

Spatial variation in nitrogen availability in three successional plant communities

KATHERINE L. GROSS, KURT S. PREGITZER*† and
ANDREW J. BURTON*

*W. K. Kellogg Biological Station and Dept of Botany and Plant Pathology, Michigan State University, Hickory Corners, MI 49060, *Department of Forestry, Michigan State University, East Lansing, MI 48823 and †School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931, USA*

Summary

1 Spatial variability in soil nitrogen and moisture levels was determined using a geostatistical analysis in a newly abandoned field, a mid-late successional field and a second-growth forest in south-western Michigan.

2 A greater proportion of the total variation for all variates associated with nitrogen availability was spatially dependent in the mid-successional field; the newly abandoned field and forest had similar patterns of spatial dependence in these variates.

3 The distance (range) over which there was spatial dependence was greater in the mid-successional field than the other two communities, indicating a more coarse-grained pattern of spatial heterogeneity in soil nitrogen, particularly in the surface soils (0–5 cm), than in the other two sites.

4 Examination of patterns of spatial dependence using different lag intervals generally gave similar results; though a nested pattern of NO₃–N availability in the mid-successional field was detected at a finer scale of analysis, indicating spatial variation at multiple scales.

5 The results suggest that patterns of spatial variation in soil nitrogen change over time in successional plant communities, perhaps reflecting changes in the species composition or size of individual plants in these communities.

Keywords: geostatistics, nutrient dynamics, old-field succession, soil nutrients, spatial heterogeneity

Journal of Ecology (1995) **83**, 357–367

Introduction

Nutrient availability is known to be highly heterogeneous in terrestrial plant communities and is often associated with variation in plant species distributions (Grime 1979; Tilman 1988; Schlesinger *et al.* 1990). Between sites, variation in plant species composition and structure has been associated with differences in the rate of and variability in nutrient cycling, particularly in a successional sere (e.g. Robertson & Vitousek 1981; Vitousek *et al.* 1989; Zak *et al.* 1989). Even within a site, nutrient levels can vary by up to an order of magnitude over relatively small spatial scales (Webster 1985; Trangmar *et al.* 1987; Robertson *et al.* 1988). Jackson & Caldwell (1993a,b) and Schlesinger *et al.* (1990) have shown that spatial heterogeneity in nutrient availability can vary at the scale of individual plants.

If plants are important in regulating nutrient avail-

ability or distribution in soils, we would expect that spatial heterogeneity in soil nutrients would change over time in successional plant communities where there is rapid turnover in species composition. Tilman (1988) has proposed that changes in the level and distribution of limiting soil resources is a major factor determining the dynamics of secondary succession on abandoned old-fields. Armesto *et al.* (1991) have proposed that resource heterogeneity increases over time in successional plant communities and that this is driven by changes in the life history and size of species that occur in these communities.

In this study we used a geostatistical analysis to quantify the magnitude and scale of spatial variability in soil nitrogen availability in three plant communities that represent a successional sere in south-western Michigan. Our initial hypotheses were that: (1) the magnitude of spatially structured variation in soil nutrients would be higher and (2) the scale would be

more coarse-grained (larger, more discrete patches) in successional mature (older) plant communities than in newly abandoned sites. Geostatistics is a powerful tool for assessing heterogeneity in below-ground resources over a broad range of scales because the parameters from the variogram model provide an index of both the magnitude and scale of spatial heterogeneity in a variate (Rossi *et al.* 1992; Robertson & Gross 1994).

This initial survey is part of a larger effort to determine how spatial variation in soil nutrients in successional plant communities relates to the abilities of species in these communities to acquire soil nitrogen. We have focused on nitrogen availability in these studies because it is the most commonly limiting nutrient in a wide range of natural and agricultural communities (Chapin 1980). Changes in total and available nitrogen have been documented in successional communities (e.g. Robertson & Vitousek 1981; Tilman 1988; Vitousek *et al.* 1989), but we know of no other study which has determined whether there are corresponding changes in the scale or pattern of spatial variation of nitrogen availability in successional fields (but see Robertson *et al.* 1993).

Methods

STUDY SITES

The research was conducted in July 1991 at Michigan State University's W. K. Kellogg Biological Station (KBS) in south-western Michigan (44°25'N, 85°23'W). Three sites, representing a range of successional communities, were chosen for study: (i) a tilled field having little plant cover at the time of sampling (Soybean Field); (ii) a 28-year-old successional field (Turner Field); and (iii) a second-growth hardwood forest with a mixture of *Quercus* and *Carya* species as canopy dominants. All three sites are located within 1 km of each other and have a similar topography (flat to gently sloping) and soils (Typic Hapludalfs).

The Soybean Field was located on Kalamazoo series soil (fine-loamy, mixed, mesic); slope in the study area was less than 2%. The field had been cropped continuously for ~50 years except during 1987–88, when it was fallowed and used for experimental studies of competition among old-field and pasture species (Miller and Werner, unpublished). In 1989 and 1990 corn (*Zea mays* L.) was grown in the field with 123 kg N ha⁻¹ added as ammonium nitrate in both years. The field was planted with soybean (*Glycine max* (L.) Merr.) in May 1991 and no fertilizer was applied. However, herbicide was misapplied to the field in late May which necessitated replanting in late June. When the field was sampled in mid-July the beans were stunted and vegetative cover was < 20% and included a mixture of summer annual weeds (e.g. *Abutilon theophrasti*, *Amaranthus* spp., *Mullugo verticillata*, and

Chenopodium album). (Nomenclature for non-crop species follows Gleason & Cronquist 1991.) The cover and composition of the weed community was similar to that of a newly abandoned field in the area (Burbank *et al.* 1992).

Turner Field was abandoned from agriculture in the mid-1960s and was selected to represent a typical mid-late successional field in this area (Burbank *et al.* 1992). Soils of the field are also a Kalamazoo series, and the study site slopes gently (about 5°) from north-west to south-east. Vegetative cover in the field approached 100% and consisted of a mixture of perennial herbs and grasses (e.g. *Solidago* spp., *Hieracium* spp., *Centaurea maculosa*, *Aster pilosa*, *Agropyron repens*, *Phleum pratense*, *Bromus inermis*), though patches dominated by moss (*Polytrichum* spp.) were scattered throughout (< 2% cover overall). Scattered small trees and shrubs (*Prunus serotina*, *Sassafras albidum*, *Juniperus virginiana*, *Quercus* spp., *Rhamnus* spp. and *Ulmus* spp.) occur primarily at the edges of the field; none were included in the area sampled for this study.

