On the nature of environmental gradients: temporal and spatial variability of soils and vegetation in the New Jersey Pinelands

JOAN G. EHRENFELD,* XINGGUO HAN,† WILLIAM F.J. PARSONS‡ and WEIXING ZHU§

*Department of Ecology, Evolution, and Natural Resources, New Brunswick, NJ 08903, USA, †Institute of Botany, Academia Sinica, Beijing, Peoples' Republic of China 100044, ‡Smithsonian Environmental Research Centre, Edgewater, MD 21037–0028, USA, and §Calder Ecological Centre, Forham University, Box K, Armonk, NY 10504, USA

Summary

1 Environmental variability can occur over various spatial scales, ranging from small patches at the scale of individual plants to long gradients over hundreds of metres.
2 In the New Jersey Pinelands, different species in the diverse shrub understorey of pitch pine (*Pinus rigida* Mill.) forests are patterned at these various scales.
3 Soil moisture, extractable NH_4-N and N mineralization rate vary in complex ways, with the scale of spatial patterning changing over time and with depth in the soil profile. Moisture in both mineral and organic horizons, and NH_4-N in the organic horizon, have patterns that are more stable over time than the mineralization rate in either horizon, or the NH_4-N concentrations in the mineral horizon.
4 Vegetation patterns, as captured in principal components analysis, were poorly explained by any of the soil properties. Only the more temporally stable properties showed any relationship with vegetation patterns.
5 These results suggest that environmental gradients reflect patterns of environmental variation in four dimensions. Variation in the vertical dimension and over time is as pronounced and important as variation in the horizontal dimensions.
6 Many methods used to analyse vegetation implicitly assume temporal and spatial stability of environmental properties. Our results suggest that a more complex, four-dimensional assessment of environmental variation should be incorporated into models of vegetation–environment relationships.

Keywords: environmental gradients, nitrogen availability, organic horizon, Pinelands, shrub communities, soil moisture, soil variability, spatial pattern, spodosol, vegetation

Journal of Ecology (1997) **85**, 785–798

Introduction

Nitrogen dynamics in forest soils are known to vary over several spatial scales. Differences in extractable N fractions and in net mineralization and nitrification have been demonstrated for deciduous forests distributed over large geographical areas (> 100s km^2: Grigal & Ohmann 1989; Zak & Pregitzer 1990; Clark 1990; Grigal *et al.* 1991), for stands of differing canopy composition (areas of 100s of m^2 to km^2; Plymale *et al.* 1987; Zak & Pregitzer 1990; Grigal *et al.* 1991),

for ecosystems with similar vegetation but occupying different topographic positions (areas of 10s to 100s of m^2; Pastor *et al.* 1984; Schimel *et al.* 1985; Zak *et al.* 1986), and for different depths within the profile of a single soil (Federer 1983). In many of these studies, variations in nitrogen content and dynamics are apparently correlated with variation in moisture or microclimate; this is particularly evident in studies across topographic gradients (Quesnel & Lavkulich 1980; Zak & Grigal 1991; Zak *et al.* 1991; Garten *et al.* 1994). In sites without strong topographic relief, however, topographic position and its correlate, soil moisture, may have little influence on spatial patterns of N mineralization (Zak *et al.* 1991).

Correspondence: Dr Joan Ehrenfeld, 126 Environment and Natural Resource Science Building, Cook College, Rutgers University, New Brunswick, NJ 08903, USA.

Variations in both N content and rates of transformation have also been frequently demonstrated on smaller spatial scales of centimetres to metres (Quesnel & Lavkulich 1980; Courtin *et al.* 1983; Arp & Krause 1984; Robertson *et al.* 1988; Grigal *et al.* 1991). In some of these studies, the intent has been to assess variability in soil nutrients as a basis for estimating the optimal number of samples needed to characterize forest soils. Only a few of these studies examine possible correlates of this variation, including physical factors such as moisture or fine-scale variation in plant community composition. For example, accumulations of coarse woody debris (Arp 1984), the chemical properties of the forest floor (Klinka *et al.* 1990; Emmer 1994), and the physical properties of treefall gaps (Vitousek & Denslow 1986; Mladenoff 1987) have been found to be correlated with the varation in N dynamics.

