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CANOPY TREE–SOIL INTERACTIONS WITHIN TEMPERATE FORESTS: SPECIES EFFECTS ON SOIL CARBON AND NITROGEN

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Abstract. In a northwestern Connecticut forest, we quantified the carbon (C) and nitrogen (N) content of the forest floor and the top 15 cm of mineral soil and the rate of midsummer net N mineralization beneath six different tree species. There were large interspecific differences in forest floor depth and mass, in the size and distribution of C and N pools at varying soil depths, and in rates of midsummer net N mineralization and nitrification. Forest floor mass ranged from 3.2 kg/m^2 to 11.0 kg/m^2 and was smallest beneath sugar maple and largest beneath hemlock. The pool size of C in the forest floor ranged from 1.1 kg/m^2 to 4.4 kg/m^2 while the N content of the forest floor ranged from 83 g/m^2 to 229 g/m^2. Forest floor C and N pools were smallest beneath sugar maple and highest beneath hemlock. Soil C:N ratios (range: 14.8–19.5) were lower beneath sugar maple, red maple, and white ash than beneath beech, red oak, and hemlock, whereas the opposite was true of the midsummer rate of net N mineralization (range: 0.91–2.02 g·m^{-2}·28 d^{-1}). The rate of net nitrification was positively correlated with the rate of net N mineralization. Interspecific differences in litter production and quality explain the large differences among species in the size of the forest floor C and N pools and in net N mineralization rates. The differences in the size and distribution of C and N pools beneath the different species suggest that the mechanisms regulating the process of species replacement in these forests will mediate the effects of anthropogenic, environmental changes in soil C and N dynamics.

Key words: carbon; ecosystem; forest; nitrogen; soils, forest.

INTRODUCTION

There is increasing interest in linking forest dynamics to ecosystem processes because human-induced environmental changes are likely to change forest composition (Bolker et al. 1995), net primary production, and consequently regional patterns of carbon (C) and nitrogen (N) cycling (Pastor and Post 1988). For example, using the LINKAGES model, Pastor and Post (1988) found that changes in temperature and precipitation resulting from an increase in atmospheric CO_2 concentrations caused a northward migration of the hardwood–conifer forest border in North America. The transition from conifer- to hardwood-dominated forests led to increases in net primary production and N availability because hardwood species had high intrinsic growth rates, high tissue N concentrations, and rapid rates of litter decomposition.

The LINKAGES model of Pastor and Post (1986) is currently the only model that links forest tree recruitment, birth, and death processes with spatial and temporal changes in C and N cycling. Simulations with LINKAGES show that C and N turnover in forests is dependent upon the species composition of forests because species differ widely in their effect on N availability. In LINKAGES, each tree occupies a single cell (0.1 ha). The submodel that describes the effect of a tree species on C and N cycling within a cell is calibrated from data on the effect of that tree species on C and N cycling in a monodominant stand. An implicit assumption of the model is that the effect of an individual tree growing in isolation is identical to the effect of several trees of the same species growing in proximity to one another.

If variation in the C and N content of soils at the scale of individual canopy trees occurs, then stand-level estimates of the sizes of these pools at any given time will depend upon the mix of species present at a site as predicted by the LINKAGES model. There is considerable evidence that temperate and conifer tree species growing in monodominant stands alter soil C and N dynamics (e.g., Challinor 1968, Mladenoff 1987, Boerner and Koslowsky 1989, Boettcher and Kalisz 1989, France et al. 1989, Binkley et al. 1992, Gower and Son 1992, Son and Gower 1992, Binkley 1995, Reich et al. 1997), and the effects of tree species on surface soil C and N dynamics can occur over short time scales (Gower and Son 1992, Binkley 1995). To date, however, there have only been a few characteri-

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zations of C and N cycling beneath individual trees. Zinke (1962) found elevated total soil N concentrations (in grams of nitrogen per gram of soil) beneath the canopy of *Pinus contorta.* Boettcher and Kalisz (1989) found significant differences in mineralizable N under tulip poplar and hemlock canopies in the mountains of Kentucky. Boerner and Koslowsky (1989) found significant differences in midsummer net N mineralization, and organic C and PO_4^{3-} concentrations beneath individual sugar maple, white ash, and beech trees growing in mixed-species forests of Ohio. These three studies were limited to one, two, and three species, respectively, and the generality of their results to more diverse forests is unknown. The objective of this study was to characterize the size of the C and N pools in the forest floor and mineral soil beneath the canopies of six different tree species dominant in mid- to late-successional forests of southern New England.

