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Topographic Influences on Nitrogen Cycling within an Upland Pin Oak Ecosystem

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ABSTRACT. Nitrogen mineralization and nitrification were studied within an upland pin oak (*Quercus ellipsoidalis* E.J. Hill) forest to determine if topography could be used to understand the spatial variability of N transformations within and among individual stands. Four upland pin oak stands were used for the study, and within each stand, transects were established on northeast (45° azimuth), southeast (135° azimuth), southwest (225° azimuth), and northwest (315° azimuth) facing aspects. Nitrogen mineralization and nitrification were measured at 5-wk intervals for 1 year at top, middle, and bottom slope position along each transect using an *in situ* soil incubation technique. Annual rates of mineralization among the four stands ranged from 3.0 to 6.7 g N m^{-2} yr^{-1}, but were not significantly influenced by aspect or slope position. Although aspect had no effect on nitrification, bottom slope positions had significantly lower (0.3 g N m^{-2} yr^{-1}) nitrification rates compared to middle (1.3 g N m^{-2} yr^{-1}) and top (1.4 g N m^{-2} yr^{-1}) slope positions. Annual N mineralization and nitrification increased with stand age. Slope position and aspect had little influence on N cycling rates within the subtle topography of east central Minnesota; time since disturbance seems to be the most important factor influencing the variability in N dynamics among upland pin oak stands. FOR. SCI. 37(1):45–53.
ADDITIONAL KEY WORDS. Nitrogen mineralization, nitrification, oak forests, spatial variability, disturbance.

NITROGEN (N) cycling within terrestrial ecosystems is a dynamic process that displays substantial variability at both large and small spatial scales (Schimel et al. 1985, Zak et al. 1986, Robertson et al. 1988, Burke 1989, Burke et al. 1989, Zak and Pregitzer 1990). Considerable effort has been devoted toward identifying the components of this variability, and several factors have been recognized as exerting a significant influence on N cycling processes (Aber and Melillo 1982, Vitousek et al. 1982, Flanagan and Van Cleve 1983, Pastor et al. 1984). Climate affects large-scale patterns of N cycling through the combined effects of precipitation and temperature. At regional scales, these effects are often modified by physiographic and edaphic factors, and several studies have found distinct patterns of N cycling along topographic and edaphic gradients (Pastor et al. 1984, Schimel et al. 1985, Burke 1989). In addition to abiotic factors, species composition and its effect on litterfall chemistry plays an important role in regulating rates of N cycling at the scale of an individual forest ecosystem (Aber and Melillo 1982, Pastor et al. 1984, Pastor and Post 1986).

Because of the factors discussed above, rates of N cycling can be expected to

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differ among forests from diverse climatic regimes. Nonetheless, spatial variability in N cycling among forests within a climatic regime can be of equivalent magnitude. In the Lake States Region, for example, N mineralization can display a twofold difference between forest ecosystems, and nitrification can differ by an order of magnitude (Pastor et al. 1984, Zak et al. 1986, 1989, Zak and Pregitzer 1990). Although local differences in species composition and soil moisture availability can account for a large proportion of this spatial variability, variability among forest stands with similar species composition and topographic position can be as large as the variability between different ecosystem types (Zak et al. 1986, 1989, Zak and Pregitzer 1990). The underlying factors or processes responsible for this variation are not fully understood.

Determining the factors that contribute to variation within and among individual forest stands (i.e., within an ecosystem type) is important because regional and global estimates of N cycling are often based on data collected from a single site within an ecosystem type. The accuracy of these estimates, therefore, depends on how well an individual stand represents an ecosystem-level mean. Because topography has a significant effect on rates of N cycling among different ecosystems (Schimel et al. 1985, Burke 1989), we hypothesized that a significant proportion of the variability in N cycling within an ecosystem type could be related to small-scale topographic gradients. To test this, we studied the influence of aspect and slope position on rates of N mineralization and nitrification within upland pin oak (*Quercus ellipsoidalis* E.J. Hill) stands located in east-central Minnesota.

METHODS

Study Site

The study was conducted at the Cedar Creek Natural History Area (CCNHA), approximately 50 km north of Minneapolis, MN. The climate of the area is continental with a mean annual temperature of 6°C and annual precipitation of 660 mm (Grigal et al. 1974). The landscape ranges from nearly level plains to gently rolling hills and is composed of well-sorted outwash sands that often extend 20 m in depth. Cedar Creek is a mosaic of wetland and upland ecosystems related to the proximity of the regional water table to the soil surface. The water table is at or near the surface in low-lying areas and is only several meters below the surface in the highest elevations. Prairie, oak savanna, upland forest, marsh, and swamp are ecosystems common to Cedar Creek (Cushing 1963).