We can distinguish three scales of variation that recur in many ecological studies of spatial patterning (Fig. 1). Variation at a scale of centimetres to metres (referred to below as 'metre-scale' variation) reflects environmental patterning at the scale of ecological interactions among individual plants. Variation at a scale of 10s of metres (referred to below as 'patch-scale' variation) presumably reflects environmental patterns associated with local changes in elevation, moisture, soil type, exposure or other factors; this scale is the one most often implied in discussions of patch dynamics. Variation at this scale can occur either as irregularly distributed patches (for example associated with an undulating ground surface), or as sequences of patches changing in a directional manner (Fig. 1). The latter pattern is usually termed a 'gradient', and extends over a scale of hundreds of metres; the term 'gradient-scale' variation is used below to refer to directional variation at this spatial scale.

Spatial variability of soil nutrients is also most frequently assessed in the two horizontal dimensions of the ground surface (e.g. studies by Courtin *et al.* 1983; Robertson *et al.* 1988; Schlesinger *et al.* 1996). However, soil is a three-dimensional environment, in which variation with depth and across different soil horizons may have profound implications for root growth and nutrient availability. Federer (1983), for example, found that the variation with depth of N mineralization accounted for much of the difference in total N availability in different forest stands. In many forest soils, a mor forest floor overlies a sharply contrasting mineral horizon of eluviated material, and much of the fine root biomass and microbial activity is concentrated in the organic layers (Clarholm & Rosswall 1980; Bååth & Söderström 1982; Hendrickson & Robinson 1984; Ehrenfeld *et al.* 1992). It is not known whether patterns of variability in the forest floor are mirrored in the underlying mineral horizons or whether the mineral soil varies independently of its surface covering. In one of the few studies of temporal and spatial variation in soil, Gupta & Rorison (1975) found that mineral horizons were more variable than organic horizons. Similarly, although seasonal patterns in N availability in both horizons are well documented (e.g. Fahey *et al.* 1985; Poovarodom *et al.* 1988; Hart & Firestone 1991), it is not known whether the two horizons vary in parallel through time. For a plant whose roots penetrate a series of soil horizons, the degree of concordance in temporal and spatial patterning between these horizons could be expected to affect the plant's response to the environment.

Patterns of variability in forest soils also need to be compared to patterns of vegetation, in order to determine the ecological significance of this variability. In most models of vegetation structure, it is implicitly assumed that variation in species occurrence is the result of their responses to variation in

10 m   **50 m**   **200 m**

Metre scale   **Patch scale**   **Gradient scale**
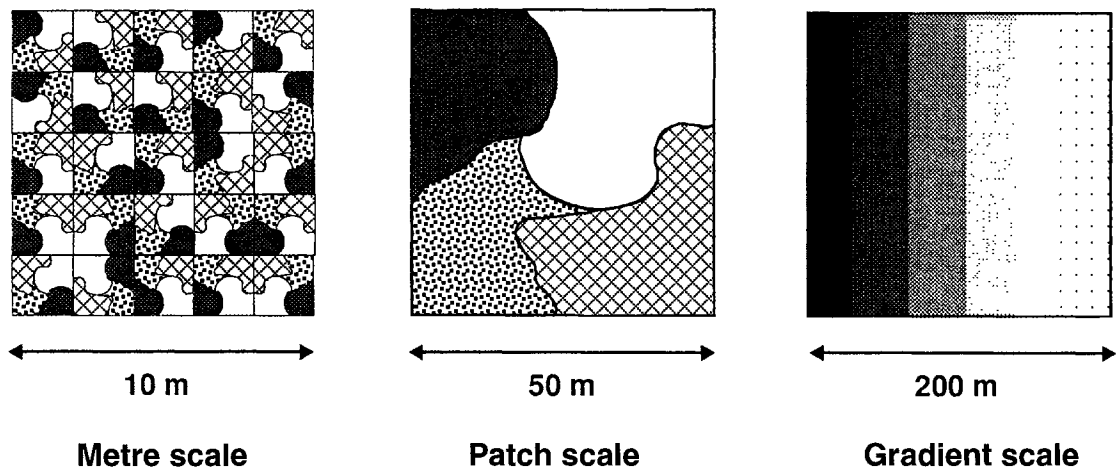
Fig. 1 Patterns of spatial variation at three scales. In metre-scale variation, significant differences in vegetation and/or environment occur at a scale of one to several metres. In patch-scale variation, such differences occur between areas that are 10s of metres in extent; vegetation and/or environmental properties are less variable within patches than between them. In gradient-scale variation, vegetation and/or environmental properties change gradually and directionally over distances of hundreds of metres; distinct patches may or may not be discernible within the gradient.

