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Decomposing litter as a sink for ^{15}N-enriched additions to an oak forest and a red pine plantation

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Abstract

The importance of surface litter as a sink for atmospheric N deposition on forests was investigated using ^{15}N tracers to quantify the effects of N input rate and litter age on retention of N inputs by forest litter. The study was conducted in plots receiving ambient (0.8 g N m^{-2} per year) and chronically elevated N inputs (ambient + 5 g NH_4NO_3-N m^{-2} per year) in both a hardwood forest and a red pine plantation. Plots (30 m × 30 m) were part of the Chronic Nitrogen Amendment Study at the Harvard Forest, Massachusetts, USA. To allow estimates of N sink strength in litter cohorts of two different ages, litterbags containing oak leaves, maple leaves, pine needles, or maple wood chips were placed in the plots in years 1 and 3 of fertilizer additions. Uptake of N inputs into decomposing litter was estimated using ^{15}N tracers applied as $^{15}NH_4$ or $^{15}NO_3$ during years 4 and 5 of fertilizer additions. Thus ^{15}N additions occurred to litters in their fourth and fifth years of decay (set out in year 1 of N additions) and to litters in their second and third years of decay (set out in year 3 of N additions).

The effect of N input level on mass loss and N dynamics varied among litter types and appeared to increase with litter age. Fertilization decreased mass loss and loss of initial N content in maple and oak leaf litters, but it enhanced mass loss in wood and had little effect on pine needles. Decomposing litter cohorts in both forests retained significant proportions of N inputs at both ambient (20% in hardwood, 9% in pine) and elevated levels (7% in hardwood, 6% in pine) over the 2 years of tracer additions. Tracer assimilation into the 2-year-old litter cohort decreased under elevated N inputs, NO_3^- assimilation decreased relative to NH_4^+, and assimilation of both forms was lower in 4-year-old material on a per unit litter mass basis. Ecosystem-scale retention of N inputs by the 2 + 4-year-old litter cohorts in both forests increased with N input level, from 0.32 and 0.15 g N m^{-2} over 2 years (ambient hardwood and pine plots) to 0.86 and 0.70 g N m^{-2} over 2 years (fertilized hardwood and pine plots). Although N sink strength of litter pools increased more strongly in the pine forest in response to elevated N inputs, the hardwood forest retained more N under both input levels, suggesting that it may be a larger sink for atmospheric N deposition than the pine forest. Recently formed litter pools assimilate more NO_3^- than NH_4^+ under ambient N deposition, but may lose capacity to assimilate NO_3^- relative to NH_4^+ under potential future increases in N deposition.

Keywords: Litter decomposition; Ammonium and nitrate additions; ^{15}N tracers; Nitrogen deposition; Forest nitrogen storage

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1. Introduction

Atmospheric nitrogen deposition is an issue of primary concern to forest health in the northeastern US and Europe. Given the potentially harmful consequences of nitrogen saturation and resulting forest decline, it is important to understand how atmospheric N deposition affects the mechanisms that control N cycling and retention in forest ecosystems. N addition experiments have shown that most of the N deposited on temperate forests is retained by soil, with a major portion retained in soil organic matter (Koopmans et al., 1996; Tietema et al., 1998; Nadelhoffer et al., 1999a,b; Magill et al., 2000). Biological N immobilization and abiotic N assimilation within decomposing litter and humus could function as sinks for atmospheric N deposition (Davidson et al., 1991; Magill and Aber, 1998; Nadelhoffer et al., 1999a; Dail et al., 2001) and could therefore play a role in ameliorating the negative impacts of N deposition (Aber et al., 1998). N deposition on forests is projected to increase over the coming decades (Galloway et al., 1994, 2003). Understanding the relationship between N deposition and soil organic matter is key to predicting future impacts on N cycling in forest ecosystems. Our study investigated the importance of recently formed litter as a sink for atmospheric N inputs, using ^{15}N tracers to track the fate of ambient and chronically elevated N additions in decomposing litter in two forest types.

It is well established that litter decomposition rates are linked to initial litter quality (Aber and Melillo, 1982; Berg, 1986; Berg and McClaugherty, 1989), and N content plays a critical role in the transition from litter to humus (McClaugherty et al., 1985; Aber et al., 1990). Different studies have reported N additions to either increase, decrease, or have no effect on litter decomposition (reviewed by Fog (1988)). It has long been held that increased N availability increases decomposition rates in early stages of litter decay (Melillo et al., 1982) but higher N content can retard decay in older, more humified material. During later stages, lignolytic enzyme efficiency may be limited by high N content or by high availability of inorganic N (Keyser et al., 1978; Berg et al., 1998). The rate of N addition also can also influence decomposition rates. Litter decay rates in pine and mixed hardwood forests declined with increasing N additions over 6 years of NH_4NO_3 inputs at 5 and 15 g N m^{-2} per year (Magill and Aber, 1998). The effects of N addition may interact with initial litter chemistry, as reported by Carreiro et al. (2000) who observed positive, negative, or no effect of increasing NH_4NO_3 additions (2 and 8 g N m^{-2} per year for 3 years) on decomposition rates in hardwood leaf litters, and the magnitude and direction of the response was controlled by initial lignin and cellulose content. Downs et al. (1996) concluded that initial litter chemistry rather than N deposition determined decay rates in hardwood and spruce leaf litters treated with NO_3^- additions (3 and 6 g N m^{-2} per year) for 4 years. The ionic composition of atmospheric N deposition, which varies regionally, is also an important factor with regard to its effects on forest ecosystems. Soil microbial preferences for NO_3^- and NH_4^+ may vary (Davidson et al., 1992), and both amount and form of N deposition have been shown to influence its assimilation into forest floors (Tietema, 1998; Nadelhoffer et al., 1999a).

The Chronic Nitrogen Amendment Study is a long-term ecosystem-level study of the effects of N deposition on forest N cycling, plant tissue chemistry, primary production, and soil solution chemistry in a red pine plantation and an oak-dominated hardwood forest located at the Harvard Forest in Petersham, MA, USA (Magill et al., 2000). Here, NH_4NO_3 has been added to experimental plots in each forest at rates of 5 or 15 g N m^{-2} per year since 1988 to simulate elevated atmospheric N inputs. In a ^{15}N tracer study carried out during the fourth and fifth years of N additions, $^{15}NO_3^-$ or $^{15}NH_4^+$ was added to separate halves of control plots receiving ambient N deposition (0.8 g N m^{-2} per year, Ollinger et al., 1993) and fertilized plots (receiving ambient + 5 g N ha^{-1} per year) in order to estimate N fluxes into plant tissues and soils under ambient and chronically elevated N deposition (Nadelhoffer et al., 1999a). After 2 years of tracer additions, soil (O horizon + mineral soil 0–20 cm depth) was a much larger sink for N inputs than was plant biomass in both forests and at both N input levels. Total tracer recovery from soil ranged from 45 to >90%, in contrast to 3–33% recovery in plant biomass. The O horizon, where microbial activity is highest, accounted for 30–77% of applied tracers and was the strongest sink for the added N in the soil profile. N loading rate influenced both the amount and form of N retained in O horizon soils: twice as much

$^{15}NO_3$ as $^{15}NH_4$ was retained in ambient plots, while differences in retention of these two N forms were smaller in the chronically fertilized plots. Clearly the forest floor is a major sink for N deposition in these forests, and N addition rate and form are important factors in their capacity to retain atmospheric N deposition.

