Pedobiologia 51 (2007) 89–97

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Pedo biologia

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Regulation of nitrogen mineralization and nitrification in Southern Appalachian ecosystems: Separating the relative importance of biotic vs. abiotic controls

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Received 20 November 2006; received in revised form 8 February 2007; accepted 8 February 2007

KEYWORDS
Forest soil;
Nitrogen availability;
Nitrogen transformations;
Elevation gradient;
Soil temperature;
Soil moisture;
Q_{10}

Summary

Long-term measurements of soil nitrogen (N) transformations along an environmental gradient within the Coweeta Hydrologic Laboratory basin in western North Carolina showed a strong seasonal pattern and suggested that vegetation community type—through its influence on soil properties—was an important regulating factor. Our objective was to determine the relative effects of biotic vs. abiotic factors on soil N transformations. During the 1999 and 2000 growing seasons we transplanted soil cores from each of the five gradient plots to all other gradient plots for their 28-day in situ incubation. N mineralization and nitrification rates in soils from the northern hardwood (NH) site were significantly increased when soils were transplanted to warmer sites. N mineralization rates also increased in transplanted soil from the dry mixed-oak/pine site to a wetter site. Multiple regression analysis of N mineralization from all five sites found that biotic (total soil N and C:N ratios) and climatic factors (moisture and temperature) regulate N mineralization. Regression analyses of individual sites showed that N mineralization rates responded to variation in temperature and moisture at only the high elevation northern hardwood site and moisture alone on the dry warm mixed-oak/pine site. N mineralization was unrelated to temperature or moisture at any of the other sites. Results indicate that soil properties plus climatic conditions affect soil N transformations along the environmental gradient at Coweeta. Environmental controls were significant only at the extreme sites; i.e., at the wettest and warmest sites and soils with highest and lowest C and N contents. The high degree of temperature sensitivity for the northern hardwood soils indicates potentially large responses to climatic change at these sites.

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0031-4056/$ - see front matter Published by Elsevier GmbH.
doi:10.1016/j.pedobi.2007.02.002

Introduction

Forests rely primarily on the internal cycling of nutrients for growth and metabolism. Total soil N pools (surface 0–10 cm) in the southern Appalachians range between 750 kg N ha^{-1} in xeric mixed-oak pine sites to 3780 kg N ha^{-1} in high-elevation northern hardwood forests (Knoepp and Swank, 1998). N mineralization (Nmin), the release of N from organic sources, results in the formation of plant available NH_4 which can also be oxidized to NO_3—a form of N available for plant uptake and readily leached from the soil. Ecosystem and nutrient cycling studies typically use measures of soil N transformation rates as indices of potential plant uptake and ecosystem loss. Rates of soil Nmin may differ with forest vegetation community, elevation, and topographic position (Garten and van Miegroet, 1994; Garten et al., 1994; Powers, 1989) due to effects on soil organic matter, temperature, and moisture. In temperate soils, Nmin displays a seasonal pattern; greatest rates are measured in summer or fall when soil temperatures are highest (Bonilla and Roda, 1992; Knoepp and Swank. 1998; Nadelhoffer et al., 1984; Strader et al., 1989). Adams and Attiwill (1986) and Polglase et al. (1992) found that soils incubated in the laboratory at constant temperatures ranging from 20 to 25 °C, did not show any seasonal patterns in Nmin rates, presumably due to high incubation temperatures.

Many studies have sought to characterize the response of soil Nmin to temperature and moisture; often to identify the optimum temperature or soil moisture content for individual soils. Maximum Nmin normally occurs when soil temperatures are between 25 and 35 °C (Nicolardot et al., 1994; Stark, 1996) and soil moisture near field capacity (Stanford and Epstein, 1974). Data from these studies may be used in simulation models to predict soil N availability or potential Nmin under climate change conditions. However, optimal Nmin conditions are rarely encountered in the field and microbial communities may differ in their temperature responses making responses difficult to generalize. Carreiro and Koske (1992) studied soil fungi from northern hardwood forests in Rhode Island and found that different fungal species have different optimum temperatures. Furthermore, the fungal species isolated from these soils differed depending on the temperature used for incubation in the laboratory (Carreiro and Koske, 1992).