Long Woods is a mature second-growth *Quercus*/*Carya* forest which is situated on Oshtemo sandy loam soil. Prior to the 1930s the site was selectively cut and in the mid-1930s the canopy was relatively open and dominated by *Quercus* spp. (*Q. velutina*, *Q. rubra*, *Q. alba*) with a fairly even mixture of *Carya glabra*, *Prunus serotina*, and *Acer rubrum* with occasional *Fraxinus americana* (Allen 1938). In the area selected for this study the canopy was closed and there was a 2° slope from east to west. The canopy dominants were *Carya glabra*, *Quercus alba* and *Fraxinus americana*. Understorey plant cover was patchy and included *Cornus florida*, *Sassafras albidum*, *Podyphyllum peltatum*, and *Solidago caesia* (Burbank *et al.* 1992).

SOIL SAMPLING AND LAB ANALYSIS

The three sites were sampled for nitrogen availability between 10 and 18 July 1991. In each site, we established a 5 × 8 sampling matrix of 40 base points. Base points within rows were set on a 2.5-m spacing, with adjacent transects offset 1.25 m to the east. At each of the 40 base points, we placed a 1-m transect in a randomly assigned cardinal direction (N, NE, E, SE, etc.) and located three additional sample points at 10, 40 and 100 cm along this transect (Fig. 1). This gave a total of 160 sampling points in a stratified-nested design which allowed us to quantify spatial patterns of variability in N-availability in each site over a broad spatial scale (10 cm to ≥ 20 m).

At each sampling point we took three 2-cm-diameter, 15-cm-deep cores from within 3 cm of each other. Cores were split into 0–5-cm and 5–15-cm depths, then composited by depth to produce a total of 320 soil samples per site. The samples were immediately placed in an ice-filled cooler and transported to the

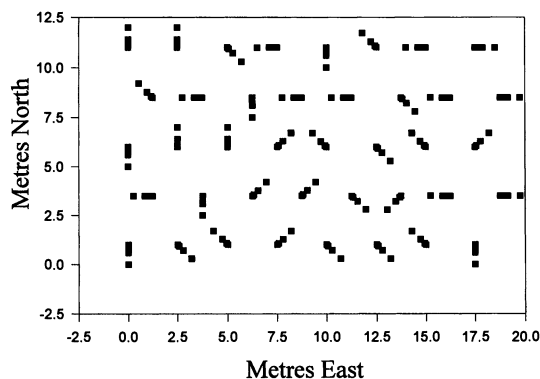


Fig. 1 Diagram of point locations sampled in the three sites. Base points are located on a 5×8 sampling matrix at 2.5-m intervals, with adjacent rows offset by 1.25 m. (See text for details.)

laboratory where they were maintained at $< 4^\circ\text{C}$ prior to analysis. Sampling and processing was completed within 48 h for each site.

Prior to extraction and incubation, field moist soils were passed through a 2-mm sieve and subsamples of 4.5 g were extracted with 40 mL of 2-M KCl. Extracted samples were shaken for 1 min and kept at room temperature for 24 h before being filtered through a $1\text{-}\mu\text{m}$ Gelman glass filter. Filtered sample extracts were stored in plastic vials at $< 4^\circ\text{C}$ until analysed for nitrogen content.

Additional 4.5-g subsamples were placed in covered plastic 50-g soufflé cups (with small holes in the lid to allow gas exchange) and incubated in the dark at 25°C and 80% relative humidity for 28 days, and then extracted as before. Gravimetric moisture content was determined for each sample point by drying subsamples at 105°C for 48 h. Prior to incubation, samples were moistened with deionized water to bring them near to field capacity (0.01–0.03 MPa) in order to maximize microbial activity. Water was added as needed during the incubation period to maintain these moisture levels. Mean gravimetric moisture contents during incubation ranged from 21.0% for the Soybean Field to 22.3% for Long Woods.

Sample extracts were analysed for NO_3^- and NH_4^+ using continuous flow colorimetry (Technicon Industrial Systems 1977). NO_3^- and NH_4^+ concentration in each sample was adjusted for initial soil moisture and expressed on a dry soil weight basis. Potentially mineralizable N was calculated as final NO_3^- -N plus NH_4^+ -N concentration minus initial concentrations. Potential nitrification was similarly calculated as the difference between final and initial NO_3^- -N concentrations. Replicate analyses were conducted on three percent of the sample extracts. The average coefficient of variation (CV) among replicate pairs for extractable NO_3^- and NH_4^+ , mineralization and nitrification was 10%, with a majority of replicate pairs having CVs of less than 5%.

STATISTICAL ANALYSES

Most variates were normally distributed (Figs 2 and 3); those that were not (e.g. NO_3^- -N at 0–5 cm in Turner Field) could be normalized by a log-transformation. For the geostatistical analyses, data were not transformed to allow for unbiased comparisons among variates and sites of scales of spatial dependence (Isaaks & Srivastava 1989). The magnitude of within and between site variability in N-availability was evaluated by one-way ANOVA using the GLM procedure in SAS-version 6.06 (SAS 1991). For the ANOVAs, data were transformed as needed.

Patterns of spatial variation in N availability in each site were examined using geostatistical analyses (Webster 1985; Robertson 1987; Rossi *et al.* 1992). Variograms for each variate were calculated using GS+, version 2.1 (Gamma Design Software 1992), using an unweighted least-square analysis for variogram model fitting. Model parameters were used to estimate both the magnitude of spatial dependence in a variate and the distance over which this spatial dependence is expressed. To estimate the magnitude of spatial dependence we calculated the proportion of the estimated total sample variation (the 'sill'; $C + C_0$) explained by structural variance (C). This index [$C/(C + C_0)$] of spatial dependence is the inverse of the 'relative nugget effect' (*sensu* Isaaks & Srivastava 1989). As this index approaches 1.0, a greater proportion of the total sample variance is spatially dependent over the distance examined. The geographic scale of this dependence is indicated by the model range (A_0). When the range is small, or where there is no detectable spatial dependence to the variation, the variate has a homogeneous (or fine-grained) distribution at the scale measured. Variance that does not appear to be spatially dependent (estimated by the y-intercept or 'nugget' [C_0] term) is either random error or represents spatial dependence at scales smaller than the minimum analysed (Isaaks & Srivastava 1989).

The adequacy of the semivariance model from which these parameters are derived can be evaluated by comparing the sample variance (σ^2) to the estimated sill ($C + C_0$) for each variate. For variates in which there is spatial dependence over the scale examined, the asymptote of the variogram should be roughly equivalent to the sample variance (Isaaks & Srivastava 1989; Barnes 1991). When the estimated sill is less than the total sample variance, this indicates there potentially is spatial dependence at multiple scales over the distance sampled (Robertson & Gross 1994).

