivory. For red pines, which retain two annual cohorts of foliage, we assumed current-year and year-old foliage to have equal masses within each 30×30 m plot. Foliar N contents by species and plot were estimated as the product of foliar mass and mean percent N as determined using 1992 samples. Foliar C:N ratios were calculated assuming leaves to be 48% C.

Wood biomass accumulation during the years of tracer additions (1991 and 1992) and during the 3 yr prior to tracer additions (1988 through 1990) was estimated as two and three times, respectively, the annual increments reported by Magill et al. (1997). Wood N content in each of these age classes on a plot was estimated as the product of wood biomass and mean percent N as determined on increment cores taken in November 1992. Bark biomass was problematic, as we were unable to locate allometric regressions predicting bark

biomass from tree diameter for the species in these forests. Therefore, we assumed that bark biomass was equivalent to 2 yr annual wood increment based on comparisons of bark thickness to the width of annual growth rings in increment cores taken from trees on the plots. Bark N content on each plot was estimated as the product of the mean N concentration of bark separated from the 1992 increment cores and our bark mass estimates. Although our estimates of bark N content are admittedly crude, the effects of uncertainties in bark N estimates are relatively minor with regard to mass balancing the fate of total N inputs. Also, errors in pool estimates for bark do not affect the comparison of fates of ammonium- and nitrate-N inputs. Wood and bark C:N ratios were calculated assuming biomass to be 48% carbon.

Fine root N contents and concentrations in the forest floor and 0–10 cm mineral soil are the 1991 estimates for individual plots reported by Magill et al. (1997). Fine root biomass and C:N ratios for each horizon within plots were calculated from percent N values assuming roots to be 48% carbon.

Forest floor (Oe and Oa) masses and N concentrations were estimated using mean values of 1992 samples taken from each plot. The N content of each organic horizon within a plot was estimated as the product of mean N concentration and mass. N contents of 0–10 cm and 10–20 cm soils in each plot were estimated as the product of mean percent N and soil mass. C:N ratios in the Oa and 0–10 cm soil were measured directly by elemental analysis (see *Elemental and ^{15}N analysis*).

^{15}N mass balances

We estimated ^{15}N tracer movements into soil and tree biomass components using N pool size estimates, changes in ^{15}N content of ecosystem pools following tracer additions, and ^{15}N mass balances (Nadelhoffer and Fry 1994, Buchmann et al. 1995, 1996). Recoveries of tracer masses in labeled ecosystem N pools were calculated using the following equation:

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

where $^{15}N_{rec}$ = mass of ^{15}N tracer recovered in the labeled N pool (kg N/ha); m_{pool} = N mass of the labeled N pool (kg N/ha); atom% $^{15}N_{pool}$ = atom percent ^{15}N in the labeled N pool; atom% $^{15}N_{ref}$ = atom percent ^{15}N in the reference (pre- or nonlabeled) N pool; and atom% $^{15}N_{tracer}$ = atom percent ^{15}N of the applied tracer or labeled fertilizer. This equation yields similar results to calculations of ^{15}N excess resulting from tracer applications (e.g., Buchmann et al. 1996). Tracers recovered in pools were expressed as proportions of total ^{15}N tracer applied to a plot through the time of sample collection.

TABLE 1. Natural ^{15}N abundances in plants and soils in a 50-yr-old oak forest and a 70-yr-old red pine plantation at the Harvard Forest Chronic N Study Plots.

	Oak forest			Red pine plantation		
Ecosystem pool	$\delta^{15}N$† (‰)	SEM	*n*	$\delta^{15}N$† (‰)	SEM	*n*
Foliage						
Oak	−2.60	0.18	4	⋯	⋯	⋯
Birch	−2.70	0.27	4	⋯	⋯	⋯
Red maple	−3.93	0.49	4	⋯	⋯	⋯
Beech	−2.33	0.04	4	⋯	⋯	⋯
All deciduous	−2.89	0.21	16	⋯	⋯	⋯
Red pine	⋯	⋯	⋯	−1.83	0.14	6
Bole wood	−3.60	0.20	16	−2.85	0.16	8
Fine roots in:						
Forest floor	−1.63	0.48	6	−1.19	0.35	6
0–10 cm soil	+0.40	0.28	6	+0.53	0.34	6
Soil						
Oi (fresh litter)‡	−2.70			−2.30		
Oe	−0.88	0.48	8	−1.49	0.07	8
Oa	+2.22	0.18	10	+1.34	0.22	9
0–10 cm mineral	+4.64	0.24	10	+4.35	0.17	10
10–20 cm mineral	+4.83	0.83	8	+5.86	0.49	8

Note: Values are means of samples collected from treated and fertilized plots within forest types before ^{15}N tracers were added.

† $\delta^{15}N$ values are expressed as positive (+) or negative (−) deviations from the atmospheric standard of 0.3663 atom% ^{15}N; see *Sampling: Soils.*

‡ Values are from P. A. Micks, M. R. Downs, and K. J. Nadelhoffer, *unpublished manuscript.*

Statistical analyses

Because N pool sizes were typically estimated using larger sample numbers than were used to estimate ^{15}N contents of ecosystem pools, we assumed that N pool sizes on the plots were well characterized. We also assumed that the ^{15}N contents of ecosystem pools in nonlabeled forests were well characterized based on the small variances in N isotope distributions observed before tracers were added (Table 1). Therefore, our statistical analyses assume fixed values for total N mass and prelabeled ^{15}N content (m_{pool} and atom% $^{15}N_{ref}$ in Eq. 1) of each pool within a plot and that variances in estimates of tracer recovery are due to variances in our estimates of ^{15}N contents of postlabeled pools (atom% $^{15}N_{pool}$ in Eq. 1).

Neither the fertilization treatments nor plot labeling are replicated within either forest at our site. Our measurements of ^{15}N recovery are replicated within experimental plots and statistical extrapolations are made at the plot scale. We used two-way analysis of variance (SYSTAT [version 5.02] 1992) on log-transformed data to test for effects of N loading rate (ambient deposition vs. chronic fertilization) and form of N tracer ($^{15}NH_4$ vs. $^{15}NO_3$) on percent ^{15}N tracer recoveries in pools within forest types. Post hoc means tests (Tukey Honestly Significant Differences, $P < 0.05$) were used to compare recoveries of ^{15}N tracers applied as either $^{15}NH_4$ or $^{15}NO_3$ under ambient or chronically elevated

TABLE 2. Masses and N contents of major ecosystem pools in ^{15}N-labeled plots in a 50-yr-old oak forest at the Harvard Forest.