Materials and Methods

Study sites and sampling protocol

This research was conducted at two sites on the Canaan Mountain Plateau at elevations of 300–500 m in northwestern Connecticut (42° N, 73°15′ W). One site was located on land belonging to the Bridgeport Hydraulic Company (BHC) near the Wangum Reservoir. The second stand was located within the Great Mountain Forest (GMF) east of Wampee pond. Soils in both sites, hereafter referred to as Wampee and Wangum, are well-drained, sandy loams classified as Typic Dystrochrepts (Hill et al. 1980). Soils at each site were sampled beneath the canopies of the six dominant tree species, which included: beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* Carr.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and northern red oak (*Quercus rubra* L.).

At each site, we randomly located six replicate trees of each species ($N = 72$). Beneath each target tree we used a galvanized iron probing rod to identify two sampling points that had a mineral soil depth of at least 15 cm. The sampling points were normally 0.5–5 m apart from one another, and each was located beyond the edge of the stemflow zone surrounding the tree (>2 m, Boerner and Koslowsky 1989) but still within the vertically projected crown of each target tree. At each sampling point we obtained two 5 cm diameter × 15 cm depth soil cores. The first core was used to sample the forest floor and several centimeters of mineral soil. The second core, located immediately adjacent to the first, contained the top 0–15 cm of mineral soil. We obtained samples using soil bulk density samplers fitted with vertically precut, polycarbonate liners. After each core was extracted, the liner was removed, capped, and brought back to the laboratory.

Laboratory methods

The cores were cut with a sharp knife along the vertical division in the polycarbonate liner and separated into three soil horizons: forest floor, 0–7.5 cm mineral soil, and 10–15 cm mineral soil. Typically, forest floor material was <7.5 cm deep, in which case the 0–7.5 cm mineral soil layer was taken from the first core. If the forest floor was >7.5 cm, the 0–7.5 cm, and 10–15 cm mineral soil layers were separated from the second soil core. In all cases, the 10–15 cm mineral soil layer was removed from the second soil core.

For each sample, forest floor depth was recorded, samples were sieved through an 8-mm mesh to remove roots, and sieved samples were dried for 4 d at 105°C and weighed. The forest floor samples were reduced to a fine powder in a tissue pulverizer prior to analysis. Mineral soil samples were first dried for 4 d at 105°C and then sieved through an 8-mm mesh sieve to remove root material and stones (>1.0 cm diameter). Dry soil and large stones were weighed. Stone bulk density was estimated from a subsample of stones (calculated to be 2.61 g/cm^3) and soil bulk density measurements were adjusted accordingly.

Characterization of C and N pools and midsummer net N mineralization

Forest floor and mineral soil were analyzed on a Carlo Erba NA 1500 Analyzer (CE Elantech, Milan, Italy). Samples were combusted at 1020°C followed by chromatographic analysis of N_2 and CO_2 using 5–20 mg of sample previously ground in a Fritsch ballmill. Acetanilide (C_8H_9N) was used as a standard for both C and N. Analytical error was <5%. The 7.5–10 cm mineral soil horizon was not analyzed. Because the dark-colored, organic-rich A horizon was usually shallower than 5 cm, and the brown B-horizon started within 7.5 cm of the mineral soil surface and extended beyond 15 cm depth, we assumed the 7.5–10 cm layer had the same soil C and N concentrations as that of the 10–15 cm mineral soil layer.

