Tree Species and Soil Textural Controls on Carbon and Nitrogen Mineralization Rates

Christian P. Giardina,* Michael G. Ryan, Robert M. Hubbard, and Dan Binkley

ABSTRACT
Terrestrial ecosystem models assume that high quality litter leads to the formation of high quality organic C and N in mineral soil, and that increased soil clay content decreases soil C and N mineralization rates. Few studies in forests, however, have examined the effects of initial litter quality and clay content on C mineralization rates (g C kg⁻¹ soil C) and net N mineralization rates (g N kg⁻¹ soil N) in soil. We used 16-mo laboratory incubations of mineral soil sampled from stands of lodgepole pine (Pinus contorta Doug. ex Loud. ssp. latifolia Englem. ex S. Wats.) and aspen (Populus tremuloides Michx.) that varied in clay content (70 to 390 g kg⁻¹ soil) to examine how soil C and N mineralization rates relate to initial litter quality and soil texture. Aspen litter quality (C/N = 52–71; lignin/N = 26) was higher than pine litter quality (C/N = 82–111; lignin/N = 40–57), but pine soils released an average of 238 g C kg⁻¹ soil C over 16 mo compared with 103 g C kg⁻¹ soil C for aspen soils. Higher microbial biomass (mg C g⁻¹ soil C) under pine also indicates that pine soil C was of higher quality than aspen soil C. Net N mineralization rates did not relate to species or to soil C mineralization rates, and neither C nor N mineralization rates were related to soil clay content.

The mineralization of soil organic C and N are important processes regulating the functioning of natural and managed ecosystems (Tieszen et al., 1994; Johnson, 1995). Because most detrital C in the terrestrial biosphere is found in mineral soil (Jobbagy and Jackson, 2000), soil C and N mineralization rates also are predicted to control how terrestrial C storage responds to changes in climate or vegetation (Vegetation/Ecosystem Modeling an Analysis Project, 1995). Accurate modeling of soil C and N mineralization rates and their response to a changing environment therefore requires a detailed understanding of the factors that control these biogeochemical processes. The quality of detrital inputs and soil texture are hypothesized to control soil C and N mineralization rates (Wedin and Tilman, 1990; Bonde et al., 1992; Schimel et al., 1994), but relative to the decomposition of fresh litter, little is known about how these variables alter C and N mineralization rates in mineral soil (Bauhus et al., 1998). Few such studies have been conducted in forests where most of the Earth’s soil C is stored (Jobbagy and Jackson, 2000).

Three competing hypotheses have been proposed for how initial litter quality influences litter decomposition rates and N release from decomposing litter. The first hypothesis suggests that litter decomposition and N release are positively related to initial litter quality (Fogel and Cromack, 1977; Berg, 1986). In early stages of litter decomposition, C/N may be the best predictor of mass loss and N release (Taylor et al., 1989), while lignin indexes become increasingly important in later stages of decay (Berg, 1986; McClugherty and Berg, 1987). In the decay filter hypothesis (Melillo et al., 1989), differences in initial litter quality (lignin/N and lignin/cellulose) alter litter decomposition and N release rates in the early stages of litter decomposition. However, as substrate quality converges to some low value during decomposition, initial litter quality has a decreasing influence on late-stage decomposition rates, which instead are controlled by climate, soil texture, and exogenous sources of labile C and nutrients. A third hypothesis suggests that litter decomposition rates and N release may relate inversely to lignin and N-based estimates of initial litter quality. For example, high N content may actually retard litter decomposition rates later in the decomposition process, particularly if lignin levels are also high (Berg, 1986; Fog, 1988; Berg and Matzner, 1997). From these three hypotheses, litter quality can be expected to positively alter, negatively alter, or have no influence on C and N mineralization rates in mineral soil.

In addition to litter quality, clay content is hypothesized to alter soil C and N mineralization rates by binding with organic matter to form soil aggregates that protect soil C and N from heterotrophic soil organisms (Oades, 1988; Six et al., 1999). In situ, ¹³C field studies show that within a site where climate, litter quality, and biota vary minimally, soil C loss occurs more slowly in clay-sized than in sand-sized soil fractions (Boné et al., 1992; Desjardins et al., 1994). Despite a near universal pattern of declining decomposition rates with decreasing particle-size, an inverse relationship between C mineralization rates and soil clay content across ¹³C field studies was not observed (Giardina and Ryan, 2000).