The upland pin oak forest is prevalent in the CCNHA, and we selected that type to determine if topographic differences could be used to explain the variability of N cycling within ecosystems. The upland pin oak forest typically occurs in the rolling portions of the landscape, extending from top to bottom slope positions. *Corylus americana* Walter and *C. cornuta* Marshall are common understory species, and often form a dense tall-shrub layer. Ovington et al. (1963) and Reiners (1971) have described the composition, structure, and biomass dynamics of these forests in detail.

Four randomly selected upland pin oak stands (ca. 1 ha) were studied; their overstory and soil properties are summarized in Table 1. Within each stand, transects were established on northeast (45° azimuth), southeast (135° azimuth),

TABLE 1.

Overstory and soil properties of four upland pin oak stands in east-central Minnesota. Values presented are stand means (n = 12) with the standard error in parentheses. Means in a row that have the same letter are not significantly different at alpha = 0.05.

	Stand			
	1	2	3	4
I. Overstory* properties				
Basal area (m^2 ha^{-1})	26ab	25b	25b	32a
	(1.4)	(2.2)	(2.4)	(2.4)
Annual radial increment (cm yr^{-1})	0.47a	0.44a	0.39a	0.39a
	(0.04)	(0.05)	(0.03)	(0.04)
Age (yr)	43a	46a	67b	63b
	(0.5)	(0.2)	(0.6)	(1.0)
II. Soil properties				
A. Forest floor				
Organic matter (g m^{-2})	3520a	2675a	3860a	3380a
	(265)	(525)	(274)	(224)
Total N (g m^{-2})	20a	11a	21a	20a
	(1.5)	(2.3)	(1.3)	(1.4)
B. Surface soil				
Organic matter (g m^{-2})	4320a	6070a	6125a	7285a
	(366)	(1150)	(862)	(866)
Total N (g m^{-2})	69a	73a	87a	91a
	(6.4)	(8.3)	(10.5)	(8.9)
pH	4.19ab	4.40b	4.11a	4.35b
	(0.09)	(0.09)	(0.09)	(0.08)
Silt + clay (%)	12.8a	9.5b	9.4b	9.1b
	(1.39)	(0.60)	(0.82)	(0.61)

* Note: Data have been summarized from Hairston (1988).

southwest (220° azimuth), and northwest (315° azimuth) facing aspects. Uniform slopes facing each aspect were identified within a stand, and one transect was randomly located on each slope. Slopes averaged 8%, and ranged from 50 to 100 m in length. Sampling points were located at top, middle, and bottom slope positions along each transect. Soils at bottom slope positions had mottling (ca. 20 cm from soil surface), indicative of poor drainage, and were typically within a few meters from the transition between upland forest and wetland. Top and middle slope positions within each stand were well drained. At each sampling point, the age of one overstory tree was determined using an increment borer.

Nitrogen Mineralization and Nitrification

Net N mineralization and nitrification were measured using an *in situ* incubation procedure (*sensu* Rapp et al. 1979). At each sampling point and date, one soil core was removed from the surface soil to determine initial NH_4^+ and NO_3^- concentrations. Cores were 10 cm in depth and 3.8 cm in diameter and were collected in a 15 cm length of PVC tubing. The initial cores were sealed within polyethylene bags and returned to the laboratory for analysis. At the same time, a second tube was driven into the soil, but the soil and tube were not removed from the soil profile. This tube was covered with a styrofoam cup to prevent leaching losses, and was incubated *in situ* for 5 weeks. Following the incubation, the soil core was removed and returned to the laboratory for analysis. Only one incubation was conducted over the period from November 12, 1987, to April 14, 1988. An additional 48 soil samples, one at each sampling point, were collected to determine soil bulk density.

A 10 g subsample of each initial and incubated core was extracted with 2 M KCl, and analyzed for NH_4^+-N and NO_3^--N (Technicon 1977, 1978). Net N mineralization was calculated as the difference in NH_4^+-N plus NO_3^--N between incubated and initial cores. Similarly, net nitrification was considered to be the increase in NO_3^--N in incubated samples. Values presented are mean weekly rates (mg N m^{-2} wk^{-1}) during the 5-week incubation and mean annual totals (g N m^{-2} yr^{-1}).

