



Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood

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Abstract

In the boreal mixed forest, stand composition generally changes from deciduous to mixed to coniferous stands during post-disturbance succession. Our objective was to determine the influence of forest composition on the quality of soil nitrogen and carbon as determined by C and N mineralization during the course of a long-term in vitro incubation (282 days). Three stand types (*Populus tremuloides*, *Betula papyrifera*, and conifers (mixture of *Abies balsamea* and *Picea glauca*)), of two ages (50 and 124 years since fire) growing on two soil types (clay and till) were considered. Expressed on an organic C basis, our results showed a greater N mineralization for deciduous than coniferous stands, both in the mineral soil and the forest floor, a higher N mineralization in the mineral soil of older stands as compared with young ones, and in till than in clay soils. Mineralization of C was higher in the forest floor of clay soils as compared to till soils while the opposite was found in the mineral soil. It was also higher in both soil layers of older sites. The observed differences in N and C mineralization among stand types, stand ages and deposits appeared to be due to differences in the most labile fraction of soil organic matter because these differences were observed within 100 days of incubation. The ratio of C mineralized–N mineralized was greater in coniferous than deciduous soils in both soil layers, indicating a lesser quality of organic matter under coniferous stands. Despite significant differences among the above-listed factors for N and C mineralization on an organic C basis, the pool size of mineralized (or mineralizable) N and C was generally not significantly different between the different forest and soil types because of an inverse relationship between quality and quantity of soil organic matter. Correlation and multiple regression analysis indicated that clay content (negatively), C–N ratio (negatively), available P as well as exchangeable Mn were related to the mineralization of N. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Boreal forest; Soil carbon; Soil nitrogen; Vegetation dynamics

1. Introduction

Boreal forest soils contain large amounts of organic nitrogen of which only a small portion is potentially available to the vegetation over a growing

season, and the productivity of these forests is often N limited. Fertilization trials have often shown a growth response to N addition in both deciduous (Van Cleve, 1973; Weetman et al., 1978) and coniferous boreal stands (Binkley and Högberg, 1997; Weetman et al., 1978). Apart from soil climate, the rate of N mineralization is dependent upon the chemical characteristics of organic matter that affect the activity of the decomposer community. Soil en-

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vironmental conditions such as temperature, pH, heavy metals, redox and texture also influence the activity of the decomposer community (DeLaune et al., 1981; Parton et al., 1987; Carreiro and Koske, 1992; Cotrufo et al., 1995).

Chemical attributes of plant litter, such as lignin, nitrogen, C–N and lignin–N ratio are believed to determine the quality of soil organic matter (SOM) for decomposers (Berg and McLaugherty, 1987; Taylor et al., 1989; Riffaldi et al., 1996). However, as noted by Ågren and Bosatta (1987), there is no universally applicable expression that provides an immediate link between litter properties and SOM decomposition rates. Litter composition can vary widely among tree species and forests of different composition and can potentially affect soil N and C dynamics (Gower and Son, 1992; Hobbie, 1992; Prescott and Preston, 1994; Paré and Bergeron, 1996). Coniferous litter has been found to reduce the availability of soil N because of its high lignin and low N content (Pastor et al., 1987). Nadelhoffer et al. (1991) showed that the quality of organic matter was more important than temperature in controlling N and C mineralization rates in tundra plant communities. In the boreal mixedwood of Quebec, current forestry practices favor the maintenance of a stable forest composition. However, without human intervention, these ecosystems will generally show a succession from deciduous to mixed, and finally to coniferous dominated forests following disturbance (Bergeron and Dubuc, 1989; Bergeron and Harvey, 1997). Our objective was to determine how forest composition can affect the dynamics of N and C mineralization and how this effect is influenced by soil type and stand age.

Several techniques can be used to assess soil N availability (Binkley and Richter, 1987); the most common include short-term incubations in the field or under controlled laboratory conditions. These techniques can be problematic in boreal forest soils because of the low and often negative rates of net N mineralization (Bonan, 1990; Paré and Van Cleve, 1993; Brais et al., 1995; Paré and Bergeron, 1996). Ruess et al. (1996) estimated that in situ incubation grossly underestimates net N mineralization in boreal forest soils. Several authors have proposed that SOM should be conceptually separated into several fractions with different turnover times (Bonde and Rosswall, 1987; Parton et al., 1987; Nicolardot et al., 1994). Commonly used terms for these pools are active, slow, and passive. The active pool, which is the most labile with regard to mineralization, can be assessed through long-term incubations. This technique allows us to determine potentially mineralizable N (N_0) and C (C_0) through following the accumulation of mineral N and soil respiration (Stanford and Smith, 1972).

2. Materials and methods

2.1. Study area

Study sites were located in the Research and Teaching Forest of Lake Duparquet (48° 30' N, 79° 20' W) in northwestern Quebec, Canada. The annual average temperature is 0.6°C and the average annual precipitation is 823 mm. This region is part of the Clay Belt of Quebec and Ontario. Clay deposits, left by the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977), are found at low elevations, while moraine deposits are found at higher elevations. All sites sampled were well to moderately well drained soils. The fine-textured soils were classified as Grey Luvisol while the moraine soils were classified as Humo-Ferric Podzols (Agriculture Canada Expert Committee on Soil Survey, 1987).

Two large stands originating from forest fires were selected. The stand ages had been determined in previous studies by dendrochronological methods (Bergeron, 1991; Dansereau and Bergeron, 1993). These stands were 50- and 124-years old and covered 298 and 555 ha, respectively (Bergeron and Dansereau, 1993). In each of these stands, three stand types and two deposits were considered. The stand types selected were aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and conifers which were stands dominated by a mixture of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss). Conifers were grouped as one forest type because it was not possible to locate pure stands of either species. The soil types considered were Grey Luvisol and Humo-Ferric Podzols. Aerial photography and field validation were used to identify units of the different species and soil combinations (6 types) in both fire years. Sampling plots were selected randomly from this site characterization. Four plots of 100 m² were selected for each soil type–stand type combination in both 50- and 124-year-old stands for a total of 48 plots. The experimental design included three stand types (species effect), two stand ages, and two soil types. The effect of these factors on the mineralization parameters and on some chemical characteristics of the soil were tested with a ANOVA. Stand age and interactions with this parameter were considered as random factors and stand type and soil type were considered as fixed factors. Stand age is a variable that is pseudoreplicated. This variable and interactions with it were considered as random factors and were not interpreted. The ANOVA was followed by Tukey's studentized range test.