In laboratory studies that control temperature and moisture, the effect of clay content on soil C mineralization is weak (Motavalli et al., 1994) or nonexistent (Sørensen, 1981; Hassink et al., 1993; Scott et al., 1996). Evidence for a relationship between soil clay content and net N mineralization is also mixed. At a grassland site, net N transformation rates were lowest in high clay soils (Hassink et al., 1993), but at other sites, clay content did not influence transformation rates (Sørensen, 1981; Motavalli et al., 1995).

The purpose of this study was to examine the effects of litter quality and soil clay content on C and net N...


mineralization rates in mineral soils sampled from two subalpine forest types of the central Rocky Mountains. We used 16-mo laboratory incubations of soil sampled from sites with contrasting litter quality inputs (pine or aspen) and a range of soil clay content (70–390 g kg\(^{-1}\) soil) to test the hypotheses that C and N mineralization rates are higher in soils receiving inputs of high quality litter, but decrease as clay content increases. Because microbes mediate the effects of species type and clay content on soil C and N mineralization rates, we also examined bacterial and fungal biomass in soil.

**MATERIALS AND METHODS**

**Study Sites**

We used differences in species litter quality and site soil texture (Table 1) as natural experiments to test our hypotheses. We selected six closed-canopy lodgepole pine and six closed-canopy aspen sites from among sites in northern Colorado, USA, previously examined by Stump and Binkley (1993). Based on traditional indexes of litter quality, aspen trees produce higher quality leaf litter (less lignin and more N) than do lodgepole pine trees. Aspen roots contain similar concentrations of lignin, but 50% more N than pine roots (Table 2). Further, aspen leaves and roots decomposed more quickly than pine material during 6-mo laboratory incubations (Stump and Binkley, 1993).

The elevation range of lodgepole pine is similar to aspen, but lodgepole pine tends to occur on drier, sandier sites, while aspen tends to occur on wetter, finer textured sites (Peet, 2000). Aspen and pine sites were chosen to represent soil texture endpoints for these forest types (Table 1). In northern Colorado, lodgepole pine and aspen occur on recently disturbed sites, as even-age patches resulting from stand-replacing disturbances, or as mixed-age climax communities (Peet, 2000). Aspen or pine can maintain dominance of a site for several forest generations (Langenheim, 1962); therefore, stand ages presented in Table 1 are minima for site occupation by these forests. Long, cold winters and cool, dry summers characterize all the sites. Mean annual precipitation for the sites ranged from 700 to 850 mm, with most falling as snow (Stump and Binkley, 1993).

**Soil Sampling, Analysis, and Incubation**

Approximately 2 kg of mineral soil (0–15 cm) were collected from three randomly selected points in stands at each of the 12 sites originally studied by Stump and Binkley (1993). Prior to sampling, forest floor material was removed. The soils were composited by site, and stored for 60 d at 2\(^{\circ}\)C without sieving before chemical analysis and incubation. Immediately prior to analysis and incubation, soils were sieved to 2 mm to remove rocks and roots. Moisture capacity of each soil was then determined by saturating 200 g of soil with water, letting soil drain freely for 24 h on cheesecloth, and weighing a subsample of wetted soil before and after oven drying at 104\(^{\circ}\)C for 24 h. Twelve 200-g samples per soil type (144 in all) were then adjusted to moisture capacity. To improve drainage during leaching, 50-g (wet weight) subsamples of each soil were mixed with 40 g (dry weight) of acid washed quartz sand. The 90-g mixture was placed in Falcon Filter micro-lysimeter cups (Becton Dickinson, Model 7102, Franklin Lakes, NJ) to permit dilute nutrient leaching during the incubation without disturbing the soil, as described by Nadellhofer et al. (1991). The soil-sand mixture was maintained at field capacity (90 g total weight) throughout the incubation by periodic additions of deionized water. Twelve laboratory replicates of each of the 12 soil types (144 in all) were incubated for 12 mo. From Months 13 to 16, only three of the 12 laboratory replicates per site were used because the other 9 laboratory replicates were used for another experiment.