Previous work by Knoepp and Swank (1998) examined Nmin rates across the elevation and vegetation gradient within the southern Appalachians. They found that rates were greatest at the highest elevation site—where temperatures were lowest and rainfall inputs were greatest indicating that vegetation, through its effects on soil biotic properties such as organic matter and soil nutrient availability, had a strong role in regulating Nmin. Furthermore, laboratory incubations indicated that soil moisture effects were only significant at non-limiting soil temperatures (Knoepp and Swank, 2002).

The objective in this study was to determine the relative importance of soil biotic properties vs. soil temperature and moisture in regulating N mineralization and nitrification rates measured in situ. We used reciprocal transplants of intact soil cores on sites spanning an environmental and vegetation gradient. Study sites represented a range of forest community types, soils, N transformation rates, soil temperature, and soil moisture conditions typical of Appalachian ecosystems. One advantage of using reciprocal transplants to determine the interaction between biotic and abiotic regulation of N cycling processes is that intact soil is exposed to natural temperature and moisture regimes.

Materials and methods

Site description

This study was conducted at the Coweeta Hydrologic Laboratory, a 2180 ha USDA Forest Service facility in the southern Appalachians of western North Carolina, USA. Annual precipitation is ~1900 mm and is >100 mm in most months. The growing season extends from early May to early October. Mean monthly temperatures are highest in June through August (~20 °C) and lowest in December through January (~5 °C). All sites are in reference watersheds (undisturbed since 1929) and represent the major vegetation community types within the Coweeta basin. Sites include dry mixed-oak pine (OP), cove hardwoods (CH), mesic mixed-oak (low elevation) (MO-L), mesic mixed-oak (high elevation) (MO-H), and northern hardwoods (NH) vegetation community types. Table 1 provides information about dominant vegetation, elevation, aspect, slope, and soils.

Field and laboratory methods

On each site one 0.08 ha (20 m × 40 m) plot was established for intensive study, the 40-m axis running along the slope contour. On each plot four transects were established parallel to the 40-m axis. Sampling points were chosen randomly along

Table 1. Selected characteristics of the elevation gradient sites.

Site	OP	CH	MO-L	MO-H	NH
Elevation (meters)	788	801	860	1094	1389
Aspect (degrees)	180	340	15	75	20
Slope (degrees)	34	21	34	33	33
Vegetation type	Oak-pine	Cove hardwoods	Mixed oak	Mixed oak	Northern hardwoods
Dominant Species	*Pinus rigida*	*Liriodendron tulipifera*	*Quercus prinus*	*Quercus prinus*	*Betula allegheniensis*
	Quercus coccinea	*Quercus prinus*	*Carya spp.*	*Quercus rubra*	*Quercus rubra*
	Quercus prinus	*Carya spp.*	*Quercus rubra*	*Carya spp.*	*Betula lenta*
	Carya spp.		*Rhododendron maximum*	*Rhododendron maximum*	*Tilia heterophylla*
	Kalmia latifolia				
Moisture regime	xeric	Mesic	Mesic	Mesic	Mesic
Soil series	Evard/Cowee Chandler Edneyville/Chestnut	Saunook Tuckaseegee	Trimont	Chandler	Plott
Soil Texture	Fine-loamy Coarse-loamy Coarse-loamy	Fine-loamy Fine-loamy	Fine-loamy	Coarse-loamy	Coarse-loamy
Soil Subgroup	Typic Hapludults	Humic Hapludults	Humic Hapludults	Typic Dystrochrepts	Typic Haplumbrepts
	Typic Dystrochrepts	Typic Haplumbrepts			

Data compiled from Coweeta Long-term Ecological Research Program records.

transects to minimize effects of soil type variation across some plots. The soil core transplant study was conducted during the growing season in 1999 and 2000; 2 transplants were conducted each season, June and July.