resource availability. For example, in an old-field community the N mineralization, nitrification and denitrification rates were strongly patterned on a scale of 20–40 m, and because this was similar to the scale of pattern in the vegetation, it was suggested that there was a causal relationship (Robertson *et al.* 1988). This implicit assumption underlies both direct and indirect ordination techniques (Jongman *et al.* 1987).

We have examined spatial and temporal patterns of N availability in a spodosolic soil in the New Jersey Pinelands, and compared them to the patterns of species occurrence in the vegetation. In the Pinelands, topographic relief is low, and although the forests have a low diversity of canopy trees, they can have considerable diversity of woody shrubs (Forman 1979). The soils have mor humus horizons that are sharply separated from the underlying highly leached, sandy mineral horizons (Ehrenfeld *et al.* 1997). The objectives of the study were therefore to (i) determine patterns of spatial variability on a horizontal plane for soil properties and vegetation; (ii) determine the concordance of spatial patterns between adjacent soil horizons; (iii) ascertain whether these three-dimensional patterns are stable or variable over time; and (iv) determine whether patterns in the occurrence of plant species reflect the patterns in soil properties.

Methods

SITE DESCRIPTION

The research was conducted in the Pinelands of the New Jersey Coastal Plain. The Pinelands is an extensive area of low topographic relief that has developed from the Cohansey Formation, a deposit of extremely nutrient-poor, Miocene-age sand (Tedrow 1979). Soils derived from this siliceous material are spodosols and entisols, which are characteristically very acidic (pH 3.5–4.0), and have surface organic matter accumulations (O horizons) ranging from 1 to 2 cm in the uplands to 6 cm in the lowlands (Ehrenfeld *et al.* 1992). The mineral soil (E horizon) is N- and C-poor (0.1 g N kg $^{-1}$ and 5 g C kg $^{-1}$) compared to the organic layers (11.4 g N kg $^{-1}$ and 407 g C kg $^{-1}$) (Par-

melee *et al.* 1993). Pitch pine, *Pinus rigida* Mill., and several species of oak, *Quercus* spp., dominate the canopy, and several species of ericaceous shrubs dominate the understorey; the vegetation is described in greater detail by Forman (1979) and Ehrenfeld *et al.* (1995).

TRANSECT ESTABLISHMENT

The study was conducted in conjunction with a study of a large set of manipulated plots located in Lebanon State Forest (Ehrenfeld *et al.* 1997). In that study, plots were established along two parallel transects on either side of a small creek in the McDonalds Branch watershed (identified as 'north' and 'south' below; Fig. 2). The transects, intended as replicates, were aligned along the contour at the lower end of the Lakewood soil series (a mesic, coated Haplaquodic Quartzipsamment). Four blocks, each 30 m long and comprising 1 m^2 plots separated by 2 m, were established along each transect, separated by 10–80 m. Sample stations for this study of the undisturbed soils were established at five random positions within each block. Blocks were separated by 10–80 m; sample stations were 2–16 m apart. Forty sample stations (five in each of eight blocks) were thus established for the study.