2.2. Sample collection and preparation

Four forest floor (FH-layer) and mineral soil (0–10

cm) subsamples were collected in each plot in October 1994 and combined to form one composite sample per replicate plot and soil layer. Forest floor (FH) samples were collected after brushing away the loose litter. Mineral soil samples were collected with a 50 mm diameter soil corer. Soil samples were refrigerated at 4°C prior to analysis. Forest floor samples were sieved (5 mm) to remove rocks, roots and coarse fragments. Mineral soil samples were sieved (2 mm) when moist, and coarse fragments and roots were removed.

2.3. Carbon and nitrogen mineralization

Soil samples were incubated in microcosms that were built from modified microlysimeters (Falcon Filter units, Becton Dickinson, Model 7102) as described by Nadelhoffer (1990). The original nitrocellulose filter of the microlysimeter was replaced by a glass-fiber filter. A thin layer of mineral wool was placed between the filter and the soil substrate to prevent the filter from blocking. Ten grams of forest floor and 40 g of mineral soil on a dry weight basis were placed into the microlysimeters. The mineral soil was mixed with 50 g of silica to facilitate the leaching of the sample. Each microlysimeter was kept in a sealed plastic container of 1.5 l containing 50 ml of 1 M NaOH to fix the evolved CO₂. The microcosms were incubated in the dark at 21°C with constant humidity for 282 days. The water content of the incubated soil was regularly determined by weighing the microlysimeter. The microlysimeters were leached with 100 ml of 5 mM K₂SO₄ at day 0, 13, 34, 54, 82, 110, 144, 193 and 282 of the incubation. The amount of CO₂ fixed by the solution and the aeration of the microcosms were measured at day 5, 13, 19, 26, 34, 41, 47, 54, 61, 68, 75, 82, 89, 96, 103, 110, 118, 128, 137, 144, 160, 172, 186, 193, 207, 222, 240, 254 and 282 of the incubation.

2.4. Chemical analyses

Mineral N (N–NH₄ and N–NO₃) extracted by percolation, was determined by Flow Injection Analysis (Tecator Fiastar 5020 Analyser). The amount of CO₂ evolved from the soil samples was determined by titration (Metrohm 702 pH meter) of the NaOH solution (50 ml, 1 M) with a solution of 1 M HCl after precipitation with 5 ml of 10% BaCl₂. Evolved CO₂ was calculated using Stotzky's equation (1965).

2.5. Other soil analyses

Subsamples of soil from each plot were oven dried at 65°C and digested in sulphuric acid and hydrogen peroxide (Allen, 1989). Concentrations of total N and P in the digests were determined colorimetrically by Flow Injection Analysis (Tecator Fiastar 5020 Analy-

ser). Concentrations of total K, Mg, Ca and Mn were determined using atomic absorption spectrophotometry. Exchangeable cations were determined by NH₄NO₃ (1 M) extraction and measured by atomic absorption spectrophotometry (Stuanes et al., 1984). Organic carbon (OC) was determined by loss on ignition at 550°C for 2 h and the OC concentration was calculated from organic matter (0.58 × O.M.) (Allen, 1989). Extractable mineral N (N–NO₃, N–NH₄) was determined in 2 M KCl extracts by Flow Injection Analysis (Tecator Fiastar 5020 Analyser). Extractable P was determined in the Bray II extraction solution and analyzed by spectrophotometer (Milton Roy, Spectronic 1001 plus) at 880 nm (McKeague, 1976). The pH was determined with an Orion pH meter at a soil–distilled water ratio of 1:2 for the mineral soil and 1:3 for the forest floor soil. Forest floor concentrations of Klaxon lignin were determined by the method described by McClaugherty et al. (1985). The soil texture of mineral soil was determined with the hydrometer technique (Sheldrick and Wang, 1993). Soil microbial C and N were determined by the chloroform-fumigation-extraction method. These results were reported by Bauhus et al. (1998).

2.6. Carbon and nitrogen mineralization kinetics

Cumulative amounts of C and N mineralized through time were fitted to non-linear equations in order to obtain an estimate of potentially mineralizable fractions of these elements although the total amount of mineralized N and C during the course of the experiment is also presented since these values are definitive analytical data, whereas equation parameters are estimated with hypothetical models (Campbell et al., 1993). Carbon mineralization kinetics were described by the simple compartment negative exponential model of Stanford and Smith (1972):

$$C_t = C_0(1 - e^{-kt}) \quad \text{or} \quad N_t = N_0(1 - e^{-kt}), \quad (1)$$

where C_t or N_t is the cumulative microbial respiration (C–CO₂) or N mineralized (NH₄ + NO₃) at time t , C_0 or N_0 is the potential mineralizable C or N, k_C or k_N is the mineralization rate constant for the mineralization of C or N, and t is time in days.

The N mineralization kinetics were described by the Gompertz model (France and Thornley, 1984). It is a three-parameter sigmoidal-shaped curve which is asymmetric about its inflection point and allows a reasonably good fit of the different phases of the curve (lag, increase and decrease and flattening out of the curve):

$$N_t = N_0e^{-he^{-kt}} - N_0e^{-h}, \quad (2)$$

where N_t is the cumulative N mineralized ($\text{NH}_4 + \text{NO}_3$) at time t , N_0 is the potentially mineralizable N, k and h are the mineralization rate constants for the mineralization of N, and t is time in days.

