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Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians

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Abstract

We measured nitrogen (N) transformation rates for six years to examine temporal variation across the vegetation and elevation gradient that exists within the Coweeta Hydrologic Laboratory. Net N mineralization and nitrification rates were measured using 28-day *in situ* closed core incubations. Incubations were conducted at various intervals, ranging from monthly during the growing season, to seasonally based on vegetation phenology. Vegetation types included oak-pine, cove hardwoods, low elevation mixed oak, high elevation mixed oak, and northern hardwoods. Elevations ranged from 782 to 1347 m. Nitrogen transformation rates varied with vegetation type. Mineralization rates were lowest in the oak-pine and mixed oak sites averaging < 1.2 mg N kg soil-’ 28 day^{-1}. Rates in the cove hardwood site were greater than all other low elevation sites with an annual average of 3.8 mg N kg soil-’ 28 day-‘. Nitrogen mineralization was greatest in the northern hardwood site averaging 13 mg N kg soil-’ 28 day-‘. Nitrification rates were typically low on four sites with rates <0.5 mg N kg soil-’ 28 day-‘. However, the annual average nitrification rate of the northern hardwood site was 6 mg N kg soil-’ 28 days-‘. Strong seasonal trends in N mineralization were observed. Highest rates occurred in spring and summer with negligible activity in winter. Seasonal trends in nitrification were statistically significant only in the northern hardwood site. Nitrogen mineralization was significantly different among sites on the vegetation and elevation gradient. While N mineralization rates were greatest at the high elevation site, vegetation type appears to be the controlling factor.

Introduction

Forest soils often contain inadequate soil nitrogen levels (N) limiting forest growth and productivity. Measured rates of soil N mineralization, used as indices of N availability, often correlate well with site productivity and forest growth (Keeney, 1980). However, when N availability exceeds the uptake capabilities of site vegetation and soil microorganisms, the site is said to be N saturated (Aber et al., 1989). Excess N leaves the system via NO_3^- leaching, often removing exchangeable cations and possibly decreasing water quality. Measured rates of the N transformation processes (mineralization of organic N and its subsequent nitrification) provide insights into the availability of N, site productivity and water quality.

Rates of soil N mineralization often differ with forest type, elevation, and topographic position (Garten and Van Miegroet, 1994; Garten et al., 1994; Powers, 1990). These differences are attributed to site variations in soil organic matter, temperature and soil water availability (Garten et al., 1994; Powers, 1990). Our objective was to characterize seasonal and annual variation in rates of *in situ N* transformation rates, mineralization, and nitrification, along a vegetation and elevation gradient within the Coweeta Hydrologic Laboratory in the southern Appalachians. Knowledge of these patterns will allow us to identify changes in N mineralization that may occur due to climate change, N saturation, insect outbreaks or other types of disturbance.