IN SITU INCUBATIONS

Nitrogen mineralization and nitrification in the O- and E-horizons along the transects were estimated from *in situ* buried-bag assays (Pastor *et al.* 1984). Soils were incubated consecutively for 42–50 days over a period of 17 months (June 1991 to October 1992; 10 samples and nine incubation periods). During each incubation period, 40 pairs of intact, adjacent soil cores (one pair per sampling station) were taken with a cylindrical corer (7.5 cm internal diameter) to a depth of 10-cm in the E horizon. Each core was separated into O- and E-horizons, which were then sealed in individual, polyethylene bags. The two bags containing the layers of the first core were reinserted into the ground in the correct order, and retrieved
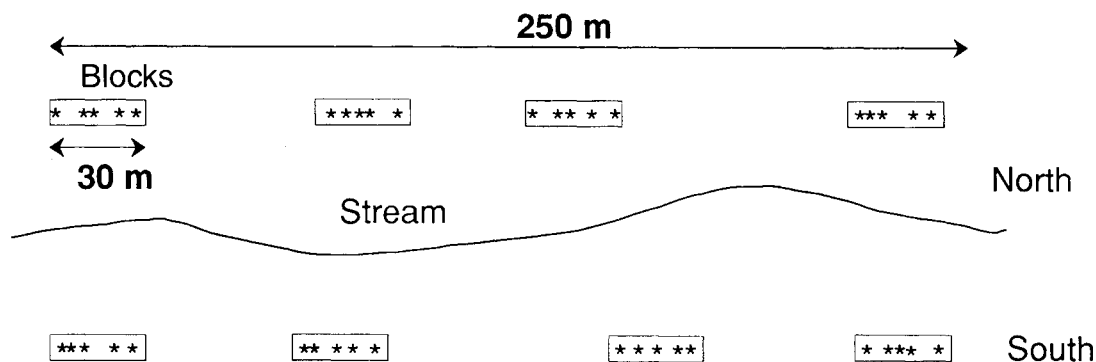
Fig. 2 Arrangement of sample points at study site on an unnamed tributary creek of McDonald's Branch. Asterisks denote locations of m^2 plots within which shrub densities were measured and all soil samples were taken.

after incubation; the second core in each pair was returned to the laboratory for immediate analysis.

The field-moist samples were mixed thoroughly, and live roots and other debris were removed prior to extraction. A 5-g organic or 20-g mineral soil sub-sample (fresh mass basis) from each core was extracted in 40 ml of 2 M KCl, filtered through Whatman no. 42 paper; NH_4-N and NO_3-N were determined in these extracts using a continuous-flow analyser (Alpkem Methods S071–00 and S170–25, respectively; Alpkem, Wilsonville, Oregon, USA). Soil moisture content was determined gravimetrically (10–30 g subsamples, oven-dried at 70 °C for 48 h). Net ammonification, net nitrification and net mineralization were calculated as the differences between final and initial concentrations of NH_4^+, NO_3^- and $NH_4 + NO_3$, respectively (mg N kg^{-1} oven-dry mass basis).

We concentrated on nitrogen and moisture, as these two properties are well known to vary over short periods of time. Phosphorous, which is present at low concentrations [60 mg kg^{-1} total P (Turner 1983), 0.5 mg kg^{-1} Bray-extractable P (Ehrenfeld *et al.* 1995)], would not be expected to vary over the month-to year-long time periods investigated here.

PLANT AND SOIL SAMPLING

We sampled the tree and shrub layers at each sample station. Canopy trees were sampled by the point-quarter method, and the diametre of each tree was recorded. Understorey composition was determined by counting shrub stems within two adjacent 50 × 50 cm quadrats, which were placed in undisturbed vegetation adjacent to the sampling point. The depth of the O-layer was determined by slicing into the forest floor with a sharpened shovel blade. Bulk densities of the O- and E-layers were determined from separate cores. Depth to the water table was also determined at each sample point on a single date in May 1994. Plants were beginning to leaf out at this date, and so the water table levels were at their annual high level.

