

SPATIAL VARIABILITY IN A SUCCESSIONAL PLANT COMMUNITY: PATTERNS OF NITROGEN AVAILABILITY¹

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Abstract. We examined the spatial variability of N mineralization, nitrification, and denitrification at a resolution of 1 m over a 0.5-ha portion of an old field in southeast Michigan. Net mineralization and nitrification rates were estimated from changes in ammonium and nitrate during 45-d laboratory incubations of soil from >300 individual sample locations. Denitrification was estimated from nitrous oxide accumulation rates during 24-h incubations of intact cores ($n = 252$) under acetylene atmospheres at a pressure of 10 kPa. We used geostatistical procedures to characterize the spatial distributions of these and other soil variates.

Semivariograms for all three N transformations showed a high degree of spatial dependence among points sampled within 1–40 m of one another. Nugget variances were 27–37% of structural variances, indicating that most of the variation within the sample populations for these rates could be attributed to spatial autocorrelation at a scale >1 m. Isopleths calculated using punctual kriging algorithms show a nonuniform distribution of these transformations across the field. High rates of all processes occurred in swales on the northern edge of the sample area, but also occurred elsewhere in the field on drier, more level sites.

These results indicate that spatial characteristics of the measured nitrogen transformations in this old field are complex, and that only some of this complexity is associated with surface topography. Whether spatial complexity affects or mainly reflects plant community structure is not known, but this small-scale heterogeneity may influence existing plant and microbial population dynamics and should be considered by those attempting to understand community dynamics or to quantify ecosystem-level nutrient fluxes.

Key words: denitrification; geostatistics; kriging; nitrification; nitrogen mineralization; nutrient cycling; old-field succession; semivariograms; soil nitrogen; spatial variability; succession.

INTRODUCTION

Soil properties can vary dramatically within plant communities. Soil pH, organic matter content, and assorted mineral element concentrations have been shown to vary in some communities by an order of magnitude at spatial scales of 5 m or less (e.g., Downes and Beckwith 1951, Raupach 1951, Trangmar et al. 1987), and in a number of cases this variation has appeared to be associated with changes in plant species distributions (e.g., Snaydon 1962, Pigott and Taylor 1964, Zedler and Zedler 1969, Turkington and Harper 1979, Montagnini et al. 1986, Inouye et al. 1987). Such results suggest that nutrient cycling properties in natural and

recently disturbed systems are spatially complex, and moreover that this complexity may significantly affect plant community structure.

Hypotheses that plant communities are structured largely in response to the availability of limiting nutrients (Bradshaw 1969, Grime 1979, Huston 1979, 1980, Tilman 1982) take these suggestions one step further. Such hypotheses argue that spatial patterns of nutrient availability constitute a critical component of the structure of plant communities, though this variability has yet to be comprehensively quantified. To evaluate potential relationships between patterns of nutrient cycling and community structure in natural plant communities first requires the demonstration that nutrient availability can vary significantly across the community.

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We report here the results of a study undertaken to test the hypothesis that nitrogen availability in an old-field community in southeast Michigan is patterned at a scale that might be expected to affect plant population dynamics within the community. We have chosen nitrogen availability to index nutrient availability because in most temperate-region ecosystems nitrogen is the nutrient that most commonly limits plant growth, and thus is the nutrient most likely to affect community structure if its availability is patterned. The measures we use to assay nitrogen availability, mineralization and nitrification potentials and intact-core denitrification assays, are sensitive indicators of N turnover and potential for loss (Keeney 1980, Tiedje 1982) and so should be reasonable indicators of the amount of N available to those portions of the plant community unable to fix atmospheric N_2 . To quantify patterning within the old-field community we use geostatistical techniques originally developed to map ore deposits (Journel and Huijbregts 1978, Krige 1981). These techniques, new to ecology (Robertson 1987), offer substantial power to detect and characterize spatial variability in two- and three-dimensional systems (Webster 1985, Trangenin et al. 1985).