We report here on the importance of decomposing litter as a sink for atmospheric N inputs as indicated by results of a litter decomposition study carried out as part of the ^{15}N tracer experiment at the Chronic Nitrogen Amendment Study. We measured mass loss, net N dynamics, and ^{15}N tracer recovery in litter samples incubated in situ in the hardwood and pine forests over a 2-year period during the fourth and fifth years of chronic N additions. A separate long-term litter decomposition study begun 2 years earlier (fertilization year 2) on the same plots (Magill and Aber, 1998) enabled us to examine ^{15}N tracer dynamics in an older litter cohort which had been decomposing for 2 years at the start of tracer additions. In this paper we present findings on how N input rate, N form, litter type, and litter age influence the strength of 1- to 4-year-old litter as a sink for atmospheric N deposition.

2. Methods

2.1. Study site

The Chronic Nitrogen Addition study, located at the Harvard Forest Long Term Ecological Research (LTER) site in Petersham, Massachusetts, USA (42°30′N, 72°10′W), has examined the long-term effects of atmospheric N deposition on two forest ecosystems since 1988. One forest is an even-aged red pine (*Pinus resinosa* Ait.) plantation established in 1926 on an old field with an Ap horizon present. The other is a mixed hardwood forest, regrown after clearcutting in the mid-1940s. The hardwood stand is dominated by oaks (*Quercus velutina* Lam. and *Q. rubra* L.) with admixtures of birch (*Betula lenta* L. and *B. papyrifera* L.), red maple (*Acer rubrum* L.), and beech (*Fagus grandifolia* Ehrh.). Soils are Inceptisols (Typic Dystrochrepts), sandy loams formed from stony glacial till. Precipitation averages 112 cm per year (Van Cleve and Martin, 1991). See Magill et al. (2000) and Bowden et al. (1990) for more detailed descriptions of the site and experimental treatments.

2.2. Chronic N additions

Four 30 m × 30 m (0.09 ha) plots, each divided into 5 m × 5 m subplots, were established in each stand in 1988 and have received the following treatments annually: control (no treatment), low N (5 g NO_3NH_4-N m^{-2} per year), high N (15 kg NO_3NH_4-N m^{-2} per year), and low N plus sulfur (as Na_2SO_4). Fertilizer is applied in six monthly applications over the growing season (May–September) with a backpack sprayer. Only the control and low N treatments are considered in this paper, referred to respectively as the 'ambient' (receiving background atmospheric N inputs) and 'fertilized' (ambient + 5 g NH_4NO_3-N m^{-2} per year) treatments. Atmospheric N deposition at Harvard Forest is estimated to be 0.8 g N m^{-2} per year consisting of approximately equal amounts of NH_4-N and NO_3-N (Ollinger et al., 1993; Currie et al., 1996).

2.3. ^{15}N tracer additions

^{15}N tracers were applied to the ambient and fertilized plots in both stands in 1991 and 1992 (years 4 and 5 of fertilization). One half of each plot was labeled with $^{15}NH_4Cl$ and the other half with $K^{15}NO_3$. Tracers were mixed with regular fertilizer additions to the fertilized plots, raising the fertilizer ammonium-N $\delta^{15}N$ value from 0 to 965‰ and nitrate-N $\delta^{15}N$ from 0 to 761‰. Ambient plot-halves received the same amounts of tracers (as ^{15}N excess) on the same dates as did the fertilized plots: 0.0176 g ^{15}N m^{-2} per year applied as dissolved $^{15}NH_4Cl$ or 0.0139 g ^{15}N m^{-2} per year as dissolved $K^{15}NO_3$ solution. See Nadelhoffer et al. (2004), for details of tracer applications.

2.4. Litterbag studies

Two separate sets of litterbags containing senesced black oak leaves (*Q. velutina* Lam.), red maple leaves (*A. rubrum* L.), and red pine needles (*P. resinosa*) were installed 2.5 years apart (set A in fall 1988 and set B in spring 1991) in the fertilized and ambient plots in the red pine plantation and oak forest. In addition to leaf litters, set B included bags of red maple bole wood

Table 1
Average annual litterfall by species in the red pine and hardwood stand ambient and fertilized plots

Litter type	Pine stand				Hardwood stand			
	Ambient		Fertilized		Ambient		Fertilized	
	Mg ha^{-1} per year	Total annual litterfall (%)	Mg ha^{-1} per year	Total annual litterfall (%)	Mg ha^{-1} per year	Total annual litterfall (%)	Mg ha^{-1} per year	Total annual litterfall (%)
Red pine needles	2.39	70	2.98	79				
Black oak leaves					2.20	78	1.96	67
Red maple leaves					0.20	6	0.27	9
Red maple wood	1.00[a]		1.00[a]		1.00[a]		1.00[a]	

Litterfall masses are averaged over 1988–1992.
[a] Estimated annual input.

chips. The 1988-emplaced litterbags used in our study were part of a larger decomposition study by Magill and Aber (1998) which involved the control, low N, and high N treatments in both forests.

We chose to study the most important species in terms of leaf litterfall mass in the two forests. Black oak and red maple together contributed 85 and 76% of total litterfall in the ambient and fertilized oak forest plots, respectively, from 1988 to 1992. Pine needle litter contributed 70% (ambient plot) and 79% (fertilized plot) of total litterfall in the red pine plantation (Table 1).

Litterbags were placed in the ambient and fertilized plots in both stands, but this paper is concerned only with the subset of leaf litters decomposing in their stand of origin: oak leaves and maple leaves in the hardwood stand and pine needles in the pine stand. We report results for maple wood chips decomposing in both stands. When final litter collections were made in 1992, set A litter had decomposed for 4 years and set B for 2 years.

3. Litterbag installation and sampling

Set A: Fresh litter was collected in the two stands away from the treated plots in the fall of 1988. Litterbags made of nylon window screening, measuring 20 cm × 20 cm, were filled with approximately 10 g of air-dry litter. In November 1988, these litterbags were placed on top of the litter layer in one subplot within each ambient and fertilized plot. Because of the single location in each plot, set A litter received only one form of tracer during 1991–1992: litterbags in both hardwood stand plots and the pine stand ambient plot received $^{15}NH_4$ tracer, while those in the pine plantation fertilized plot received $^{15}NO_3$. This paper considers set A litterbag collections made each November from 1989 through 1992, in which four bags of each litter type were taken from each plot. Litterbags were collected twice per year, but we chose to examine only November collection data, in order to compare year-to-year variation with set B which was collected only in the fall. See Magill and Aber (1998) for more information on the experimental design.