The two-component model described by Bonde and

Rosswall (1987) was also tested:

$$C_{\text{min}} = C_0(1 - e^{-kt}) + xt \quad \text{and}$$

$$N_{\text{min}} = N_0(1 - e^{-kt}) + xt, \quad (3)$$

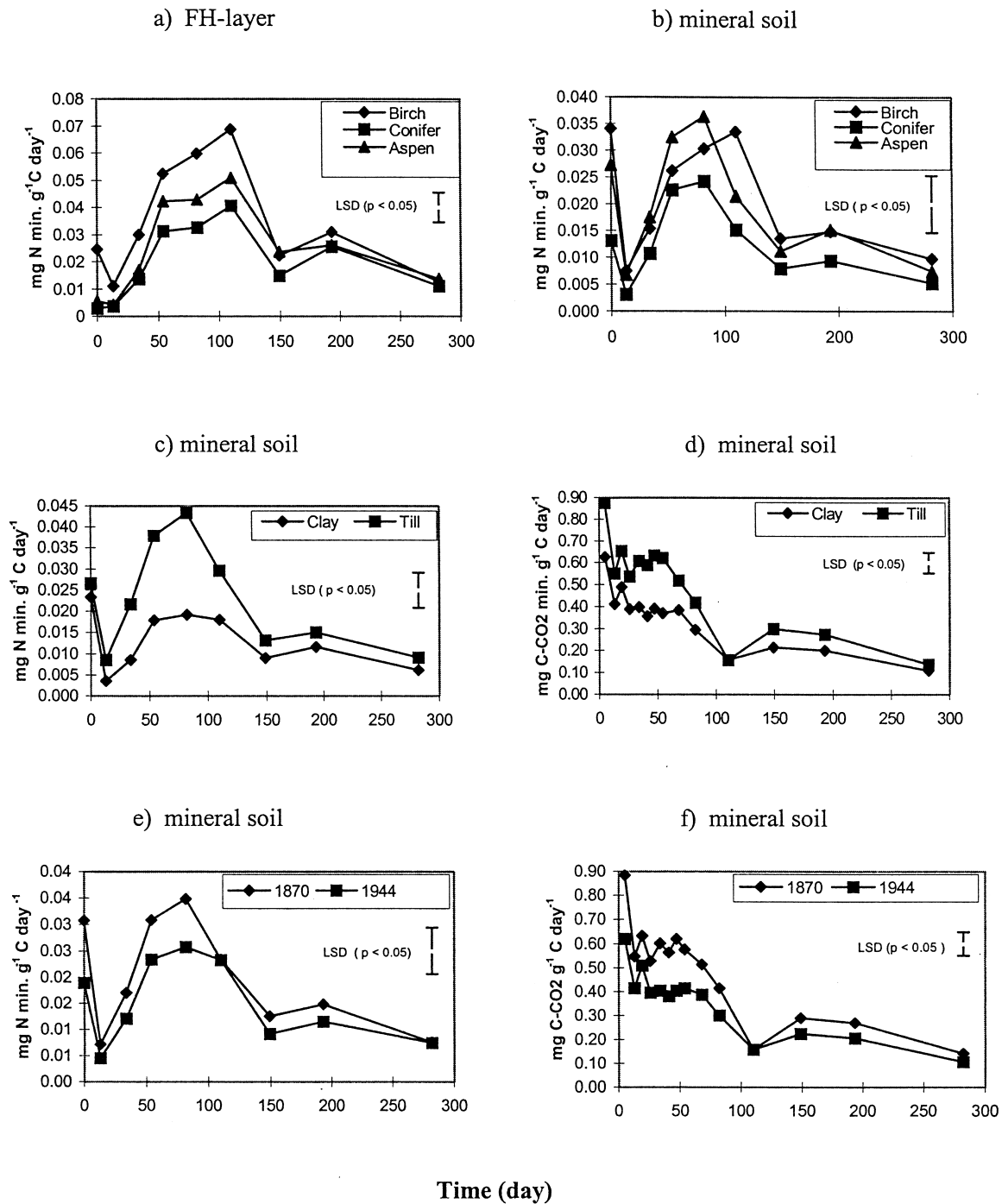


Fig. 1. Nitrogen and carbon mineralization (mg N or C mineralized $\text{g}^{-1} \text{C day}^{-1}$) during the course of a 282-day incubation. (a) Effect of stand type on N mineralization in the FH-layer. (b) Effect of stand type on N mineralization in the upper mineral soil. (c) Effect of deposit on N mineralization in the upper mineral soil. (d) Effect of deposit on C mineralization in the upper mineral soil. (e) Effect of stand age on N mineralization in the upper mineral soil. (f) Effect of stand age on C mineralization in the upper mineral soil.

where $x = k_{CR}$ or k_{NR} (R is the portion of recalcitrant C or N). Other kinetic models (double exponential, hyperbolic, power function) were tested, but they either yielded lower predictive values or no convergence of the parameters.

2.7. Other statistical analyses

Non-linear regressions were performed to estimate the derivatives of the first-order equation (1) using the Marquardt iteration procedure, allowing estimation of the equation parameters. For simplicity in illustrating the main results, the LSDs were calculated on the time-effect units and reported in Fig. 1(a–f). Calculation of the LSDs for the trend in C and N mineralization will only give close approximation of error, because the time-effect units are not randomized. Correlations between the parameters of C and N mineralization and soil chemical properties were performed. The significance level for all statistical analyses was 5%. All statistical analyses were performed using the SAS procedure (SAS Institute Inc., 1985).

3. Results

The general trends in the mineralization of C and N over time are presented in Fig. 1 for the principal significant effects observed with species, age and soil type in the FH-layer and the mineral soil. At the beginning of the incubation, N mineralization (Fig. 1(a–c,e)) increased to reach a peak at 100 days of incubation and gradually decreased thereafter. Microbial respiration (Fig. 1 (d,f)) decreased from the beginning to the end of the incubation. Significant differences generally occurred between 50 and 100 days for N and during the first 100 days of incubation for C mineralization. The rate of microbial respiration over time fitted well the single-compartment negative exponential model. Convergence of the k_C and C_0 occurred for 98% of the incubated samples. The pattern of mineralized N over time showed in general a S-shaped curve which fitted better the Gompertz model than the negative exponential model. This latter model also often generated very high estimates of N_0 . Using the Gompertz model convergence of the K_n , h_n and N_0 occurred for 95% of the samples. The negative exponential model was therefore chosen for comparison among sites for C mineralization and the Gompertz model for N mineralization.