We calculated semivariograms at two lag-intervals (1.4 m and 0.4 m) in order to examine patterns of spatial dependence at two scales of resolution (defined here as 'macro' and 'fine-scale', respectively). At the macro-scale, the mean distance between points at the first and second lag intervals was 0.57 and 2.4 m,

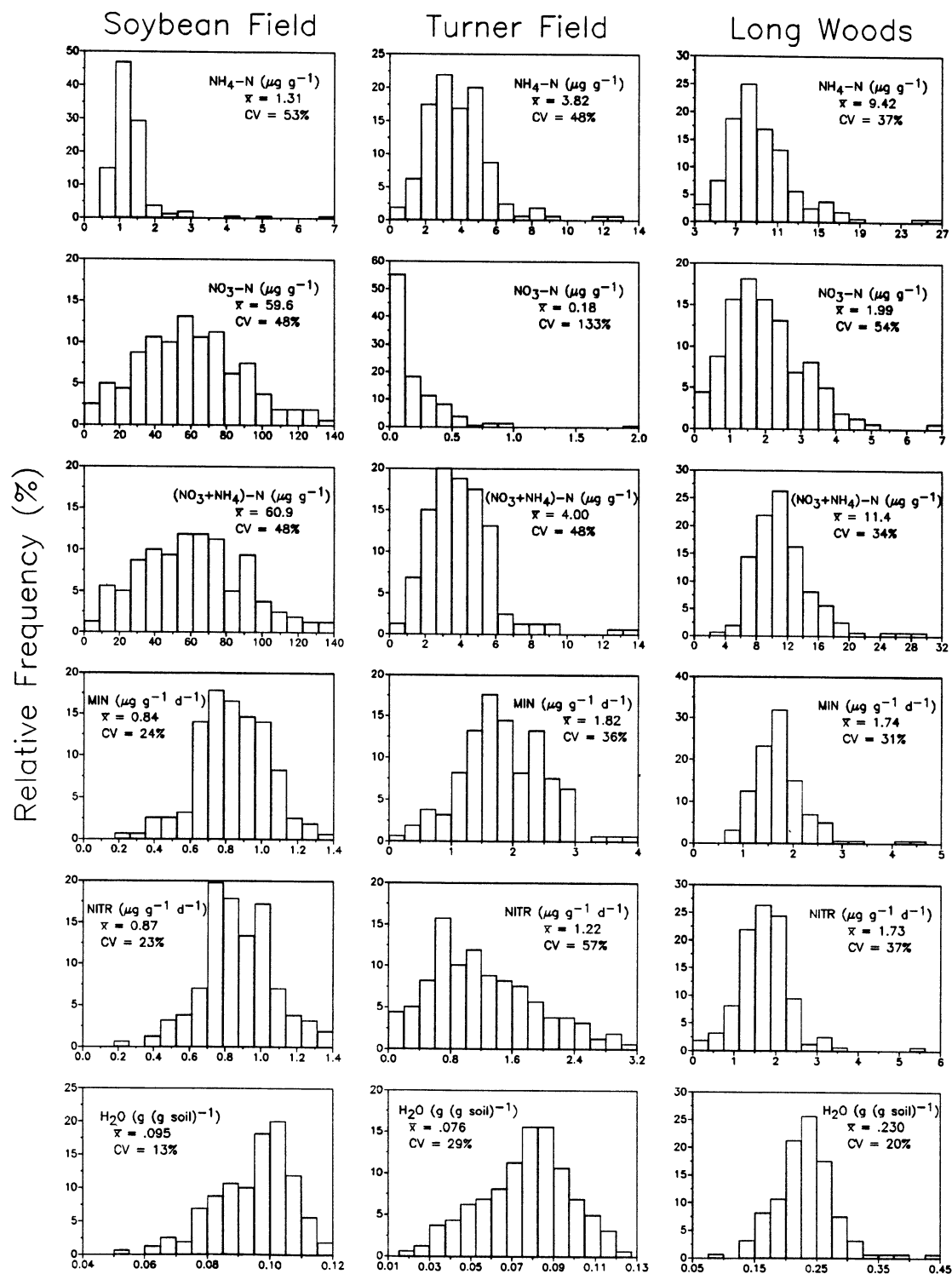


Fig. 2 Frequency distributions for soil properties in the three sites at 0–5 cm. Mean and coefficient of variation (CV) for each variate are given on each histogram. The scale for the relative frequency axis differs for sites and variates.

respectively. At the fine-scale the mean distance between points for the first four lags was 0.25, 0.54, 0.96 and 1.5 m. This finer-scale analysis allowed us to compare the sensitivity of the models to detect spatial dependence at scales likely to reflect that experienced by individual plants (< 1 m).

At the macro-scale, the number of pairs per lag

interval ranged from 249 to ≥ 1600 , with most variogram points calculated on the basis of over 1100 pairs; at the fine-scale, this range was 31 to ≥ 600 , with most points having greater than 300 pairs. For comparative purposes, all variogram models were calculated over a 16-m range (75% of maximum) and fitted to either a spherical or linear function depending