Set B: Freshly fallen leaf litter was collected in the fall of 1990 in the same manner as set A. Maple wood chips came from bark-free bolewood of a red maple tree harvested at the Harvard Forest. Fifteen to 20 g of air-dry material was weighed into 25 cm × 30 cm litterbags constructed of fiberglass window screening. In the early spring of 1991 before fertilizer and tracer additions began, 25 bags of each litter type were placed on the surface of the litter layer in four subplots in the ambient and fertilized plots, located such that two subplots received additions of $^{15}NH_4$ and the other two received $^{15}NO_3$. Litterbags were collected once in the fall (October or November) from 1991 through 1995. Each collection consisted of five bags of each litter type from each subplot, for a total of 10 bags per litter type per ^{15}N label per plot. For this paper we consider set B data from the 1991 and 1992 collections.

4. Litter pools

Initial leaf litter masses for the two litter cohorts represented by sets A (1988) and B (1990) were

Table 2
Beginning and final masses of the decomposing litter pools during the 2-year tracer application period 1990–1992

Set	Litter type	Stand	Litter mass in 1990 (Mg ha^{-1})		Litter mass in 1992 (Mg ha^{-1})	
			Ambient	Fertilized	Ambient	Fertilized
A	Red pine needles	Pine	1.21	1.51	0.92	0.90
	Black oak leaves	Hardwood	1.02	0.84	0.50	0.75
	Red maple leaves	Hardwood	0.09	0.12	0.07	0.12
B	Red pine needles	Pine	2.39[a]	2.98[a]	1.40	1.69
	Black oak leaves	Hardwood	2.20[a]	1.96[a]	0.92	0.90
	Red maple leaves	Hardwood	0.20[a]	0.27[a]	0.11	0.16
	Red maple wood	Hardwood	1.00[a,b]	1.00[a,b]	0.68	0.53
Total needle + wood pool in pine stand			4.60	5.49	3.00	3.12
Total leaf + wood pool in hardwood stand			4.51	4.19	2.28	2.46

Notes: Pine stand totals include wood pool mass data taken from the hardwood stand on the assumption that mass loss of decomposing native wood in the pine stand is more realistically represented by maple wood decomposing in its native hardwood stand. In 1992, set B litter had decomposed for 2 years and set A for 4 years.

[a] Data from Table 1.

[b] Estimated annual input.

assumed to be the same. Initial mass was determined for each litter species from litter basket collections averaged over the 4-year period 1989–1992. The amount of initial litter remaining in 1990 in the pool represented by set A was calculated from set A 1988–1990 litterbag mass loss data, averaged by plot. Litter mass remaining in 1991 and 1992 was determined from litterbag mass loss data from the respective sets. 1990 and 1992 litter masses are given in Table 2. No data for woody litterfall exist for the site; we assumed an annual input of 1 Mg ha^{-1}, which is half the measured woody litter input in a hardwood forest at Hubbard Brook, New Hampshire (Whittaker et al., 1979). N mass in initial and decomposing litters was determined from N analyses and litter mass calculations.

4.1. Analytical methods

Mass loss was determined for each litterbag on an oven-dry weight basis (set A: 70 °C, set B: 50 °C). Percent N in set A initial material and litterbags was determined by near-infra red spectroscopy at the University of New Hampshire. Percent N in set B initial material and in all individual set B litterbags was determined with a Perkin-Elmer 2400 elemental analyzer, using acetanilide as a reference standard. Percent N determination methods were not intercalibrated, and we made no direct comparison of %N results between set A and set B.

^{15}N analysis of set A 1991 and 1992 litterbags was carried out on material composited into two samples per species, plot, and year, with each sample containing material from two litterbags. Percent N and ^{15}N content in the composited samples were determined at the Marine Biological Laboratory with a Finnegan MAT delta S isotope ratio mass spectrometer, according to the methods of Fry et al. (1992). Analytical errors are typically less than 0.2‰ δ^{15}N. ^{15}N in set B was determined by mass spectrometry as above in initial litters and in four individual litterbags per plot, ^{15}N label form, and year (1991 and 1992).

4.2. ^{15}N mass balance and ^{15}N uptake

We calculated the recovery of the applied ^{15}N tracers in 2- and 4-year-old litter pools at the end of the second year of tracer additions. This was accomplished using estimates of litter N pool sizes derived using initial litter masses, 1990–1992 litterbag data, ^{15}N content of initial and decomposed material, mass of fertilizer N applied, the known ^{15}N content of the $^{15}NH_4$ and $^{15}NO_3$ labels, and ^{15}N mass balance equations (Nadelhoffer and Fry, 1994). Tracer recovery in the labeled litter, expressed as percent of the total ^{15}N

tracer applied, was calculated with the following equation:

$$\mathrm{PR}^{15}\mathrm{N} = \frac{{}^{15}\mathrm{N}_{\mathrm{pool}} - (m_{\mathrm{pool}} \times \mathrm{at.\%\,init}) \times 0.01}{m^{15}\mathrm{N}_{\mathrm{tracer}} \times ((\mathrm{at.\%}\,{}^{15}\mathrm{N}_{\mathrm{tracer}} - \mathrm{at.\%\,init}) \times 0.01) \times 100}$$

where $\mathrm{PR}^{15}\mathrm{N}$ is the percent of tracer recovered in the labeled pool; ${}^{15}\mathrm{N}_{\mathrm{pool}}$ is the mass of ${}^{15}\mathrm{N}$ in the labeled pool (kg N ha^{-1}); m_{pool} is the mass of N in the labeled pool (kg N ha^{-1}); at.% init is the atom percent ${}^{15}\mathrm{N}$ in the initial, 1990 pre-labeled pool; $m^{15}\mathrm{N}_{\mathrm{tracer}}$ is the mass of tracer applied over 2 years; and at.% ${}^{15}\mathrm{N}_{\mathrm{tracer}}$ is the atom percent ${}^{15}\mathrm{N}$ of the applied tracer or labeled fertilizer.

Tracer recovery in set B litter was calculated using individual litterbag %N, $\delta^{15}\mathrm{N}$, and mass loss data. Tracer recovery calculations for set A used $\delta^{15}\mathrm{N}$ and %N values for the composited samples and the average mass loss for litterbags in each plot.

We calculated the proportion of applied ${}^{15}\mathrm{N}$ tracer recovered in the individual litter pools at the end of the labeling period using the above equation and the initial and final litter masses of the two cohorts. To examine the ability of the different litter types and ages to assimilate tracers on a per-unit-mass basis we calculated percent tracer recovery per Mg 1990 litter mass. Uptake of N inputs into litter pools was estimated by multiplying percent tracer recovery in the litter pools by the masses of N inputs to the plots over 2 years.

4.3. Statistical analyses

t-Tests were performed on ambient and fertilizer treatment means for initial mass remaining and percent initial N remaining, within each set, litter type, and year to determine whether mass loss and net N immobilization or mineralization were influenced by N input level. Two-way analysis of variance was used to test set B litters for N input level and N form effects on percent recovery of tracers in the litter pools, and on percent tracer recovery per Mg initial litter mass, after 2 years of tracer additions. Tukey HSD was used for post-hoc pair wise comparisons. *t*-Tests were used to compare percent tracer recovery per Mg initial litter mass between sets A and B for cases in which set A and B litters received the same N input level and form of ${}^{15}\mathrm{N}$ tracer. All statistical tests were performed using SYSTAT 9 software (Systat Inc., 1998).