STATISTICAL ANALYSES

Because the samples were not collected on a regular two-dimensional array of points, but were grouped according to the location of the blocks, conventional methods of spatial analysis (Rossi *et al.* 1992) could not be used. Rather, analyses of variance (both parametric and non-parametric) comparing the sample blocks (Fig. 2) were used to distinguish variation between blocks (patch-scale variation) from variation within blocks (metre-scale variation). The normality of the data was assessed using probit plots, and the homogeneity of variance assumption was tested using Levene's *F*-test (Levene 1960). Data not meeting these assumptions were subjected to Friedman's tests (non-parametric completely randomized block ANOVA) and

Kruskal–Wallis one-way ANOVAs (Marascuilo & McSweeney 1977).

Gradient-scale patterns were detected by regressing the observed values for each sample station against its distance from the beginning of the series of plots (Fig. 2), testing both linear and curvilinear models. These regressions were calculated separately for the north and south sets of blocks (Fig. 2), because our hypothesis was that the samples are arranged over an environment that changes regularly over distances of hundreds of metres. Thus, each set of 20 samples constituted an independent test of the gradient structure of spatial variation. Initial analyses showed that in almost all cases in which significance was found, a curvilinear (second-order polynomial) model fitted the data better than a linear model, and thus only the curvilinear results are reported; deviations from this pattern are noted in the text.

Temporal variation was analysed in three ways. First, the coefficients of variation within each sample period were examined to assess changes in variability over time. Secondly, Friedman's tests followed by rank tests of interaction between sample date and location (block position) (de Kroon & van der Laan 1983) were used to determine whether spatial patterns among the blocks were concordant over time; that is, whether certain blocks were reliably higher or lower than the others for each soil property throughout the year. Thirdly, correlations between consecutive sample periods were calculated to determine whether soil properties were consistent over season-long periods.

Concordance between organic and mineral horizons was examined in two ways. First, the correlation between horizons was tested for each sample period (10 sample periods, $n = 40$ sample points per period). Secondly, correlations were computed between O- and E-horizons using the differenced data, i.e. the absolute positive or negative changes in the soil properties within a horizon from one sample interval to the next. We wanted to know if, from month to month, systematic changes in soil properties in the organic horizon were accompanied by similar changes of amplitude and direction in the mineral horizon.

Both the vegetation and the environmental data were subjected to principal components analysis (PCA). This method was selected, as opposed to correspondence analysis, because the study design provided only a relatively small amount of environmental variability, and it was assumed that the species would have linear responses over this short environmental gradient, rather than unimodal responses as assumed for correspondence analysis (Jongman *et al.* 1987). Parallel analysis was used to test the significance of the components and the significance of the loadings of variables on the components (Buja & Eyuboglu 1992; Franklin *et al.* 1995). The axes of the environmental ordinations were then used as regressors in backwards, step-wise multiple regression analyses,

which sought to determine the environmental factors accounting for variation in the vegetation axes.

All analyses were conducted using SuperANOVA and StatView 4.02 for the Macintosh (Abacus Concepts Inc., Berkeley, CA).

Results

SPATIAL PATTERNS OF VEGETATION

The canopy consisted exclusively of *P. rigida* (mean density 1400 stems ha^{-1}), and no significant variation in tree density among blocks was detected. The shrub layer was very dense, with an overall mean density of 160.6 + 12.5 stems m^{-2} (mean + SE), a value similar to other studies in the same area (Ehrenfeld *et al.* 1992). *Gaylussacia baccata* dominated the upper stratum (to approximately 50 cm), while *Gaultheria procumbens* formed a dense layer on the forest floor (Table 1). Five species (*Vaccinium pallidum, Kalmia angustifolia, Lyonia mariana, Leucothoë racemosa* and *Clethra alnifolia*) showed significant heterogeneity in their patterns of occurrence among blocks (patch-scale variation), but only two (*G. procumbens* and *L. mariana*) showed gradient-scale patterning (based on the density of stems per sample; Table 1). Total stem density did not show either patch- or gradient-scale spatial patterning.