Statistical Analyses

Mineralization and nitrification rates (mg N m^{-2} wk^{-1}) were analyzed using an analysis of variance for a split-plot design (SAS 1982). An analysis of variance for a randomized block design was employed to determine differences in annual rates (g N m^{-2} yr^{-1}) due to stand, aspect, and slope effects; stands were used as the blocking variable. Mean rates were compared using a Fisher's protected least significant difference procedure. Significance for all analyses was accepted at alpha = 0.05. We used linear regression analysis to correlate soil organic matter and N content to annual rates of N mineralization. Linear regression analyses were also used to explore the relationships between stand age and N mineralization, nitrification, soil organic matter, soil total N, forest floor organic matter, and forest floor total N (SAS 1982).

RESULTS

Average weekly rates of N mineralization and nitrification were significantly different among the seven sampling dates (Figure 1a and 1b). In general, rates were greatest during the growing season and minimal during winter. Slope and aspect had little influence on temporal patterns of N mineralization and nitrification; neither of these variables or their interaction were significant. Differences among the four upland pin oak stands were, however, significantly different. Weekly rates of N mineralization and nitrification (averaged over date, aspect and slope) displayed a two-fold difference among the stands.

Annual N mineralization rates were not significantly different between northeast, southeast, southwest, and northwest facing slopes (Table 2). Values ranged from 6.0 g N m^{-2} yr^{-1} on southeast facing slopes to 4.3 g N m^{-2} yr^{-1} on northwest facing slopes. Annual rates of nitrification were not significantly different among any of the aspects, and ranged from 1.9 g N m^{-2} yr^{-1} on the southeast aspect to 0.8 g N m^{-2} yr^{-1} on the northwest aspect (Table 2). Although rates of annual N mineralization were not significantly different among the three slope positions, slope position had a significant influence on nitrification. Rates at the top (1.4 g N m^{-2} yr^{-1}) and middle (1.3 g N m^{-2} yr^{-1}) slope positions were significantly greater than those at the bottom slope position (0.3 g N m^{-2} yr^{-1}; Table

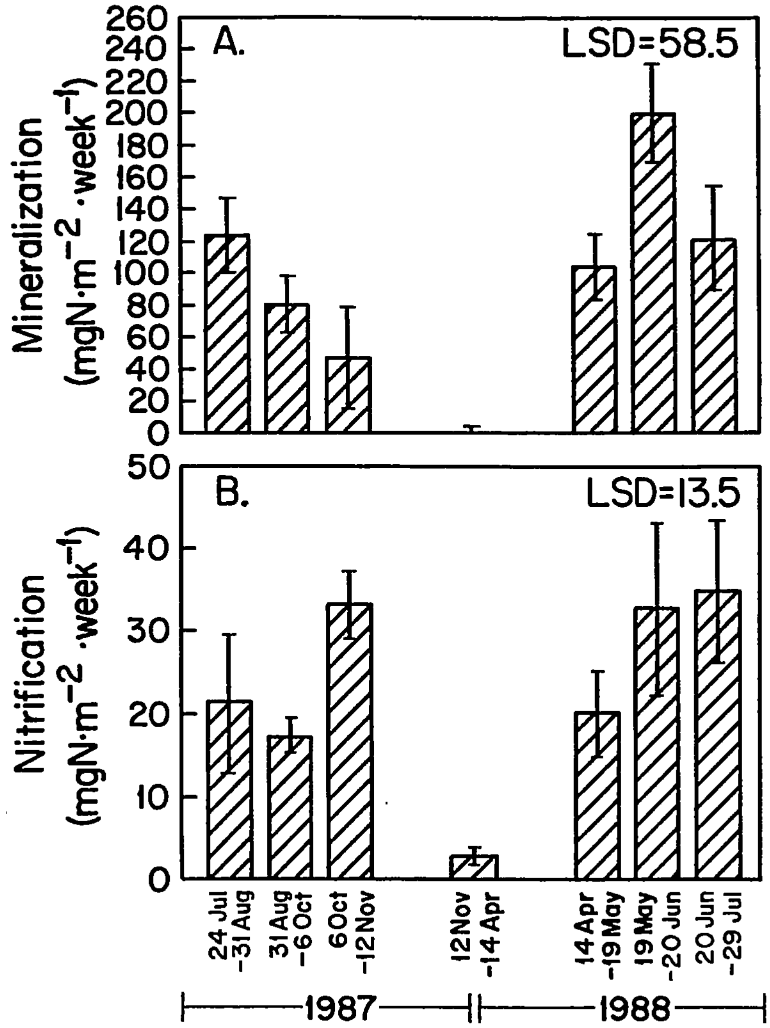

FIGURE 1. Mean N mineralization (A) and nitrification (B) for an upland pin oak ecosystem in east-central Minnesota. Values are mean weekly rates (n = 48) during the *in situ* soil incubation. The standard error of each mean is indicated.