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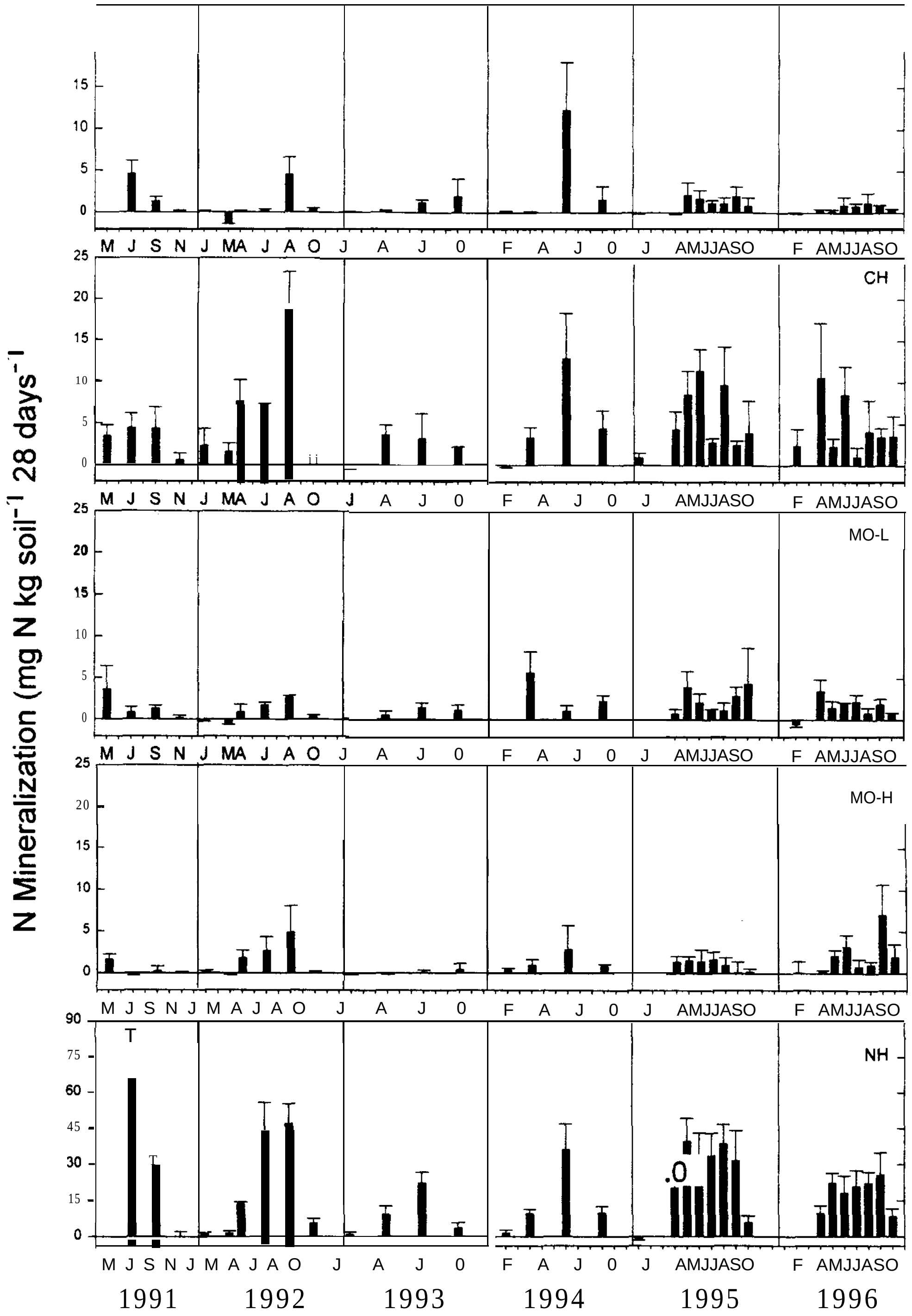

Figure I. Nitrogen mineralization rates measured using *in situ* closed core 28-day incubations. Data are presented for five sites representing a gradient in vegetation and elevation: OP – xeric oak-pine; CH – cove hardwoods; MO-L – low elevation mixed-oak; MO-H – high elevation mixed-oak: NH – northern hardwoods. Measurements began in May 1991 and were conducted at various intervals through October 1996. Values represent the mean of four transects from each site with standard error bars shown. Note differences in scale on vertical axes.

Materials and methods

Site description

This study was conducted at the Coueeta Hydrologic Laboratory, a 2 180 ha USDA Forest Service facility in the southern Appalachians of western North Carolina. USA. The climate is characterized by 1900 mm of precipitation annually with most months receiving at least 100 mm. 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).

The sites examined represent a gradient in vegetation and elevation and are a part of the Coweeta Long-term Ecological Research (LTER) project, funded by the National Science Foundation. All sites are on reference watersheds and represent the major vegetation community types within the Coweeta basin. Table 1 provides information about dominant vegetation, elevation, aspect, slope and soil. The Gradient project took a multi-disciplinary approach to study ecosystem processes and nutrient cycling within the range of elevation and vegetation types in the southern Appalachian forest. Intensive measurements, besides N mineralization, have been conducted on these sites including, throughfall chemistry, soil solution chemistry, forest floor mass and chemistry, aboveground productivity, root phenology and productivity, and many other parameters.