5. Results

5.1. Mass loss

All leaf litters experienced rapid mass loss during the first 2 years (Fig. 1) but in most cases set A lost more than did set B. This apparent difference may be due to the fact that set A litter had experienced a full year of decomposition before the first collection, whereas set B litter had only been in the field for 6

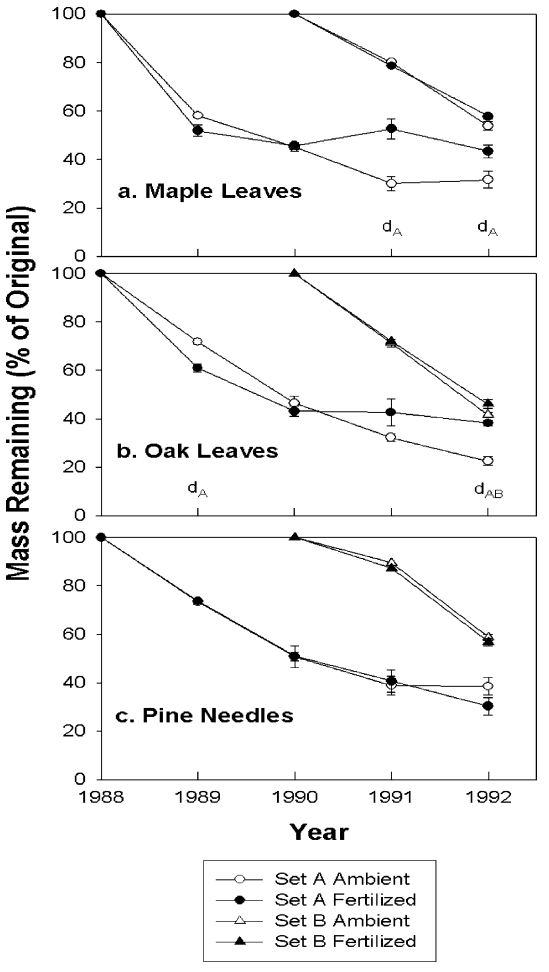

Fig. 1. Percent of original mass remaining of two sets of litter incubated on fertilized (low N) and ambient (control) plots. (a) Maple and (b) oak litter data are from the hardwood stand and (c) pine needle litter data are from the pine stand. Error bars are ±1 S.E.M. (set A: $n = 4$; set B: $n = 20$). Letter 'd' indicates a yearly significant difference ($P < 0.05$) between the two N input levels; subscript denotes set A and/or B.

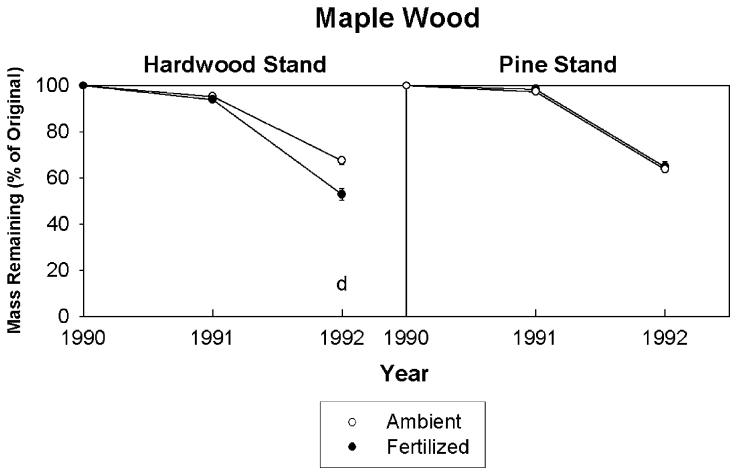

Fig. 2. Percent of original mass remaining in maple wood chips incubated on fertilized (low N) and ambient (control) plots in the hardwood stand and pine stand. Error bars are ±1 S.E.M. ($n = 20$). Letter 'd' indicates a yearly significant difference ($P < 0.05$) between the two N input levels.

months when it was first collected. By 1992, the 4-year-old set A litters lost 57–78% of initial mass and 2-year-old set B leaf litters lost 41–58% (Fig. 2). Maple wood mass declined by only 3–6% in the first year but in its second year nearly equaled pine needle mass loss rate for a total of 33–48% mass lost by 1992.

Nitrogen input level had no significant effect on leaf litter mass loss after 2 years of decomposition in either set with the exception of set B oak leaves, in which fertilizer addition slightly reduced mass loss. The effects of fertilizer inputs became apparent as litter aged, however. After 3 and 4 years, respectively, fertilizer additions significantly reduced mass loss in set A maple and oak leaves (Fig. 1a and b). Pine needle mass loss was not affected by N input level in either set (Fig. 1c). Fertilization increased maple wood mass loss in the hardwood stand after 1 year but not in the pine stand (Fig. 2); otherwise, wood decomposition rates were similar in both stands.

Mass loss rates for both sets of litter in their first year were related to initial litter quality. Mass loss in set B litters decreased with increasing initial C:N ratios: maple and oak leaves (C:N 52) decayed the most rapidly, followed by pine needles (C:N 88), then wood (C:N 312). Initial lignin:nitrogen ratios were similarly correlated, ranging from 21 in red maple leaves, 34 in oak leaves, 40 in white pine needles to 109 in red maple wood (data from Magill and Aber (1998) and Downs et al. (1996)).

5.2. N dynamics

Net N accumulation and release were calculated as an increase or decrease in the mass of N remaining in the litterbags relative to the initial N mass.

N input level influenced litter N dynamics and this effect appeared to increase with litter age, although set A and B results were somewhat different. In general, fertilized plot leaf litters accumulated N while ambient plot leaf litters lost N or accumulated less N than the fertilized leaf litters. (Fig. 3). Where the percent of initial N mass remaining differed significantly between N treatments, fertilized plot litter contained more N than did ambient plot litter. Set A maple and oak leaves generally accumulated N under fertilization and released N under ambient inputs, and differences between the two treatments were significant after 2–4 years. Set A oak leaves strongly accumulated N during the first year, then showed net N loss in year 2, while set B oak leaves experienced only modest net N uptake by the second year. Set A pine needles slowly and steadily released N over time (Fig. 3c) while set B pine needles showed net N accumulation after 2 years. N treatment had no effect on N dynamics in either set of pine litter beyond the first year. As noted above, differences in N dynamics between the two sets of leaf litters may have been influenced by the fact that the two sets had decomposed for different lengths of time prior to their first collection.