METHODS

Study site

We conducted this study at the E. S. George Reserve, a 490-ha natural area in southeast Michigan (42°30' N, 83°50' W, \approx 300 m elevation) maintained as an ecological reserve by the University of Michigan. The climate, physiography, soils, and cultural history of the reserve have been detailed by Evans and Dahl (1955). Mean monthly temperature ranges from -4.1° (January) to 23° (July); annual precipitation (40-yr average) is 800 mm.

Our study site is a 0.5-ha portion of a 6.6-ha old field under long-term study by F. C. Evans and colleagues (Evans and Cain 1952, Evans and Dahl 1955, Wiegert and Evans 1964, Murdoch et al. 1972). The field lies on a large glacial outwash plain with undulating topography; relief across our 69×69 m site varies by 2.5 m (Fig. 1). Soils of the site are Typic Hapludalfs in the Fox sandy loam series (USDA 1977).

Original vegetation was probably oak-hickory forest. Prior to 1870 most of the reserve was cleared of this forest and converted to cropland; in the early 1900s cultivation ceased and most of the upland areas were abandoned to pasture. Livestock were removed when the reserve was established in 1928, though grazing pressure from a resident white-tail deer (*Odocoileus virginianus*) population remains high, explaining in part the persistence of the study site in a relatively early successional state (Evans and Dahl 1955). Vegetation at the time of this study were similar to those in earlier reports, and included various forbs (*Solidago* spp., *Hieracium* spp., *Liatriis aspera*, *Rubus flagellaris*,

grasses and sedges (*Poa* spp. in particular), and a number of mosses and lichens. Scattered shrubs (especially *Juniperus communis*) provided \approx 7% cover. The transition from forbs to shrubs is occurring more quickly now that some shrubs have attained sufficient height to escape grazing (F. C. Evans, *personal communication*).

Soil sampling and nitrogen availability assays

We sampled our 69×69 m study area using the existing grid system (based on 20×20 yard cells) on 4.6-m centers (Fig. 1). In addition to these 256 points, we sampled 45 additional points within a smaller grid on 0.9-m centers located in the northeast quadrat of the main sample area, for a total of 301 sample locations. We removed two sets of soil samples from each of these locations in early fall before first frost. The first set of samples included three 2 cm diameter \times 15 cm deep soil cores taken within a few centimetres of one another at each grid point and then composited by grid point. Sample depth was designed to include the Ap horizon. These samples were used for all analyses except denitrification and soil respiration assays.

The second set of samples consisted of single 2.2 cm diameter \times 15 cm deep intact cores also taken at each of the 301 grid points. These cores were taken by fitting an acrylic tube into a sharpened metal sleeve that was then driven slowly into the soil (Robertson et al. 1987); soil compaction within the acrylic tubes was negligible. Cores were kept in the collection tubes until after analysis in order to maintain the existing soil structure as much as possible: soil structure can be an important determinant of denitrification and of soil respiration rates. All composite and intact soil cores were taken within the same 36-h period, and immediately stored at 3° until analysis within the following 3 d.

We estimated N mineralization and nitrification potentials at each sample point by means of 45-d soil incubations (Keeney 1980). At the start and end of the incubation period triplicate 5-g soil samples were extracted in 50 mL 2 mol/L NaCl, and the extracts then analyzed for NH_4^+ and NO_3^- via continuous flow colorimetry (Technicon Instruments 1973). Analytical variability was low, with standard deviations for replicate extracts almost always $<5\%$ of mean values. Soils from a subset of 20 sample points were extracted at 5–10 d intervals to check for linearity over the 45-d period. Soils were incubated in polyethylene bags in a darkened 25° incubator. No water was added to soils initially; gravimetric water loss during the course of incubation was low and additional water was added to each bag during the incubation to maintain initial levels $\pm 5\%$. At the beginning of the incubation period two replicate soil subsamples were also analyzed for pH in a suspension of 10 g soil (fresh mass) in 20 mL of added water, and one 100-g subsample was analyzed for moisture content by drying at 105° . Potential N mineralization is the net amount of NH_4^+ -N plus NO_3^- -N