Ecosystem pool	Ambient plot				Fertilized plot			
	Mass (kg/ha)	N (%)	C:N	N (kg/ha)	Mass (kg/ha)	N (%)	C:N	N (kg/ha)
Foliage								
Oak	2 352	2.14	22	50.3	2 014	2.11	23	42.5
Birch	310	2.34	21	7.3	372	2.53	19	9.4
Maple	186	1.46	33	2.7	272	1.75	27	4.8
Other	154			nd	367			nd
Total foliage	3 002			60.3	3 025			56.7
Bark + new wood								
Wood (1991–1992)	9 000	0.16	300	14.4	9 600	0.21	229	20.2
Wood (1988–1990)	13 500	0.13	369	17.6	14 400	0.12	400	17.3
Bark	9 000	0.40	120	36.0	9 600	0.41	117	39.4
Total bark + 1988–1992 wood	31 500			68.0	33 600			76.8
Fine roots								
Fine roots (forest floor)	3 323	1.3	37	43.2	6 043	1.4	34	84.6
Fine roots (0–10 cm)	2 536	1.1	44	27.9	3 336	1.1	44	36.7
Total fine roots	5 859			71.1	9 379			121.3
Tree biomass (1988–1992 wood only)	40 361			199.4	46 004			254.8
Forest floor								
Oe	7 039	1.34	nd	94	11 962	1.69	nd	202
Oa	86 170	1.13	26	974	62 488	1.70	23	1062
Total forest floor	93 209			1068	74 450			1264
Mineral soil								
0–10 cm	670 000	0.26	23	1742	670 000	0.29	19	1943
10–20 cm	800 000	0.18	nd	1440	800 000	0.16	nd	1240
Mineral soil (0–20 cm)				3182				3183
Total				4449				4702

Note: Ambient plots received only atmospheric N inputs (about 8 kg $N \cdot ha^{-1} \cdot yr^{-1}$), and fertilized plots received N additions of 50 kg $\cdot ha^{-1} \cdot yr^{-1}$ (as NH_4NO_3) from 1988 through the 1992 sampling (and thereafter through at least 1997); nd = no data.

N loading. Although the fertilizer treatments are not replicated within either forest, the small variances in ^{15}N contents in ecosystem pools both before and after ^{15}N additions indicate that significant differences in ^{15}N recoveries are due to treatments rather than to natural variations in ^{15}N abundances. Therefore, we use our estimates of tracer movements within plots to make inferences about the fates of atmospheric ammonium and nitrate inputs to these forests.

RESULTS

Natural ^{15}N abundances

Prior to ^{15}N additions, $\delta^{15}N$ values of forest N pools ranged from −3.6‰ in deciduous tree bolewood to +5.9‰ in 10–20 cm soil in the red pine forest (Table 1). Natural ^{15}N abundances in tree tissues increased as follows: wood < foliage < forest floor roots < mineral soil roots in both forests. Leaf litter $\delta^{15}N$ values were similar to values of green foliage within species. Abundances of ^{15}N in forest floor and mineral soil horizons increased with depth, with $\delta^{15}N$ values typically increasing by 1–3‰ between adjacent horizons. Ranges of $\delta^{15}N$ values for individual ecosystem pools were narrow, with standard errors of means ≤0.8‰. These narrow ranges show that ecosystem N pools were well defined with respect to their isotopic compositions, thereby supporting the assumption implicit in our budget analyses (this paper) and simulations (Currie et al. 1999) that ^{15}N was well mixed within sampled pools.

Ecosystem N pools

Ecosystem N contents (excluding soils >20 cm deep and wood >5 yr old) were 4.4 Mg/ha in the ambient and 4.7 Mg/ha in the fertilized oak forest plots (Table 2) and were 5.6 Mg/ha in the ambient and 5.8 Mg/ha in the fertilized red pine plots (Table 3). Of pools measured, mineral soils contained the most N, with 0–20 cm soils accounting for ~70% of total N in both forests. Tree biomass (foliage, fine roots, bark, and wood produced between 1988 and 1992) accounted for 5–6% of the N mass in measured oak forest pools and 3–4% of N in red pine pools. Newly formed wood (1988–1992) plus bark accounted for only 1.5% and 0.5% of the sums of measured N pools, respectively, in the oak and in red pine forests.

Tracer fluxes into ecosystem components

We used ^{15}N contents of plant tissue, forest floor, and soil samples collected after two seasons of tracer applications, together with plot-specific information on N pool sizes and prelabeling ^{15}N contents, to construct budgets quantifying the movements of ^{15}N tracers (ap-

TABLE 3. Masses and N contents of major ecosystem components in ambient and fertilized plots in a 70-yr-old red pine plantation at the Harvard Forest. Treatments were the same as for plots in a nearby oak forest (See Table 2.).

	Ambient plot				Fertilized plot			
Ecosystem pool	Mass (kg/ha)	N (%)	C:N	N (kg/ha)	Mass (kg/ha)	N (%)	C:N	N (kg/ha)
Foliage								
Red pine, current	3 115	1.13	42	35.2	4 513	1.32	36	59.6
Red pine, second year	3 115	1.15	42	35.8	4 513	1.42	34	64.1
Other	124			n.a.	64			n.a.
Total foliage	6 354			71.0	9 090			123.7
Bark + new wood								
Wood (1991–1992)	6 600	0.08	623	5.3	6 600	0.11	436	7.3
Wood (1988–1990)	9 900	0.04	1200	4.0	9 900	0.05	960	5.0
Bark	6 600	0.28	171	18.5	6 600	0.36	133	23.8
Total bark + 1988–1992 wood	23 100			27.8	23 100			36.0
Fine roots								
Fine roots (forest floor)	1 400	1.7	28	23.8	2 276	2.1	23	47.8
Fine roots (0–10 cm)	1 650	1.2	40	19.8	2 559	1.7	28	43.5
Total fine roots	3 050			43.6	4 835			91.3
Tree biomass (1988–1992 wood only)	32 504			142.4	37 025			250.9
Forest floor								
Oe	11 958	1.93	nd	231	14 642	1.58	nd	231
Oa	79 140	1.46	22	1155	79 140	1.73	26	1369
Total forest floor	91 098			1386	93 782			1600
Mineral soil								
0–10 cm	770 000	0.29	21	2233	770 000	0.29	26	2233
10–20 cm	900 000	0.20	nd	1800	900 000	0.19	nd	1710
Mineral soil (0–20 cm)				4033				3943
Total				5562				5794

plied as either $^{15}NH_4$ or $^{15}NO_3$) into ecosystem components in both forests. Also, in order to provide insights into movements of N inputs to these forests over the longer term, we followed movements of the ^{15}N tracers into foliage and fine roots during the 2 yr of tracer additions and during 3 more yr in foliage and 1 more yr in fine roots.

Foliage.—Analysis of variance indicated that tracer movements into foliage were influenced by N loading rate (ambient deposition vs. chronic fertilization) and form ($^{15}NH_4$ vs. $^{15}NO_3$) of tracer addition in both the oak (Table 4) and pine (Table 5) forests. Percent recoveries of tracers in foliage of dominant species were greater under chronic fertilization than under ambient N deposition and when ^{15}N was added as nitrate. By August 1992, mean percentage recoveries of ^{15}N tracers (averages of $^{15}NH_4$ and $^{15}NO_3$ additions) in deciduous forest foliage were 0.5% on the ambient and 5.9% on the fertilized plot (Table 4). Recoveries were highest in oak foliage, reflecting the dominance of oaks in the mixed hardwood forest (Table 2). In the pine forest, tracer recoveries in foliage averaged 0.5 and 9.6% on ambient and fertilized plots, respectively. Current-year needles were stronger sinks for tracers than were year-old needles (Table 5). It should be noted that because foliage was sampled in mid-August (before senescence), these samples were collected after 4 of the 6 tracer applications in 1991 and after 10 of the 12 tracer applications made through 1992.