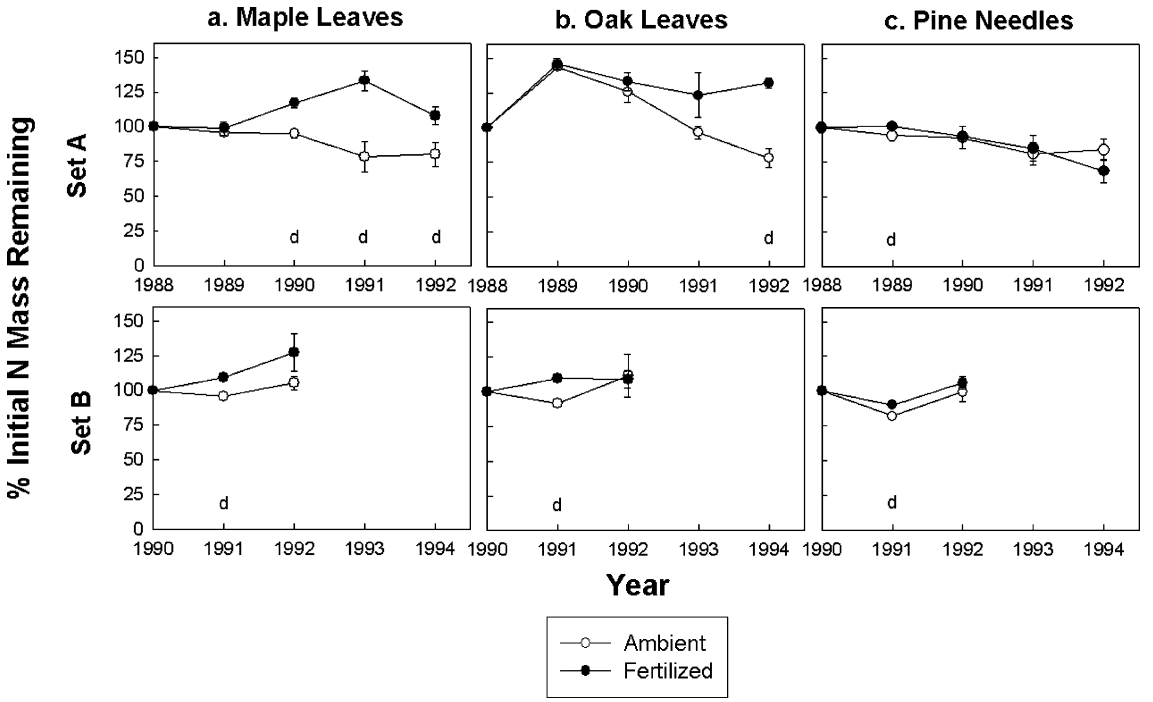

Fig. 3. Percent of original N mass remaining in litter incubated in fertilized (low N) and ambient (control) plots. (a) Maple and (b) oak litter data are from the hardwood stand and (c) pine needle litter data are from the pine stand. Error bars represent ±1 S.E.M. ($n = 6–8$). Letter 'd' indicates a yearly significant difference ($P < 0.05$) between the two N input levels.

Maple wood had the highest net N accumulation rates, taking up an additional 100–222% beyond the initial N mass (Fig. 4). Wood accumulated slightly more N in the hardwood stand than in the pine stand. Where significant treatment differences occurred, fertilization increased net N uptake. After 1 year, net N uptake rates were higher in the hardwood stand than in the pine stand where net changes were small. After 2 years, fertilization significantly increased net N accumulation in the pine stand but did not affect N dynamics in the hardwood stand.

5.3. ^{15}N content

^{15}N content increased in all litters during the first year of tracer additions. In the second year of additions, $\delta^{15}N$ values further increased, decreased, or remained the same. Differences between pre- and post-labeled material were always large, with average $\delta^{15}N$ values ranging from −4.2 to −2.3 in the former and from 45.8 to 404.1 in the latter.

5.4. ^{15}N tracer assimilation per unit mass

We examined whether litter types differed in their inherent ability to assimilate ^{15}N tracers on a per-unit-mass basis with regard to age, N loading, and tracer form. We calculated the proportion of applied tracer that was recovered, after 2 years of tracer additions, per Mg of the 1990 litter mass (Figs. 5 and 6). Any differences in tracer recovery are expected to be related to the inherent physical and chemical properties of the individual litter materials, although initial litter chemistry did not appear to be related to uptake of the two tracers.

Results of two-way ANOVA on 2-year-old set B litters indicate that N input level was a significant factor in percent recovery per Mg 1990 litter mass for all leaf litter types ($P < 0.001$), and tracer form was significant in maple leaves ($P < 0.001$) and pine needles ($P = 0.02$). The interaction term was significant for oak ($P = 0.02$) and maple leaf litters ($P < 0.001$). Maple leaf material had the highest

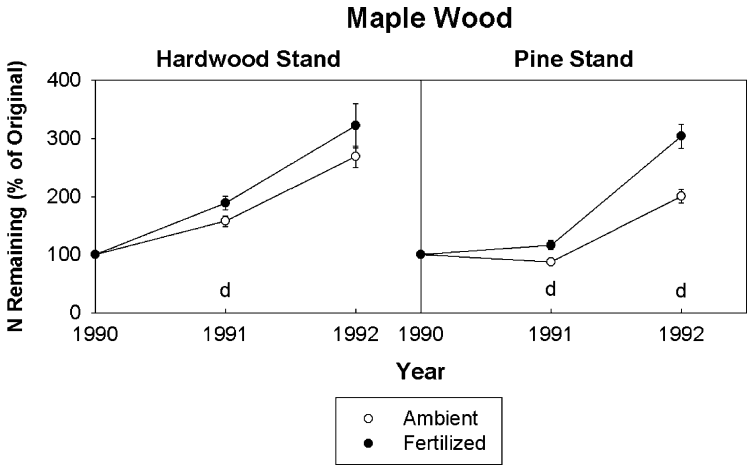

Fig. 4. Percent of original N mass remaining in maple wood chips incubated on fertilized and ambient (non-fertilized) plots in the hardwood stand and pine stand. Error bars represent ±1 S.E.M. ($n = 8$). Letter 'd' indicates a yearly significant difference ($P < 0.05$) between the two N input levels.

recoveries of both tracer forms per unit mass (Fig. 5). Pine needle material retained roughly half as much tracer as the other leaf litters (Fig. 5). Tracer uptake into wood was similar to pine needles, and was not different across both stands. Within the hardwood stand alone, only N input level was significant ($P = 0.007$), and $^{15}NO_3^-$ retention declined significantly with increased N load (Fig. 6). Overall, 2-year-old oak and maple leaf litters retained more tracer per unit mass than 2-year-old pine needles or wood.

For any given N input level and stand, retention of both tracer forms was similar except for ambient-treated maple leaf material which retained twice as much $^{15}NO_3^-$ as $^{15}NH_4^+$. However, increasing N inputs resulted in significantly decreased $^{15}NO_3^-$ uptake per unit mass in all 2-year-old litters.

Only limited comparisons were possible between the 2- and 4-year-old litters because set A litterbags received only one form of ^{15}N tracer per plot. Also, two set A sample ^{15}N results were determined to be outliers and their data were not used; so small sample size ($n = 1$ or 2 samples of set A materials) further limited our ability to detect significant differences. The only significant difference occurred in set A pine needle material under increased N input, which retained significantly less $^{15}NO_3^-$ than B material (t-test, $P = 0.03$). The data suggest that the capacities of 2- and 4-year-old litters to assimilate $^{15}NH_4^+$ do not differ greatly, and that the ability of maple and oak leaf material to assimilate $^{15}NH_4^+$ may decrease somewhat with age under ambient N inputs but not under increased N loading. Because set A maple and oak leaf litters did not receive $^{15}NO_3^-$, we do not know whether the strong $^{15}NO_3$ retention observed in set B was also present in the set A material.