Net rates of N transformations were measured using a modified in situ closed core method (Adams and Attiwill, 1986). Six 15-cm long, 4.3-cm i.d., PVC cores were driven 10 cm into the mineral soil, 25 cm apart. One soil core was removed immediately for time zero determination of soil NH_4 and NO_3–N concentrations. One core was capped and incubated in place for 28 days; the other 4 cores were capped and transplanted to the other 4 gradient plots, incubated for 28 days and then collected for soil analysis. Collected soil cores were kept cool; returned to the laboratory; and stored at 4 °C until analyzed, within 24 h. Soils were sieved to <6 mm. 20 g of soil was oven-dried at 105 °C. Five gram of soil was shaken with 20 ml of 2 M KCl for 1 h to extract NH_4 and NO_3–N. The soil/KCl mixture was centrifuged for 15 min at 6000 rpm. Supernatant was analyzed for NH_4- and NO_3–N on an autoanalyzer using alkaline phenol (USEPA, 1983a, b) and cadmium reduction (USEPA, 1983a, b) techniques. All N data are presented on an oven dry weight basis. Net N mineralization rates equal soil NH_4+NO_3–N concentrations in incubated/transplanted cores minus NH_4+NO_3–N concentrations at time zero. Net nitrification rates equal soil NO_3–N concentrations in incubated/transplanted cores minus NO_3–N at time zero. In nitrification rate calculations any NO_3 concentrations in extracted solutions reading below zero were set equal to zero; negative values were included in calculations of mean soil NO_3 concentrations. N transformation rates and concentrations were transformed to area basis (kg ha^{-1}) using previously determined bulk densities.

Total soil C and N were determined each year for each site on $t = 0$ soil samples composited by transect ($n = 8$ per site). Soil temperature data were collected continuously using a thermocouple placed at 5 cm deep in the mineral soil in the center of each 20 × 40 m plot. Soil moisture content was determined for N concentration calculations. Moisture content at $t = 0$ was used to characterize site difference. Moisture content at $t = 1$ (incubated soils) was used in regression analyses of climatic controls on N transformation rates.

Statistical analyses

Data were analyzed as a split plot design with sample date serving as the plot. Plot means of the four transects from each sample date were used in all statistical analyses. In strict terms, the experimental design was unreplicated because transects were located in a single plot on each forest site. Significant differences among sites in biotic and abiotic characteristics were determined using the GLM Procedure of SAS; means comparisons were conducted using the PDIFF option adjusted for Tukey mean comparisons in the LSMEANS statement (SAS, 2000). Transplant effects on N mineralization and nitrification rates and soil moisture content were determined for soil from each site using a paired T-test analysis comparing rates or soil moisture in soil cores left on site with means from cores transplanted to other sites.

We used stepwise multiple regression techniques (Stepwise Procedure of SAS) (SAS, 1985) to explore the regulation of N mineralization and nitrification by soil temperature and moisture and soil biotic characteristics, total soil carbon and nitrogen and C:N ratios. We examined these relationships across all sites using N transformation rates on an area basis. The five sites were examined individually to examine the relationship between N transformation rates and climatic variables. We used soil concentration changes ($\mu g\,g^{-1}$) rather than changes in content ($kg\,ha^{-1}$) for individual site comparisons. We used the NLIN Procedure of SAS (SAS, 2000) to describe the curve responses between soil temperature and N mineralization and nitrification to allow computation of Q_{10} values for soil from each site.