Sequential sampling showed that excess ^{15}N in foliage due to tracer additions was easily detected during the first season of labeling on the chronically fertilized plots and during the second season on the ambient plots (Fig. 2). Tracer recoveries in foliage on the ambient plots increased for 3 yr after tracer additions were stopped (Fig. 2a, c). Recoveries in fertilized plots, however, increased for only 1 yr after tracer additions were stopped and decreased thereafter (Fig. 2b, d). Patterns of tracer recoveries in year-old needles were similar to those in current-year needles (Fig. 2c, d), but were less pronounced. Decreases in tracer recoveries on fertilized plots after 1993 were greater after labeling with $^{15}NO_3$ than with $^{15}NH_4$ (Fig. 2b, d). Three years after the end of ^{15}N additions, tracer recoveries in current-year and year-old needles converged within each fertilization-tracer form combination (Fig. 2c, d).

Fine roots.—Tracer movements into fine roots in oak forest floor and mineral soils were influenced by rate and form of N addition (Table 4). Recoveries in oak forest roots increased with N loading rate, with forest floor roots averaging 2.1 and 9.0% recoveries of ^{15}N additions, respectively, under ambient deposition and chronic N fertilization. ^{15}N recoveries in mineral soil roots averaged 0.4% at ambient and 6.0% at elevated N deposition in the oak forest plots. Although ANOVA indicated tracer assimilation by roots differed according to form of N addition, the effects were smaller for the form of N than for N loading rate.

TABLE 4. Tracer ($^{15}NH_4$ and $^{15}NO_3$) recoveries in ambient and chronically fertilized plots in a 50-yr-old oak forest.

Ecosystem component	Ambient N deposition (8 kg·ha^{-1}·yr^{-1})			Fertilizer plus ambient N (58 kg·ha^{-1}·yr^{-1})			Significant effects (two-way ANOVA)		
	$^{15}NH_4$	$^{15}NO_3$	Mean	$^{15}NH_4$	$^{15}NO_3$	Mean	N load *P*	N form *P*	Interaction *P*
Foliage: oak	0.28^{a}	0.64^{b}	0.46	3.06^{c}	5.72^{d}	4.39	***	***	0.242
Foliage: birch	0.02^{a}	0.08^{a}	0.05	0.87^{b}	1.12^{b}	1.00	***	*	*
Foliage: maple	0.00^{a}	0.02^{a}	0.01	0.34^{b}	0.66^{b}	0.50	**	*	0.330
Total foliage	0.31	0.74	0.52	4.28	7.50	5.89			
Wood: 1991–1992	0.10^{a}	0.19^{b}	0.15	1.37^{c}	2.34^{d}	1.86	***	***	0.657
Wood: 1988–1990	0.08^{a}	0.13^{b}	0.11	0.79^{c}	1.19^{d}	0.99	***	***	0.170
Bark	0.26^{a}	0.24^{a}	0.25	1.01^{b}	2.15^{b}	1.58	***	*	0.258
Total wood + bark	0.44	0.56	0.50	3.17	5.68	4.43			
Fine roots: forest floor	1.28^{a}	2.05^{a}	1.66	6.43^{b}	9.04^{b}	7.73	***	*	0.577
Fine roots: 0–10 cm soil	0.29^{a}	0.57^{a}	0.43	2.63^{b}	9.31^{c}	5.97	***	**	*
Total fine roots	1.56	2.62	2.09	9.05	18.35	13.70			
Tree biomass	2.31	3.92	3.11	16.50	31.53	24.02			
Litter (0 to 2 yr old, Oi)†	13.1	21.3	17.2	13.0	8.4	10.7			
Oe horizon	3.2^{a}	4.5^{a}	3.8	8.2^{b}	8.1^{b}	8.2	***	0.340	0.290
Oa horizon	12.2^{a}	20.3^{ac}	16.2	28.2^{bc}	23.1^{bc}	25.7	**	0.296	*
0–10 cm mineral soil	1.3^{a}	1.8^{a}	1.5	11.0^{b}	30.4^{c}	20.7	***	***	***
10–20 cm mineral soil	3.5^{a}	3.6^{a}	3.6	4.3^{a}	9.0^{a}	6.7	0.139	0.246	0.273
Forest floor + mineral soil	33.2	51.5	42.3	64.7	79.1	71.9			
Total	35.5	55.4	45.4	81.2	110.6	95.9			

Notes: Values are percent recoveries of ^{15}N tracers at the end of 1992 that were applied in 1991 and 1992 as $^{15}NH_4$ or $^{15}NO_3$ to forest floors in separate halves of plots. Significant main effects and interactions (two-way ANOVA) for individual ecosystem compartments are indicated as follows: * = $P < 0.10$, ** = $P < 0.01$, and *** = $P < 0.001$. Significant differences ($P < 0.05$, Tukey HSD posthoc tests) in percent recoveries of $^{15}NH_4$ vs. $^{15}NO_3$ tracers across both levels of N loading are shown using different superscript letters within rows.

† Values are from P. A. Micks, M. R. Downs, and K. J. Nadelhoffer, *unpublished manuscript.*

Tracer recoveries in red pine forest roots were also influenced by N loading rate in both the forest floor and mineral soil (Table 5). Recoveries in forest floor roots averaged 0.7 and 4.5% of tracer inputs in the ambient and fertilized pine plots, respectively. Recoveries in pine mineral soil roots averaged 0.3% under ambient N loading and 4.2% under chronic N fertilization. N form influenced tracer recoveries in roots in mineral soil, but not in the forest floor ($P = 0.120$), in the pine plots. In mineral soil, significantly greater recovery of nitrate-applied tracer occurred only in the fertilized plot.

TABLE 5. Tracer recoveries in ambient and chronically fertilized plots in a 70-yr-old red pine plantation. See Table 4 for units and statistical comparisons, and Table 4 notes for units and statistical tests.

Ecosystem component	Ambient N deposition (8 kg·ha^{-1}·yr^{-1})			Fertilizer plus ambient (58 kg·ha^{-1}·yr^{-1})			Significant effects (two-way ANOVA)		
	$^{15}NH_4$	$^{15}NO_3$	Mean	$^{15}NH_4$	$^{15}NO_3$	Mean	N load *P*	N form *P*	Interaction *P*
Foliage: current-year needles	0.21^{a}	0.44^{b}	0.33	3.34^{c}	8.80^{d}	6.07	***	***	0.163
Foliage: year-old needles	0.10^{a}	0.19^{b}	0.14	1.87^{c}	5.12^{d}	3.49	***	***	0.463
Total foliage	0.30	0.64	0.47	5.21	13.92	9.56			
Wood: 1991–1992	0.03^{a}	0.04^{a}	0.04	0.15^{b}	0.42^{c}	0.28	***	***	*
Wood: 1988–1990	0.01^{a}	0.01^{a}	0.01	0.08^{b}	0.20^{c}	0.14	***	**	*
Bark	0.05^{a}	0.10^{b}	0.07	0.48^{c}	1.40^{d}	0.94	***	**	0.578
Total wood + bark	0.08	0.15	0.12	0.71	2.02	1.36			
Fine roots: forest floor	0.58^{a}	0.89^{a}	0.73	4.42^{b}	4.63^{b}	4.52	***	0.120	0.388
Fine roots: 0–10 cm soil	0.24^{a}	0.38^{a}	0.31	2.76^{b}	5.67^{c}	4.22	***	**	0.467
Total fine roots	0.81	1.27	1.04	7.18	10.30	8.74			
Tree biomass	1.20	2.05	1.63	13.10	26.23	19.67			
Litter (0 to 2 yr old, Oi)†	8.1	7.6	7.9	12.9	8.8	10.9			
Oe horizon	5.5^{a}	8.7^{a}	7.1	10.8^{a}	6.8^{a}	8.8	0.256	0.854	*
Oa horizon	8.8^{a}	16.1^{a}	12.5	18.3^{a}	10.0^{a}	14.2	0.640	0.926	*
0–10 cm mineral soil	2.9^{a}	2.9^{a}	2.9	7.4^{a}	13.8^{b}	10.6	***	*	*
10–20 cm mineral soil	1.2^{a}	1.1^{a}	1.2	2.7^{a}	6.5^{a}	4.6	0.184	0.481	0.453
Forest floor + mineral soil	26.5	36.4	31.4	52.2	45.9	49.0			
Total	27.7	38.4	33.1	65.3	72.1	68.7			