The cumulative amounts of mineralized C at the end of incubation ranged from 109 to 287 mg g^{-1} OC in the forest floor and from 33 to 128 mg g^{-1} OC in the mineral soil. These values represented 11–23% of total OC in the forest floor and 3–13% of OC in the mineral soil, respectively. The estimated potentially miner-

alizable C (C_0) varied from 12 to 32% of total OC in the forest floor and from 4 to 13% of OC in the mineral soil. The daily C mineralization rate varied between 0.0039 and 0.012 for the forest floor and from 0.0044 to 0.0152 for the mineral soil. The amount of mineralized N during the course of the experiment ranged from 3.28 to 12.93 mg N g^{-1} C in the forest floor and from 1.04 to 9.09 mg N g^{-1} C in the mineral soil. These values corresponded to a proportion of total N that varied between 13 and 35% in the forest floor while the corresponding values for the mineral soil varied from 3 to 20%. The pool of potentially mineralizable N (N_0) estimated with the Gompertz equation varied between 3.33 and 13.36 mg N g^{-1} C in the forest floor and 1.22 and 12.06 mg N g^{-1} C in the mineral soil and represented between 13 and 35% of total N in the forest floor and between 3 and 22% of total N in the top mineral soil. The rate of N mineralization (k_n) and (h_n)/day varied between 0.0080 and 0.037 for the k_n and 2.279–9.999 for the h_n in the forest floor and between 0.0068 and 0.036 for the K_n and 1.559–8.360 for the h_n in the mineral soil. Comparison between cumulative values of N and C mineralized at the end of the incubation and estimated values of potentially available N and C can be found in Tables 1–4. The values of the estimated parameters were always slightly higher than the total amounts of mineralized elements.

The results of the analyses of variance and the average values per stand type, stand age and soil types are presented in Tables 1–4. The mineralization rate of C in the FH horizon differed significantly between stand types and was higher in the birch than in the aspen and the coniferous forest floor. In the forest floor, the amount of OC on an area basis, as well as the amount of organic N, were significantly affected by stand type (Table 1), stand age (Table 3) and also by the Age*Species and Age*Soil interactions (data not presented). The old coniferous plots contained more C in the forest floor than all other stand types except old aspen stands. The amount of total N and OC in the forest floor on till sites was significantly greater on old than on young sites, and no significant difference in C mineralization rates or in total C pools was observed between stand types in the mineral soil.

The amount of N mineralized over the course of the experiment was, on an OC weight basis, significantly higher in deciduous than in coniferous stands in both the forest floor and the mineral soil (Tables 1 and 2). However, on an area basis, neither N mineralization nor total N differed significantly among stand types. The ratio of mineralized C–mineralized N was significantly higher in coniferous than in deciduous stands in both soil layers (Tables 1 and 2).

Several indices of C and N dynamics indicated a significantly higher quality of SOM for N and C mineralization in old stands as compared with

Table 1
Forest floor species effects^a

Parameter	Birch	Aspen	Conifer
k_C (day ⁻¹)	0.0086 (0.0015) a	0.0075 (0.0011) ab	0.0068 (0.0015) b*
C_0 (mg g ⁻¹ OC)	203.79 (45.00) a	207.69 (48.71) a	215.95 (29.22) a
Cmin (mg g ⁻¹ OC)	183.16 (34.97) a	182.86 (37.93) a	178.68 (13.69) a
Cmin (kg m ⁻²)	0.360 (0.080) a	0.429 (0.111) a	0.510 (0.210) a
OC (kg m ⁻²)	2.02 (0.46) z	2.41 (0.45) z	2.88 (1.19) z
k_N (day ⁻¹)	0.018 (0.005) a	0.016 (0.003) a	0.016 (0.007) a
h_N (day ⁻¹)	4.13 (1.28) a	4.57 (1.65) a	4.35 (1.90) a
N_0 (mg g ⁻¹ OC)	9.38 (2.25) a	7.64 (1.82) ab	6.49 (2.26) b*
Nmin (mg g ⁻¹ OC)	8.80 (2.02) a	7.18 (1.50) ab	5.70 (1.86) b**
Nmin (kg m ⁻²)	0.018 (0.005) a	0.017 (0.006) a	0.016 (0.006) a
ON (kg m ⁻²)	0.083 (0.021) z	0.082 (0.036) z	0.073 (0.021) z
Cmin–Nmin	21.49 (5.23) a	26.19 (6.03) ab	34.25 (10.49) b**

^a Mean values with standard error in parentheses of parameters describing the dynamics of C and N mineralization in relation to species effect (stand types). Values followed by the same letter are not significantly different ($P < 0.05$) based on a one-way ANOVA. Z indicates a significant interaction between species and age or species and deposit. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$ (significance level of F ratios)).

young ones (Table 3). The amount of mineralized C and of potentially available C on an OC weight basis were significantly greater at the older sites than on the young sites in both soil layers. The amount of mineralized C in the forest floor on an areal basis was also significantly higher at the older sites. The amount of mineralized N on an OC weight basis was higher in the mineral soil of old stands.

The rate of C mineralization was significantly higher in the forest floor overlying clay soils than in that of till soils (Table 4). No other difference in the forest floor between soil types was significant. In the mineral soil, the cumulative amounts of mineralized C and N on an OC basis, as well as the potentially mineralizable C, were significantly higher in till soil than in clay soil. However, the amounts of total and mineralizable

N and C on an area basis were not different among soil types. The mineralization rates of C and N were significantly greater in till. In the mineral soil, the ratio of mineralized C–mineralized N was significantly greater in clay.