Results

Site differences

N transformation rates were similar to rates measured during the years 1991–1996 (Knoepp and Swank, 1998). Only the MO-L had rates outside the previously measured range (Table 2). Nmin rates over the two growing seasons of measurement ranged from $12.32\,kg\,N\,ha^{-1}\ 28\,days^{-1}$ on NH to $0.66\,kg\,N\,ha^{-1}\ 28\,days^{-1}$ on OP, but did not differ

Table 2. Comparison of nitrogen transformation data collected in 1999–2000 compared to data collected during the summer 1991–1996; all data are presented in $kg\,ha^{-1}$.

Site	N Mineralization ($kg\,N\,ha^{-1}\ 28\,d^{-1}$)			Nitrification ($kg\,N\,ha^{-1}\ 28\,d^{-1}$)		
	1991–1996	1999–2000	Q_{10} ($n = 20$)	1991–1996	1999–2000	Q_{10} ($n = 20$)
OP	1.52 (0.11–5.29)	0.66a	0.62	0.01 (−0.02–0.10)	−0.02b	n.e.
CH	5.44 (0.76–14.52)	11.15a	0.18	0.48 (0.05–2.58)	0.25b	0.70
MO-L	1.47 (0.66–3.13)	5.64a	1.41	−0.01 (−0.10–0.36)	0.12b	n.e.
MO-H	1.32 (−0.02–3.65)	0.82a	n.e.	0.04 (−0.14–0.25)	−0.01b	n.e.
NH	18.39 (9.67–35.38)	12.35a	8.86	8.48 (3.62–13.40)	3.66a	2.76

For 1991–1996, values in parentheses are minimum and maximum rates measured. Values for 1999–2000 are the mean of four sample dates for soil cores incubated on the same site from which they were collected, values within a column with different letters are significantly different ($p \leqslant 0.10$). Q_{10} values, were from temperature response curves parameterized using the NLIN procedure of SAS, values are presented that had a probability of significance <0.10. n.e. represents Q_{10} values that were non-estimable.

Table 3. Soil edaphic characteristics of 0–10 cm of soil collected from forested sites including, dry mixed-oak/pine (OP); cove hardwood (CH); mixed-oak, low elevation (MO-L); mixed-oak, high elevation (MO-H); northern hardwood (NH).

Site	C ($Mg\,ha^{-1}$)	N ($Mg\,ha^{-1}$)	NO_3–N ($kg\,ha^{-1}$)	NH_4–N ($kg\,ha^{-1}$)	Temp (°C)	H_2O ($g\,cm^{-3}$)
OP	25.2	0.80c	0.01b	1.11	18.5a	0.13b
CH	45.9	2.75b	0.01b	2.32	18.5a	0.37a
MO-L	32.7	1.49c	0.01b	0.95	17.7c	0.20ab
MO-H	28.33	1.12c	0.00b	1.08	17.8b	0.22ab
NH	59.57	3.97a	0.16a	2.37	15.6d	0.38a

Chemical and soil moisture data represent site means from $t = 0$ soil samples, soil temperature was collected continuously in the center of each plot; values presented are the mean of all days during the in situ incubation. Values in a column with different letter designations are significantly different as determined in the GLM procedure of SAS using LSMEANS analysis with PDIFF adjusted for Tukey.

significantly among sites. Nitrification rates were significantly greater on NH compared to all other sites; rates ranged from slightly less than zero on OP and MO-H to 3.66 kg N ha^{-1} 28 $days^{-1}$ on NH.

Sites varied significantly in total soil N, and NO_3 and concentrations, soil temperature, and soil moisture content (Table 3). Total soil N was also greatest in NH with 3.97 Mg N ha^{-1}, other sites ranged from 0.80 Mg ha^{-1} on OP to 2.75 Mg ha^{-1} in CH soils. Total soil C content did not differ significantly among sites, however, C:N ratios ranged from 32 in OP soils to 15 in NH and differed significantly among sites. Average soil temperature (5 cm depth) during the 28-day soil in situ incubations differed significantly among sites. The highest temperatures (18.5 °C) were measured on the low elevation OP and CH sites and the lowest temperature was observed on the high elevation NH (15.6 °C) site (Table 3). Soil water content also differed significantly among sites. NH had the greatest soil water content averaging 0.38 g H_2O cm^{-3} soil; water content was lowest on OP averaging 0.13 g H_2O cm $soil^{-3}$ (Table 3).