† Values are from P. A. Micks, M. R. Downs, and K. J. Nadelhoffer, *unpublished manuscript.*

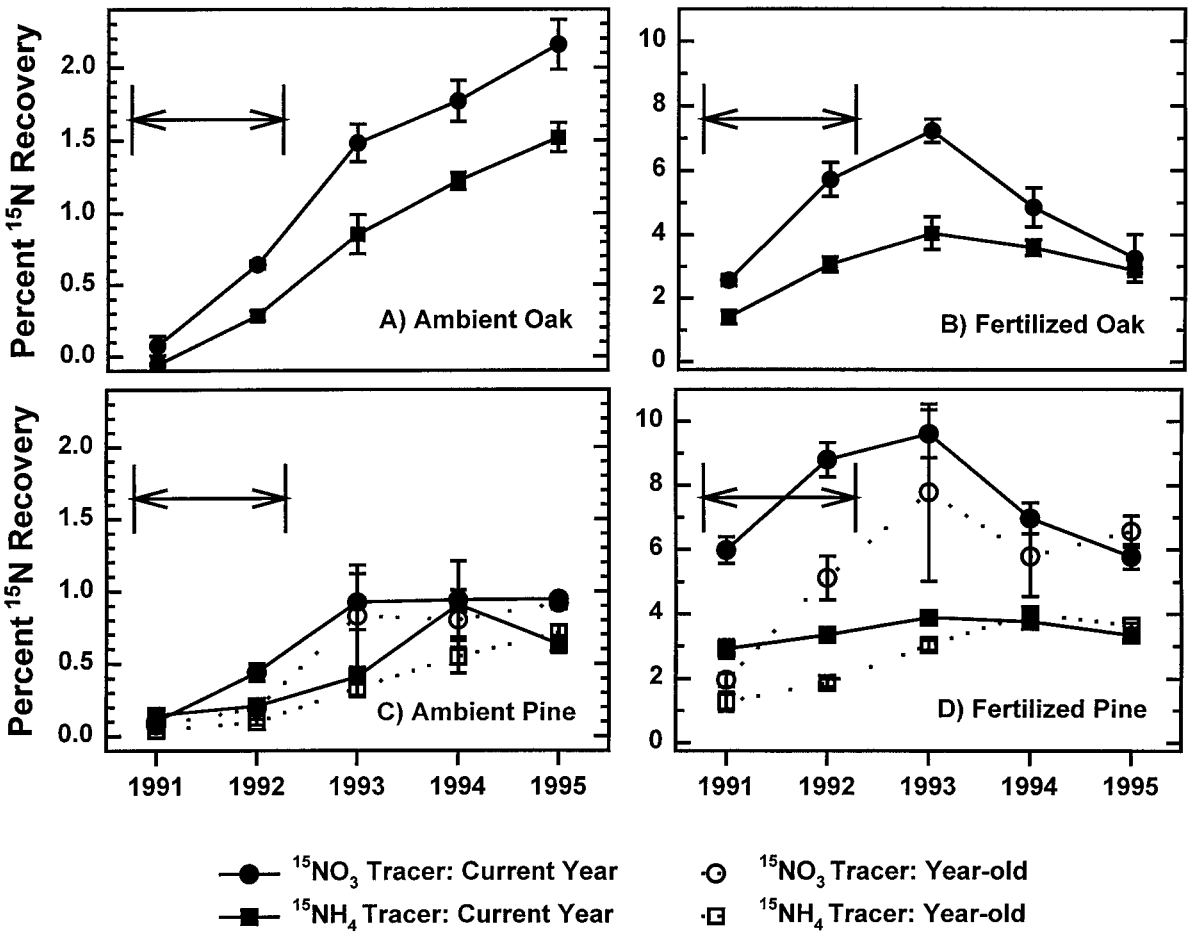

FIG. 2. Recoveries of $^{15}NH_4$ and $^{15}NO_3$ tracers in foliage on ambient and chronically fertilized plots in an oak forest and a pine plantation at the Harvard Forest. Tracers were applied to soil surfaces during the 1991 and 1992 growing seasons (indicated by ↔). Values are mean (±1 SE) percent recoveries of tracers applied to forest floors. Fertilization began in 1988 and continued throughout the course of measurements.

Of all measured oak forest vegetation components, fine roots were the dominant sink for N inputs under both levels of N addition (Table 4). ^{15}N recoveries in oak forest fine roots were 2.1% on the ambient and 13.7% on the fertilized plot in both soil strata combined. Fine roots were also strong sinks for tracers applied to the red pine forest (Table 5). On the fertilized red pine plot, however, foliage was nearly as strong a sink as were fine roots. Recoveries in pine forest fine roots were 1.0% on the ambient and 8.7% on the fertilized plot (Table 5).

Forest floor roots accumulated more tracer than did mineral soil roots at ambient N loading in both forests (Tables 4 and 5); tracer recoveries in forest floor roots on ambient plots were 2–4 times higher than were recoveries in mineral soil roots on the same plots. However, recoveries on the fertilized plots were higher in forest floor roots only when $^{15}NH_4$ was applied. When $^{15}NO_3$ was added to fertilized plots, recoveries in forest floor and mineral soil roots did not differ appreciably within either forest type.

Excess ^{15}N was detectable in forest floor and 0–10 cm soil fine roots after 1 yr of labeling at both levels of N inputs in the oak (Fig. 3) and red pine (Fig. 4) forests. Although we analyzed fine root samples collected through only the first year after the end of labeling, the trends of continued tracer accumulation, as observed in foliage (Fig. 2), were not evident in roots. Rather, recoveries in fine roots either did not change or decreased slightly one year after tracer additions were stopped (Figs. 3 and 4).