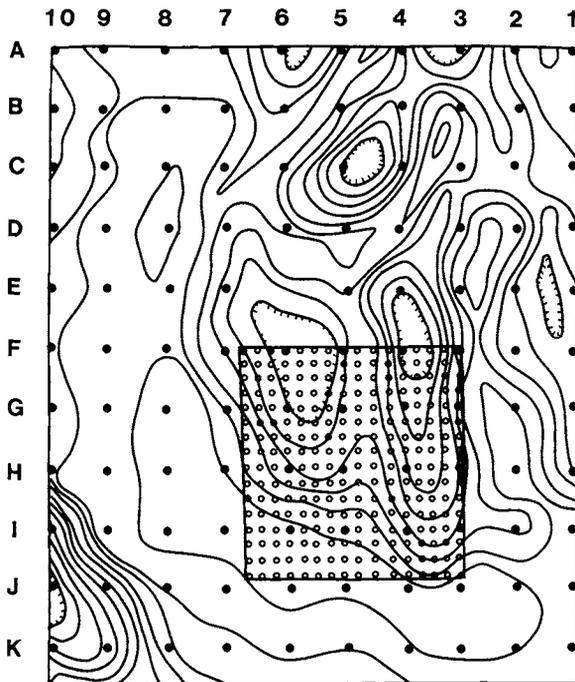


FIG. 1. Location of 0.5-ha sampling grid in the old-field study area. Contour lines represent elevation at 0.3-m intervals; hatched lines indicate depressions (redrawn from Evans and Dahl 1955). Points within the sample grid are on 4.6-m centers; points outside the sample grid are permanent plot markers on 18.3-m (20 yard) centers.

produced over the 45-d incubation period, and potential nitrification is the NO_3^- -N portion of net N mineralization. Neither of these measures estimate actual in situ N turnover; we use them here as indices of relative rates in the field.

Denitrification was assayed by a static-core acetylene inhibition technique (Robertson et al. 1987). Intact cores were vented at the beginning of a 24-h incubation period, capped with rubber serum stoppers, and then amended with acetone-free acetylene to bring core atmosphere concentrations to 10 kPa (10% v/v) acetone-free acetylene and 90 kPa air. Headspace samples were removed at 2, 12, and 24 h from all cores and stored in glass collection tubes at a 130 kPa overpressure; these gas samples were later analyzed simultaneously

for N_2O and CO_2 via automated gas chromatography (Robertson and Tiedje 1984). Denitrification rates in individual cores were based on regressions through the three time points.

Statistical analysis

Analyses of spatial variability were performed using recently developed geostatistical techniques (Vieira et al. 1983, Webster 1985, Trangmar et al. 1985). These techniques offer considerable power for detecting and quantifying autocorrelation in serial data, and offer in addition an optimal means for interpolating across a sample area if spatial dependence is present. Interpolated values are based on values for nearby sample points weighted by distance and the degree of autocorrelation among measured points separated by similar distances elsewhere in the sample area. This interpolation, termed "kriging," can be used to provide detailed isopleths for measured properties of a site with known confidence limits for each interpolated point.

We used computer programs available in Robertson (1987) to calculate semivariograms and perform punctual kriging prior to mapping isopleths. Data for all variates that exhibited spatial dependence were interpolated by kriging to 1-m resolution across the site. Semivariogram models were fit using a weighted least-squares technique (SAS 1985) that assumed that the small scale (1–5 m) autocorrelation found for each variate in our smaller grid was typical for the site as a whole. Where variates were log-normally distributed, log-normal transformations were performed on the data to normalize frequency distributions; back-transformations followed Haan (1977:107). Optimal neighborhood sizes for interpolation were determined for each variate by jackknifing (Vieira et al. 1983). Regression statistics were calculated using procedures available in SAS (1985).