The relationships between soil chemical and biological characteristics and amounts and rates of C and N mineralization were examined with the use of linear correlation (Table 5). In the forest floor, the amount of mineralized C and the estimate of potentially available C are positively related to exchangeable Mn and negatively related to base saturation and the lignin content. The rate of C mineralization in the forest floor is positively related to pH, available P, exchangeable cations, C–N ratio, clay content and microbial C and N concentrations. The amount of N mineralized was negatively related to the C–N and lignin–N ratios

Table 2
Mineral soil species effects^a

Parameter	Birch	Aspen	Conifer
k_C (d ⁻¹)	0.0072 (0.0016) a	0.0072 (0.0014) a	0.0062 (0.0013) a
C_0 (mg g ⁻¹ OC)	89.98 (20.52) a	82.40 (29.08) a	87.79 (18.42) a
Cmin (mg g ⁻¹ OC)	78.80 (20.49) z	73.83 (29.02) z	72.42 (19.19) z
Cmin (kg m ⁻²)	0.29 (0.12) a	0.29 (0.09) a	0.27 (0.12) a
OC (kg m ⁻²)	3.84 (1.16) a	4.53 (2.46) a	3.98 (1.67) a
k_N (day ⁻¹)	0.017 (0.006) a	0.018 (0.008) a	0.018 (0.007) a
h_N (day ⁻¹)	3.84 (1.39) a	3.86 (1.39) a	4.36 (1.60) a
N_0 (mg g ⁻¹ OC)	5.07 (1.84) z	4.92 (3.04) z	3.32 (1.56) z
Nmin (mg g ⁻¹ OC)	4.81 (1.87) a	4.52 (2.57) a	3.02 (1.28) b*
Nmin (kg m ⁻²)	0.017 (0.007) a	0.016 (0.007) a	0.011 (0.005) b*
ON (kg m ⁻²)	0.18 (0.07) a	0.16 (0.04) a	0.14 (0.07) a
Cmin–Nmin	17.32 (4.72) a	20.39 (12.35) ab	26.04 (7.39) b*

^a Mean values with standard error in parentheses of parameters describing the dynamics of C and N mineralization in relation to species effect (stand types). Values followed by the same letter are not significantly different ($P < 0.05$) based on a one-way ANOVA. Z indicates a significant interaction between species and age or species and deposit. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$ (significance level of F ratios)).

Table 3
Stand age (year)^a

Parameter	Forest floor		Mineral soil	
	124	50	124	50
k_C (day ⁻¹)	0.0075 (0.0016) a	0.0078 (0.0015) a	0.0072 (0.0013) a	0.0065 (0.0016) a
C_0 (mg g ⁻¹ OC)	221.77 (40.42) a	196.51 (38.88) b*	96.98 (21.20) a	76.47 (19.99) b***
Cmin (mg g ⁻¹ OC)	191.83 (27.48) a	171.71 (30.15) b*	85.87 (21.67) a	64.16 (19.06) b***
Cmin (kg m ⁻²)	0.51 (0.18) a	0.36 (0.08) b*	0.31 (0.10) a	0.26 (0.12) a
OC (kg m ⁻²)	2.73 (1.01) z	2.14 (0.50) z	3.84 (1.42) a	4.42 (2.17) a
k_N (day ⁻¹)	0.016 (0.006) a	0.017 (0.007) a	0.016 (0.005) a	0.019 (0.008) a
h_N (day ⁻¹)	4.26 (1.27) z	4.45 (1.90) z	3.48 (1.16) z	4.37 (1.56) z
N_0 (mg g ⁻¹ OC)	7.95 (2.74) a	7.72 (2.05) a	4.99 (2.76) a	3.88 (1.70) a
Nmin (mg g ⁻¹ OC)	7.23 (2.46) a	7.23 (1.92) a	4.54 (2.43) a	3.70 (1.64) b*
Nmin (kg m ⁻²)	0.018 (0.005) a	0.015 (0.005) b*	0.015 (0.005) a	0.014 (0.008) a
ON (kg m ⁻¹)	0.085 (0.031) z	0.072 (0.020) z	0.171 (0.077) a	0.147 (0.042) a
Cmin–Nmin	29.17 (9.10) a	25.46 (9.01) a	3.29 (11.21) a	19.34 (6.48) a

^a Mean values with standard error in parentheses of parameters describing the dynamics of C and N mineralization in relation to stand age. Values followed by the same letter are not significantly different ($P < 0.05$) based on a one-way ANOVA. Z indicates a significant interaction between species and age or species and deposit (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$ (significance level of F ratios)).

and to the OC content per unit area. However, the amount of potentially available N and the rate of N mineralization were not correlated to any soil properties. In the mineral soil, mineralized C, mineralizable C, as well as mineralized N, were negatively related to the parameters typical of fine-textured soil. These mineralization parameters were negatively related to pH, exchangeable cations, clay content and the amount of C per area, and positively related to available P. Again, potentially mineralizable N was not significantly correlated to soil chemical parameters. The rate of N mineralization was negatively related to pH, exchangeable cations, C–N ratio, clay content and microbial N. It is noteworthy that both in the forest

floor and the mineral soil, the C–N ratios of the microbial biomass (data from Bauhus et al., 1998) and of total soil organic matter were significantly correlated with the ratio of mineralized C–mineralized N, suggesting that the stoichiometry of the mineralization and microbial immobilization processes are dependent on the C–N ratio of total soil organic matter.

The best multiple regression models for N mineralization are presented in Table 6. In the forest floor, C–N, C mineralization and exchangeable Mn explained 50% of the observed variation in mineralized N, whereas in the mineral soil, the C–N ratio and the amount of mineralized C explained 70% of the observed variation in mineralized N.