PCA analysis was based on eight shrub species; rare species (*V. corymbosum, Q. ilicifolia* and *Smilax rotundifolia*), which together accounted for < 1% of the stem densities, were excluded. The first two principal components extracted from the shrub data were significant (determined using the methodology in Franklin *et al.* 1995), and accounted for 48.0% of the variation in vegetational composition along the

transects. The first component (Fig. 3) reflected a contrast between *G. baccata*, which extends into the most xeric soils of the region, and *L. racemosa*, which extends into adjoining wetlands (loadings significant at 90% quantile; Buja & Eyuboglu 1992). On the second axis, two species were significantly loaded (*G. procumbens* and *L. mariana*), both at the same end of the axis. Both species are found broadly across the topographic gradient from xeric to hydric soils, whereas the other species are less widely distributed. *Vaccinium pallidum*, whose loading on the second axis corresponds to approximately the 85% quantile, and which is associated with xeric uplands, is found at the opposite end of this axis, suggesting that the axis might represent a contrast between broad and narrow ecological amplitudes. As the two axes explained nearly equal amounts of variance (Fig. 3), the lack of obvious explanation for the second axis, and the failure of more species to load significantly on the axes, suggests that species' distributions do not reflect a simple moisture gradient, and that other environmental factors may be involved in differentiating their occurrence.

SPATIAL PATTERNS OF SOIL CHARACTERISTICS

The O horizon was 3.0–5.6 cm thick (mean ± SE, 4.4 ± 0.2 cm) and there was significant patch-scale spatial variation (Table 2). Both transects also showed gradient-scale variation, but with different patterns. In the north transect, O horizon thickness varied in a curvilinear fashion, with greatest thickness in the centre of the transect, whereas on the south side, O horizon thickness decreased linearly from one end of the set of plots to the other.

Table 1 Density (stems m^{-2}) and frequency of occurrence among plots ($n = 40$) of shrubs in McDonalds Branch watershed. χ^2 tests of homogeneity of species occurrence among blocks test for patch-scale variation, and regressions (r^2 and P-value) of density as a function of distance test for gradient-scale variation. Regressions are reported separately for the north (N) and south (S) sets of samples

Species	Occurrence (%)	χ^2	Mean density (range)	Regression Side: P	r^2
Gaylussacia baccata (Wang.) K. Koch	100.0	NS	63.7 (60.0–114.0)	N, S	NS
Gaultheria procumbens L.	97.5	NS	58.2 (0–178.0)	N: S: 0.049	NS 0.299
Kalmia angustifolia L.	85.0	16.97*	25.5 (0–172.0)		NS
Vaccinium pallidum Aiton.	45.0	19.96**	57.5 (0–72.0)		NS
Leucothoë racemosa (L.) Gray	20.0	23.53**	25.0 (0–30.0)		NS
Clethra alnifolia L.	25.0	19.05**	15.0 (0–12.0)		NS
Lyonia mariana (L.) D. Don	22.5	28.24**	1.50 (0–12.0)	N: 0.0007 S: 0.066	0.572 0.273
Ilex glabra (L.) Gray	20.0	NS	1.0 (0–10.0)		NS
Smilax rotundifolia. L.	20.0	NS	0.5 (0–6.0)		NS
Quercus ilicifolia Wang.	12.5	NS	0.5 (0–4.0)		NS
Vaccinium corymbosum L.	2.5	NS	0.1 (0–4.0)		NS