RESULTS

On average, soil biological activity was low across the site. Mean N mineralization and nitrification potentials (Table 1) were comparatively low at the time soils were collected relative to rates reported for other successional sites (Robertson 1982), as were denitrification rates (Melillo et al. 1983, Robertson and Tiedje 1984) and rates of soil respiration. Low activity not-

TABLE 1. Properties of soil samples taken across the site at 15-cm soil depths. $n = 301$ sample locations less as many as nine missing values per measure except for denitrification ($n = 252$). All values are measured rates or concentrations before transformation (cf. Fig. 2).

Measure	Units	Mean value	SD	CV (%)
N mineralization	($\mu\text{g} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$)	3.36	1.95	57.9
Nitrification (NO_3^- -N production)	($\mu\text{g} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$)	2.52	1.69	67.0
Denitrification (N)	($\text{ng} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$)	4.73	13.0	275
CO_2 production	($\mu\text{g} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$)	55.5	33.7	60.7
$[\text{H}^+]$	($\mu\text{mol/L}$)	5.77	3.27	56.6
Moisture	($\mu\text{g}/\text{cm}^2$)	0.65	0.38	58.7
Soil nitrate-N	($\mu\text{g}/\text{cm}^2$)	5.90	3.84	65.0

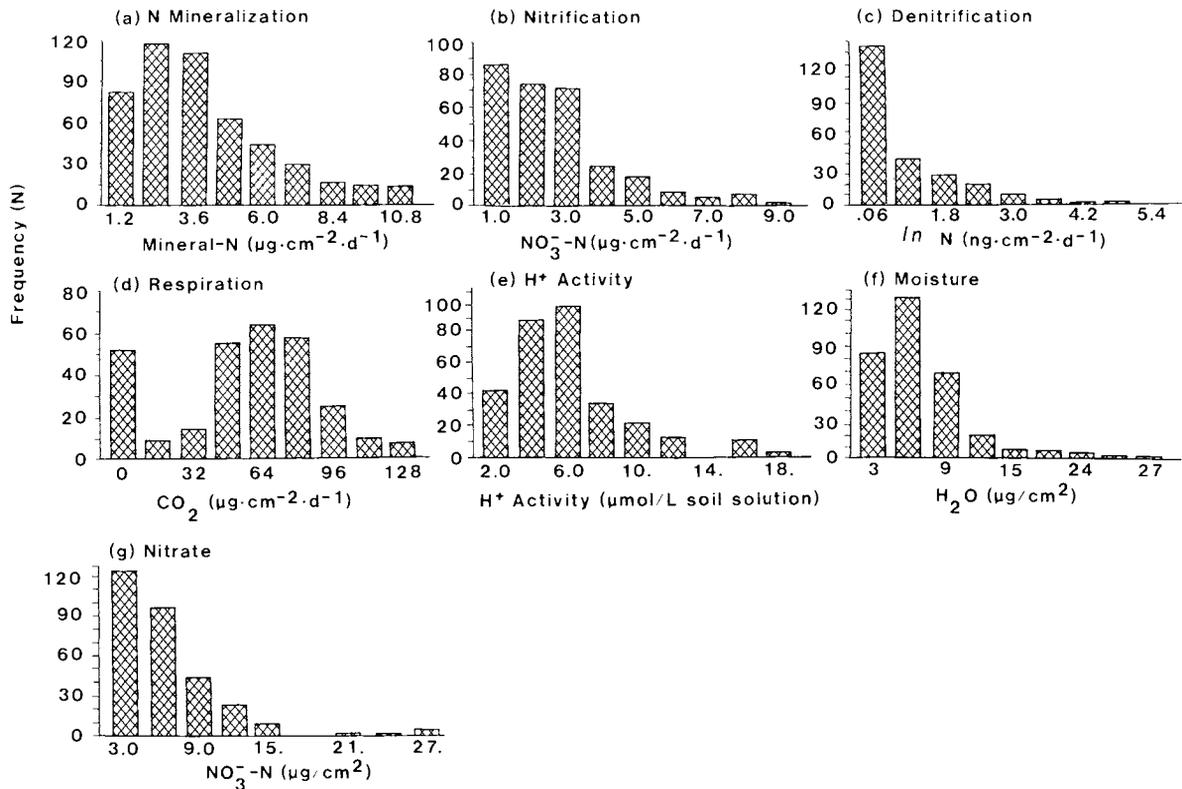


FIG. 2. Frequency distributions for the soil properties described in Table 1.