In situ rates of net N mineralization beneath each of the canopy tree species ($N = 72$) were measured for a 28-d period from mid-July to mid-August during the summer of 1991 at the sample locations used for the analysis of C and N, using a modification of the buried bag procedure (Eno 1960). We used a soil corer (2.5 cm diameter × 15 cm depth) to obtain an initial sample that was placed in a plastic bag and brought back to the laboratory for analysis. Immediately adjacent to the initial sample, we cored soils using a soil bulk density sampler (5 cm diameter × 15 cm depth). Each intact soil core was wrapped in a polyethylene bag, capped, replaced into the hole from which it was extracted, and retrieved after 28 d (herein referred to as the incubated sample). Both the initial and incubated soil cores contained the forest floor and mineral soil. Identical laboratory procedures were used for both the initial and the incubated samples. The samples were sieved through an 8-mm mesh to remove fine roots and large stones. Twenty-gram subsamples were placed into extraction cups to which 200 mL of 2 mol/L KCl was

TABLE 1. Between-site comparisons of forest floor mass, soil C and N pools, C:N ratio, and midsummer net N mineralization and nitrification.

Soil property	Wampee	Wangum
Forest floor mass (kg/m^2)^{NS}	6.3 ± 0.8	6.1 ± 0.6
Mass carbon (kg/m^2)***	9.8 ± 0.3	8.2 ± 0.3
Forest floor^{NS}	2.6 ± 0.3	2.1 ± 0.3
0–7.5 cm mineral soil^{NS}	4.0 ± 0.1	3.6 ± 0.1
7.5–15 cm mineral soil***	3.2 ± 0.2	2.6 ± 0.1
Mass nitrogen (g/m^2)***	630.1 ± 23.1	482.4 ± 17.2
Forest floor	137.1 ± 13.6	128.8 ± 17.5
0–7.5 cm mineral soil***	270.0 ± 9.2	211.5 ± 9.3
7.5–15 cm mineral soil***	223.0 ± 15.8	142.1 ± 7.2
C:N ratio**	16.6 ± 0.4	17.7 ± 0.4
Forest floor*	18.9 ± 0.7	16.8 ± 0.9
0–7.5 cm mineral soil***	15.5 ± 0.6	17.3 ± 0.6
7.5–15 cm mineral soil***	15.2 ± 0.5	18.9 ± 0.7
Net N mineralization ($g\ N \cdot m^{-2} \cdot 28\ d^{-1}$)*	1.18 ± 0.14	1.82 ± 0.23
Net nitrification ($g\ NO_3 \cdot m^{-2} \cdot 28\ d^{-1}$)*	0.44 ± 0.09	1.26 ± 0.24

Note: Each entry is the mean ± 1 SE. Significance levels are: NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

added. The extraction cups were capped and the samples were shaken for eight 1-min periods over 1 h and allowed to settle overnight. The supernatant was analyzed for NH_4^+ and NO_3^- concentrations on an Alpkem Enviroflow Analyzer (Model 3590, Alpkem Flow Solutions III, Alpkem, Wilsonville, Oregon, USA). Ammonium concentrations were measured using the phenate method. NO_3^- concentrations were measured using cadmium diazotization. The remaining sample material was dried for 4 d at 70°C to determine soil bulk density and soil dry mass.

Net N mineralization was calculated as the difference in the concentration of inorganic N (NH_4^+ and NO_3^-) ions in the incubated and initial sample. Net nitrification was calculated as the difference in the NO_3^- concentration in the incubated and initial sample. Net N mineralization and nitrification are expressed in units of grams per square meter per 28 d.

Statistical analysis

The data were analyzed as a factorial design using PROC GLM in SAS (1987). There were two independent variables: sites (two levels), and species (six levels). The dependent variables were forest floor mass, the C and N content of each soil horizon, the C:N ratio of each soil horizon, and midsummer net N mineralization and net nitrification. Because of the strong depth gradient in C and N content, we analyzed differences among species and sites separately for each soil horizon. Assumptions of normality and homogeneity of variance were met. We used Tukey's test for post hoc mean comparisons for each of the main effects (site, species). This test protects the experimentwise alpha at 0.05.