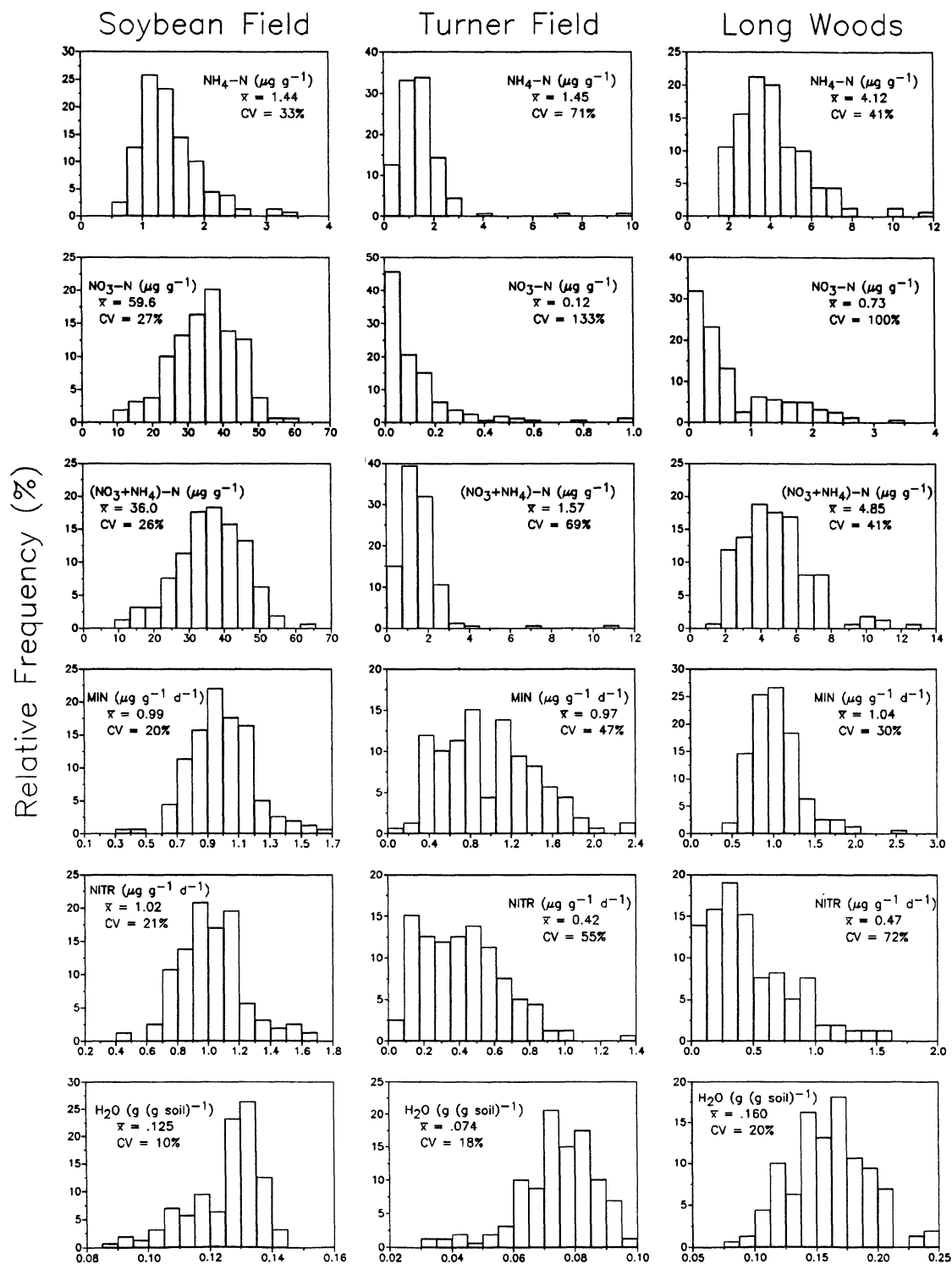


Fig. 3 Frequency distributions for soil properties in the three sites at 5–15 cm. Mean and coefficient of variation (CV) for each variate are given on each histogram. The scale for the relative frequency axis differs for sites and variates.

on the better fit (Webster 1985; Isaaks & Srivastava 1989). One exception to this was nitrate in the surface soil (0–5 cm) at the fine-scale in Turner Field; inspection of the variogram suggested a nested structure to the variation at this scale. To resolve this, separate variograms were calculated over a range of 8 and 16 m for this variate.

Results

VARIATION AMONG SITES

There were highly significant differences between sites in all measures of N-availability, except nitrification at the lower depth (5–15 cm; Table 1). Total extractable inorganic N in the surface (0–5 cm) soil was low-

Table 1 Summary statistics and results of ANOVAS for site differences in soil variates (d.f. = 2,477 for all variates). Site differences were significant ($P < 0.0001$) for all variates, except N-mineralization at 5–15 cm. Comparisons of site means based on Tukey's studentized range test; sites which differ ($P < 0.05$) are indicated by superscript different letters. Values shown are means \pm SD; units given in Fig. 2

| Variate | Soybean | Turner | Long | F |
|--|--------------------------------|-------------------------------|-------------------------------|------|
| 0–5 cm depth | | | | |
| NO ₃ -N | 59.60 \pm 28.40 ^a | 0.18 \pm 0.24 ^b | 1.99 \pm 1.08 ^b | 680 |
| NH ₄ -N | 1.31 \pm 0.69 ^a | 3.82 \pm 1.85 ^b | 9.42 \pm 3.47 ^b | 520 |
| (NO ₃ + NH ₄)-N | 60.90 \pm 28.42 ^a | 4.00 \pm 1.93 ^b | 11.40 \pm 3.82 ^c | 556 |
| N-mineralization | 0.84 \pm 0.20 ^a | 1.82 \pm 0.66 ^b | 1.74 \pm 0.53 ^a | 184 |
| Nitrification | 0.87 \pm 0.20 ^a | 1.22 \pm 0.64 ^b | 1.73 \pm 0.64 ^b | 95 |
| Soil moisture | 0.095 \pm 0.01 ^a | 0.076 \pm 0.02 ^b | 0.23 \pm 0.05 ^c | 1180 |
| 5–15 cm depth | | | | |
| NO ₃ -N | 34.50 \pm 9.42 ^a | 0.12 \pm 0.16 ^b | 0.73 \pm 0.73 ^b | 2086 |
| NH ₄ -N | 1.44 \pm 0.48 ^a | 1.45 \pm 1.03 ^a | 4.12 \pm 1.70 ^b | 273 |
| (NO ₃ + NH ₄)-N | 35.98 \pm 9.32 ^a | 1.57 \pm 1.09 ^b | 4.85 \pm 1.99 ^b | 1875 |
| N-mineralization | 0.99 \pm 0.20 | 0.97 \pm 0.46 | 1.04 \pm 0.31 | 1.6 |
| Nitrification | 1.02 \pm 0.21 ^a | 0.42 \pm 0.22 ^b | 0.47 \pm 0.03 ^c | 244 |
| Soil moisture | 0.13 \pm 0.01 ^a | 0.074 \pm 0.04 ^b | 0.16 \pm 0.03 ^c | 684 |

est in Turner Field, intermediate in Long Woods, and highest in the Soybean Field (Table 1). The same ranking of sites existed for extractable inorganic N at the 5–15-cm depth, with mean values at each site generally half those found at the 0–5-cm depth.

The importance of NO₃- and NH₄-N also differed among sites. Nitrate was the dominant form of inorganic N in the Soybean Field, comprising 98% of inorganic N at 0–5 cm and 96% at 5–15 cm. Nitrate accounted for only 17% and 15% of inorganic N, respectively, in the two depths in Long Woods, and 5% and 8% in Turner Field. Nitrate levels did not differ in Turner Field and Long Woods (Table 1). Ammonium (NH₄-N) levels were higher in Long Woods at both depths than in the two field sites; the two field sites differed in NH₄-N levels in the surface soils, but had similar concentrations at 5–15 cm (Table 1).

Mean potential mineralization differed among sites at 0–5 cm and was significantly higher in Turner Field and Long Woods than the Soybean Field (Table 1). Mineralization rates at 5–15 cm did not differ among sites. Nitrification rates differed among sites at both depths sampled, but the ranking of sites was reversed at the two depths sampled (Table 1). Gravimetric soil moisture content at the time of sampling also differed among the three sites, and was highest in Long Woods and lowest in Turner Field at both depths (Table 1).