Table 4
Soil texture^a

Parameter	Forest floor		Mineral soil	
	Clay	Till	Clay	Till
k_C (day ⁻¹)	0.0080 (0.0013) a	0.0072 (0.0016) b*	0.0065 (0.0011) a	0.0073 (0.0017) b*
C_0 (mg g ⁻¹ OC)	200.45 (43.82) a	219.41 (36.32) a	78.16 (21.49) a	96.84 (20.56) b***
Cmin (mg g ⁻¹ OC)	179.84 (35.41) a	183.61 (23.33) a	65.98 (19.10) z	85.70 (22.95) z
Cmin (kg m ⁻²)	0.44 (0.12) a	0.43 (0.19) a	0.30 (0.11) a	0.27 (0.11) a
OC (kg m ⁻²)	2.51 (0.63) a	2.35 (1.05) a	4.63 (1.89) a	3.25 (1.28) a
k_N (day ⁻¹)	0.017 (0.007) a	0.0017 (0.003) a	0.016 (0.006) a	0.019 (0.007) b*
h_N (day ⁻¹)	4.87 (1.86) a	3.83 (1.09) a	4.06 (1.59) a	3.78 (1.27) a
N_0 (mg g ⁻¹ OC)	7.74 (220) a	7.93 (2.63) a	3.09 (1.42) z	5.78 (2.32) z
Nmin (mg g ⁻¹ OC)	7.23 (2.08) a	7.23 (2.35) a	3.06 (1.48) a	5.37 (2.03) b***
Nmin (kg m ⁻²)	0.018 (0.005) a	0.016 (0.006) a	0.013 (0.007) a	0.015 (0.007) a
ON (kg m ⁻²)	0.082 (0.023) a	0.075 (0.030) a	0.171 (0.064) a	0.137 (0.048) a
Cmin–Nmin	26.70 (8.63) a	28.04 (9.89) a	24.80 (10.43) a	17.20 (5.49) b*

^a Mean values with standard error in parentheses of parameters describing the dynamics of C and N mineralization in relation to soil texture. Values followed by the same letter are not significantly different ($P < 0.05$) based on a one-way ANOVA. Z indicates a significant interaction between species and age or species and deposit. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$ (significance level of F ratios)).

Table 5

Correlation coefficient R and probability for the relationships between C and N mineralization parameters and some soil properties in FH-layer and surface mineral soil. Microbial biomass Nmic and Cmic from Bauhus et al. (1998)

	C-CO ₂ min (282 days)	C ₀ (mg C-CO ₂ g ⁻¹ OC)	k _C (day ⁻¹)	Nmin (282 days)	C-N (ratio)	Cmin-Nmin (ratio)
pH	-0.25 (0.086)	-0.45 (0.001)	0.53 (0.0001)	0.22 (0.131)	-0.15 (0.298)	-0.40 (0.0044)
P ext (mg g ⁻¹ C org)	0.02 (0.862)	-0.20 (0.167)	0.57 (0.0001)	0.23 (0.108)	-0.01 (0.925)	-0.19 (0.194)
Mn ext (mg g ⁻¹ C org)	0.61 (0.0001)	0.48 (0.0006)	0.06 (0.692)	0.29 (0.047)	-0.04 (0.812)	0.08 (0.567)
E.C. (K, Ca, Mg)	-0.49 (0.0005)	-0.53 (0.0001)	0.30 (0.035)	0.07 (0.622)	-0.17 (0.243)	-0.35 (0.016)
Lignin (mg g ⁻¹ C)	-0.32 (0.027)	-0.33 (0.021)	-0.01 (0.933)	0.03 (0.831)	-0.25 (0.084)	-0.19 (0.206)
C-N total	0.08 (0.579)	0.17 (0.235)	-0.30 (0.038)	-0.61 (0.0001)	1.00	0.71 (0.0001)
Lignin-N	-0.160 (0.280)	-0.093 (0.529)	-0.231 (0.114)	-0.434 (0.0021)	0.58 (0.0001)	0.411 (0.0036)
Clay (%)	-0.16 (0.272)	-0.32 (0.025)	0.30 (0.036)	-0.07 (0.643)	0.11 (0.449)	-0.05 (0.751)
ON (g m ⁻²)	-0.27(0.071)	-0.15 (0.322)	-0.12 (0.414)	-0.05 (0.723)	-0.29 (0.045)	-0.03 (0.834)
OC (g m ⁻²)	-0.17 (0.2601)	-0.02 (0.899)	-0.28 (0.055)	-0.37 (0.009)	0.22 (0.128)	0.35 (0.016)
Cmic (μg g ⁻¹)	0.06 (0.673)	-0.05 (0.712)	0.31 (0.033)	0.12 (0.430)	-0.15 (0.317)	-0.15 (0.317)
Nmic (μg g ⁻¹)	-0.04 (0.773)	-0.20 (0.170)	0.47 (0.0008)	0.44 (0.0019)	-0.41 (0.004)	-0.51 (0.0002)
Cmic-Nmic	0.16 (0.283)	0.28 (0.053)	-0.37 (0.0103)	-0.44 (0.002)	0.71 (0.0001)	0.55 (0.0001)
<i>Mineral soil</i>						
pH	-0.59 (0.0001)	-0.63 (0.0001)	-0.22 (0.131)	-0.36 (0.011)	0.27 (0.069)	0.03 (0.838)
P ext (mg g ⁻¹ C org)	0.47 (0.0008)	0.46 (0.0013)	0.27 (0.06)	0.40 (0.006)	-0.36 (0.014)	0.00 (0.979)
Mn ext (mg g ⁻¹ C org)	0.26 (0.073)	0.25 (0.088)	0.20 (0.164)	0.06 (0.607)	0.15 (0.315)	0.23 (0.110)
E.C. (K, Ca, Mg)	-0.60 (0.0001)	-0.62 (0.0001)	-0.32 (0.025)	-0.53 (0.0001)	0.37 (0.010)	0.26 (0.071)
C-N total	-0.52 (0.0001)	-0.47 (0.0007)	-0.31 (0.030)	-0.65 (0.0001)	1.00	0.57 (0.0001)
Clay (%)	-0.51 (0.0002)	-0.51 (0.0002)	-0.19 (0.198)	-0.60 (0.0001)	0.48 (0.0005)	0.44 (0.0016)
N org (g m ⁻²)	-0.30 (0.054)	-0.30 (0.0519)	-0.17 (0.295)	-0.25 (0.105)	0.15 (0.359)	0.06 (0.692)
C org (g m ⁻²)	-0.47 (0.0015)	-0.46 (0.0024)	-0.33 (0.0345)	-0.48 (0.0013)	0.50 (0.0007)	0.30 (0.0512)
Cmic (μg g ⁻¹)	-0.15 (0.313)	-0.17 (0.263)	0.03 (0.846)	-0.37 (0.0125)	0.61 (0.0001)	0.51 (0.0003)
Nmic (μg g ⁻¹)	-0.15 (0.3433)	-0.21 (0.1579)	0.22 (0.1350)	-0.20 (0.178)	0.50 (0.0004)	0.36 (0.013)
Cmic-Nmic	0.04 (0.808)	0.13 (0.389)	-0.25 (0.097)	-0.30 (0.043)	0.22 (0.143)	0.35 (0.018)

4. Discussion

Our results indicated that in both the forest floor and the surface mineral soil, the quality of soil organic matter with regard to N mineralization, when expressed on an organic C or total N basis, was affected by stand type, soil type and stand age with few significant interactions between these variables. The results showed that N mineralization on C weight basis was higher in soils of deciduous stands, in the soils of older stands and in mineral soil with a coarser texture. This is reflected in the C-N ratio of mineralized substrate, which is an index of N immobilization by microbes. High ratios indicate high immobilization rates relative to the amount of C mineralized (Burke et al., 1989).