RESULTS

Forest floor mass and soil bulk density

Forest floor mass did not differ between sites (Table 1) but differed significantly beneath the different tree species (Table 2). Forest floor mass was lowest beneath sugar maple and highest beneath hemlock. Soil bulk density increased significantly with increasing depth (forest floor = 0.17 g/cm^3, 0–7.5 cm mineral soil = 0.63 g/cm^3, lower 10–15 cm mineral soil = 0.99 g/cm^3, df = 2, 201, $F = 529.3$, $P < 0.001$). The bulk density at a given depth did not differ among species.

Soil carbon

Carbon pools were largest in the upper 7.5 cm of mineral soil and lowest in the forest floor (forest floor = 2335 g/m^2, 0–7.5 cm = 3772 g/m^2, 7.5–15 cm = 2877 g/m^2, df = 2, 168, $F = 47.4$, $P < 0.001$). Carbon pools in the forest floor and mineral soil layers were slightly but consistently higher at Wampee than at Wangum, leading to a significant difference in the total quantity of C (=forest floor C + 0–15 cm mineral soil C) between sites (Table 1).

The total quantity of C was lowest beneath white ash and significantly greater beneath hemlock (Table 2). There was no significant variation in total C among the five hardwood species (Table 2). Forest floor C varied from 1.1 kg/m^2 beneath white ash to 4.4 kg/m^2 beneath hemlock (Fig. 1A). The variation among species in the mass of C in the forest floor paralleled the variation among species in forest floor mass (Table 2).

TABLE 2. Differences in forest floor mass, soil C and N pools, and soil C:N ratio among tree species. Mean values are reported ± 1 SE.

Variable	Sugar maple	White ash	Red maple	Beech	Red oak	Hemlock
Forest floor mass (kg/m^2)***	3.2 ± 0.6^c	3.2 ± 0.8^c	5.6 ± 0.9^{bc}	6.1 ± 0.8^{bc}	8.1 ± 0.1^{ab}	10.9 ± 1.6^a
Mass carbon (kg/m^2)***	8.1 ± 0.6^b	8.1 ± 0.6^b	8.7 ± 0.5^b	8.2 ± 0.5^b	9.4 ± 0.4^{ab}	10.8 ± 0.6^a
Mass nitrogen (g/m^2)*	555.0 ± 45.8^{ab}	563.2 ± 54.8^{ab}	589.6 ± 47.9^a	462.9 ± 31.1^b	507.7 ± 21.2^{ab}	577.6 ± 26.8^{ab}
C:N ratio***	15.0 ± 0.6^b	14.8 ± 0.6^b	15.3 ± 0.7^b	18.5 ± 0.5^a	19.2 ± 0.7^a	19.5 ± 0.6^a
Forest floor***	15.0 ± 1.4^b	15.1 ± 1.0^b	14.4 ± 0.1^b	20.7 ± 0.7^a	21.1 ± 1.3^a	20.2 ± 1.0^a
0–7.5 cm mineral soil***	14.1 ± 0.3^c	13.9 ± 0.5^c	17.1 ± 1.9^{bc}	17.2 ± 0.8^{ab}	19.4 ± 1.1^a	19.4 ± 0.8^a
10–15 cm mineral soil^{ns}	17.1 ± 0.9	15.4 ± 1.0	14.4 ± 0.6	17.5 ± 0.8	17.2 ± 0.7	18.9 ± 1.4

Note: Row values with different superscript letters are significantly different from one another. Significance levels are: NS = not significant, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