5.5. ^{15}N tracer uptake into litter pools

We determined percent ^{15}N tracer recovery in 2- and 4-year-old litter pools for each litter type and added the results to obtain total percent tracer recovery at the stand level (Table 3). These values integrate differences in initial pool size and mass loss rates among litter types and N input levels as well as inherent species characteristics that affect litter ability to accumulate $^{15}NH_4^+$ and $^{15}NO_3^-$. Because set A data were available for only one or the other form of ^{15}N, we assumed equivalent uptake of $^{15}NH_4$ and $^{15}NO_3$ in set A litters. For woody litter pools, we let tracer recoveries observed in the hardwood stand represent recoveries in both stands, because we felt that the N dynamics of dominant species woody litter in the pine stand are more realistically represented by the N uptake properties of maple wood in its native hardwood stand.

Values given in Table 3 do not completely represent tracer assimilation into the recent (2- and 4-year-old) litter pool, for only the dominant species are repre-

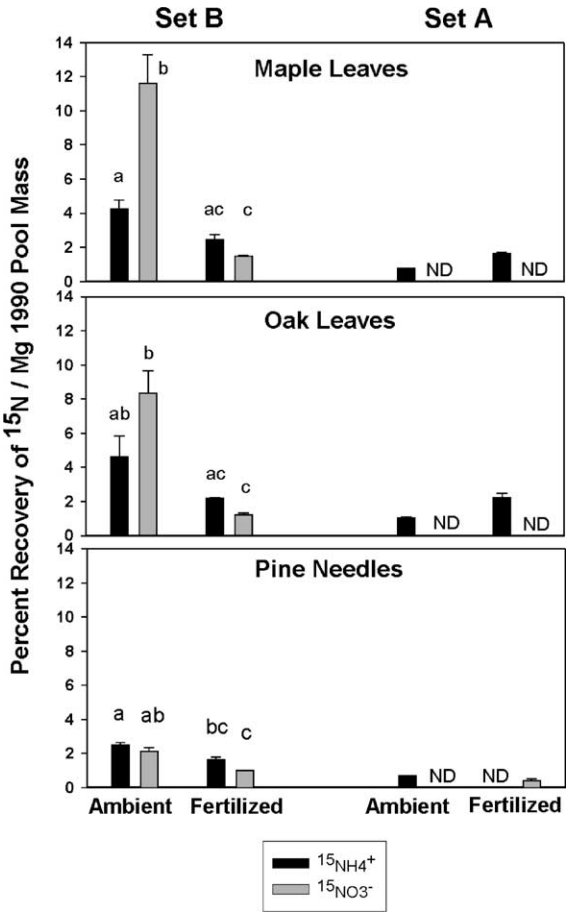

Fig. 5. Sink strengths of decomposing litter material for ^{15}N tracers, calculated as percent recovery of $^{15}NH_4^+$ and $^{15}NO_3^-$ labels per Mg initial litter mass under ambient and fertilized conditions after 2 years of label additions. Significant differences among set B means (two-way ANOVA and Tukey HSD post-hoc comparisons) are indicated by lower case letters. Error bars are ±1 S.E.M. (set A: $n = 2$, set B: $n = 2$–4) (note: $n = 1$ for set A ambient $^{15}NH_4^+$-treated maple leaves and oak leaves, for which values represent only one composited sample). Set A means were not significantly different from the corresponding means in set B. ND: data not available.

sented and woody litter input is estimated. However, litter masses are roughly comparable among the stands and treatments, and permit some general comparisons.

Litter pools assimilated significant amounts of tracers in both stands. Recoveries of the two tracer forms in the 2 + 4-year-old pools averaged 6–9% in pine stand plots and the hardwood fertilized plot. The hardwood stand ambient plot assimilated 20%, due to the high retention of $^{15}NH_4^+$ and especially $^{15}NO_3^-$ by the 2-year-old leaf litters. Differences among stands, plots, and N form retention in individual pools follow the same patterns as for tracer uptake per unit mass. The hardwood stand retained more tracer than the pine stand under each N input level even though the 2 + 4-year-old pools in 1992 were 23% smaller than pine stand pools (Table 2). Total 2 + 4-year-old pools in both stands retained more tracer under ambient compared to elevated inputs. Ambient plots accumulated more $^{15}NO_3^-$ than $^{15}NH_4^+$, although this difference was very slight in the pine stand. Fertilized plots in both stands accumulated less $^{15}NO_3^-$ than $^{15}NH_4^+$. Over all plots and tracer N forms, total tracer recovery in the combined 2 + 4-year-old pools ranged from 8 to 22% of total recovery in O horizon + mineral soil. ANOVA and post-hoc test results for tracer recoveries in set B pools are given in Table 3.

5.6. Uptake of N inputs into litter at stand level

N sink strength of the 2- and 4-year-old litter pools for ambient N deposition and fertilizer N inputs were estimated by multiplying tracer recoveries in the individual litter pools (Table 3) by the mass of N inputs over the 2-year labeling period. Results are given in Table 4.

Assimilation of $NH_4^+ + NO_3^-$ inputs into the 2 + 4-year-old litter pools ranged from 0.15 (pine ambient plot) to 0.86 g N m^{-2} (hardwood fertilized plot) over the 2 years. The greater N load with fertilization resulted in higher uptake in those plots even though tracer recoveries were lower than for ambient plots. The hardwood stand retained more N under both N input levels than did the pine stand as a result of higher tracer uptake per unit mass, despite its smaller 2 + 4-year-old litter pools. Retention of N inputs in pine stand litter increased five-fold under higher N inputs while the retention in the hardwood stand increased only three-fold.

Retention of NH_4^+ and NO_3^- inputs follows patterns of ^{15}N tracer uptake per unit mass by litter materials. Ambient pine plot litter retained similar amounts of the two N forms while ambient hardwood plot litter retained more NO_3^- than NH_4^+. Litter in fertilized plots in both stands assimilated more NH_4^+ than NO_3^-.

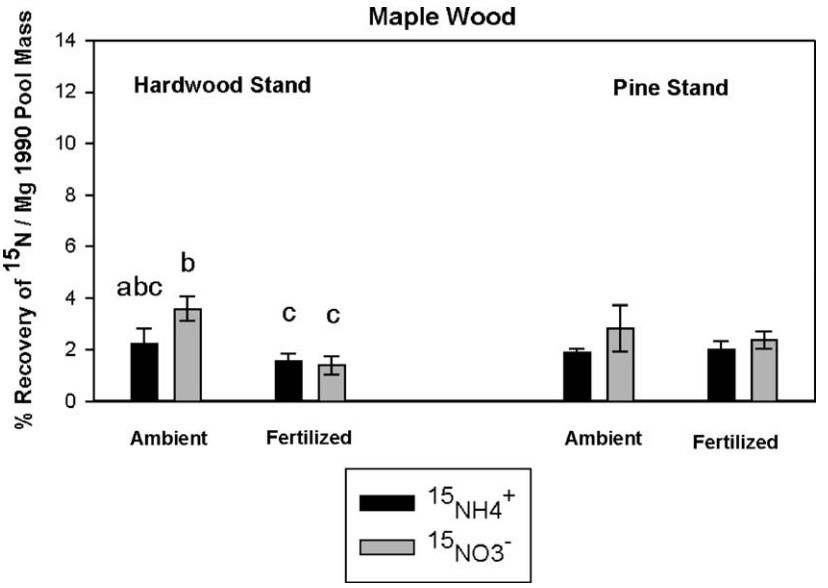

Fig. 6. Sink strength of decomposing maple wood for ^{15}N tracers, calculated as percent recovery of $^{15}NH_4^+$ and $^{15}NO_3^-$ labels per Mg estimated initial maple wood litter mass under ambient and fertilized conditions after 2 years of label additions. Significant differences among pine stand means (ANOVA, Tukey HSD post-hoc tests) are indicated by lower case letters. No significant differences were present in hardwood stand-incubated material. Error bars are ±1 S.E.M. ($n = 4$).