Plot sampling and soil analysis

On each site one 0.08 ha (20 m x 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. Transects were at 1, 7, 13 and 19 m along the 20 m axis. Sampling points on each transect were chosen randomly due to variation in soil type in some plots. Plots were established and measurements of *in situ N* transformations were initiated in May and June 1991. Measurement intervals in 1991 and 1992 were bimonthly. In 1993 and 1994, N transformation measurements were conducted four times a year, with season definitions based on plant phenology: winter, dormant season (December, January and February); spring, bud break (March and April); summer, full leaf (May, June, July, August and September); and fall, abscission layer formation and leaf fall (October and November). In 1995 and 1996, we measured N transformation rates once during the dormant season and monthly, April through October. Thirty-four net N transformation measurements were made from May 199 1 through October 1996.

Net rates of N transformations were measured using an *in situ* closed core method modified from Adams and Attiwill (1986). Two 15-cm long, 4.3-cm inside diameter, PVC cores were driven 10 cm into the mineral soil within 25 cm of each sample point. One PVC core was removed immediately for the time zero determination of soil NH_4^+– and NO_3^-–N concentrations. The second core of each pair was capped and retrieved after incubating in the field for 28 days. All collected soil cores were kept cool until returned to the laboratory, stored in a refrigerator at 4 °C until analyzed, within 24 h. Soils were moist sieved to <6 mm. One subsample (20 g) was placed in a 105 °C oven for > 12 h to obtain oven-dry weight. One 5-g subsample was shaken with 20 mL of 2 *M* KC1 for 1 h to extract NH_4^+– and NO_3^-–N. The soil/ KC1 mixture was then centrifuged for 15 min at 6000 rpm. The supernatant was analyzed for NH_4^+– and NO_3^-–N on an autoanalyzer using alkaline phenol (USEPA,1983a) and cadmium reduction (USEPA, 1983b) techniques, respectively. All soil N data are presented on an oven dry weight basis. Net N mineralization rates were calculated as soil NH_4^++NO_3^-–N concentrations at 28 days minus NH_4^++NO_3^-–N concentrations at time zero. Net nitrification rates equaled soil NO_3^-–N concentrations at 28 days minus NO_3^-–N concentrations at time zero.

Characterization of soil chemical properties was conducted on a subset of samples collected for time zero inorganic N determinations. The remaining soil was air-dried and sieved to <2 mm. Total percent soil C and N were determined by combustion on a ground subsample. Soil pH was measured in a 1: 1 soil: 0.0 1 *M* $CaCl_2$ slurry. Soil base cation concentrations were determined using a dilute double acid extraction procedure, in which, subsamples (5 g) were extracted with 20 mL 0.05 *M* H_2SO_4 plus 0.05 *M* HCl. Calcium, Mg and K concentrations in solution were determined using atomic absorption spectroscopy.

Seasonal net mineralization and nitrification rates were calculated using plot means ($n = 4$) from each sample date. Sample dates were assigned a season, based on plant phenological stages as previously described. Analysis of variance was conducted using the GLM procedure of SAS (SAS, 1985) to examine the effects of SITE and SEASON on rates of net N mineralization and nitrification.

Table 1. Site characteristics for the oak-pine (OP), cove hardwood (CH), low elevation mixed oak (MO-L), high elevation mixed oak (MO-H), and northern hardwood (NH) rite\. including dominant overstory and shrub vegetation, elevation (m), aspect (°), slope (°) and soil series and classification