Transplanting Effects

Only NH and OP soils exhibited significant changes in Nmin rates when soils were transplanted to other sites. T-test comparisons found that soil in cores from NH had increased Nmin rates when transplanted to CH and MO-L (from 12 kg N ha^{-1} 28 day^{-1} on the NH site to 22 and 18 kg N ha^{-1} 28 day^{-1} in soil cores transplanted to CH and MO-L, respectively) (Fig. 1). Soil from OP had increased Nmin rates in soil cores transplanted to MO-H (from 0.7 kg N ha^{-1} 28 day^{-1} on the OP site to 1.8 kg N ha^{-1} 28 day^{-1} on the MO-H site) (Fig. 1). Soils from NH also had significantly greater rates of nitrification in cores transplanted to CH and MO-L, increasing from 3.7 kg N ha^{-1} 28 day^{-1} to 5.7 and 6.5 kg N ha^{-1} 28 day^{-1} on CH and MO-H, respectively (Fig. 2).

Transplanting soil had a significant effect on soil moisture content in a few cases; transplanting soil cores from OP to MO-H resulted in an increase ($p = 0.10$) in soil moisture content after 28 d of incubation as did cores transplanted from MO-L to NH ($p = 0.08$). Soil cores transplanted from NH to MO-L had decreased soil moisture ($p = 0.06$).

Regulation of N mineralization

Multiple regression analyses of Nmin and nitrification rates with soil biotic and abiotic variables across soils from all sites indicated that both