withstanding, however, all soil properties examined varied substantially across the site. Many properties varied by several orders of magnitude (Table 1). Rates of net N mineralization, for example, varied from 0.2 to $11.4 \mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ with a coefficient of variation (cv) of 58%. Rates of net nitrification varied to a somewhat greater extent, with a cv of 67% ($0.01\text{--}9.31 \mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$). Soil respiration, acidity, and moisture content varied at rates similar to those for N mineralization, with cvs between 56 and 61%. Denitrification, on the other hand, was considerably more inconstant, varying from <0.1 to $>100 \text{ ng}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ with a cv of 275%.

Frequency distributions for all nitrogen transformations and for soil acidity, moisture, and nitrate con-

tents were positively skewed; this skew was particularly extreme for denitrification activity (Fig. 2). Soil respiration, on the other hand, appeared to be negatively skewed, with >50 soil cores producing CO_2 at rates close to or below detection limits.

We used spatial autocorrelation analysis to quantify spatial dependence among sample points within the field. For all three nitrogen fluxes examined, the resulting semivariograms demonstrated strong spatial dependence among sample locations. This dependence was strongest for locations within 25–30 m of one another for N mineralization, and within a 40 m radius for nitrification, denitrification, and nitrate pool size (Fig. 3). In all three cases autocorrelation was strongest

TABLE 2. Model parameters for semivariograms in Fig. 3. h is the distance (m) between sample location points. γ is the semivariance.

Property	Model	Nugget variance (C_0)	Structural variance (C)	Range (a_0)	r^2
N mineralization	Exponential*	0.074	0.198	8.22	0.985
Nitrification	Exponential*	0.076	0.234	10.51	0.982
Denitrification	Exponential*	0.229	0.835	11.49	0.976
Respiration	Linear + sill†	2.466	2.735	30.43	0.231
Soil acidity	Spherical§	0.080	0.197	18.28	0.976
Soil moisture	Spherical§	0.018	0.038	11.63	0.939
Soil nitrate	Exponential*	0.056	0.283	17.67	0.981

* $\gamma(h) = C_0 + (C - C_0) \cdot (1 - e^{-h/a_0})$.

† For $h < a_0$, $\gamma(h) = h \cdot ((C - C_0)/a_0) + C_0$; $h \geq a_0$, $\gamma(h) = C$.

§ For $h < a_0$, $\gamma(h) = C_0 + (C - C_0) \cdot (1.5 \cdot h/a_0 - 0.5 \cdot (h/a_0)^3)$; $h \geq a_0$, $\gamma(h) = C$.