Site	Dominant vegetation	Elevation (m)	Aspect (°)	Slope (°)	Soil classification
OP	*Quercus prinus* Q. *rubra* *Carya* spp. *Kalmia latifolia*	7x2	180	34	Cowee-Evard complex fine-loamy, oxidic/mixed Typic Hapludults: Chandler series a coarse-loamy, micaceous mesic Typic Dystrochrepts: Edneyville-Chestnut complex coarse-loamy. mixed mesic Typic Dystrochrepts
CH	*Liriodendron tulipifera* *Q. rubra* *Tsuga canadensis* *Carya* spp.	795	340	21	Tuckasegee series a tine-loamy. mixed mesic Typic Haplumbrepts: Saunook series a tine-loamy. mixed mesic Humic Hapludults
MO-L	*Q. coccinea* *Q. prinus* *Rhododendron maxima*	865	15	34	Trimont series a tine-loamy mixed. mesic Humic Hapludults
MO-H	Q. *rubra* *Carya* spp. *R. maxima*	1001	75	33	Chandler series a coarse-loamy. micaceous. mesic Typic Dystrochrepts
NH	*Betula allegheniensis* *L. tulipifera* Q. *rubra*	1347	20	33	Plott series a coarse-loamy, mixed, mesic Typic Haplumbrepts

Table 2. Mean seasonal rates of N mineralization and nitrification for O-IO cm of surface soil measured using in *situ* closed cores. Values represent seasonal means of plot means for each of the five vegetation types examined. Values in parentheses are standard errors of the mean

	Mineralization Rate (mg N kg soil-’ 28 day-‘)			
Site[a]	Winter	Spring	Summer	Fall
OP	0.05 (0.04)	-0.1 l (0.25)	1.90 (0.48)	0.86 (0.29)
CH	1.06 (0.54)	5.17 (1.34)	6.35 (1.14)	2.60 (0.63)
MO-L	-0.29 (0.12)	1.77 (0.94)	1.87 (0.22)	1.45 (0.64)
MO-H	0.09 (0.1 I)	0.73 (0.32)	1.89 (0.44)	0.61 (0.29)
NH	3.81 (3.10)	IO.55 (2.50)	33.07 (3.07)	5.48 (1.42)
	Nitrification Rate (mg N kg soil-’ 28 day-’)			
	Winter	Spring	Summer	Fall
OP	-0.01 (0.03)	-0.01 (0.01)	0.14 (0.12)	0.16 (0.13)
CH	0.01 (0.03)	0.25 (0.02)	0.70 (0.21)	0.77 (0.62)
MO-L	0.00 (0.03)	0.00 (0.01)	0.16 (0.17)	0.80 (0.71)
MO-H	0.10 (0.11)	0.00 (0.01)	0.24 (0.19)	0.06 (0.04)
NH	1.02 (0.37)	6.10 (1.59)	16.04 (1.18)	2.62 (0.87)

[a] OP = xeric oak-pine, CH = cove hardwood, MO-L = low elevation mixed oak. MO-H = high elevation mixed oak and NH = northern hardwood.

Results and discussion

Analysis of variance showed that site and season of year significantly affected in *situ N* mineralization rates (*P* = 0.0001). The site x season interaction term was also significant. Average seasonal rates of net N mineralization were generally greatest in summer, ranging from 1.9 mg N kg soil-t 28 day-t on the low elevation mixed oak (MO-L), high elevation mixed oak (MO-H) and oak-pine (OP) sites to 33 mg N kg soil-’ 28 day-’ on the northern hardwood (NH) (Table 2). On two sites, cove hardwood (CH) and MO-L, summer rates were not significantly greater than those measured in the spring and fall. Rates in the winter were negligible (< 1 .0 mg N kg soil-t 28 day-‘) on all sites except NH, where N was mineralized at a rate of 3.8 mg N kg soil-’ 28 day-t. Nitrification rates on four sites were very low regardless of season, ≤0.8 mg N kg soil-’ 28 day^{-1} (Table 2) while rates for the fifth site (NH) ranged from a low of 1 .O mg N kg soil-’ 28 day-’ in the winter, to 16.0 mg N kg soil-’ 28 day-’ in the summer.