VARIATION WITHIN SITES

Although site differences were highly significant, they accounted for less than 50% of the total variation observed as there was a high degree of within site variation in all of these variates. Coefficients of variation (CVs) for all measures of N-availability tended to be highest for Turner Field, intermediate for Long Woods and lowest for the Soybean Field (Figs 2 and 3). The magnitude of the within site variation differed

most for initial NO₃⁻; CVs for this variate ranged from 27% at 5–15 cm in the Soybean Field to 133% at both depths in Turner Field (Figs 2 and 3).

Soil moisture content at the time of sampling was also variable within sites, but not to the same extent as nitrogen availability. Coefficients of variation for moisture content ranged from 10 to 29% in the three sites (Figs 2 and 3).

MACRO-SCALE SPATIAL VARIATION WITHIN SITES

In all three sites, the correspondence between the total sample variance and estimated variance from the spherical variogram model (sill; $C + C_0$) was relatively high (Table 2). In the Soybean Field and Long Woods the estimated sill for all measures of nitrogen availability was $\geq 90\%$ of the sample variance; in Turner Field it was somewhat lower and ranged from 70 to 99%. At the macro-scale of analysis (1.4-m lag interval), r^2 s for the semivariance models were relatively high and tended to be somewhat higher for the surface (0–5-cm) than deeper (5–15-cm) samples (Table 2).

The magnitude of spatial dependence [$C/(C + C_0)$] in nitrogen and moisture availability in the surface soil (0–5 cm) was consistently higher in Turner Field than in the other two sites (Table 2). In Turner Field, the index of spatial dependence in the surface soils ranged from 0.54–0.80 (Table 2). In the Soybean Field and Long Woods the ratio of spatial dependence did not exceed 0.35 at this depth. The range (distance) over which there was spatial dependence in these variates also differed among these sites. In the Soybean Field and Long Woods the range over which there was spatial dependence in nitrogen availability tended to be less (2.5–8.1 and 2.5–10.3 m, respectively) than in Turner Field, where only N-mineralization and soil moisture had a range less than 10 m (Table 2).

Table 2 Summary of variogram model parameters for soil variates calculated at 1.4-m lag (macro-scale) over 16 m at the three sites. The best model fit to the data (S = spherical, L = linear) is indicated. Proportion structural variation ($C/C + C_o$) is used as an index of the magnitude of spatial dependence for each variate

| Site (depth) | Model | r^2 | Nugget (C_o) | Sill ($C + C_o$) | Range (m) | ($C/C + C_o$) | σ^2/sill |
|--|-------|-------|-------------------------|-----------------------|-----------|-----------------|------------------------|
| Soybean (0–5 cm) | | | | | | | |
| NO ₃ –N | S | 0.70 | 542 | 814 | 2.5 | 0.33 | 0.99 |
| NH ₄ –N | L | 0.34 | 0.34 | – | ≥ 16 | – | – |
| (NO ₃ + NH ₄)–N | S | 0.71 | 544 | 816 | 2.5 | 0.33 | 0.99 |
| N-mineralization | S | 0.74 | 0.03 | 0.04 | 7.2 | 0.33 | 0.99 |
| Nitrification | S | 0.75 | 0.03 | 0.04 | 8.1 | 0.29 | 0.95 |
| Soil moisture | S | 0.84 | 10 ^{–4} | 2 × 10 ^{–4} | 5.8 | 0.50 | 0.72 |
| Soybean (5–15 cm) | | | | | | | |
| NO ₃ –N | S | 0.81 | 38.2 | 89.60 | 2.5 | 0.57 | 0.99 |
| NH ₄ –N | S | 0.53 | 0.13 | 0.23 | 2.5 | 0.47 | 0.98 |
| (NO ₃ + NH ₄)–N | S | 0.82 | 37.8 | 88.00 | 2.5 | 0.57 | 0.99 |
| N-mineralization | S | 0.87 | 0.03 | 0.04 | 4.4 | 0.22 | 0.98 |
| Nitrification | S | 0.85 | 0.03 | 0.04 | 2.9 | 0.27 | 1.01 |
| Soil moisture | S | 0.63 | 9.95 × 10 ^{–5} | 10 ^{–4} | 4.6 | 0.005 | 0.94 |
| Turner Field (0–5 cm) | | | | | | | |
| NO ₃ –N | L | 0.81 | 0.03 | – | ≥ 16 | – | – |
| NH ₄ –N | S | 0.91 | 1.64 | 4.28 | 15.5 | 0.62 | 0.80 |
| (NO ₃ + NH ₄)–N | S | 0.93 | 1.74 | 4.73 | 15.6 | 0.63 | 0.79 |
| N-mineralization | S | 0.86 | 0.20 | 0.45 | 5.4 | 0.54 | 0.99 |
| Nitrification | S | 0.94 | 0.17 | 0.59 | 13.1 | 0.70 | 0.69 |
| Soil moisture | S | 0.90 | 0.0001 | 0.0005 | 4.0 | 0.80 | 0.97 |
| Turner Field (5–15 cm) | | | | | | | |
| NO ₃ –N | L | 0.35 | 0.22 | – | ≥ 16 | – | – |
| NH ₄ –N | L | 0.29 | 1.09 | – | ≥ 16 | – | – |
| (NO ₃ + NH ₄)–N | L | 0.27 | 1.23 | – | ≥ 16 | – | – |
| N-mineralization | S | 0.46 | 0.14 | 0.21 | 5.6 | 0.34 | 0.99 |
| Nitrification | L | 0.94 | 0.02 | – | ≥ 16 | – | – |
| Soil moisture | S | 0.94 | 5.5 × 10 ^{–5} | 0.0002 | 3.8 | 0.73 | 0.85 |
| Long Woods (0–5 cm) | | | | | | | |
| NO ₃ –N | S | 0.59 | 0.85 | 1.2 | 2.5 | 0.28 | 0.99 |
| NH ₄ –N | S | 0.57 | 8.34 | 12.8 | 8.2 | 0.35 | 0.94 |
| (NO ₃ + NH ₄)–N | S | 0.66 | 10.2 | 15.6 | 8.4 | 0.35 | 0.93 |
| N-mineralization | S | 0.83 | 0.22 | 0.31 | 9.8 | 0.27 | 0.92 |
| Nitrification | S | 0.49 | 0.33 | 0.44 | 10.3 | 0.24 | 0.93 |
| Soil moisture | L | 0.92 | 0.001 | – | ≥ 16 | – | – |
| Long Woods (5–15 cm) | | | | | | | |
| NO ₃ –N | S | 0.26 | 0.44 | 0.54 | 2.4 | 0.17 | 0.99 |
| NH ₄ –N | L | 0.66 | 2.32 | – | ≥ 16 | – | – |
| (NO ₃ + NH ₄)–N | S | 0.58 | 2.41 | 4.04 | 3.6 | 0.40 | 0.98 |
| N-mineralization | S | 0.11 | 0.09 | 0.10 | 6.1 | 0.10 | 0.96 |
| Nitrification | S | 0.33 | 0.08 | 0.12 | 2.5 | 0.33 | 0.97 |
| Soil moisture | S | 0.62 | 0.0003 | 0.0011 | 5.8 | 0.73 | 0.91 |