Wood and bark.—As for foliage and roots, tracer movements into recently formed wood (≤5 yr old) and into bark in both forests were influenced by N loading rate and the form of labeled N applied (Tables 4 and 5). In the oak forest, tracer recovery in wood formed during labeling years (1991 and 1992) was 0.2% on the ambient plot vs. 1.9% on the fertilized plot (Table 4). Wood formed in the 3 yr prior to labeling (1988 to 1990) showed a similar pattern, with this age class accumulating 0.1 and 1.0% of tracers applied to the ambient and fertilized plots, respectively. Within each

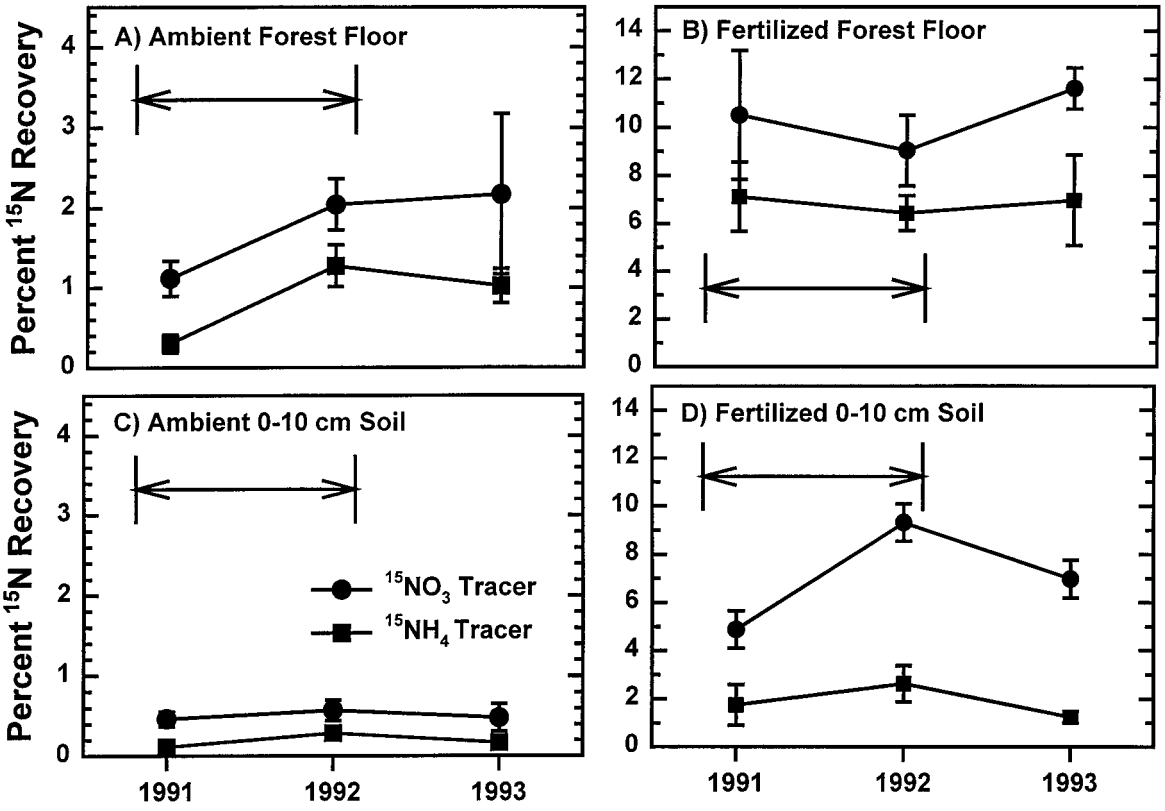

FIG. 3. Recoveries of $^{15}NH_4$ and $^{15}NO_3$ tracers in fine roots on ambient and chronically fertilized plots in an oak forest. Tracers were applied to soil surfaces during the 1991 and 1992 growing seasons (indicated by ↔). Values are mean (±1 SE) percent recoveries of tracers applied to forest floors. Fertilization began in 1988 and continued throughout the course of measurements.

wood age class and N loading level in the oak forest, tracer recoveries were about two times greater when $^{15}NO_3$ vs. $^{15}NH_4$ was applied. Tracer recoveries in oak bark also increased with N loading rate; from 0.2% in the ambient to 1.6% in the fertilized plot.

In the red pine forest, recoveries in 1991–1992 wood were <0.1 and 0.3% of tracer additions on the ambient and fertilized plots, respectively (Table 5). Recoveries in wood formed in the 3 yr prior to labeling the pine plots were <0.1% in the ambient and 0.1% in the fertilized plots. The form of tracer applied to the pine plots influenced tracer recoveries in both age classes of wood. Post hoc tests showed that this effect was important only in the fertilized plot, where recoveries were >2 times greater when $^{15}NO_3$ was applied. Recoveries of ^{15}N in pine bark increased from 0.1 to 0.9% of addition from ambient to fertilized conditions. Although there was a significant effect of N form on ^{15}N recovery in bark, only in the fertilized plot in the pine forest was recovery greater after $^{15}NO_3$ than after $^{15}NH_4$ additions.

In the oak forest, tracer recoveries in bark plus recently formed wood (1988–1992) were about 0.5% of tracer additions to the ambient plot and about 4.4% of tracer additions to the fertilized plot (Table 4). These values are similar to percent recoveries in foliage but are considerably lower than recoveries in fine roots on the oak plots. In the pine forest, recoveries of tracers in bark plus recently formed wood were 0.1 and 1.4% of ^{15}N additions to the ambient and fertilized plots, respectively (Table 5). In contrast to the oak plots, recoveries in the pine wood plus bark pool were considerably smaller than were recoveries in pine foliage. Although we are less confident about our estimates of bark N pool sizes than of our estimates of other pool sizes (*Methods*), any biases in our estimates of bark N masses are unlikely to affect the overall results. With regard to the overall importance of bark as a sink for N, estimates of recoveries in bark ranged from <0.1 to 2.2% of ^{15}N additions across forest types, N loading rates, and N forms. Systematic errors as great as a factor of 2 would thus have small effects on estimates of total tracer recovery, or on comparisons with soil and nonwoody biomass pools.

Decomposing litter.—Analyses of litter collected from nonlabeled plots at Harvard Forest and subsequently incubated on the plot forest floors during the 2 yr of ^{15}N tracer additions showed that decomposition of recently formed litter (<2 yr old) was an important sink for both ammonium and nitrate deposition under ambient and fertilized conditions (P. A. Micks, M. R. Downs, and K. J. Nadelhoffer, *unpublished manu-*