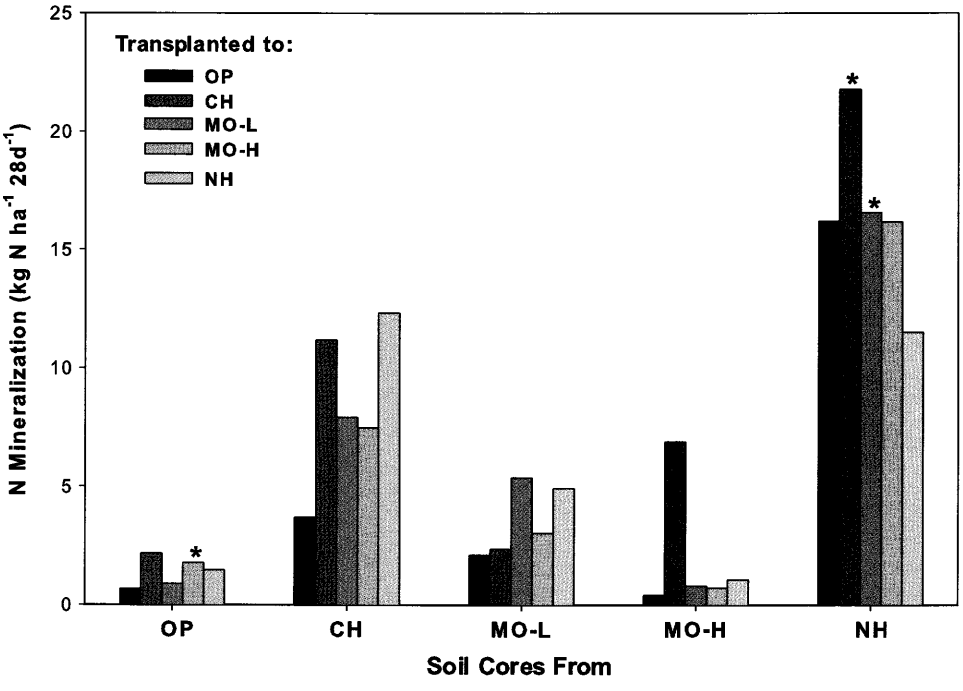

Figure 1. Effect of soil core transplanting on rates of N mineralization (kg ha^{-1} 28 d^{-1}). Bars represent mean N mineralization rates of four sample dates for soil cores collected from one site and transplanted to each of 4 different sites. Sites represent the following vegetation types: dry mixed-oak/pine (OP); cove hardwood (CH); mixed-oak, low elevation (MO-L); mixed-oak, high elevation (MO-H); northern hardwood (NH). '*' = significant difference between soil cores incubated on the site of origin and cores moved to another site as determined using a paired *T*-test analysis (SAS, 1985).

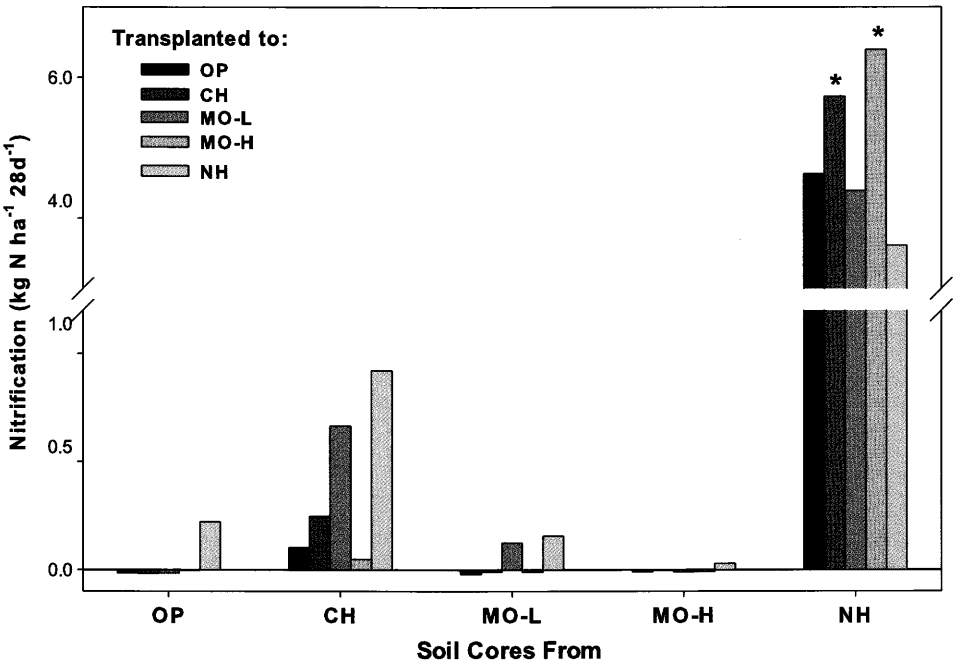

Figure 2. Effect of soil core transplanting on rates of nitrification (kg ha^{-1} 28 d^{-1}). Bars represent mean nitrification rates of four sample dates for soil cores collected from one site and transplanted to each of 4 different sites. Sites represent the following vegetation types: dry mixed-oak/pine (OP); cove hardwood (CH); mixed-oak, low elevation (MO-L); mixed-oak, high elevation (MO-H); northern hardwood (NH). '*' = significant difference between soil cores incubated on the site of origin and cores moved to another site as determined using a paired *T*-test analysis (SAS, 1985).

factors are important regulating factors. Total soil N, C:N ratio, soil water content, and soil temperature were significantly correlated with Nmin ($r^2 = 0.61$). Variables regulating nitrification rates included all factors tested, total C and N, C:N ratio, soil temperature and moisture ($r^2 = 0.75$). Total N was the variable first identified in the stepwise regression procedure for both N transformation processes; that variable alone had an r^2 of 0.55 and 0.62 for Nmin and nitrification, respectively. The relationship between N transformation rates and abiotic variables were examined for the five sites individually. Significant relationships were found only for NH and OP. Nmin rates on NH were positively correlated with both soil temperature and moisture ($r^2 = 0.83$) (Fig. 3). Nitrification rates on NH were positively correlated with soil temperature ($r^2 = 0.32$). On OP, N mineralization was positively correlated with soil H_2O content ($r^2 = 0.22$).