At the 5–15-cm depth, the Soybean Field exhibited a higher degree of spatial structure than the other two sites. Spatial dependence in extractable nitrogen was higher at 5–15 cm than in the surface soils at this site (0.57 vs. 0.33). In Turner Field, only N-mineralization and soil moisture exhibited spatial dependence at 5–15 cm; all the other variates had linear patterns of spatial dependence (Table 2). In Long Woods, total extractable nitrogen and nitrification exhibited similar degrees of spatial dependence at 0–5 and 5–15 cm; however, all other variates exhibited less spatial dependence in the deeper fraction (Table 2). The distance over which the variates were spatially dependent again was less in the Soybean Field and Long Woods than in Turner Field. In all three sites, for variates in

which there was spatial dependence, the range was less than 6.1 m (Table 2).

FINE-SCALE SPATIAL VARIATION WITHIN SITES

For all variates, except notably NO₃–N in Turner Field, there were similar patterns of spatial dependence at the macro (1.4-m lag) and fine-scale (0.4-m lag) of resolution (cf. Fig. 4). For most variates, the variogram at the fine-scale had a similar estimated sill and nugget as at the macro-scale; though in some cases where there was spatial dependence, a smaller range was detected at the finer scale. In all cases there was considerably more scatter in the fit to the esti-

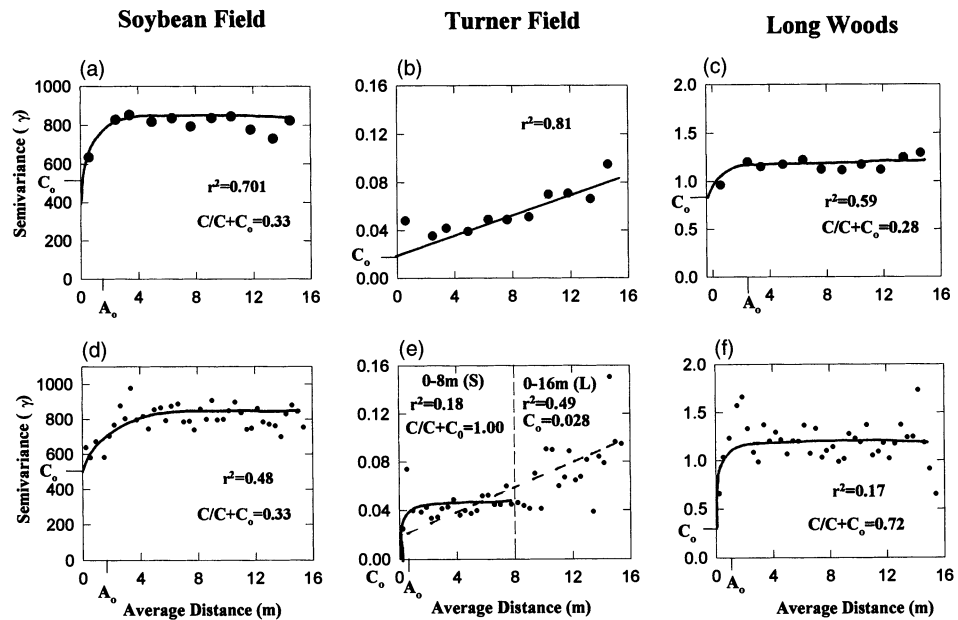


Fig. 4 Variograms for soil nitrate availability in the surface soils (0–5 cm) in the three sites. Graphs in the top row (a–c) are for models calculated at the macro-scale (1.4-m step); those in the bottom row (d–f) are calculated at the fine-scale (0.4-m step) of resolution. The model r^2 and index of spatial dependence ($C/(C + C_0)$) estimated from the model parameters is given for each variogram. In (e) separate statistics and plots are shown for variograms calculated over an 8- and 16-m range (solid and dashed line, respectively).

mated semivariance model at the fine-scale than the macro-scale, and the model r^2 s were consequently generally lower at the fine scale resolution (Fig. 4).

For $\text{NO}_3\text{-N}$ in Turner Field a linear model gave the best fit at both the macro and fine-scale of resolution. However, examination of the variogram at the fine-scale suggested that there might be two scales of variation for this variate; one between 0 and 8 m, another between 8 and 16 m (Fig. 4). The estimated sill for an exponential model (which had an equivalent fit as a linear model) was only 50% of the total population variance, which also suggested a nested structure to the spatial pattern. A spherical variogram model estimated over 0–8 m for $\text{NO}_3\text{-N}$ in Turner Field indicated that nearly 100% of the total variation was spatially dependent at this spatial scale [$C_0 = 0.0001$; $C_0 + C = 0.044$; $C/(C_0 + C) = 0.999$]. The range for this model suggested that spatial dependence was expressed over a smaller distance (0.55 m) than had been detected for any other variate.

Discussion

In all three sites, we found a high degree of variability in several indices of nitrogen availability within the 12.5-m \times 20-m area sampled. Coefficients of variation for nitrogen availability ranged from 20 to 133% across the sites and were most extreme in Turner Field (48–133%). This degree of within-site variability is consistent with observations by Beckett & Webster (1971) in their review of soil variability. They concluded that in cultivated lands, up to half of the variability in soil nutrients in a field may be present

within any m^2 in the field. In the studies they reviewed, variability was lower in grazed fields and 'waste lands' than cultivated lands, though few data were available for natural areas.

In the three communities we studied, variability in nitrogen availability was highest in the mid-successional site (Turner Field), and much of this variability (54–90%) in the surface soils was spatially dependent at 1–10 m. In contrast, in both the newly abandoned (Soybean) field and the forest, only about 30% of the total variation was spatially dependent at the scale we sampled. Several recent studies have documented spatial variation in nutrients at scales similar to those we have measured, and suggested that the patterning is possibly a consequence of variation in plant cover or composition (e.g. Robertson *et al.* 1988; Palmer 1990; Lechowicz & Bell 1991; Jackson & Caldwell 1993a,b). It is often inferred from such results that the spatial scale and magnitude of variation in nutrient availability can change over time in successional systems (Robertson *et al.* 1988; Olff *et al.* 1994; Robertson & Gross 1994), as plant controls on biogeochemical processes increase. Rarely have comparative studies been made among sites that differ in species composition, cover or successional status (but see Robertson *et al.* 1993) that would allow comparisons of spatial structure in soil nutrients among sites to evaluate these hypotheses.