2). The interaction of slope and aspect did not have a significant influence on either mineralization or nitrification.

Annual N mineralization and nitrification were significantly different among the four upland pin oak stands. Mineralization rates in Stand 3 (6.2 g N m^{-2} yr^{-1}) and Stand 4 (6.7 g N m^{-2} yr^{-1}) were twice those measured in Stands 1 and 2 (Figure 2a). A similar pattern was present for nitrification (Figure 2b). Annual N mineralization in the four stands was highly correlated to soil total N and well correlated to organic matter content (NMIN = $-8.79 + 0.17$ (TN), $r^2 = 0.99$; NMIN = $-2.60 + 0.001$ (OM), $r^2 = 0.71$; where NMIN = g N m^{-2} yr^{-1}, TN = soil total N in g N m^{-2}, and OM = soil organic matter in g m^{-2}). Soil organic matter ($r^2 = 0.50$), total N ($r^2 = 0.91$), N mineralization ($r^2 = 0.93$), and nitrification ($r^2 = 0.99$) were linearly correlated to mean stand age.

TABLE 2.

The influence of slope position and aspect on rates of nitrogen mineralization and nitrification within an upland pin oak forest. Values presented are mean annual rates for four stands in east-central Minnesota (n = 12 for aspect, n = 16 for slope). The standard error (in parentheses) is listed below each mean.

	Mineralization	Nitrification
	($g\ m^{-2}\ yr^{-1}$)	
I. Aspect		
Northeast	4.7	1.0
	(1.01)	(0.23)
Southeast	6.0	1.9
	(1.75)	(0.56)
Southwest	4.6	0.8
	(0.92)	(0.23)
Northwest	4.3	1.1
	(0.79)	(0.25)
LSD	n/s	n/s
II. Slope position		
Top	5.6	1.4 a
	(1.25)	(0.36)
Middle	4.6	1.3 a
	(0.84)	(0.32)
Bottom	4.5	0.3 b
	(0.91)	(0.09)
LSD	n/s	0.72

Note: means in a column that have the same letter are not significantly different at alpha = 0.05. The interaction of slope and aspect was not significant at alpha = 0.05.

DISCUSSION

In the subtle landscape of east-central Minnesota, topography significantly influences the distribution of upland and wetland ecosystems. The regional water table lies at a shallow depth in the CCNHA, and small topographic changes can result in large differences in edaphic conditions. Moreover, these changes can occur across relatively short (3 to 5 m) distances. Although topographic variation within the upland pin oak stands was subtle, it was a logical source of variation because they all had similar species composition and occurred on similar soils. The topographic gradients we studied extended from excessively well-drained top-slope positions to imperfectly drained bottom-slope positions and encompassed four different aspects. Topography, or distance from the water table, significantly influences community composition; however, it seems to have a limited influence on N dynamics within the upland pin oak forest.

Whereas N mineralization was little affected by slope position or aspect, nitrification was significantly greater in the well-drained top and middle slope positions compared to the imperfectly drained bottom slope position. This pattern could be explained by two alternative mechanisms. Nitrification is an aerobic process requiring O_2 for the two-step oxidation of NH_4^+ to NO_3^- (Alexander 1977, Schmidt 1982). The regional groundwater table lies near the soil surface in the lower slope