The differences observed between stand types in the amounts of N mineralized on an OC basis, as well as in the ratios of mineralized C-N, are consistent with the C-N and lignin-N ratios of litter-fall. The C-N ratio of foliar litterfall was estimated to be 45, 84 and 178 for birch, aspen and spruce, respectively, while the lignin-N ratio for these species was estimated at 30, 49 and 92, respectively

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Table 6

Multiple regression between N mineralization and C respiration and some soil chemical and physical properties in FH-layer and surface mineral soil

FH-layer					
Regression model	Nmin	-0.222 C-N	+ 0.026 Cmin	+ 0.28 Mn	+ 8.46
Probability	0.0001	0.0001	0.0051	0.0094	0.00001
Total and partial r^2	0.58	0.36	0.14	0.07	
Mineral soil					
Regression model	Nmin	0.058 Cmin	-0.163 C-N	+ 3.899	
Probability	0.0001	0.0001	0.0011	0.0213	
Total and partial r^2	0.700	0.623	0.0848		

(Côté, unpublished). Differences in forest floor soil N mineralization rates among deciduous and coniferous stands have been reported by Harris and Riha, (1991) and Zak et al. (1993). However, we do not know of any report of such changes in the mineral soils. These changes could be caused by a greater decomposability of fine roots of deciduous trees than of coniferous fine roots. Finér et al. (1997) described a higher decomposition rate of aspen fine roots as compared with coniferous fine roots in the same forest ecosystem. Alternatively, the organic matter that is incorporated in the mineral soil through biological activity and the soluble organic matter that is leached from forest floor horizons may be of higher quality in deciduous than in coniferous forests.

While the amounts of N mineralized on a total N or OC basis as well as the stoichiometry of the mineralization of C and N contrasted between stand types, the amount of mineralizable C generally did not show any significant difference between stand types. This could be related to the relatively similar concentration of lignin that was observed in the litter of the studied tree species. Lignin concentrations were estimated at 32, 29 and 25% for birch, aspen and spruce foliar litter, respectively (Côté, unpublished). Apart from N and lignin concentrations, another variable, exchangeable Mn, was correlated to N mineralization in the forest floor. This factor also increased the significance of multivariate models predicting N mineralization. This element has been found to play an important role in lignin degradation as Mn-peroxydase is involved in lignin degradation (Berg et al., 1996) and could be important in the late phases of organic matter decomposition when N is released (Berg, 1986). Chemical analysis of foliar litter indicated that paper birch litter contained high concentrations of this element. Manganese concentrations were 1.30, 0.19 and 0.70 mg g⁻¹ for birch, aspen and spruce litter, respectively (Côté, unpublished).

Soil type had a great influence on mineralization of C and N but did not appear to alter the effect of stand type or stand age, suggesting that these factors may affect the dynamics of C and N over a range of soil types. It was apparent that the fine texture of clay soil reduces the amount of C and N mineralized. Protection of soil organic matter by fine particles is well known (Sorensen, 1981; Hassink, 1994b). The ratio of mineralized C–N was greater in clay suggesting a stronger N than C limitation of the microflora in clay soils reflected in a higher immobilization of N in the microflora. Bauhus et al. (1998) found that a higher proportion of total soil N was incorporated into microbial biomass in clay than in till soils. Fine textured soils also offer more protection for microbial biomass

from grazing and desiccation. This protection is more important for bacteria than fungi, which are more efficient in their carbon use. The specific microbial respiration, unit C respired per unit of biomass C, in clay soils was half that in till soils (Bauhus et al., 1998). The higher C–N ratio of mineralized substrate may thus also indicate a larger proportion of bacteria in the microflora in clay soils than in till soils.

Hassink (1994a) reported that the ratio of mineralized C per unit of microbial biomass was not related to soil texture while the ratio of mineralized N per unit of microbial biomass was related to texture. Because soil pH and exchangeable cations are positively related to the clay content, these factors are negatively related to the mineralization of C and N. However, there is probably no causal relationship between these variables. It is likely that, given the relatively high pH of these soils, a change in soil pH does not significantly affect mineralization rates in the mineral soil. In the forest floor however, which is more acidic, there is a positive relationship between pH and C mineralization rates.

The multiple regression models that were developed suggest that N mineralization could be predicted from total C–N and soil respiration rates. While the determination of soil C–N ratio is easily performed, the determination of soil heterotrophic respiration rates is more tedious. However, the measurement of this flux has received much attention recently and may be technologically more easily and reliably measurable (Pongracic et al., 1997) or estimated using simulation models (Hanson et al., 1993) than N mineralization in the field.