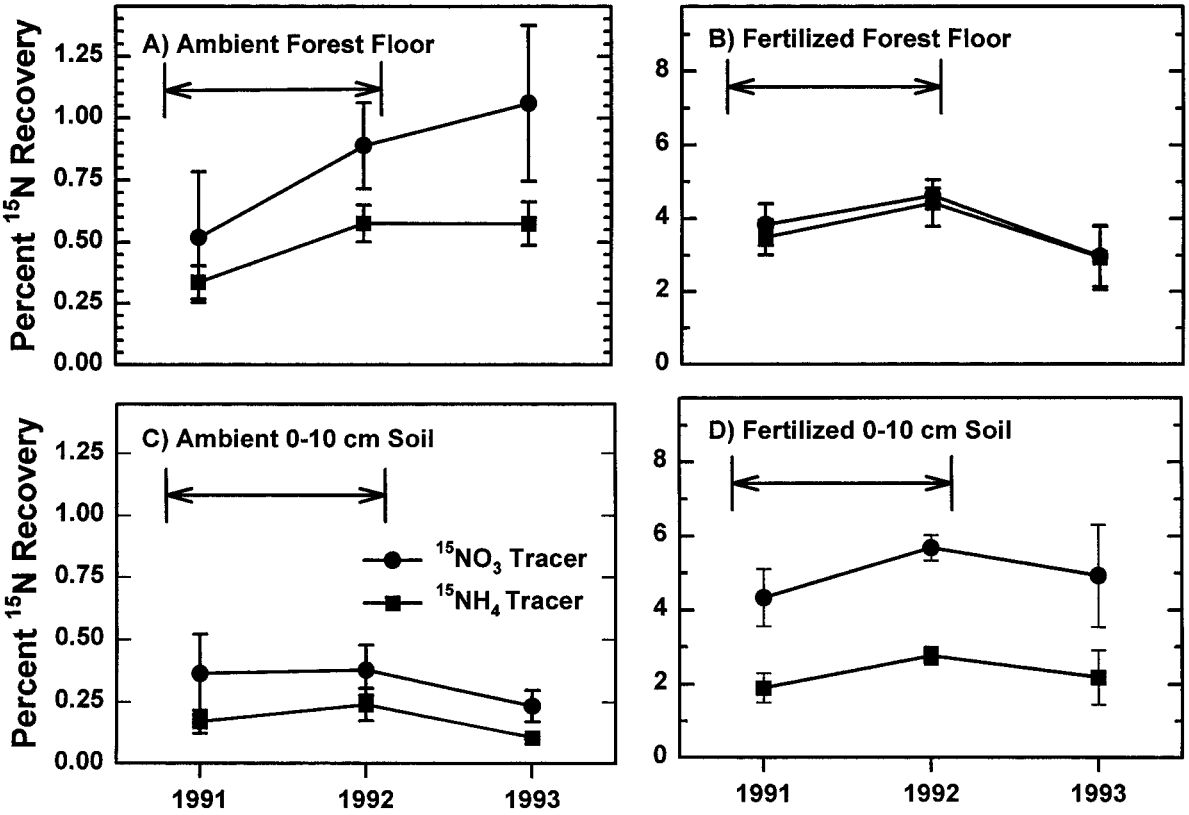

FIG. 4. Recoveries of $^{15}NH_4$ and $^{15}NO_3$ tracers in fine roots on ambient and chronically fertilized plots in a red pine plantation. Tracers were applied to soil surfaces during the 1991 and 1992 growing seasons (indicated by ↔). Values are mean (±1 SE) percent recoveries of tracers applied to forest floors. Fertilization began in 1988 and continued throughout the course of measurements.

script). We incorporate summary data from this study in order to compare the importance of decomposing litter as a sink for N additions with plant tissues and soils as N sinks.

Results from Micks et al. (P. A. Micks, M. R. Downs, and K. J. Nadelhoffer, *unpublished manuscript*) indicate that N immobilized by decomposing oak and maple leaf litter plus woody litter (estimated to be 1 $Mg \cdot ha^{-1} \cdot yr^{-1}$) in the oak forest during the 2 yr of labeling could have accounted for 17% of N inputs under ambient conditions and 11% of N inputs under fertilized conditions (Table 4). On the pine plots, immobilization in needle litter and woody litter during the 2 yr of tracer additions accounted for 8 and 11% of applied tracers under ambient and fertilized conditions, respectively (Table 5).

Forest floor and mineral soil.—Recoveries of tracers from Oe horizons (recognizable litter fragments) after tracer additions ranged from 3 to 11% of ^{15}N additions across both forest types and levels of N addition. In the oak forest Oe horizon, recoveries were significantly higher under fertilized than under ambient conditions, but tracer recoveries did not differ between $^{15}NH_4$ and $^{15}NO_3$ tracer additions within either level of N input (Table 4). In the pine forest, no differences in tracer recovery were detected between levels of N input or between the two labeled ions within either level of N input (Table 5).

Tracer recoveries in Oa horizons (''humus'' layers) were higher than in Oe horizons or in mineral soil layers under ambient conditions in both forests (Tables 4 and 5). Recoveries increased with N loading rate in the Oa horizon of the oak forest (Table 4), but not in the pine forest (Table 5). Tracer recoveries in Oa horizons were not significantly influenced by the form of N label applied in either forest type.

Small fractions of tracers were recovered in mineral soils under ambient conditions in both forests, and recoveries from mineral soils did not differ between $^{15}NH_4$ and $^{15}NO_3$ additions (Tables 4 and 5). Recoveries were $<5\%$ for both mineral soil layers combined under ambient N loading in both forests. Under chronic fertilization, however, tracer recoveries were higher in 0–10 cm soils and were greater when ^{15}N was applied as nitrate than as ammonium. This is in contrast to forest floors where tracer recoveries after $^{15}NO_3$ labeling were equal to or less than recoveries after $^{15}NH_4$ labeling. Tracers were detectable in 10–20 cm mineral soils, but recoveries in this deeper soil layer were not signifi-

cantly influenced by either N loading rate or the form of tracer applied.

Discussion

^{15}N natural abundances

Natural ^{15}N abundances (Table 1) followed the general pattern for forests observed elsewhere in which plant tissues are slightly depleted and soils are slightly enriched in ^{15}N relative to the atmospheric standard (e.g., Nadelhoffer and Fry 1988, Gebauer and Schulze 1991, Garten 1993, Garten and Van Miegroet 1994, Buchmann et al. 1995). The patterns of ^{15}N abundances in these two forests are consistent with conceptual models (summarized in Nadelhoffer and Fry 1994) in which slight fractionations during litter and organic matter decomposition lead to gradual enrichments of forest floor and mineral soil in ^{15}N with age and depth. Plant tissues are depleted in ^{15}N relative to soils because soil ammonium and nitrate have slightly lower ^{15}N contents than the organic matter from which they are mineralized, and, to some extent, because mineral N inputs from the atmosphere in the northeastern U.S. are slightly depleted in ^{15}N relative to the atmospheric N_2 standard (Nadelhoffer et al. 1998). Our data also suggest that plant processes associated with N translocation discriminate against ^{15}N in that foliar $\delta^{15}N$ values were lower than fine root values and bolewood values were lower than foliar values. The narrow ranges of $\delta^{15}N$ values in nonlabeled pools facilitated detection of excess ^{15}N in samples collected after tracers were applied to forest floors in 1991 and 1992. Also, the large differences between $\delta^{15}N$ values in nonlabeled forests and the labeled N additions ($\delta^{15}N > 750‰$) minimized the influence of isotopic discrimination on our estimates of ^{15}N tracer retention.

^{15}N tracer recoveries

The sums of tracers recovered in measured pools ranged from 30 to 113% of ^{15}N additions (Tables 4 and 5). Total percent recoveries were higher under fertilized than under ambient conditions, after $^{15}NO_3$ additions than after $^{15}NH_4$ additions, and in the oak than in the pine forest. Incomplete recoveries in the ambient plots were likely due to the extremely small N masses that were added to these plots (<0.4 kg/ha as nearly pure ^{15}N over 2 yr, vs. 100 kg ^{15}N-labeled fertilizer added during 2 yr to the low N plots). Some of these small masses of ^{15}N additions may have been leached, denitrified, volatilized, or immobilized in nonsampled pools such as large woody roots or deep mineral soils (>20 cm depth). We suspect, however, that large fractions of tracers applied without fertilizers were retained in thin surface layers on forest floors that are subject to horizontal mixing with materials from adjacent, nonlabeled areas. Because litter and soil samples were collected within 1–5 m of plot boundaries, mixing of surface litter between labeled plots and adjacent, nonlabeled areas probably served to dilute the N labels when such small masses of N were added. This mixing of litter between labeled and nonlabeled areas was probably less important in fertilized plots where N fertilizer additions overwhelmed retention capacities of the surface materials and served to carry tracers to lower forest floor and soil horizons. Also, some of the small masses of N tracer applied to the ambient plots could have adsorbed to litterbag material or to nonsampled fresh litter (e.g., fine woody material). Therefore, low recoveries in ambient plots more likely resulted from errors in forest floor and soil sampling than from errors in biomass sampling.