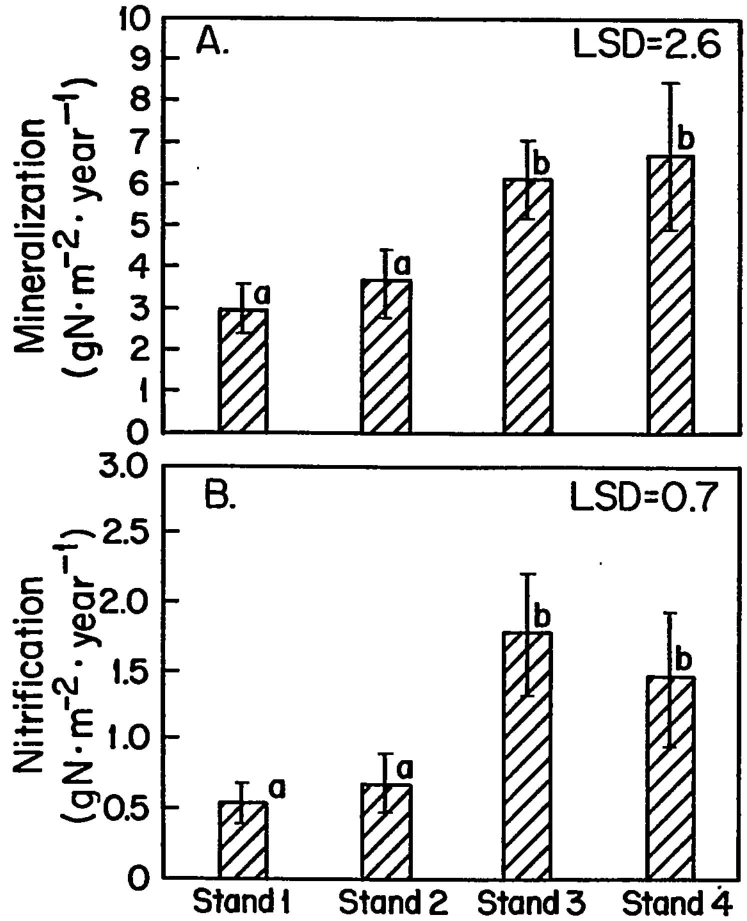

FIGURE 2. Mean annual N mineralization (A) and nitrification (B) for each of the four upland pin oak stands ($n = 12$) in east-central Minnesota. Means with the same letter are not significantly different at alpha = 0.05. The standard error of each mean is indicated.

positions, and could create conditions unfavorable to nitrification (i.e., anaerobiosis). Alternatively, denitrification can be an important process in poorly drained landscape positions (Groffman and Tiedje 1989), and could consume a large proportion of the NO_3^- produced in aerobic microsites. Further study of these processes would be required to determine the exact mechanism responsible for the low net nitrification rates we observed.

In the Lake States region, N mineralization can range from 5.3 to 8.3 g N m^{-2} yr^{-1} in oak-dominated forests (calculated from Nadelhoffer et al. 1983, Pastor et al. 1984, Zak and Pregitzer 1990). Rates that we measured in the upland pin oak stands varied from 3.0 to 6.7 g N m^{-2} yr^{-1} and are comparatively low. More importantly, our study sites all occurred within a 5.2 km^2 area, and the differences among them were as large as those in the aforementioned studies. Topographic gradients are obviously not responsible for the variability we observed among the four upland pin oak stands.

Effects of disturbance on nutrient cycling, biomass accrual, and forest floor dynamics are well documented (Bormann and Likens 1979, Covington 1981). The upland pin oak stands we studied were even-aged, and all probably regenerated following fire. Therefore, stand age should be a relative measure of time since disturbance. The correlation between N transformations and stand age suggests that disturbance is an important factor regulating rates of N cycling within the upland pin oak forest. In the old-field ecosystems of CCNHA, soil C and N pools are highly correlated to field age, i.e., length of time following agricultural abandonment (Zak et al. 1990). Our data suggest that disturbance, and it influence on soil organic matter dynamics, is an equally important factor regulating N availability within the forested ecosystems of the CCNHA.

A similar magnitude of difference in N cycling rates has been observed among several northern hardwood stands in Lower Michigan (Zak et al. 1986, Zak and Pregitzer 1990). Although these stands were of similar age, the differences among them were directly related to soil organic matter content; mineralization rates were low in stands with low organic matter contents (Zak and Pregitzer 1990). Soil total N and organic matter content were highly correlated to annual rates of N mineralization in the northern pin oak stands. The relationship between soil organic matter content and stand age in the northern pin oak stands, and the absence of this correlation in the Michigan northern hardwood forest suggests that the magnitude of disturbance and recovery time are important factors regulating N cycling variability within individual ecosystems.

Our results suggest that variability among forest stands with similar species composition and soil development can be significant. More importantly, small changes in topography within and among forest stands are relatively unimportant compared to the time-dependent influence of disturbance on soil organic matter dynamics. The two-fold difference in N mineralization and nitrification rates that we observed further suggests that studying a single stand within an ecosystem type may not provide an accurate estimate of ecosystem-level processes.

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