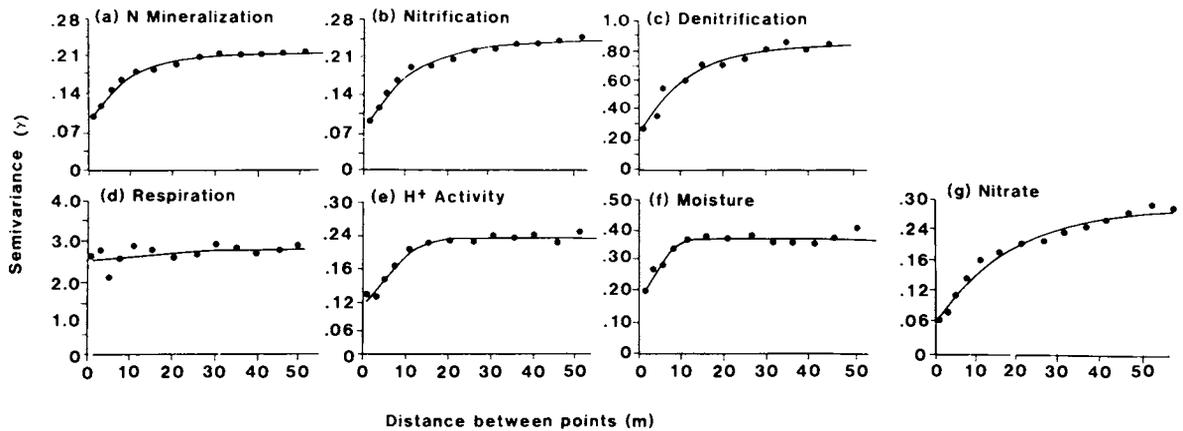


FIG. 3. Semivariograms for (a) N mineralization potentials, (b) nitrification potentials, (c) denitrification, (d) soil respiration, (e) [H⁺], (f) soil moisture, and (g) soil nitrate across the 0.5-ha study site. Solid lines are best-fit models; see Table 2 for parameter descriptions.

at the 0–20 m scale. Nugget variance represents the portion of population variance not contributing to autocorrelation at the lowest scale examined; it is estimated by extrapolating a *y* intercept for the semivariogram. For the three N fluxes examined, nugget variance was between 27 and 37% of the structural or estimated population variance (Table 2), suggesting that much of the population variance is a function of spatial autocorrelation. This was also true for soil nitrate pool, for which nugget variance was 20% of structural variance. The remaining variance is due either to experimental error or to autocorrelation at scales below those explicitly examined; in this study such scales would be at <1 m.

In contrast to soil N transformations, soil respiration did not appear to be spatially autocorrelated at any of the scales examined (1–>80 m). The semivariogram for this property exhibited almost a pure nugget effect

(Fig. 3d), indicating that variance among points close to one another was no different than variance among points farther apart. Both soil acidity (Fig. 3e) and soil moisture (Fig. 3f) exhibited stronger spatial dependence, about equal to that demonstrated by the N transformations, with nugget variances at 41–47% of structural variances (Table 2) and almost all dependence among sample points occurring at scales of <20 m apart for acidity and <10 m for moisture.

Punctual kriging at 1-m intervals resulted in isopleths for N fluxes diagrammed in Figs. 4–6. All three fluxes were strongly patterned across the old field. Potential N mineralization (Fig. 4) was greatest in the northeast and northwest quadrants, corresponding broadly to the locations of two swales in the study area (Fig. 1). Patterning was nevertheless equally strong in the southern half of the field where topography is more uniform. Patterns of net nitrate production (Fig. 5)

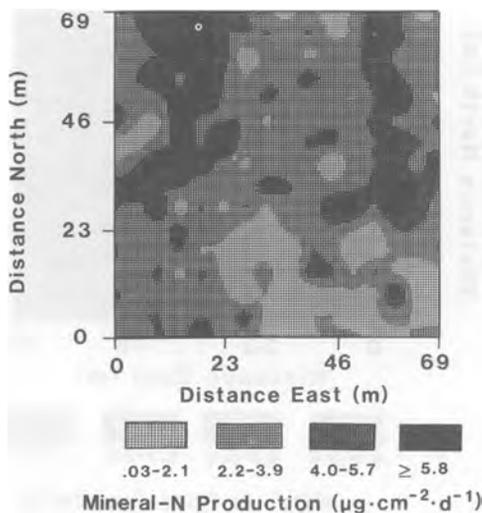


FIG. 4. Isopleths for N mineralization potentials across the study site. Estimation standard deviations for interpolated points range from 0.97 to 1.34 $\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$.

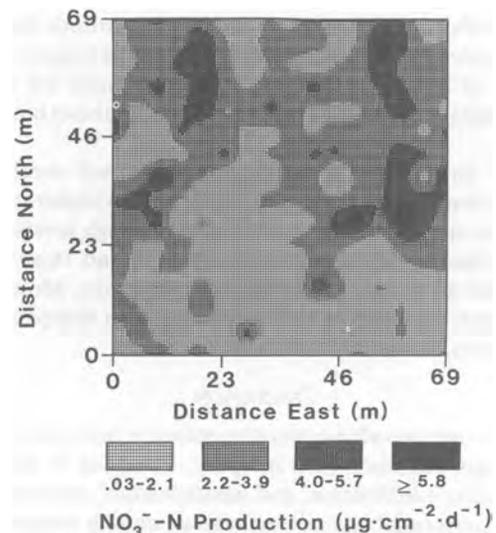


FIG. 5. Isopleths for nitrification potentials across the study site. Estimation standard deviations for interpolated points range from 0.70 to 1.00 $\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$.