Soil C mineralization rates were measured by placing microlysimeter cups plus soil into sealed 1-L glass jars with 2 M NaOH traps (Anderson, 1982). For the 16-mo incubation period, NaOH traps were sampled and replaced at ~30-d intervals. After addition of 1.0 mL of 0.75 M BaCl\(_2\), 1.0-mL subsamples of the NaOH were titrated with 1.0 M HCl to determine the quantity of NaOH neutralized by absorbed CO\(_2\). Empty microlysimeter cups (blanks) were incubated concurrently throughout the 16-mo incubation period. Changes in base concentration caused by water absorption were estimated by weighing base traps before and after each incubation period and assuming that water absorption caused any increases in weight. Based on CO\(_2\) production, the highest O\(_2\) consumption rate observed was 0.006 mol 31 d\(^{-1}\). Because a 1-L mason jar contains ~0.015 mol O\(_2\), the incubations should have been aerobic for the entire course of study. Incubation temperature was selected to match mean annual air temperature, and was held at 5 ± 1\(^{\circ}\)C throughout the incubation.

**Table 2. Litter quality for aspen and lodgepole pine foliage and fine roots.†**

<table>
<thead>
<tr>
<th>Plant Material</th>
<th>C</th>
<th>N</th>
<th>Lignin</th>
<th>Cellulose</th>
<th>Lignin/N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foliage, aspen</td>
<td>7.3</td>
<td>194</td>
<td>406</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Foliage, pine</td>
<td>4.5</td>
<td>253</td>
<td>370</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td>Fine roots, aspen</td>
<td>8.8</td>
<td>224</td>
<td>444</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Fine roots, pine</td>
<td>5.5</td>
<td>214</td>
<td>434</td>
<td>40</td>
<td></td>
</tr>
</tbody>
</table>

† Data from Stump and Binkley (1993).
Soil $\text{NH}_4^+$ and $\text{NO}_3^-$ were initially extracted from a subsample of each soil by shaking 10 g of sieved, field-moist soil with 100 mL of 2 $M$ KCl on a reciprocating shaker for 60 min. Extracts were settled for 30 min, and then passed through preleached (2 $M$ KCl) #42 Whatman filters (Whatman International, Kent, England); extracts were stored frozen until analysis (Keeney and Nelson, 1982). To estimate net N mineralization rates and to limit the accumulation of $\text{NO}_3^-$ in soils, each of the soil incubations and blanks were leached at the end of Months 4, 8, 12, and 16 with 100 mL of dilute, N-free nutrient solution (Nadelhoff et al., 1991), and samples were frozen until analysis. At the end of Month 16, a final 2 $M$ KCl extraction was performed to remove any mineral N that had not been previously removed by the final dilute nutrient leaching. Sample extracts were analyzed for $\text{NH}_4^+$ and $\text{NO}_3^-$ on a Lachat Instruments AE Flow Injection Autoanalyzer (Lachat Instruments, Milwaukee, WI) according to Lachat Instruments QuikChem Method 12-107-06-2-A (1990) for $\text{NH}_4^+$ and QuikChem Method 12-107-04-1-B (1992) for $\text{NO}_3^-$ and nitrite ($\text{NO}_2^-$). To estimate net N mineralization rates for the 16-mo incubations, we made the following calculations: net N mineralization rate equals the initial, time-zero KCl extract plus the $\text{NH}_4^+$ and $\text{NO}_3^-$ removed in the final KCl extraction minus the $\text{NH}_4^+$ removed during the four leaching events minus $\text{NH}_4^+$ removed in the initial, time-zero KCl extract. We assumed no N was lost to denitrification.

Concentrations of C and N in soil were determined on a Leco 1000 CHN analyzer (Leco, St. Joseph, MI) by dry combustion. The Soil Testing Lab at Colorado State University determined soil clay content by hydrometer method (Gee and Bauder, 1986), pH by glass electrode in a 1:2 mixture with deionized water, and total soil P by NHClO$_4$ digestion followed by inductively coupled plasma-spectrometry (Kuo, 1996). At the end of the incubations, a direct count method was used to analyze the three remaining laboratory replicates of each of the 12 soil types for total and active fungal and bacterial biomass (Hendricks et al., 1998). All C, N, and P data are presented on an oven dried soil basis (24 h at 104°C). We express soil C and N mineralization rates as g C or N released per kg soil C or N. Monthly estimates of soil C mineralization are based on soil C content for that month rather than on initial soil C content; the quantity of soil C released during previous months was subtracted from initial soil C. Cumulative release rates are based on soil C content at the beginning of the measurement period in question.