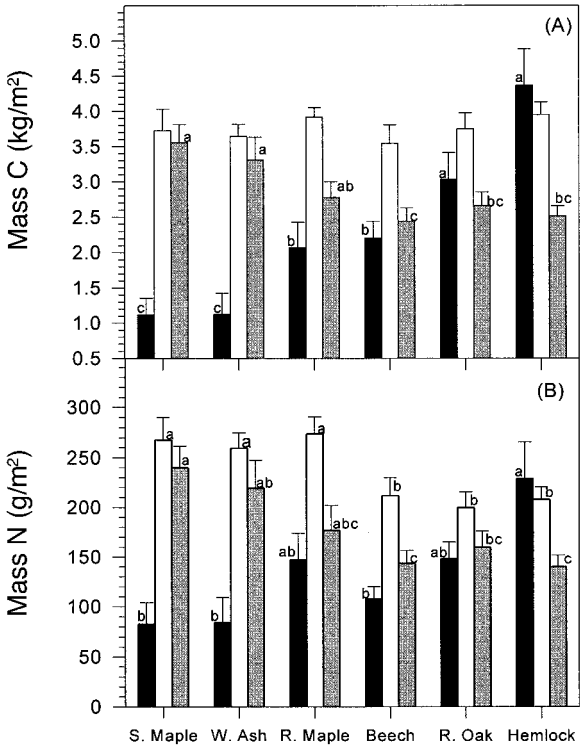

FIG. 1. (A) The mean (+1 SE) content of C beneath the canopies of the six tree species at three depths. (B) The mean (+1 SE) content of N beneath the canopies of the six tree species at three depths. In each panel, bars of the same color with different superscript letters are significantly different from one another at the $P < 0.001$ level. Black bars correspond to forest floor. White and gray bars correspond to the 0–7.5 and 7.5–15 cm mineral soil horizons, respectively. S. Maple = sugar maple, W. Ash = white ash, R. Maple = red maple, R. Oak = red oak.

The C pool in the 0–7.5 cm mineral soil layer was not significantly different among species (Fig. 1A). The C pool in the 7.5–15 cm mineral soil layer was significantly higher under sugar maple (3.6 kg/m^2) than under beech (2.4 kg/m^2), red oak (2.7 kg/m^2), and hemlock (2.6 kg/m^2, Fig. 1A). The differences among species in the size of the forest floor C pool were offset by differences in the 7.5–15 cm mineral soil layer, leading to relatively small differences among species in total soil C (Fig. 1A, Table 2).

Soil nitrogen

Nitrogen in the 0–7.5 cm mineral soil layer (241 g/m^2) was significantly greater than in the 7.5–15 cm mineral soil layer (181 g/m^2), which was significantly greater than in the forest floor (133 g/m^2, df = 2, 168, $F = 51.69$, $P < 0.0001$). The N content of the three soil layers was significantly lower at Wangum than at Wampee (Table 1).

The total quantity of N was significantly higher beneath red maple than beech (Table 2) and the total quantity of N beneath all species was greater at Wampee than at Wangum with the exception of hemlock (Table 3). The N pool in the forest floor was smallest beneath white ash (81.1 g/m^2) and largest beneath hemlock (229.1 g/m^2) with the differences among species paralleling those of the forest floor mass (Fig. 1B, Table 2). The N pool in the 0–7.5 cm mineral soil layer was significantly smaller beneath beech, red oak, and hemlock, than beneath red maple, white ash, and sugar maple (Fig. 1B). The N pool in the 7.5–15 cm mineral soil layer was largest beneath sugar maple (242.8 g/m^2) and smallest beneath hemlock (140.1 g/m^2, Fig. 1B). As with C, the large differences among species in the size of the forest floor N pool were offset by the differences in the N pool size of the mineral soil horizons, leading to relatively few differences among species in total soil N (Table 2).

Soil C:N ratio

The forest floor C:N ratio (17.8) was significantly higher than the 0–7.5 cm of mineral soil (16.4) but not significantly different from the C:N ratio in the lower 7.5–15 cm of mineral soil (17.0) (df = 2, 173, $F = 3.37$, $P < 0.05$) (Table 1). The C:N ratio of the forest floor at Wangum was higher than at Wampee, whereas the opposite was true of the mineral soil layers (Table 1). Averaged across the forest floor and mineral soil horizons, C:N ratios were significantly higher at Wangum (17.7) than at Wampee (16.4, Table 1).