Robertson *et al.* (1993) contrasted the spatial patterning of several soil properties in a cultivated and an adjacent uncultivated site in south-western Michigan. They found that the proportion of structural variance did not differ among these two sites, but that the

distance over which spatial dependence was expressed was greater in the cultivated site. For example, ~40% of the total sample variance in N-mineralization was structural in both sites, but the range in the uncultivated site was about 10 m as compared to over 100 m in the cultivated site. In contrast, we found a somewhat higher degree of spatial structure in N-mineralization in Turner Field than in the newly-abandoned site (Soybean Field; 0.54 vs. 0.33) and in both sites the range was less than 8 m.

Differences in the magnitude and range over which spatial dependence is detectable in these two studies (though they were conducted at sites within a few kilometres of each other) may be due to differences in the scale of sampling and geostatistical analysis used in each study. Robertson *et al.* (1993) examined variation over a much larger distance (0–120 m) and used a larger lag interval (8 m) than we did. As evidenced by our analysis of spatial variation in initial nitrate level in Turner Field, where the pattern of spatial structure was different at the fine (0.4 m) and macro (1.4 m) scales, both the ability to detect spatial structure and the distance (range) over which there is structure can be affected by the scale sampled and analysed.

We had initially hypothesized that the magnitude (proportion structural) and scale (distance) of spatial dependence would increase in relation to the successional maturity of these sites, reflecting increasing 'biological controls' by plants on nutrient availability. Although we found evidence of spatial structure in all three sites, the patterns in the newly abandoned field (Soybean Field) and the forest (Long Woods) were similar. In both of these sites, the range over which there was spatial dependence was small (2–10 m) relative to Turner Field, suggesting that there was a finer-grained, more homogeneous, distribution to nitrogen availability in these sites. Whether these patterns of spatial variability are related to the size and rooting distribution of the plants in these systems remains to be determined.

Several recent studies of spatial variation in forests have documented similar patterns of spatial variation in soil nutrients to those we found in Long Woods. Palmer (1990) quantified spatial patterns of plant–environment relationships among hardwood stands in the Duke Forest in North Carolina, USA. He found weak spatial dependence in most of the 12 edaphic variables he measured, and most of the spatial dependence was at small scales (within 10-m subplots). He used this evidence to support an analysis of plant–environment relationships in which he found that species composition in these stands varied in relation to calcium (or some unmeasured variate correlated with calcium) availability among plots. Within plots (e.g. at small spatial scales) this relationship was only apparent in plots with low calcium availability.

Lechowicz & Bell (1991) quantified spatial heterogeneity in three edaphic variables (pH, NO₃, and K) in an old-growth forest in Quebec, Canada, and

found a high degree of spatial dependence within a 2-m range in all three variates. They interpreted these results in relation to the maintenance of genetic variation among locally adapted subpopulations of *Impatiens pallida*, an understory herb with localized seed dispersal, that is common in such sites. They suggested that such fine-scale heterogeneity in a forest understory can arise from individual tree-level effects on nutrient availability mediated through differences in stem-flow (e.g. Boerner & Koslowsky 1989) or litter deposition and decomposition (e.g. France *et al.* 1989; Roy & Singh 1994).

Spatial dependence in soil properties in cultivated fields has been attributed to land management practices (Trangmar *et al.* 1987), macrotopography (Beckett & Webster 1971), and microtopography (Robertson *et al.* 1988). Robertson *et al.* (1993) concluded that the greater distance over which there was spatial dependence in soil nutrients in the cultivated than the uncultivated sites they sampled reflected the effects of chronic soil physical disturbance. In the cultivated field there was spatial dependence over a greater distance (20–100 m) than in the uncultivated field (7–25 m). Using a similar sampling design in a field 40 years post-abandonment, Robertson *et al.* (1988) found the range of spatial dependence in soil variates was intermediate (1–40 m) to that observed in these sites.

Effects of spatial heterogeneity on individual plants in herb and shrub-dominated plant communities have been inferred from small-scale sampling of spatial dependence in soil nutrients (Jackson & Caldwell 1993a,b; Schlesinger *et al.* 1990). Further evidence for heterogeneity at the scale of individual plants comes from Wedin & Tilman (1990). They found that within 3 years, N-mineralization rates diverged among plots in which five species of perennial grasses were grown in monoculture and suggested that these results might be extendable to the field. In the field these effects are likely to be more difficult to detect, due to species differences in litter N, lignin concentration, and below-ground production (Stewart *et al.* 1993; Olff *et al.* 1994).

A recent study by Wedin & Pastor (1993) demonstrated that plant species need only cause a small change (< 3%) in the labile fraction of soil organic matter to have large effects on local N dynamics at a site. Berendse (1994) has developed a model suggesting that species differences in litter decomposability can produce positive and negative feedback effects that can effect succession. Thus it seems likely that scale and magnitude of spatial variation in N availability in successional plant communities can be influenced by changes in the abundance and distribution of plant species. In particular, as these communities change from dominance by annuals and short-lived dicots to long-lived clonal herbs and grasses, the size and scale of patches of nutrients could be strongly influenced by the vegetation.

The results of our survey of three successional sites indicate that variation in N availability can be nearly as great in small areas within a community as it is between different ecosystems (Vitousek *et al.* 1982; Vitousek & Matson 1988; Zak *et al.* 1989). This variability can be highly patterned spatially at a scale that can influence the occurrence of individual plants, and therefore community composition. Though limited to three sites, and unreplicated, the results suggest that spatial variability in N availability changes as succession occurs. In this study, nitrogen levels were high and had a fairly uniform distribution (e.g. 'fine-grained') in the newly abandoned site, a situation that favours the growth of annual plants that can effectively exploit large uniform patches of nutrients (Pregitzer & Gross, unpublished). As succession occurs, competition for N becomes severe and distinct patches with varying degrees of N availability can form, favouring perennials, shrubs and small trees with root systems capable of foraging for N over a larger area. In late succession sites, N availability is concentrated in the surface soil and is greater and more uniform than in mid-successional sites due to an accumulation of organic matter over many years, but patches associated with decaying organic matter do occur.