Statistical Analyses

Twelve laboratory replicates for Months 1 to 12 and three laboratory replicates for Months 13 to 16 were used to estimate measurement means for the 12 sites. We used analysis of covariance with species type (aspen or pine) as a fixed factor ($n = 6$) and clay content as the covariate to examine the effects of initial litter quality and clay content on soil C and N mineralization rates, extracted N pools, and microbial biomass (SPSS, version 8.0, Chicago, IL). Patterns of N release during the leaching events were analyzed by repeated measures ANOVA with species and clay content as fixed factors; soils with <18% clay were classified as low clay, while soils with >18% clay were classified as high clay. Relationships among soil clay content, total C and N content, C and N mineralization rates, and microbial biomass were analyzed by means of simple and multiple linear regression. Data were log transformed when the assumption of homogeneity of variance was not met. In all comparisons, $\alpha = 0.05$ was used to protect against Type I errors.

RESULTS

Soil Carbon Mineralization Rates and Soil Carbon Content

Throughout the incubation, C mineralization rates (g C kg$^{-1}$ soil C) were significantly higher in pine than in aspen soils (Fig. 1). At the end of the first 152 d of incubation, cumulative soil C release for pine was 136 g C kg$^{-1}$ soil C compared with 51 g C kg$^{-1}$ soil C for aspen ($P < 0.01$; Fig. 2). Differences between species persisted throughout the incubation; from Day 377 to 483, cumulative soil C release for pine was 22 g C kg$^{-1}$ soil C compared with 12 g C kg$^{-1}$ soil C for aspen ($P < 0.01$; Fig. 2). By the end of 16 mo, total soil C release for pine was 238 g C kg$^{-1}$ soil C compared with 103 g C kg$^{-1}$ soil C for aspen ($P < 0.01$). In contrast, C loss kg$^{-1}$ soil over 16 mo did not differ between species (pine: 4.58 g C kg$^{-1}$ soil; aspen: 6.14 g C kg$^{-1}$ soil; $P = 0.74$).

Cumulative soil C mineralization rates declined with increasing soil clay content ($P = 0.04$), but a near signifi-
significant interaction between species type and clay content ($P = 0.06$) suggests that the effect of clay on soil C mineralization rates differed between species. Linear regression analyses showed that within each species total C release did not relate to soil clay content (pine: $R^2 = 0.51$, $P = 0.11$; aspen: $R^2 = 0.14$, $P = 0.46$; Fig. 3A). Within species, soil C content was strongly related to soil clay content (pine: $R^2 = 0.91$, $P < 0.01$; aspen: $R^2 = 0.67$, $P = 0.05$; Fig. 3B), and in a multiple linear regression, clay content and species type (as a dummy variable) explained nearly all of the variation in soil C content ($R^2 = 0.89$, $P < 0.01$).

Net Nitrogen Mineralization Rates and Total Soil Nitrogen Content

More NH$_4^+$ (g N kg$^{-1}$ soil N) was released from pine than from aspen soils during the four leaching events ($P < 0.01$; Fig. 4A), and the release of NO$_3^-$ did not relate to soil clay content ($P = 0.37$). Total NO$_3^-$ (g N kg$^{-1}$ soil N) recovered during the four leaching events did not relate to species type (Fig. 4B) or soil clay content ($P = 0.74$ and $P = 0.32$, respectively). Neither species type nor soil clay content altered total N recovered (NO$_3^-$ + NH$_4^+$) during the four leaching events ($P = 0.55$ and $P = 0.29$, respectively), largely because NO$_3^-$ represented 84% of the N recovered from pine soils and 97% of the N recovered from aspen soils. An interaction between time and species type ($P < 0.01$) in an analysis of repeated measures indicated that patterns of total N release differed between species (Fig. 4C). However, over the 16-mo incubation, net N mineralization rates were unrelated to species (pine: 24.6 g N kg$^{-1}$ soil N; aspen: 28.3 g N kg$^{-1}$ soil N; $P = 0.60$). Net N mineralization rates also were unrelated to soil clay content ($R^2 = 0.02$, $P = 0.68$) or C mineralization rates ($R^2 = 0.08$, $P = 0.37$). Species type and soil clay content explained most of the variation in soil N content ($R^2 = 0.85$, $P < 0.01$).