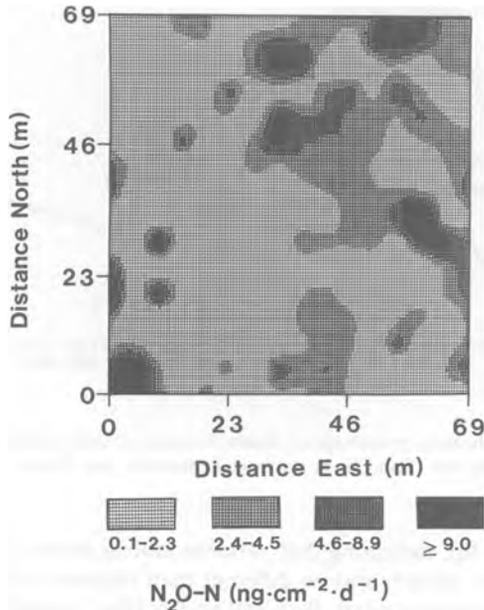


FIG. 6. Isopleths for denitrification across the study site. Estimation standard deviations for interpolated points range from 2.56 to 3.89.

followed closely the patterns of net N mineralization, as predicted by a strong positive correlation between potential N mineralization and potential nitrification rates ($r = 0.88$, $n = 288$).

Denitrification activity in our site (Fig. 6) was more discontinuous in its distribution across the field than the other N fluxes examined, reflecting its highly skewed frequency distribution (Fig. 2c). As for N mineralization and nitrification, a number of high-activity, denitrification "hotspots" appeared within the site, but denitrification hotspots tended to be more intense than hotspots for other properties. In some of these spots denitrification was over an order of magnitude higher than rates in the surrounding locale, and a nugget variance of 27% (Fig. 3c) suggests the potential for substantial spatial dependence even within hotspot boundaries.

As for patterns of N mineralization, soil moisture and nitrate levels (Figs. 7, 8) tended to be higher in the northern swales than in other areas, though levels in a few other locations were equally high and there was overall no direct relationship to topography. Moisture hotspots did tend to be less evident than hotspots for N fluxes, however.

DISCUSSION

Nitrogen transformations examined in this study were strongly autocorrelated in space. Potential N mineralization, nitrification, and denitrification rates exhibited substantial spatial dependence among sample locations 1 to >20 m distant (Fig. 3), and nugget variances of 27–37% of structural variances (Table 2) suggest a potential for autocorrelation at scales <1 m.

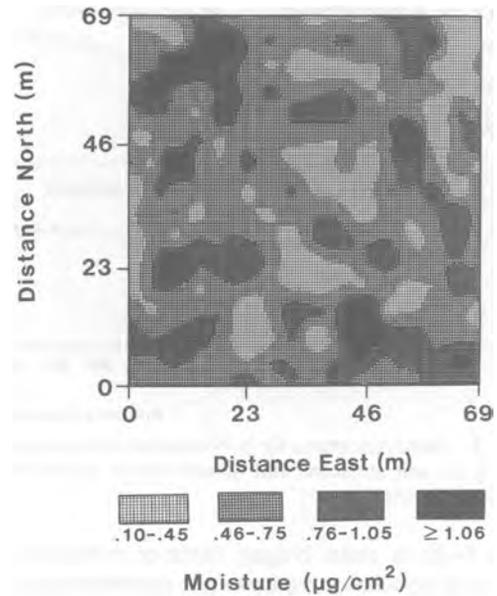


FIG. 7. Isopleths for soil moisture across the study site. Estimation standard deviations for interpolated points range from 0.09 to 0.12 $\mu\text{g}/\text{cm}^2$.