The results of this initial study are strongly suggestive that there are changes in the magnitude and scale of spatial dependence in soil nutrients over succession that reflect changes in the cover, composition or size of the plants in these communities. However, these results are only preliminary as they are based on only one site of each stage. We are currently studying a series of successional fields to define further the changes in N availability, N homogeneity, and patch size that occur during succession.

Acknowledgements

We thank Andy Peters, Jennifer Klug, Michelle Keagle, and Lisa Huberty for their assistance in field sampling and laboratory analysis involved in this project. We also appreciate the valuable and perceptive comments on earlier drafts of this manuscript provided by Phil Robertson, Bill Schlesinger, Lisa Huberty, Kevin Kosola, Andrea Corbett, Melissa McCormick and Michel Cavigelli. This work was supported by funding from NSF to KLG and KSP (DEB 91-07481) and to the LTER project at KBS (DEB 92-11771). This is KBS contribution number 787.

References

- Allen, D.L. (1938) Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. *Ecological Monographs*, **8**, 347–436.
- Armesto, J.J., Pickett, S.T.A. & McDonnell, M.J. (1991) Spatial heterogeneity during succession: A cyclic model of invasion and exclusion. *Ecological Heterogeneity* (eds J. Kosola & S. T. A. Pickett), pp. 256–269. Springer-Verlag, New York.
- Barnes, R.J. (1991) The variogram sill and the sample variance. *Mathematical Geology*, **23**, 673–678.
- Beckett, P.H.T. & Webster, R. (1971) Soil variability: a review. *Soils and Fertilizers*, **34**, 1–15.
- Berendse, F. (1994) Litter decomposability – a neglected component of plant fitness. *Journal of Ecology*, **82**, 187–190.
- Boerner, R.E.J. & Koslowsky, S.D. (1989) Microsite variation in soil chemistry and nitrogen mineralization in a beech-maple forest. *Soil Biology and Biogeochemistry*, **21**, 795–801.
- Burbank, D.H., Pregitzer, K.S. & Gross, K.L. (1992) *Vegetation of the W.K. Kellogg Biological Station, Kalamazoo County, Michigan*. Michigan State University Agricultural Extension Research Report 510, East Lansing, Michigan.
- Chapin, F.S. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.
- France, E.A., Binkley, D. & Valentine, D. (1989) Soil chemistry changes after 27 years under 4 tree species in southern Ontario. *Canadian Journal of Forestry Research*, **19**, 1648–1650.
- Gamma Design Software (1992) *GS+: Geostatistics for the Environmental Sciences*, Version 2.1. Gamma Design, Plainwell, Michigan.
- Gleason, H.A. & Cronquist, A. (1991) *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd edn. The New York Botanical Garden, New York, New York.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Ltd, New York.
- Isaaks, E.H. & Srivastava, R.M. (1989) *Applied Geostatistics*. Oxford University Press, New York.
- Jackson, R.B. & Caldwell, M.M. (1993a) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology*, **74**, 612–614.
- Jackson, R.B. & Caldwell, M.M. (1993b) Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology*, **81**, 683–692.
- Lechowicz, M.J. & Bell, G. (1991) The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *Journal of Ecology*, **79**, 687–696.
- Olf, H., Berendse, F. & de Visser, W. (1994) Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application to mown grassland. *Journal of Ecology*, **82**, 611–620.
- Palmer, M.W. (1990) Spatial scale and patterns of species–environment relationships in hardwood forest of the North Carolina Piedmont. *Coenoses*, **5**, 79–87.
- Robertson, G.P. (1987) Geostatistics in ecology: interpolating with known variance. *Ecology*, **68**, 744–748.
- Robertson, G.P. & Gross, K.L. (1994) Assessing the heterogeneity of belowground resources: quantifying pattern and scale. *Exploitation of Environmental Heterogeneity by Plants* (eds M. M. Caldwell & R. W. Pearcy), pp. 237–252. Academic Press, New York.
- Robertson, G.P. & Vitousek, P.M. (1981) Nitrification potentials in primary and secondary succession. *Ecology*, **62**, 376–386.
- Robertson, G.P., Crum, J.R. & Ellis, B.G. (1993) The spatial variability of soil resources following long term disturbance. *Oecologia*, **96**, 451–456.
- Robertson G.P., Huston M.A., Evans, F.C. & Tiedje, J.M. (1988) Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology*, **69**, 1517–1524.
- Rossi, R.E., Mulla, D.J., Journel, A.G. & Franz, E.H. (1992) Geostatistical tools for modeling and interpreting eco-

- logical spatial dependence. *Ecological Monographs*, **62**, 277–314.
- Roy, S. & Singh, J.S. (1994) Consequence of habitat heterogeneity for availability of nutrients in a dry tropical forest. *Journal of Ecology*, **82**, 503–509.
- SAS (1991) *SAS/STAT Users Guide*, Version 6.06 edn. SAS Institute, Cary, NC.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, **247**, 1043–1048.
- Stewart, G.R., Pate, B.B. & Unkovich, M. (1993) Characteristics of inorganic nitrogen assimilation of plants in fire-prone Mediterranean-type vegetation. *Plant, Cell and Environment*, **16**, 351–363.
- Technicon Industrial Systems (1977) Nitrite and nitrate in water and wastewater. Method no. 102–70W/C. Technicon Ind. Syst., Tarrytown, NY.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Trangmar, B.B., Yost, R.S., Wade, M.K., Uehara, G. & Sudjadi, M. (1987) Spatial variation of soil properties and rice yield on recently cleared land. *Soil Science Society of America Journal*, **51**, 668–674.
- Vitousek, P.M. & Matson, P.A. (1988) Nitrogen transformations in a range of tropical forest soils. *Soil Biology and Biochemistry*, **20**, 361–367.
- Vitousek, P.M., Matson, P.A. & Van Cleve, K. (1989) Nitrogen availability and nitrification during succession: primary, secondary and old field seres. *Plant and Soil*, **115**, 229–239.
- Vitousek, P.M., Gosz, J.R., Grier, C.C., Mellilo, J.M. & Reiners, W.A. (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological Monographs*, **52**, 155–177.
- Webster, R. (1985) Quantitative spatial analysis of soil in the field. *Advances in Soil Science*, Vol. 3 (ed. B. A. Stewart), pp. 1–70. Springer-Verlag, New York.
- Wedin, D.A. & Tilman, D. (1990) Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia*, **84**, 433–441.
- Wedin, D.A. & Pastor, J. (1993) Nitrogen mineralization dynamics in grass monocultures. *Oecologia*, **96**, 186–192.
- Zak, D.R., Host, G.E. & Pregitzer, K.S. (1989) Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. *Canadian Journal of Forest Research*, **19**, 1521–1526.

Received 27 May 1994

Revised version accepted 15 August 1994