Microbial Biomass

Analysis of covariance showed that pine soil C supported more active fungal, total active, and total bacterial biomass (mg biomass kg$^{-1}$ soil C) than did aspen soil C ($P = 0.03$, $P = 0.01$, and $P = 0.01$, respectively; Fig. 5). Higher levels of active bacterial biomass in pine soils were nearly significant ($P = 0.07$). Total fungal biomass (97% of total microbial biomass) was higher in pine soils ($P = 0.03$), but a species by clay content interaction ($P = 0.04$) indicated that the effect of species varied with clay content. Active fungal biomass increased linearly with soil clay content ($P = 0.04$). Total active biomass, total bacterial biomass, and total fungal biomass increased with soil clay content, but not significantly ($P = 0.07$, $P = 0.06$, $P = 0.10$, respectively). Active bacterial biomass did not relate to soil clay content ($P = 0.17$). Ratios of active fungi/active bacteria were higher in pine than in aspen soils (3.7 and 0.5,
predict, soil C mineralization rates for pine exceeded those for aspen throughout the incubation (Fig. 1).

Our results are consistent with long-term litter decomposition studies showing that rapid decomposition rates for high quality litter are typically not sustained. In later stages of litter decay, decomposition rates for high quality litter may slow down more rapidly than do rates for low quality litter (Berg, 1986; Prescott et al., 2000). For example, Berg (1986) found that low N content Scot’s pine (Pinus sylvestris L. Dict. Gard) litter decomposed more slowly in the first two years than high N content Scot’s pine litter, but after two years, decomposition rates for the high N content litter declined while decomposition rates for low N content litter continued unchanged. By Year 3, total mass loss and lignin mass loss for low N content litter had surpassed losses for high N content litter (Berg, 1986). Similarly, Prescott et al. (2000) found that first year mass loss for lodgepole pine litter was lower than for aspen litter (30% and 40%, respectively), but by Year 2, differences had disappeared (50%), and by Year 4, mass loss for pine had surpassed aspen (70% and 60%, respectively). Overall, high quality litter from broad leaved trees decomposed more quickly in the first two years compared with conifer litter, but in subsequent years, mass loss for conifer litter often surpassed broad leaved litter (Prescott et al., 2000). In line with these results, Kaye et al. (2000) reported that soil C of grass origin decomposed more slowly when sites were planted to Albizia falcataria (L.) Fosberg, a N-fixing tree that produces high quality litter, than when planted to Eucalyptus saligna Sm., a similarly fast-growing tree that produces relatively low quality litter. Berg (1986) hypothesized that inverse relationships between litter quality and decomposition were caused by: high N availability inhibiting lignase production or activity; low quality lignin occurring in overall high quality litter; or, decomposition of high N litter leading to the formation of organic matter that is more resistant to decay than organic matter formed from low N content litter.

At the end of our incubations, pine soil C supported microbial communities with a higher proportion of active fungi to active bacteria (Fig. 6). Because certain groups of fungi decompose low quality substrates more effectively than do bacteria (Paul and Clark, 1996), the fungi dominated communities in pine soils may decompose the low quality remains and byproducts of litter decomposition more effectively than the bacteria dominated communities in aspen soils. Conversely, high quality aspen litter may select for organisms that are adapted to higher quality litter, but would do poorly with the low quality remains and byproducts of aspen litter decomposition. Hence, the apparent negative effect of high litter quality on soil C mineralization rates may reflect the influence of tree species on the composition of soil microbial communities.

The C/N of soil did not explain species differences in soil C mineralization rates. Soil C/N did not differ between species (pine: 20.4; aspen: 17.4, $P = 0.81$), and was unrelated to both C/N of initial litter ($P = 0.75$;...
Tables 1 and 2) and soil C mineralization rates (pine: \( R^2 = 0.33, P = 0.23 \); aspen: \( R^2 = 0.07, P = 0.60 \)). While soil C/N has been used to index soil C quality (Parnas, 1976; Schimel et al., 1994), soil C/N was a poor predictor of C mineralization rates across our sites.

**Soil Clay Content, Soil Carbon Mineralization Rates, and Soil Carbon Content**

In line with previous studies (Sørenson, 1981; Hassink et al., 1993; Motavalli et al., 1994; Scott et al., 1996), soil C availability was unrelated (aspen) or weakly related (pine) to soil clay content. Variation in climate is unlikely to have masked a relationship between soil C mineralization rates and clay content because climate was similar across sites (Stump and Binkley, 1993). Secondary indexes of soil C quality (microbial biomass and composition) showed mixed results. After 16 mo of incubation, most measures of microbial biomass were unrelated to soil clay content, suggesting that C quality did not vary with clay content (Bauhus et al., 1998). In contrast, analysis of covariance showed that the ratio of active fungi/active bacteria increased with clay content (\( P = 0.03 \); Fig. 6), suggesting lower soil C quality in high clay soils.