These N fluxes were also distinctly patterned across the site, with high activities most frequent in the northern swales but with equally high activities elsewhere (Fig. 4–6). Localized "hotspots," areas <20–30 m^2 in which fluxes were substantially higher than those in the surrounding locale, were common. Denitrification hotspots were especially significant, reflecting the highly skewed frequency distribution within the site for denitrification rates (Fig. 2) and a high coefficient of

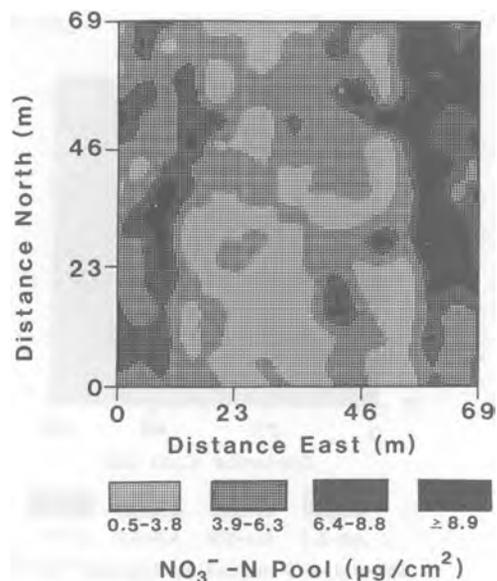


FIG. 8. Isopleths for soil nitrate-N across the study site. Estimation standard deviations for interpolated points range from 1.5 to 2.5 $\mu\text{g}/\text{cm}^2$.

TABLE 3. Predictors of N transformations in the old-field site based on stepwise regression procedures (SAS 1985). Within each category r^2 values are cumulative going down the column.

Category variate	Coefficient of determination (r^2)	Probability level
Potential mineralization		
Soil moisture	0.109	.0001
CO ₂ production	0.142	.0017
Acidity	0.170	.0027
Potential nitrification		
Potential mineralization	0.809	.0001
Soil nitrate	0.834	.0001
Soil moisture	0.837	.013
Acidity	0.839	.031
CO ₂ production	0.839	.597
Denitrification		
CO ₂ production	0.257	.0001
Potential nitrification	0.366	.0004
Moisture	0.370	.157
Acidity	0.371	.553

variation (Table 1). Such strong discontinuities for denitrification rates have been noted for a number of agricultural sites (e.g., Folorunso and Rolston 1985, Parkin et al. 1985).

Moisture availability across the site was also strongly patterned (Figs. 3 and 7), and helps to explain some of the patterning in N transformations. N mineralization, nitrification, and denitrification were all moderately correlated with soil moisture content ($r = 0.34, 0.36, 0.23$ respectively; $P < .0001, n > 251$), which in general was low at the time of sampling (Table 1). Soil acidity on the other hand did not vary as much across the site, and was not as strong a predictor for the N fluxes examined ($r = 0.28, 0.20, \text{ and } 0.10$; $P < .11, n > 251$). Other predictors included CO₂ production (a measure of soil organic matter availability), mineralization potentials (as a predictor of potential nitrification), nitrification potentials (as a measure of nitrate availability and as a predictor for denitrification), and nitrate pool sizes (as a predictor for potential nitrification). All told, various combinations of predictors (Table 3) could explain up to 17% of the variability we found for potential N mineralization across our site, up to 84% of the variation in nitrification potentials, and up to 37% of the variation in denitrification rates. Despite its value as a predictor for N transformation rates, we found little spatial dependence within the site for soil CO₂ production, a measure of soil organic matter availability. Presumably factors that operate at smaller spatial scales than the 1-m resolution in this study combine to keep soil respiration spatially dependent mainly at scales $\ll 1$ m; rhizosphere influences may play a part in this scaling.

We conclude that nitrogen availability in this old-field community is highly patterned at scales $< 20\text{--}40$ m. These scales are similar to those over which plant

community composition varies during early succession, suggesting the possibility that the spatial heterogeneity of available nutrients in this community may significantly influence community structure.

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