The seasonal patterns of N mineralization and nitrification we observed were consistent from year to year and similar to those observed by others. Rates were generally greatest during the growing season and

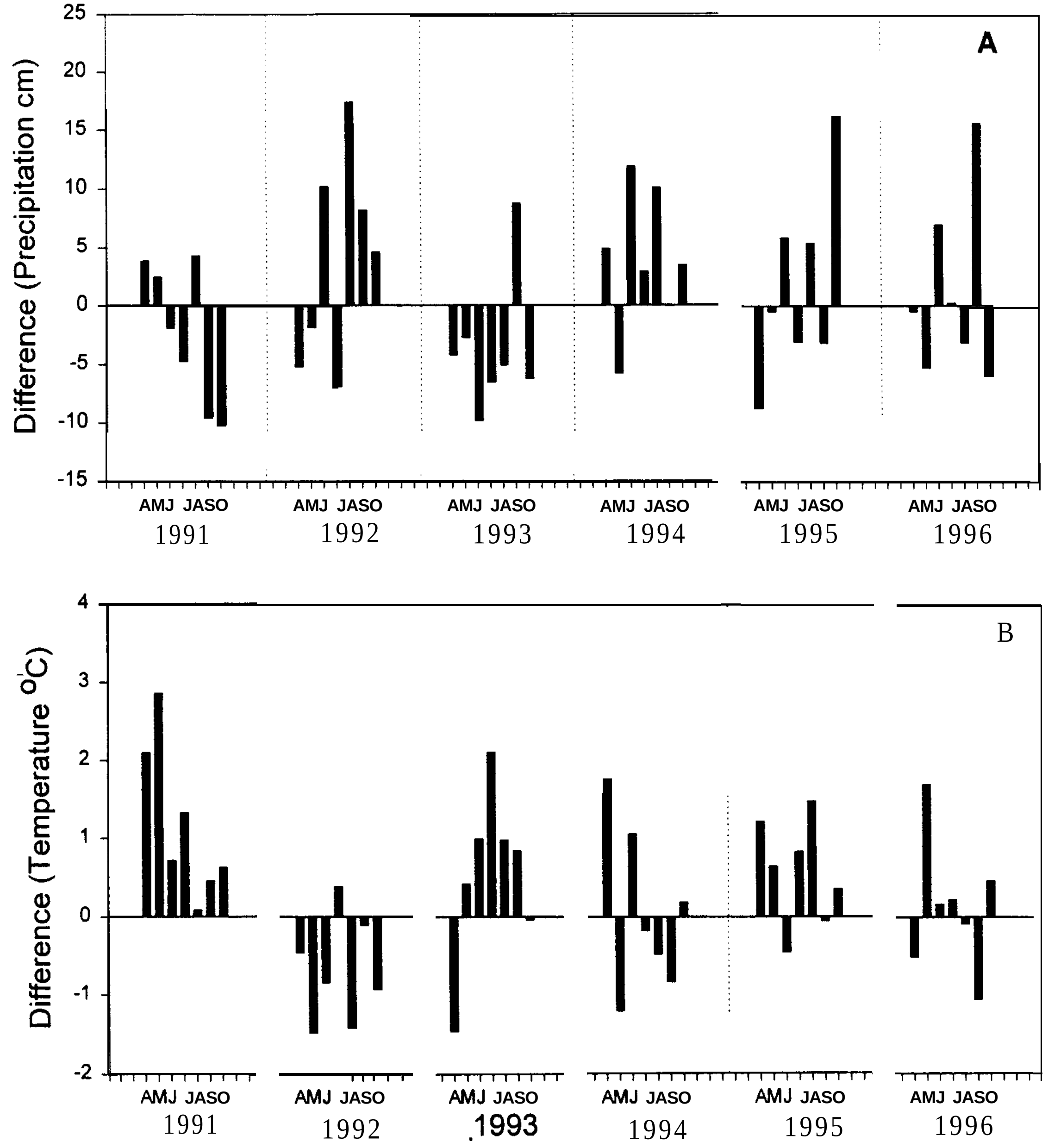

Figure 2. The 1991 through 1996 growing season differences from the 62-yr monthly mean in (A) precipitation and (B) air temperature.