Despite a weak relationship with soil C mineralization rates, soil clay content was a strong predictor of soil C content across our sites (Fig. 3B). These findings appear contradictory, but soil clay content can influence plant productivity (Pastor et al., 1984), and higher soil C content in high clay soils may represent an effect of clay on detritus production rather than an effect on soil C mineralization rates. For example, soil texture can influence water holding capacity and nutrient availability, both of which can influence plant productivity. Similarly, Sørenson (1981) found that while high clay soils retained more \(^{14}\text{C} \) labeled cellulose than low clay soils, with differences established in the first 10 d of incubation, soils that retained more cellulose also mineralized proportionally more cellulose over the 4 yr incubation.

**Net Nitrogen Mineralization Rates**

Large differences between pine and aspen litter quality did not lead to species differences in soil C/N or net N mineralization rates (\( P = 0.81 \) and \( P = 0.68 \), respectively). These results are consistent with the decay filter hypothesis (Melillo et al., 1989): early in the decomposition process, low quality litter will release less N than high quality litter because available nutrients are immobilized more rapidly by microbes decomposing low quality, nutrient poor litter. As the quality of diverse litter types converges during decomposition, the influence of initial litter quality on N release should also decline. In contrast to soil N mineralization rates, \( \text{NH}_4^+ \) was leached at higher rates from pine than aspen soils (Fig. 4A), possibly because abiotic fixation or microbial competition for \( \text{NH}_4^+ \) were greater in aspen soils. Overall, differences in leached \( \text{NH}_4^+ \) were small relative to mineralization rates. Cumulative N release increased more rapidly in pine than in aspen soils, suggesting that species differences in N mineralization rates may have emerged had the incubations continued.

Previous studies have shown mixed effects of initial litter quality on net N mineralization rates. In a common garden experiment with perennial grasses, increasing litter quality led to increased net N mineralization rates kg\(^{-1}\) soil N (Wedin and Tilman, 1990). In a common garden study with trees, Scott (1998) found that soils under European larch (Larix decidua P. Mill.), which had the highest leaf litter and root quality of five trees examined, had the highest net N mineralization rates kg\(^{-1}\) soil N. In contrast, red oak soils had moderate N mineralization rates, but red oak roots and leaf litter were lowest and second lowest in quality.

The decay filter hypothesis predicts that soil texture, climate, and new sources of labile C will control N release in later stages of litter decomposition (Melillo et al., 1989). Across our sites, soil N mineralization rates did not relate to soil clay content, despite constant temperature and moisture during the incubation, and no inputs of labile C. Clay content did not influence quantities of N leached from soil, and analysis of repeated measures showed that clay content did not alter patterns of N release (\( P = 0.23 \)). Our findings are consistent with two long-term studies reporting no relationship between N mineralization rates and soil clay content (Sørenson, 1981; Motavalli et al., 1995), but conflict with a grassland study reporting lower N mineralization rates in high clay soils (Hassink et al., 1993).

Most N in soil is covalently bound to soil C, and the fate of soil N is assumed to follow that of soil C (Schimel et al., 1994), soil C/N was a poor predictor of soil N mineralization rates. Our results suggest, however, that these relationships may be relevant only over the time scales from which they were developed. For the pine and aspen soils compared here, low quality litter resulted in high quality soil C, and faster mineralization of pine C appears to be the explanation for the lower C content of pine soils. Similarly, while large-scale relationships between soil C

**CONCLUSIONS**

Based on short-term litter decomposition studies (1 to 2 yr), ecosystem models identify C/N and lignin/N as important predictors of soil C formation and mineralization. Our results suggest, however, that these relationships may be relevant only over the time scales from which they were developed. For the pine and aspen soils compared here, low quality litter resulted in high quality soil C, and faster mineralization of pine C appears to be the explanation for the lower C content of pine soils.
and clay content are used to make inferences about how soil C mineralization rates are altered by soil clay content, we found that despite a strong relationship between soil C and clay content, clay was a weak predictor of soil C and N mineralization rates. While in agreement with previous incubation and cross-site comparison studies examining the effects of soil clay content on C mineralization rates, these results conflict with $^{13}$C-based particle-size fractionation studies at individual sites reporting a strong influence of soil texture on C turnover. Overall, our results suggest that current assumptions about litter quality and soil textural controls on soil C formation and turnover need to be reevaluated.