Soil C:N ratios were significantly lower beneath sugar maple, white ash, and red maple than beneath hemlock, beech, and red oak (Table 2). The largest differences among species were in the C:N ratio of the forest floor and the 0–7.5 cm mineral soil layer (Table 2). There were no significant differences among species in the C:N ratio of the 7.5–15 cm mineral soil layer (Table 2).

Midsummer net N mineralization

Midsummer net N mineralization and nitrification were significantly higher at Wangum than at Wampee (Table 1). Rates of midsummer net mineralization and

TABLE 3. The total mass of N (= forest floor + mineral soil layers) beneath the six study species at each study site. The site × species interaction term was significant: df = 5, 53, $F = 3.72$, $P < 0.01$.

Variable	Sugar maple	White ash	Red maple	Beech	Red oak	Hemlock
Mass nitrogen (g/m^2)						
Wampee	661 ± 44	726 ± 82	686 ± 82	553 ± 27	552 ± 28	545 ± 33
Wangum	485 ± 55	455 ± 21	510 ± 33	388 ± 24	463 ± 20	617 ± 40

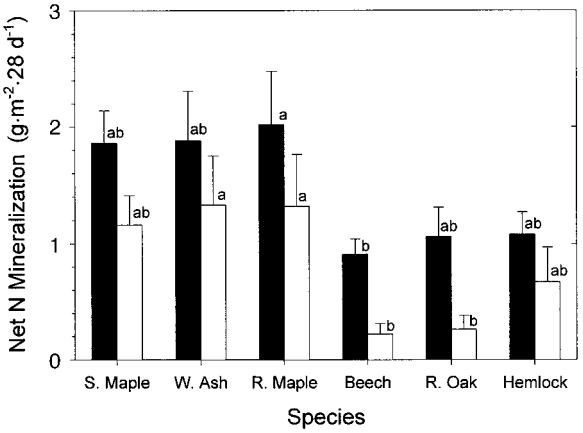

FIG. 2. The mean (+1 SE) rate of net N mineralization and net nitrification beneath the canopies of the different tree species. Bars of the same color with different superscript letters are significantly different from one another at $P < 0.05$. Black bars correspond to net N mineralization; white bars correspond net nitrification. S. Maple = sugar maple, W. Ash = white ash, R. Maple = red maple, R. Oak = red oak.

nitrification were nearly twofold higher beneath red maple, sugar maple, and white ash than beneath red oak, beech, and hemlock (Fig. 2). However, net N mineralization was only significantly different between red maple and beech. Net nitrification was highest beneath red maple and white ash, and significantly different from beech and red oak (Fig. 2). Averaged for each tree species, the rate of net N mineralization was negatively correlated with the C:N ratio of the forest floor and mineral soil (Fig. 3A, $N = 6$, $P < 0.01$, $r^2 = 0.94$). Conversely, the average rate of net nitrification was positively correlated with the average rate of net N mineralization (Fig. 3B, $N = 6$, $P < 0.01$, $r^2 = 0.90$).