Trees were much smaller sinks for N inputs than were soils under ambient conditions in both forests (Tables 4 and 5). Tracer recoveries in the ambient plots suggest that only ~3 and 1.5% of annual background N inputs to the reference plots in the oak and pine forests, respectively, are assimilated into tree biomass. Direct uptake of N deposition into foliage could result in somewhat greater uptake of atmospheric N inputs than our tracer study indicates. However, Currie et al. (1996) showed no differences in inorganic N fluxes between wet deposition and throughfall in either of these forests, thereby suggesting little direct N uptake into canopies. Our tracer results suggest that background N inputs taken up by trees are assimilated mainly into fine roots and foliage and that wood and bark accumulate extremely small fractions of N inputs at current deposition levels (~8 kg $N \cdot ha^{-1} \cdot yr^{-1}$). Longer term measures are needed to assess whether this is true at decadal time scales as well. Wood and bark are of particular interest as C:N mass ratios are high (C:N wood >200, C:N bark ≈100 to 200) compared to foliage, roots and soils (C:N ≈20 to 50). Despite the uncertainties in tree N pool sizes (e.g., Bark N is a rough estimate; woody roots and twigs are not included, etc.), it is likely that <5% of the 8 kg $N \cdot ha^{-1} \cdot yr^{-1}$ deposited on these forests, or <0. 4 kg $N \cdot ha^{-1} \cdot yr^{-1}$, is taken up by trees (unless large amounts of N deposition are taken up directly by foliage). Furthermore, $\ll$0.1 kg $\cdot ha^{-1} \cdot yr^{-1}$ of N deposition was taken up into woody biomass. Assuming C: $N_{wood+bark}$ = 500, this amount of N assimilation into woody tissues contributed <50 kg $\cdot ha^{-1} \cdot yr^{-1}$ of C accumulation in tree boles. As wood production ranges from 1.75 to 2.40 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ in these forests (from Magill et al. 1997: Table 3), only small fractions of wood accumulation (2–3%) in these plots can be attributed to ambient N deposition. Although fluxes of tracers into tree biomass were small, the fact that ^{15}N recoveries in tree tissues were typically higher after $^{15}NO_3$ than after $^{15}NH_4$ additions, suggests that nitrate deposition could have a greater effect on tree growth than ammonium deposition.

Tracer recoveries show that the importance of trees as sinks for N inputs increased with N loading rates in both forests. Percentages of tracers recovered within tree tissues were at least 10-fold greater under elevated

N loading than under ambient N deposition (Tables 4 and 5). As in the ambient plots, woody tissues in the fertilized plots assimilated smaller percentages of applied tracers than did fine roots or foliage. If, as indicated by tracer recoveries, only 4.4% (oak) and 1.4% (pine) of the 58 kg $N \cdot ha^{-1} \cdot yr^{-1}$ inputs to the fertilized plots were taken up into woody tissues, then assimilation of elevated N inputs into wood plus bark was 2.6 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the oak and 0.8 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the pine forest. Assuming $C:N_{wood+bark}$ to be 250 in the fertilized oak and 500 in the fertilized red pine plots, wood C accumulation resulting from N inputs would be 650 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the oak forest and 400 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the pine forest. These values are ~25% of the 2.4 and 1.7 $Mg \cdot ha^{-1} \cdot yr^{-1}$ of wood C increments (from Magill et al. 1997) in the chronically fertilized oak and pine plots. It should be noted, however, that Magill et al. (1997) found no detectable increase in wood production between ambient and plots fertilized with 50 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (''low N'' treatment) in these same forests. Therefore, movement of labeled fertilizers into woody biomass on these plots did not necessarily stimulate wood increment appreciably. In fact, Magill et al. (1997) reported decreases in tree growth in these forests by 1993 after 6 yr of higher rates (150 kg $N \cdot ha^{-1} \cdot yr^{-1}$) of N addition. Movements of tracers into woody tissues under both ambient and fertilized conditions show that wood is a minor sink for N deposition in these forests. Very small percentages of C accumulation in wood are directly attributable to N inputs, particularly under ambient levels of N deposition at our site.

Soils (including forests floors) were much stronger sinks for N inputs than were trees under ambient conditions. This finding is consistent with smaller scale, pulse-labeling studies of forest soils indicating much higher exchanges between soil microbes and inorganic N pools than between tree roots and inorganic N pools (Davidson et al. 1992, Stark and Hart 1997). Mean tracer recoveries (averaged across both N forms) in forest floor plus soil in ambient plots were 45% of excess ^{15}N applied to the oak (Table 4) and 34% of excess ^{15}N applied to the pine (Table 5) forest. The strongest sinks for N in soils under ambient conditions (8 $kg \cdot ha^{-1} \cdot yr^{-1}$ N deposition) were Oi (recent litter) and Oa horizons. These two horizons accounted for more than two-thirds of tracer recoveries from soil profiles in both ambient plots. If tracer recoveries underestimated the importance of N assimilation into upper forest floors (mainly Oi), then the importance of forest floors as sinks for ambient N deposition was also underestimated.

Mean tracer recoveries in forest floor plus mineral soil in fertilized plots were ~75% in the oak (Table 4) and >50% in the pine (Table 5) forest. As these values are greater than in ambient plots, chronic fertilization appears to have increased the importance of soils as sinks for N inputs. However, the likelihood of incomplete tracer recoveries, particularly in ambient plots (above), probably led to underestimates of N assimilation into forest floors. Therefore, we cannot conclude that the importance of soil profiles as sinks for N deposition increased with N deposition rates. In contrast, although soils (including forest floor) were more important sinks than were trees under both levels of N deposition, the clear increase in assimilation of N inputs by trees under chronically elevated N deposition indicates that the relative importance of soil profiles as N sinks decreased with N deposition. Our results do indicate that the importance of mineral soils as sinks for N inputs increased with N deposition rates: Mean ^{15}N recoveries in 0–10 cm soils increased more than 10-fold with chronic fertilization in the oak forest (Table 4) and more than three-fold in the pine forests (Table 5). These results suggest that chronic N additions may have decreased the proportions of inorganic N immobilized by forest floor microbes, thereby resulting in greater N transport from forest floors to mineral soils and greater uptake by tree roots. Nitrate assimilation capacities of forest floors were more likely exceeded under chronic N additions than were the ammonium assimilation capacities, as tracer recoveries from mineral soils were greater when $^{15}NO_3$ rather than $^{15}NH_4$ was applied with fertilizer.