ACKNOWLEDGMENTS

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REFERENCES


LONG-TERM PATTERNS IN FOREST-FLOOR NITROGEN-15 NATURAL ABUNDANCE AT HUBBARD BROOK, NH

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Abstract

To test the hypothesis that δ15N in the forest floor remains constant over time, we measured δ15N in forest-floor samples from 1969, 1978, 1987, and 1992 at the reference watershed, W6, at the Hubbard Brook Experimental Forest (HBEF), New Hampshire. The δ15N of the Oa horizon increased significantly (P < 0.05) from 3.00‰ in 1969 to 4.89‰ in 1978, then decreased significantly to 3.81‰ in 1987 and remained near that level in 1992. In the Oie horizon, δ15N increased significantly from 0.17‰ in 1969 to 0.91‰ in 1978 and remained at the higher level for the later years. Thus δ15N was not at steady state in either the Oie or Oa horizon for the period 1969 to 1992 in the reference watershed. These data suggest that even relatively short-term disruptions of the N cycle (either by anthropogenic or natural disturbance) can alter the δ15N in the forest floor, and should be considered in evaluating natural abundance data.

Natural abundance of 15N has been used to help evaluate N cycling and N losses (Johannisson and Högberg, 1994; Austin and Vitousek, 1998; Emmett et al., 1998), to compare plant species patterns of N uptake (Nadelhoffer et al., 1996), and to compare land-use history (Piccolo et al., 1994). An underlying assumption that soil δ15N is at steady state is made in many studies, including laboratory experiments evaluating the change in soil δ15N in response to mineralization and nitrification (Nadelhoffer and Fry, 1988), comparisons of N deposition gradient in the NITREX study (Emmett et al., 1998), and models (Shearer et al., 1974; Hobbie et al., 1999). Although it is reasonable to assume that the δ15N in the mineral soil changes very little over time because of the large pool size and long residence time, the steady-state assumption in the forest floor has not been established.

The stable N isotope ratio (15N to 14N) is useful in ecological research because it records the net effects of N transformations on the soil (Högberg, 1997). Microbiologically mediated processes discriminate against the heavier 15N, creating products that are depleted in 15N and leaving the source pool enriched in 15N and 14N (Mariotti et al., 1981; Shearer and Kohl, 1986). If the depleted product is exported from the soil (via uptake or leaching after nitrification or gaseous losses after denitrification), the remaining soil becomes enriched in 15N (Létolle, 1980; Shearer and Kohl, 1986; Nadelhoffer and Fry, 1994). The fractionation during nitrification, 15 to 14‰ (Högberg, 1997), is significantly higher than that during mineralization (+1‰; Högberg, 1997; Kendall, 1998).

Because litter δ15N values are consistently lower than soil values, litterfall inputs tend to lower the δ15N of the forest floor (Fry, 1991; Nadelhoffer and Fry, 1994; Högberg, 1997). Likewise, because soil is typically enriched relative to the atmosphere, N fixation also decreases soil δ15N. Nitrogen fixation incorporates atmospheric N, which has a δ15N of 0‰, into plant material and subsequently into soil with a fractionation that typically ranges from −1 to +1‰ (Shearer and Kohl, 1986).

Other N fluxes may either deplete or enrich soil 15N; these include deposition and immobilization. The δ15N of ammonium and nitrate in deposition varies considerably, the former from −14 to 9‰ (Hoering, 1957; Freyer, 1978; Paerl and Fogel, 1994), and the latter from −7 to 6‰ (Hübner, 1986; Garten, 1992; Kendall, 1998; Pardo et al., 1998). At the HBEF, the δ15N of precipitation nitrate is −2‰ (Pardo, unpublished data, 1996–1998); δ15N has not been measured for ammonium. Ammonium deposition may be more enriched (Hoering, 1957; Nadelhoffer et al., 1999) or less enriched (Freyer, 1978; Garten, 1992) in δ15N than nitrate deposition. The effect of N deposition on forest soil, therefore, cannot be predicted a priori. At the HBEF, because nitrate deposition is depleted relative to soil (as is ammonium for the nearest site with data available; Nadelhoffer et al., 1999),

Abbreviations: HBEF, Hubbard Brook Experimental Forest; LOI, loss on ignition; W6, reference Watershed 6.