DISCUSSION

Carbon and nitrogen pools

Variation in the size and distribution of C and N pools and in net N mineralization among sites and species appears to be regulated by a combination of interspecific differences in litter production and the rate of litter decomposition (Melillo et al. 1982, 1989, Prescott et al. 1993, Stump and Binkley 1993). Ferrari (1993) measured leaf litter production in hemlock- and sugar-maple-dominated stands growing on the same soil type in Sylvania, northern Michigan. Using the field-calibrated models of leaf litter disperal from adult trees presented in Ferrari and Sugita (1996), we calculated that a 50 cm diameter sugar maple tree produces 5.7 $kg \cdot m^{-2} \cdot yr^{-1}$ of leaf litter while the same size hemlock produces 11.9 $kg \cdot m^{-2} \cdot yr^{-1}$ of the leaf litter. Although leaf litter production is likely to differ between northern Michigan and northwestern Connecticut due to regional variation in temperature and precipitation, the large differences in litter production between these species is likely to have contributed to the difference in the mass and size of the forest floor C and N pools beneath their canopies. Assuming that the rates of litter production in Ferrari and Sugita (1996) are representative of the differences in litter production between sugar maple and hemlock at GMF, the ~2.1-fold difference in litter production between these two species is smaller than the difference in forest floor mass (~3.4-fold), C content (~3.9-fold), and N content (2.8-fold) despite similar leaf litter C and N concentrations (sugar maple: 49.2% C, 0.81% N; hemlock: 54.5% C, 082% N; A. C. Finzi, *unpublished data* for adult trees at GMF). Thus, interspecific differences in litter production alone are not sufficient to explain the differences in sizes of these pools beneath sugar maple and hemlock.

Litter with a high carbon : nitrogen (C:N) ratio or a high lignin : nitrogen ratio decomposes more slowly than litter with a low C:N or lignin : N ratio (Melillo et al. 1982, Prescott et al. 1993, Stump and Binkley 1993, Prescott 1995). Subtle differences in the rate of litter decomposition spanning temporal scales of decades to centuries can lead to large differences in organic matter accumulation and the C and N content of soils (Parton et al. 1987). C:N and lignin : N ratios are typically lower in sugar maple, white ash, and red maple leaf litter than in beech, red oak, and hemlock leaf litter (Melillo et al. 1982, Pastor et al. 1984, Finzi and

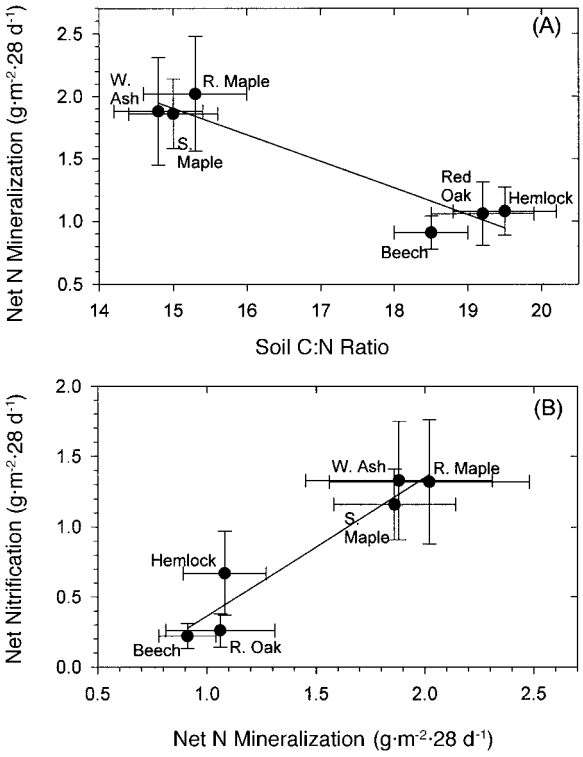

FIG. 3. (A) A regression of net N mineralization on the average C:N ratio of the forest floor and mineral soil beneath each canopy tree. (B) A regression of net nitrification on the average rate of net N mineralization beneath each canopy tree during a single midsummer incubation.

Canham, *in press*). Hemlock litter is also high in tannic acid content, which reduces its rate of decomposition (White 1986, 1991). Therefore interspecific differences in litter quality (C:N and lignin : N ratios) are likely to have influenced the mass, C, and N content of the forest floor beneath the different tree species.