Other studies of temperate forest N sinks

Our approach of adding ^{15}N tracers to large forest plots across entire growing seasons to simulate atmospheric N inputs has been used only recently (Nadelhoffer et al. 1995, 1998, Koopmans et al. 1996, Gundersen 1998, Tietema et al. 1998) and differs from earlier studies that used single applications of ^{15}N-labeled fertilizers (e.g., Hulm and Killham 1990), often to small plots (<10 m^2) with single mature trees (e.g., Mead and Pritchett 1975, Heilman et al. 1982*a*, *b*, Melin et al. 1983, Preston and Mead 1994) or small numbers of seedlings (e.g., Nambiar and Bowen 1985). However, although various studies using ^{15}N additions to intact forests differ with respect to plot size, forms and methods of tracer additions, soil types, tree species, and stand age, they can be used to make inferences regarding the fates of N deposition on forests.

Studies using single applications of ^{15}N-labeled fertilizers suggest, as do the results of our repeated applications of ^{15}N tracers, that soils (forest floor and mineral) are more important sinks for N deposition than trees as evidenced by low tracer recoveries in tree biomass. For example, recoveries of applied ^{15}N in 11-yr-old slash pine (*Pinus elliottii* Engelm.) tree biomass were 10.5% after one-time additions of labeled fertilizers (ammonium sulfate at either 56 or 220 kg N/ha) to single-tree plots in Florida (Mead and Pritchett 1975). Tracer recoveries in tree biomass one or two years after single ^{15}N-fertilizer applications were 10% in a 20-yr-old Sitka spruce (*Picea sitchensis*) stand in Scotland (Hulm and Killham 1990), 25–36% in 7–9 yr old Douglas-fir (*Pseudotsuga menziesii*) stands in the

Pacific Northwest (Heilman et al. 1982*a*), 40% in a radiata pine (*Pinus radiata*) plantation in New Zealand (Worsnop and Will 1980), and 12–28% in mature Scots pine (*Pinus sylvestris*, L.) stands in Sweden (Melin et al. 1983). Preston and Mead (1994) reported that tracer recoveries in lodgepole pine (*Pinus contorta* Dougl.) biomass were 2–10% one year after ^{15}N-fertilizer additions in a British Columbia plantation and were lower after 8 yr.

Soils appear to be stronger sinks for ^{15}N tracers when they are applied at low rates (without fertilizers). For example, 8 mo after adding trace amounts (0.62 kg/m^2) of ^{15}N as either $^{15}NH_4$ or $^{15}NO_3$ to a 15-yr-old Norway spruce (*P. abies*) stand in Bavaria, only 3% of ammonium label and 7% of the nitrate label were recovered in tree biomass, while soils accounted for 87% of the ammonium and 79% of the nitrate label (Buchmann et al. 1996). The percentage recoveries of $^{15}NH_4$ and $^{15}NO_3$ in tree biomass at this Norway spruce site were 2 to 3 times greater than were recoveries in tree biomass under ambient N deposition in the Harvard Forest oak and red pine forests. However, wet N deposition at this Bavarian site was 15 kg·ha^{-1}·yr^{-1} (equal amounts of ammonium and nitrate in throughfall; Buchmann et al. 1995), or twice that at Harvard Forest. Greater recoveries of tracers in tree biomass in the Bavarian spruce forest than in the Harvard Forest pines and oaks are consistent with the greater recoveries of tracers in tree biomass under fertilization at our site (Tables 4 and 5).

Studies in which tracers have been applied to forest floors across one or more growing seasons also suggest that soils are a stronger sink for N deposition than trees. For example, soils were stronger sinks than tree biomass for experimentally elevated N inputs to a beech–maple–red spruce forest in eastern Maine where ^{15}N-labeled ammonium and nitrate fertilizers were added separately across several growing seasons (Nadelhoffer et al. 1993, 1995, 1998). In four western European conifer forests, tracer recoveries in tree biomass typically were less than in soils when ^{15}N ions were added to forest floors in throughfall (no fertilizer) or as ^{15}N-labeled fertilizer additions across an entire year (Tietema et al. 1998). These studies also support higher recoveries in tree biomass with higher N inputs: Only when throughfall N inputs were high (>50 kg·ha^{-1}·yr^{-1}) or when N leaching losses were at least 30% of N inputs did tracer recoveries in tree biomass approach recoveries in soils in these European forests.

Some, but not all, other tracer studies are consistent with our finding that trees compete better against soil sinks for nitrate than for ammonium inputs. For example, Preston and Mead (1994) reported that tracer recoveries in lodgepole pine tree biomass were greater after fertilizing with $^{15}NH_4NO_3$ than with $NH_4{}^{15}NO_3$, both 1 and 8 yr after plot labeling. It is not possible to distinguish whether greater recoveries of N tracers in trees following $^{15}NO_3$ additions in our study were due to tree species preferences for nitrate, to greater competition between tree roots and soil microbes for ammonium, or to more rapid movement of nitrate to root surfaces. Any or all of these processes could have contributed to greater recoveries of tracers after $^{15}NO_3$ than $^{15}NH_4$ additions. It is clear, however, that whatever processes were responsible, greater proportions of nitrate-N than ammonium-N inputs accumulated in tree biomass in the oak and red pine forests under both ambient and chronically elevated N deposition.

Our results are consistent with Johnson's (1992) conclusion that soil microbes are better competitors than trees for atmospheric N inputs to forest. As with other studies, the relative importance of trees as short-term sinks for elevated N inputs increased after fertilization. Nevertheless, soils remained the dominant sink for inorganic N inputs, with trees accumulating less than a third of total inputs even after 5 yr fertilization with NH_4NO_3 at 50 kg N·ha^{-1}·yr^{-1}.

Conclusions

Because we applied N tracers to plots 3 yr after the start of fertilization, tracer recoveries in our study are less likely to reflect short-term responses of forests to N enrichment and can be used to assess longer term responses to elevated N deposition with some confidence. Also, because $^{15}NH_4$ and $^{15}NO_3$ tracers were applied separately to plots receiving ammonium nitrate inputs at ambient (8 kg N·ha^{-1}·yr^{-1}) and at experimentally elevated (58 kg N·ha^{-1}·yr^{-1}) deposition rates, our results can be used to assess how forms and rates of N inputs affect the partitioning of N inputs among ecosystem components in these two forest types. What are the possible fates of N deposition to forests in the Northeastern U.S. under current (but nonpristine) and chronically elevated deposition rates? Our tracer studies at Harvard Forest suggest that:

1) Forest floors and mineral soils dominate over trees as sinks for both ammonium and nitrate deposition.

2) Trees are more important sinks for nitrate than for ammonium inputs under both ambient and elevated N deposition rates.

3) The importance of trees as sinks for N inputs increases with N deposition rates.

4) Small fractions of N inputs to temperate forests, generally $\ll$10% of deposition, are likely to be assimilated into woody tissues (C:N >200). Of the inputs that are not lost to leaching or gaseous fluxes, remaining N inputs are assimilated into soils and nonwoody plant tissues (C:N =20 to 50).

Our results, together with ^{15}N tracer studies in other forests, have important implications for assessments of the effects of N deposition on forest carbon balances in temperate regions. In particular, realistic simulations of forest C–N interactions should assume that forest floor and soil pools are the dominant sinks for N deposition, while woody biomass is a relatively minor sink for N inputs. Overestimating the importance of woody

biomass as a sink for N deposition could lead to overestimates of the role of temperate forests as sinks for atmospheric CO_2.

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