When the results are expressed on an areal basis, the studied factors (stand type, soil type and stand age) rarely showed a significant effect on C and N mineralization. That is a reflection of an inverse relationship between total pool sizes and organic matter quality that cancels the effects of soil organic matter quality on N and C fluxes (Fig. 2 (a–d)). This relationship is suggested by the negative correlations that were observed in both soil layers between pool sizes of total N and C and mineralizable portions of C and N (Table 6). This relationship holds when comparing soils with different permanent or abiotic properties such as texture. For example, clay soil contains more organic matter than till soil, but a smaller proportion is potentially accessible to microbes. The inverse relationship between pool sizes and mineralizable fraction is also apparent when comparing sites of different biotic properties. The pool size of organic matter of coniferous sites is generally greater than that of deciduous ones, however, a smaller proportion is potentially accessible to microbial activity. This relationship has the effect of flattening out differences in ecosystem fluxes on an areal basis, which would be suggested by

the quality of SOM. However, the absence of significant differences on an areal basis could also be an artifact of the method used. In the laboratory, the soil samples are incubated at a constant temperature while in the field, the temperature in the humus may decrease as it thickens as demonstrated by Van Cleve et al. (1981). This would imply that in the field, thicker humus, such as observed in coniferous stands, may show smaller fluxes of N and C than those derived from laboratory experiments. Field measurements of soil CO₂ evolution (Paré et al., unpublished) indicated no difference between coniferous and deciduous stands suggesting that, if the stoichiometry of C and N respiration is similar both in the field and the laboratory, the actual N mineralization in the field may be lower in coniferous than deciduous stands.

The differences in the amount of mineralized N and C among stand types, stand age and soil type were observed early in the incubation and they are the result of differences in the active SOM fraction

(Fig. 1), which represents a relatively small percentage of total SOM (between 3 and 35% depending on element and soil layer). Given the relatively rapid turnover of this fraction, it is likely that species effects would not be long lasting if there is a change in litter quality or quantity such as the one that might be induced by forest harvesting. Nevertheless, changes caused by the composition of the tree community may affect N cycling within the ecosystem. This study focussed on relatively pure stands and may not provide adequate insight into the behavior of soil in mixed stands, which predominate in the boreal mixedwood. Further investigation into the role of deciduous trees in mixed forest stands is warranted.

It is difficult to draw conclusions regarding the effect of tree species on in situ soil fluxes of C and N from laboratory measurements. Nevertheless, the results presented indicated that the quality of SOM for N mineralization as well as the stoichiometry of C and N

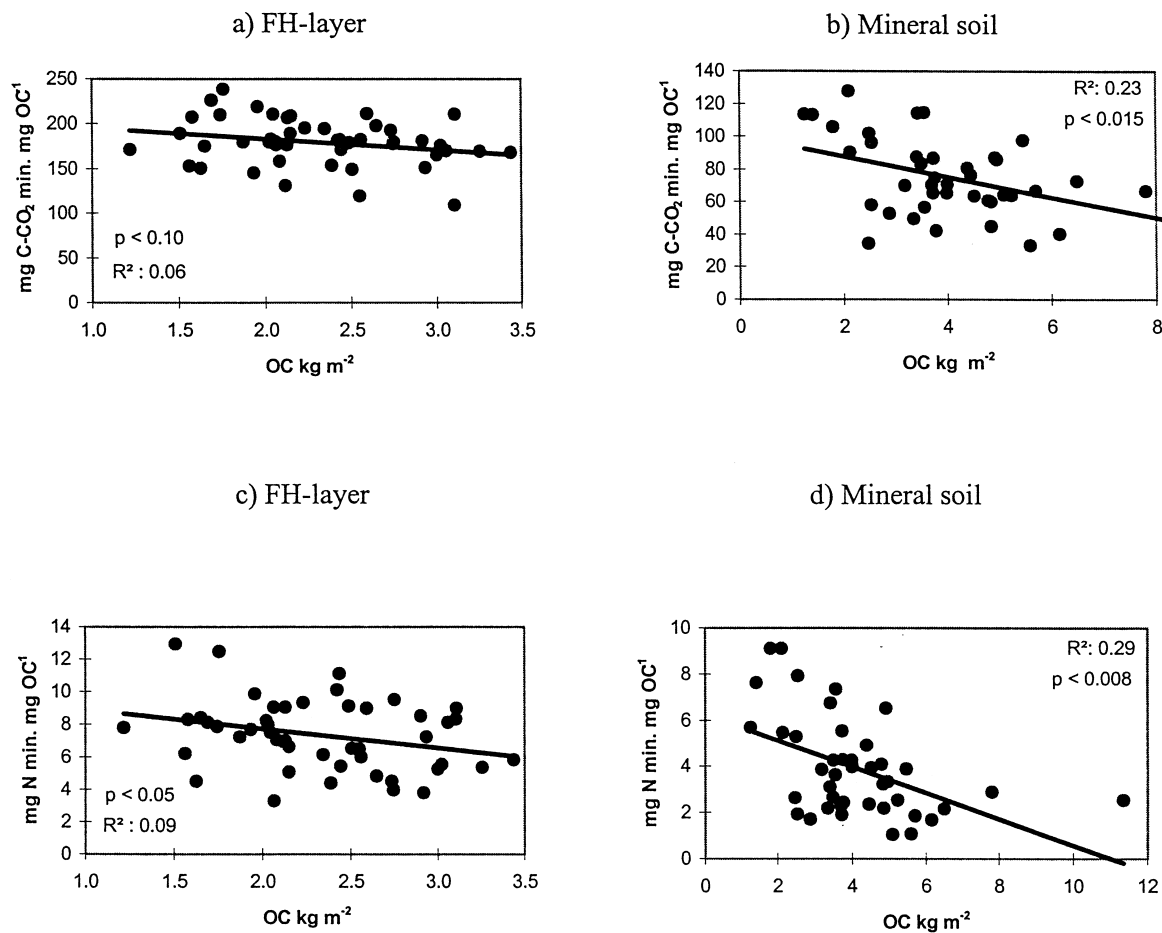


Fig. 2. Relationships between cumulative soil C and N mineralization (mg element mineralized g OC⁻¹) and the amount of soil OC (kg m⁻²) for the FH-layer and mineral soil (10 cm depth). (a) Relationship between C mineralization and the SOC m⁻² in the FH-layer. (b) Relationship between C mineralization and the SOC m⁻² in the mineral soil. (c) Relationship between N mineralization and the SOC m⁻² in the FH-layer (d) Relationship between N mineralization and the SOC m⁻² in the mineral soil.

mineralization is affected by stand type, stand age and soil type in both soil layers. The positive relationships between mineralized C–N, total C–N as well as microbial C–N ratios suggest that litter quality affects the decomposer community (reflected in changes in microbial C–N ratio) and determines the total C–N ratio of SOM and the stoichiometry of the mineralization of C and N.

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