Biological processes regulated by temperature are often described by an exponential relationship and the strength of temperature dependence can be characterized by the Q_{10} value (i.e., a higher Q_{10} value indicates a higher temperature dependence). The Q_{10} value for N transformations for all soils on all sites was 3.4 for Nmin and 1.9 for nitrification. Examining soils from each site separately we found that NH soils had the greatest Nmin Q_{10} value at 8.9, other sites Q_{10} values ranged from 0.2 for CH to 1.4 for MO-L (Table 2). Nitrification rate Q_{10} values were only estimable for NH soils, 2.8 and CH, 0.70.

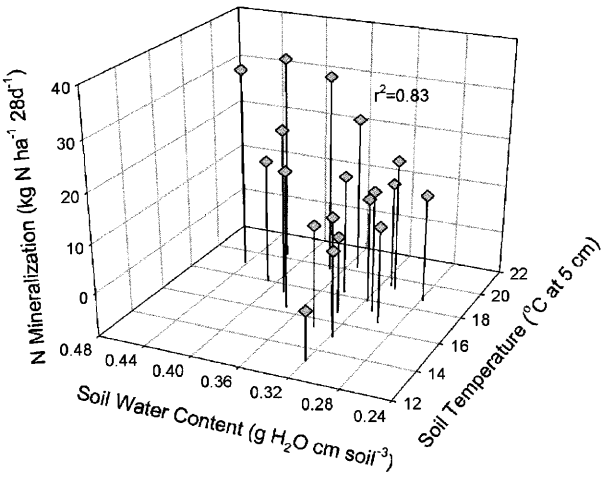

Figure 3. Graph of northern hardwood (NH) soil cores, both transplanted and incubated on the site of origin and the relationship between soil temperature (°C), soil moisture content (g H_2O cm soil^{-3}), and nitrogen mineralization (kg ha^{-1} 28 d^{-1}). Data shown include plot means for each sample date.

Discussion

Vegetation effects

Vegetation has long been recognized for its importance as a soil forming factor (Jenny, 1941) due to its impact on soil biological and chemical characteristics including microbial populations and soil organic matter composition. The five sites in our study represent four vegetation communities in the southern Appalachians and were found in previous studies to differ significantly in soil biological and chemical characteristics including Nmin and nitrification rates (Knoepp et al., 2000; Knoepp and Swank, 1998) (Table 2). Many other researchers have examined the relationships between N cycling patterns and vegetation community type (Fernandez, et al., 2000; Garten, 2004; Knoepp and Swank, 1998; Ross et al., 2004). These studies have shown that soil and forest floor N concentrations and C:N ratios often vary significantly among sites with differing vegetation types (Fernandez, et al., 2000; Garten, 2004; Knoepp and Swank, 1998; Ross et al., 2004). These variations occur not only between conifer and deciduous species (Fernandez et al., 2000) but also among deciduous communities (Garten et al., 1994; Knoepp and Swank, 1998; Ross et al., 2004). N transformation rates and N availability were greatest in sites with the greatest N concentrations and lowest C:N ratios (Fernandez et al., 2000; Garten, 2004; Knoepp and Swank, 1998; Ross et al., 2004). Knoepp et al. (2000) and Garten (2004) examined indicators of soil C quality and the relationship of these indicators with N cycling rates in southern Appalachian forests. The indicators examine the relationship between CO_2 flux rates, total C, and microbial biomass. Soil C quality and turnover rates were greatest in high elevation sites, the sites with the greatest N availability and the lowest temperatures.