negligible in the winter. Casals et al. (1995) examined four sites with pine hardwood vegetation in Spain and found the greatest net NH_4^+ formation occurred in the spring while nitrification was greatest in the summer. Polglase et al. (1992) found that *in situ* rates of N mineralization were greatest in the summer. They noted however, that the seasonal differences were observed only with *in situ* methods. Anaerobic N mineralization measurements showed little seasonal or annual variation. In our study, differences among N mineralization rates in spring, summer, or fall were not always significant; only NH exhibited significant differences among seasonal rates. We observed similar seasonal responses in nitrification rates: on NH nitrification rates changed with season; on the remaining sites seasonal changes were not statistically significant ($p = 0.35$ to 0.8).

In addition to seasonal patterns in net N mineralization rates, data show differences in patterns of N mineralization among years. Annual variation could be a response to annual differences in rainfall and temperature. Temperature and soil moisture were used to explain more than 90% of the variation in laboratory N mineralization measurements made by Goncalves and Carlyle (1994). Figure 2 shows the deviation from the 62-yr monthly mean of growing season air temperature and precipitation. Elevated N mineralization rates in August 1992 were associated with a very wet month. 15 cm above average rainfall. Net N mineralization rates were very low in 1993 corresponding with below average precipitation that year. However, in our study annual temperature patterns do not necessarily affect annual patterns of N mineralization. Monthly mean air temperatures were below average in, 1992 (Figure 2) with no apparent effect on N mineralization rates (Figure 1).

Analysis of variance showed significant differences in N mineralization rates among the five sites ($P = 0.000 I$). The oak-pine (OP), low elevation mixed oak (MO-L) and high elevation mixed oak (MO-H) sites had the lowest rates, averaging ≤ 1.2 mg N kg soil-’ 28 day-’ (Table 2). Mineralization rates in soils on the cove hardwood site (CH) were significantly greater. averaging 3.8 mg N kg soil^{-1} 28 day-‘. The high elevation northern hardwood site (NH), had the greatest mineralization rates of all sites examined, averaging 13 mg N kg soil-’ 28 day-‘.

Rates of nitrification were low and few differences existed among four sites. OP, MO-L, MO-H and CH (Table 2). averaging ≤ 0.4 mg N kg soil-’ 28 day-‘. Less than 15% of the net N mineralized was transformed into NO_3^-. NH had the greatest nitrification rates; those soils produced an average of 6 mg kg soil-’ 28 day-’ as NO_3^-–N, about 50% of the net N mineralized.

Differences in rates of net N mineralization among forest types are well documented. Liu and Muller (1993) examined forested sites with vegetation types very similar to those we examined. In their study, they found that mesophytic sites had greater rates of N mineralization than more xeric sites. This observation is similar to the differences we observed between CH and NH and the more xeric sites, OP, MO-L and MO-H.

Garten and Van Miegroet (1994) sampled sites that represented low to high elevations in the Great Smoky Mountains National Park. Sites above 700 m had the greatest rates of N mineralization and nitrification, but did not differ significantly from low elevation sites. Our five sites had significantly different rates of N mineralization and nitrification and all were located at >700 m elevation. Powers (1990) examined N mineralization along a 2000 m gradient crossing six different vegetation types in northern California. Patterns of N mineralization did not follow site characteristics of temperature and moisture. However, when N mineralized was expressed as a percent of total N. a positive correlation with soil temperature became significant. Therefore, he attributed differences along the elevation and vegetation gradient to interactions of soil temperature, moisture and substrate quality.