6. Discussion

6.1. Mass loss and N dynamics

Fog (1988) concluded that N additions generally have either no effect or a negative effect on decomposition in the long term. We observed all three effects over the 2–4 years of decomposition: fertilizer N additions depressed mass loss in maple and oak leaf litters, had no effect on pine needles, and increased mass loss in maple wood.

Where N input level influenced mass loss, this effect appeared to increase with litter age. Reduced decomposition rates in the fertilized oak and maple leaf litters could be caused by a shift in the decomposer population to a less efficient microflora (Fog, 1988), or by increased consumption of labile carbon in the early stages of decay as a consequence of N additions. N additions may also retard decomposition through suppression of lignolytic enzyme production (Keyser et al., 1978; Carreiro et al., 2000). Oak leaf lignin content is relatively high (25%), and lignin decomposition is known to decrease when the labile C supply is low and N availability is high (Reid, 1979; Magill and Aber, 1998). The high uptake of N into the maple wood chips during the second year served to enhance decomposition in this high C:N ratio material. Fertilization increased this effect in the hardwood stand but not in the pine stand, however, suggesting that the two stands possess different soil microflora. Magill and Aber (1998) found that pine needles and red maple leaves decomposed more rapidly in the hardwood stand than in the pine stand, further suggesting that soil microflora are functionally different in the two forests. Differences in soil microbial community structure among forest types and along fertility gradients has been demonstrated by Blagodatskaya and Anderson (1998) and Pennanen et al. (1999).

The effect of N addition on net N dynamics was also related to litter type and age, but data variability also increased with litter age, making it difficult to demonstrate trends or significant differences in older litter. Maple wood chips showed strong net N accumulation during the 2 years for which we have data; however, Downs et al. (1996) observed decomposition of the same material fertilized with NO_3^- at a separate site in eastern Maine (USA). They noted that although N content of maple wood chips was initially high under

Table 3
Percent recovery of 2-year tracer additions in 2-year-old (set B) and 4-year-old (set A) litter pools in 1992

Set	Litter type	Pine stand						Hardwood stand						Significant effects (two-way ANOVA)		
		Ambient			Fertilized			Ambient			Fertilized			N load	N form	Interaction
		$^{15}NH_4$	$^{15}NO_3$	Average	$^{15}NH_4$	$^{15}NO_3$	Average	$^{15}NH_4$	$^{15}NO_3$	Average	$^{15}NH_4$	$^{15}NO_3$	Average	*P*	*P*	*P*
B	Red maple leaves							0.88 a	2.40 b	1.64	0.67 ac	0.40 c	0.54	<0.001	<0.001	<0.001
	Black oak leaves							10.19 ab	18.30 b	14.28	4.26 ac	2.39 c	3.32	<0.001	0.148	0.023
	Red pine needles	6.01 a	5.12 ab	5.57	4.92 bc	2.97 c	3.95							<0.001	0.019	0.462
	Red maple wood	2.25[a]	3.59[a]	2.92[a]	1.55[a]	1.41[a]	1.48[a]	2.25 abc	3.59 b	2.92	1.55 c	1.41 c	1.48	0.007	0.204	0.122
A	Red maple leaves							0.07	0.07[b]	0.07	0.20	0.20[b]	0.20			
	Black oak leaves							1.05	1.05[b]	1.05	1.88	1.88[b]	1.88			
	Red pine needles	0.89	0.89[b]	0.89	0.62[b]	0.62	0.62									
Total		9.15	9.60	9.37	7.09	5.00	6.05	14.43	25.49	19.96	8.56	6.28	7.42			

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 differences (ANOVA and Tukey HSD post-hoc test, $P < 0.05$) in percent recoveries of $^{15}NH_4^+$ vs. $^{15}NO_3^-$ tracers across both levels of N loading are shown using different letters within rows. ANOVA was not possible for set A litters because they received only one form of tracer, due to litterbag locations within plots.

[a] Estimated to be equivalent to wood in the hardwood stand.

[b] Estimated values.

Table 4
Total ambient N and fertilizer plus ambient N inputs assimilated by litter pools over 2 years

Set	Litter type	Pine stand						Hardwood stand					
		Ambient N deposition			Fertilizer plus ambient N			Ambient N deposition			Fertilizer plus ambient N		
		NH_4 (0.8 g N m^{-2} for 2 years)	NO_3 (0.8 g N m^{-2} for 2 years)	Total	NH_4 (5.8 g N m^{-2} for 2 years)	NO_3 (5.8 g N m^{-2} for 2 years)	Total	NH_4 (0.8 g N m^{-2} for 2 years)	NO_3 (0.8 g N m^{-2} for 2 years)	Total	NH_4 (5.8 g N m^{-2} for 2 years)	NO_3 (5.8 g N m^{-2} for 2 years)	Average
B	Red maple leaves							0.007	0.019	0.026	0.039	0.023	0.062
	Black oak leaves							0.081	0.147	0.229	0.247	0.139	0.386
	Red pine needles	0.048	0.04	0.089	0.285	0.172	0.458						
	Red maple wood	0.018[a]	0.029[a]	0.047[a]	0.090[a]	0.082[a]	0.172[a]	0.018	0.029	0.047	0.090	0.082	0.171
A	Red maple leaves							0.0006	0.0006[b]	0.001	0.012	0.012[b]	0.023
	Black oak leaves							0.008	0.008[b]	0.017	0.109	0.109[b]	0.218
	Red pine needles	0.007	0.007[b]	0.014	0.036[b]	0.036	0.072						
Total N mass assimilated	0.07	0.08	0.15	0.41	0.29	0.70	0.12	0.20	0.32	0.50	0.36	0.86	

Notes: Atmospheric inputs are assumed to be composed of equal amounts of NO_3^- and NH_4^+. Set B was 2 years old and set A was 4 years old at the end of the 2 years.

[a] Estimated to be equivalent to wood in the hardwood stand.

[b] Estimated values.

increased N deposition, it fell below that of unfertilized maple wood chips after 3 years. That N immobilization in maple wood was more enhanced by fertilization in the pine stand than in the hardwood stand again suggests that the microflora were functionally different in the two stands.