The size of the forest floor and its C and N content may also be related to soil pH. In a companion study, Finzi et al. (1998) found that forest floor pH ranged from 3.8 to 4.8 and increased in the order hemlock < red oak < beech < red maple < white ash < sugar maple. Similar but more gradual declines were observed at successive depths. The quantity of C in the forest floor increases from sugar maple to hemlock but decreases in the 7.5–15 cm mineral soil layer. This pattern is consistent with the observation that an increase in pH and ensuing earthworm activity increases the mixing of organic matter between the forest floor and mineral soil horizons (Lee 1985). Earthworms were present in several of the soil cores taken beneath sugar maple and white ash trees (A. C. Finzi, N. Van Breemen, and C. D. Canham, *personal observations*).

Midsummer N mineralization

The rate of midsummer net N mineralization was nearly twofold higher under sugar maple, white ash, and red maple than under beech, red oak, and hemlock (Fig. 2). Similar patterns were observed for net nitrification. Thus there were differences among species in both the quantity and the form of N available during the growing season.

The differences among species in net N mineralization reported here are consistent with Boerner and Koslowsky (1989), who found a twofold higher rate of net N mineralization in autumn beneath sugar maple and white ash trees than beneath beech trees growing in mixed-species forests in Ohio. Ferrari (1993) also found a twofold difference in the annual rate of N mineralization in sugar maple and hemlock stands on the same soil type. In contrast, Mladenoff (1987) found no significant difference in the rate of annual net N mineralization beneath sugar maple and hemlock trees in Wisconsin.

Interspecific differences in SOM (soil organic matter) quality (e.g., C:N ratio) rather than quantity appear to regulate the rate of net N mineralization in these forests. The soils beneath sugar maple, white ash, and red maple had significantly lower C:N ratios than the soils beneath beech, red oak, and hemlock (Table 2). The average soil C:N ratio beneath the six species' canopies was negatively correlated with the rate of midsummer net N mineralization, consistent with other studies (e.g., Pastor et al. 1984, Plymale et al. 1987). Rates of midsummer net N mineralization per gram of soil organic matter were also higher beneath sugar maple, white ash, and red maple than beneath beech, red oak, and hemlock (data not shown). Soil cores in which net N mineralization was measured differed in the quantity of forest floor mass; soil cores beneath beech, red oak, and hemlock had larger quantities of forest floor material than did soil cores beneath sugar maple, red maple, and white ash (Table 2). If the mass rather than the quality of the C or N in soil cores regulated the rate of net N mineralization, we would have expected the highest rates of net N mineralization beneath beech, red oak, and hemlock, whereas the opposite was true.

Low rates of net nitrification are observed in many acid forest soils (e.g., Paul and Clark 1988, Davidson et al. 1992, Stark and Hart 1997) and increases in the pH of soils can increase the rate of net nitrification (Vitousek and Matson 1985). The pH of the forest floor and the surface soil beneath beech, red oak, and hemlock is within the range of values for which low rates of net nitrification have been observed (Davidson et al. 1992, Finzi et al. 1998). We tested for a pH effect on net nitrification using a multiple regression analysis with net mineralization and pH as independent variables. At GMF, there is no evidence that the rate of net nitrification is controlled by soil pH (pH partial $F = 0.52$, df = 1, 5, $P > 0.05$; net mineralization partial $F = 18.07$, df = 1, 5, $P < 0.05$). Rather, the rate of net nitrification at GMF appears to be controlled by the production of NH_4^+ ions that can be oxidized to NO_3^-.

Conclusion

In this study, the effect of an individual tree of a given species growing in isolation was similar to the effect of several trees of the same species growing in monodominant stands in other regions of the northeastern United States (e.g., Boerner and Koslowsky 1989, Ferrari 1993). In addition, the controls over net N transformations in the soils beneath the different tree species were similar to those commonly observed at the landscape scale (e.g., the correlation between soil C:N ratio and net N mineralization). The associations between canopy tree species, the pool sizes of C and N in soils, and the quantity and form of N available to plants during the growing season suggest that forest floor and surface soil C and N dynamics are likely to track changes in the species composition of these forests. As a first approximation to modeling forest dynamics and ecosystem processes, it is reasonable to assume that individual trees influence C and N dynamics in a uniform manner beneath their canopies.

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