Table 3. Chemical characteristics of surface 0–10 cm soils collected for $t = 0$ nitrogen transformation measurements. Values presented are means with $n = 32$ for pH. $n = 16$ for C and N and $n = 12$ for cation concentations. Values in parentheses are standard errors

Site[a]	pH	Total C (%)	Total N (%)	Ca (mg kg^{-1})	Mg (mg kg^{-1})	K (mg kg^{-1})
OP	3.9 (0.04)	3.3 (0.3)	0.1 (0.01)	28 (6.9)	19 (2.0)	61 (6.0)
CH	4.2 (0.04)	5.5 (0.3)	0.3 (0.02)	112 (14.0)	38 (2.9)	89 (6.8)
MO-L	4.0 (0.05)	4.4 (0.2)	0.2 (0.01)	49 (7.8)	25 (1.9)	69 (5.5)
MO-H	4.0 (0.03)	5.6 (0.4)	0.2 (0.01)	28 (6.7)	20 (1.5)	67 (6.2)
NH	4.0 (0.03)	9.9 (0.4)	0.7 (0.03)	441 (81.4)	55 (9.4)	83 (4.5)

[a] See Table 2

Studies by Garten and Van Miegroet (1994) and Powers (1990) and the data we present suggest that separating environmental effects from vegetation type is complex. Their data indicate that temperature and rainfall influence rates and patterns of mineralization. Both of these factors vary with elevation, with rainfall increases, and temperature decreases as elevation increases. In our study, rates are greatest at the high elevation sites where temperatures are lowest. This suggests that vegetation is the overriding regulator of net N mineralization rates in southern Appalachian forests. Casals et al. (1995) also found that vegetation type dominated regulation of N mineralization in a pine hardwood system in the Pyrenees mountains of Spain. They observed similar rates among four sites with different aspects. Nadelhoffer et al. (1984) also concluded that substrate quality regulates N mineralization rates. Our study also points to the regulation of N mineralization by substrate quality which is directly linked to vegetation type. Our sites cover a wide range in exchangeable cation concentration, percent total C and N, while soil pH is very consistent, ranging from

3.9 to 4.2 (Table 3). OP and MO-H have the lowest exchangeable Ca concentration. 28 mg kg^{-1}; MO-L soils contain 49 mg Ca kg^{-1}; CH 129 mg kg^{-1} and NH 441 mg Ca kg $soil^{-1}$, the same ranking pattern as summer rates of N mineralization. This pattern generally holds for percent total N. lowest in OP at 0.1%; 0.7% in MO-L and MO-H soils, 0.3% in CH and 0.7% in NH.

We examined the N mineralization data as a proportion of total N mineralized annually, mg N mineralized g N^{-1} (Nmin/Ntot). This approach was used by Powers (1990), who found that the analysis removed some site variability and produced a strong positive relationship between mineralization and mean annual soil temperature ($r^2 = 0.68$) which decreased along an elevational gradient. We calculated annual rates of N mineralization by multiplying seasonal means by the number of months in that season (see methods section) and summing them. Annual rates were: OP – 11 mg N kg soil-‘: CH – 50 mg N kg soil-‘; MO-L – 15 mg N kg soil-‘; MO-H – 12 mg N kg soil-‘: NH – 209 mg N kg soil-). This resulted in Nmin/Ntot ratios of 11 for OP. 17 for CH, 7 for MO-L, 6 for MO-H, and 30 for NH. In contrast to Powers' (1990) findings. a positive relationship between mg N mineralized g N^{-1} and temperature was not evident on our sites. NH the highest elevation site, with the lowest mean annual temperature. had the greatest Nmin/Ntot ratio. This also supports the conclusion that vegetation. not climate. is the main factor controlling N mineralization along the gradient in vegetation and elevation.

Summary

Nitrogen mineralization and nitrification rates measured for six years on five sites showed strong seasonal response with greatest rates occurring in the spring and summer. Significant differences were measured among sites in both mineralization and nitrification where elevation ranged from 782 to 1347 m and vegetation types from xeric oak-pine to mesic northern hardwood. Nitrogen mineralization and nitrification rates were greatest on the northern hardwood and lowest on the oak-pine sites. Greatest rates occurred on the high elevation site, suggesting that vegetation type may regulate N transformations by controlling substrate quality.

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