Some differences in mass loss and net N dynamics were observed between the two sets of leaf litters during their initial 2 years. Because set B decomposed for only 6 months before its first collection while set A had a full initial year in the field, set B decomposition may have been at an earlier stage than set A when first-year analyses were made. Taking this into account, the first-year mass loss, net N immobilization, and net N mineralization rates in set B litter would be somewhat higher than reported here. This could account for some but not all of the variation we observed between the two sets. Differences between the two sets may also be related to possible shifts over time in decomposer populations and degree of C limitation, as a consequence of continuing N additions. Climatic variation between the two periods (1988–1990 and 1990–1992) was not likely a factor, for differences were negligible except that summer temperatures in 1992 averaged 4 °C lower than the other years. We would expect labile C stocks to have decreased in the fertilized plots over time, slowing decomposition and reducing net N immobilization in the litter (Flanagan and Van Cleve, 1983; Bååth et al., 1981) However, three of the litters experienced higher net N incorporation in the fertilized plots than in the ambient plots, over time. This suggests that pine stand litter should decay more slowly in the fertilized plot, but we did not observe this in pine needles or maple wood in that stand, and N loading had only minor effects on N dynamics in the pine needles. Magill and Aber (1998) did observe decreased pine needle mass loss in the pine stand under higher fertilizer N inputs (1.5 g N m^{-2} per year) after 4 years. For longer-term N input effects on decomposition in these stands, see Magill and Aber (1998) for results of their 6-year study.

6.2. NH_4^+ and NO_3^- assimilation

Litter assimilation of labeled NH_4^+ and NO_3^- per unit mass was stronger in the maple and oak leaf litters than pine needles and wood, suggesting that the hardwood stand litter has a higher inherent capacity to assimilate atmospheric N inputs, especially NO_3^-, than does pine forest litter.

Two-year-old materials showed decreased assimilation of $^{15}NO_3$ per unit mass relative to $^{15}NH_4$ with increasing N addition, and this decrease was strongest in the hardwood leaf litters. This suggests that the dominant litters in the two stands will be less capable of assimilating future increases in atmospheric N deposition, particularly with regard to NO_3^- deposition to hardwood leaf litter.

How retention of NH_4^+ and NO_3^- per unit initial mass change as decomposition progresses is less clear. It appears that the sink strength of litter materials decreases somewhat with age in most cases, and that, in contrast to the younger litter, inherent N sink strength in older oak and maple leaf litter material may increase under higher N deposition loads.

6.3. Litter retention of N inputs to the ecosystem

We estimate that on an annual basis the 2 + 4-year-old decomposing litter pools in the pine and hardwood stands retained 0.08 and 0.16 g N m^{-2} per year, or 10 and 20% of current atmospheric N deposition. Estimated retention of fertilizer + ambient inputs are 0.35 and 0.42 kg N m^{-2} per year (pine and hardwood stands), or 12 and 15% of elevated inputs. We expect that retention would be significantly greater if 1- and 3-year-old pools were included in the estimates. These decomposing litter pools clearly demonstrate the potential to assimilate a significant proportion of N deposition at current and future predicted rates.

Our results are comparable to findings of other field decomposition studies. Koopmans et al. (1998) found that, after 1 year of decomposition, Douglas-fir and Scots pine needle litter retained 0.03 g N m^{-2} per year of ^{15}N-labeled throughfall NH_4^+ inputs at low input rates (0.4–0.6 g N m^{-2} per year), or 9% of the NH_4^+ inputs. Litter in plots receiving ^{15}N-labeled NH_4^+ at the rate of 4–4.5 g N m^{-2} per year retained 0.2 g NH_4^+-N m^{-2} per year, or 4–7% of inputs. In a mixed forest in Maine where plots received chronic additions of ^{15}N-labeled HNO_3^-, Downs et al. (1996) estimated that over 4 years, one cohort of decomposing litter could immobilize 0.10–0.15 g NO_3^--N m^{-2} per year, or about half the ambient NO_3^- deposition rate at that site. Magill and Aber (1998) calculated

higher N retention when they considered long-term changes in litterfall inputs, and changes in accumulation and N content of newly formed humus as a result of reduced litter decay under high N additions at the Chronic Nitrogen Amendment study. They estimated that up to 1.5 g N m^{-2} per year can be incorporated into the forest floor, which is nearly twice the ambient deposition rate and also equivalent to 10% of the annual high N addition rate.

Nitrogen uptake and release have been found to occur simultaneously during litter decomposition. Litter decomposition studies using ^{15}N tracers or ^{15}N-labeled litter (Berg, 1988; Van Vuuren and Van Der Eerden, 1992; Downs et al., 1996; Koopmans et al., 1998; Zeller et al., 2000) observed that exogenous N inputs were both incorporated and released along with net release of litter N over time. Undoubtedly, litters in our study released a portion of the labeled N inputs they assimilated during the 2 years. Percent tracer retention and calculated uptake of N reported here represent net uptake of tracers into litter at the end of the period.

The 2 + 4-year-old litter pool assimilated more N inputs in the hardwood stand than in the pine stand at both N loading rates. This may be attributable to a greater inherent ability of hardwood leaf litter to assimilate N. As such, recently formed decomposing litter in the hardwood forest may be a larger sink for atmospheric N deposition than in the pine forest. However, with increased N loading, N uptake into the pine forest litter increased at a greater rate than the oak forest litter, suggesting that N sink strength of the pine stand litter pool may become relatively more important under higher N deposition loads.

At the current N deposition rate, hardwood stand litter assimilated more NO_3^- than pine stand litter. This suggests that the effects of NO_3^- leaching, which increases with the approach of N saturation, may be ameliorated to some degree by the litter in the hardwood forest. This idea is consistent with results from the Chronic Nitrogen Amendment study in which increased NO_3^- leaching losses in the High N plots began to occur much sooner in the pine stand (year 3 of fertilizer additions) than in the hardwood stand (year 7 of fertilizer additions) (Magill et al., 2000). However, under increased N inputs, our results indicate that litter pools in both forests assimilate less NO_3^- relative to NH_4^+, suggesting that litter sink strength for NO_3^- inputs will effectively decline relative to increasing N deposition rates.

Our limited results for the 4-year-old litter suggest that inherent NH_4^+ sink strength per unit mass did not decrease greatly over the second and fourth years of decomposition. We speculate that the 4-year-old litter pool may be a more important N sink under future increased N deposition than it is under present rates.

7. Conclusion

In this paper we make ecosystem-scale estimates of the importance of recently formed litter as a sink for atmospheric N deposition. Our results demonstrate that litter type, litter age, N input level, and form of N inputs influence the retention of N inputs to litter pools into a pine plantation and a mixed hardwood forest ecosystem.

Although our study did not examine total litterfall inputs, it is clear that the two cohorts of dominant leaf litters we studied are capable of retaining significant amounts of N deposition in the two forests. Decomposing 2 + 4-year-old litter pools in both stands assimilated significant amounts of both ambient and elevated N inputs and they represented a significant proportion of tracer N uptake in the soil profile. Our results demonstrated differences in litter sink strength for NH_4^+ and NO_3^- deposition between the two forests, and that the potential for these forests to assimilate N may change with litter age and the rate and chemical composition of N deposition. Knowledge of these factors will be useful in predicting changes in forest N storage as forests continue to be exposed to increasing atmospheric N deposition.

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