Temperature and moisture response

Transplanting soil cores resulted in significant responses on soil N transformation rates only on soils from the two most extreme sites: OP (lowest moisture and highest temperature) and NH (lowest temperature and highest moisture). OP soil had increased Nmin when transplanted to MO-H. OP has the lowest moisture content ($0.13\,g\,cm^{-3}$) of all sites studied. Transplanting OP soil cores to MO-H resulted in increased soil moisture content, explaining the positive relationship between Nmin and soil water content on this site. The soil Nmin for NH was significantly affected by transplanting to CH and MO-L, two low elevation sites. Nmin on NH had a strong relationship with temperature, evidenced by the high Q_{10} values for Nmin rates and the significant regression relationship for both Nmin and nitrification, suggesting that soil temperatures limit N transformations on this site. Interestingly, soil moisture content was also significant in multivariate analyses of Nmin regulation on NH. This suggests that moisture may limit Nmin even on this site where soil moisture is quite high, averaging 38% by volume (Table 3). The importance of temperature and moisture interactions on regulating Nmin were examined by Wang et al. (2004) in 18 soils with a range of textures and C content. They found that net N mineralization increased with increasing temperature and moisture. Their data showed that N mineralization patterns were linear at lower temperature and curvilinear at higher temperatures. They found no relationship between net nitrification rates and incubation temperature.

In an examination of the regulation of N transformations by soil temperature and moisture, Knoepp and Swank (2002) found that when temperature was not limiting—moisture became a regulating factor of N mineralization. This is a similar finding to Zaman and Chang (2004), in laboratory studies they found that soil moisture had no affect on N mineralization at the low incubation temperatures. Rodrigo et al. (1997) reported greater relative differences in Nmin response to H_2O content at low soil H_2O levels. This supports our finding that only OP had a significant H_2O response and the lowest H_2O content.

Researchers have used transplant studies to predict ecosystem response to global climate change, specifically increased temperatures, and altered rainfall patterns (Bottner et al., 2000). Our results suggest that in the vegetation communities we studied, which represent up to 80% of the land area in the southern Appalachians (Elliott et al., 1999), biotic variables (i.e., soil N, soil C) exert substantial influence over N transformation processes. This is evidenced by the measurement of the greatest N transformation rates at the site with the lowest temperature in ours and other gradient studies (Fernandez et al., 2000; Knoepp et al., 2000; Knoepp and Swank, 1998). Environmental controls were significant regulating factors only at the wettest and warmest sites, and in soils with the highest and lowest C and N contents. The Nmin Q_{10} value for NH (8.9) suggests that increased temperatures would result in large releases of N, mineralized from the soil organic matter, unless moisture becomes limiting; nitrification rates may

also increase although more slowly ($Q_{10} = 2.8$). This site already shows signs of excess N availability with elevated NO_3 concentrations in soil solution below the rooting zone compared to low elevation sites (Knoepp et al., 2000), a sign this site may be approaching early N saturation (Aber et al., 1989). These data suggest that increases in soil temperatures resulting from global change could accelerate N saturation in northern hardwood or high elevation forests which extend from the southern Appalachians to the NE United States.

Acknowledgements

This paper was presented at: Through the Ped Darkly: Functional Ecology Belowground, a symposium honoring Dr. David C. Coleman, Distinguished Research Professor of Soil Ecology, Institute of Ecology, University of Georgia, Athens, GA, USA. Due to space constraints this contribution could not appear in the Pedobiologia Festschrift issue (Volume 50, Issue 6). In the spirit of the Festschrift, this work is dedicated to Dr. Coleman and acknowledges his collegiality, collaboration, and lifelong contribution to soil biology. This work was funded by the USDA Forest Service and the Coweeta LTER program (NSF Grant DEB 9632854 and DEB-0218001).

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