$*P < 0.05; **P < 0.01.$
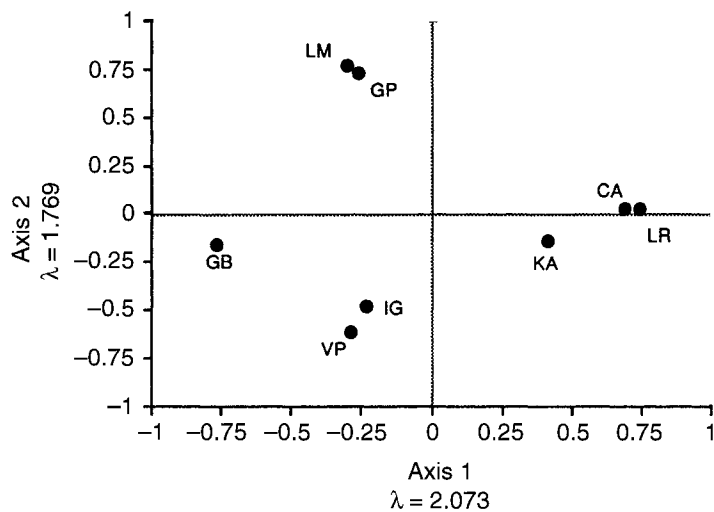
Fig. 3 Principal components ordination of shrub species. Eigenvalues and percentage of variance explained are given for the first two axes. Plant species: CA, *C. alnifolia*; GB, *G. baccata*; GP, *G. procumbens*; IG, *I. glabra*; KA, *K. angustifolia*; LR, *L. racemosa*; LM, *L. mariana*; VP, *V. pallidum*.

Table 2 Spatial heterogeneity in soil properties. Metre- vs. patch-scale patterns compared by one-way ANOVA among the eight blocks. Gradient patterns were tested by separate regression analyses for each set (north and south) of blocks. All regression results are for a second-order polynomial equation (d.f. = 2,17), except as noted

Property	n per block	Metre vs. patch scale ANOVA $F_{7,32}$	P	Side	Gradient-scale regression F	P	r^2
Organic matter thickness (cm)	5	5.820	0.0002	N	11.496	0.0007	0.575
				S	13.545†	0.0017	0.429
O horizon bulk density (g cm^{-3})	2	NS			NS		
E horizon bulk density (g cm^{-3})	2	NS			NS		
Depth to water table (cm)	2	NS			NS		
Cumulative N min, E horizon	5	NS			NS		
Cumulative N min, O horizon	5	NS			NS		
Mean soil moisture (%), E horizon, 12 months	5	5.000	0.0007	N	8.431	0.0029	0.498
				S	NS		
Mean soil moisture (%), O horizon, 12 months	5	7.459	0.0001	N	12.418	0.0005	0.594
				S	4.758	0.0229	0.359
Mean extractable NH$_4$-N O horizon	5	4.783	0.0009	N	7.731	0.0041	0.476
				S	6.007	0.0106	0.414
Mean extractable NH$_4$-N E horizon	5	3.008	0.0152		NS		

† Linear regression (d.f. = 1,18).

Organic horizon bulk density varied from 0.25 g cm^{-3} to 0.78 g cm^{-3} (overall mean 0.41 ± 0.05 g cm^{-3}, n = 16), and bulk density of the E horizon soil varied from 1.04 to 1.32 g cm^{-3} (mean 1.17 ± 0.46 g cm^{-3}). In neither horizon did bulk density show patch- or gradient-scale variation (Table 2). Depth to the water table ranged from 47 to 90 cm, and it also varied only at the metre scale. Similarly, the cumulative N mineralized in each horizon of the profile over the course of a 12-month period (May 1991–92) varied only at the metre scale (Table 2).

Mean soil moisture over the study period (May 1991–October 1992) is shown in Fig. 4(a,b). In both horizons, soil moisture rose in late autumn, and remained high until spring. Moisture in both horizons decreased in spring as the plants leafed out in early May, but the decrease in the O horizon was pro-

portionately greater than the decrease in the E horizon. Conversely, the E horizon was more sensitive to late-season drought than the O horizon. In both horizons, patterning at the patch scale and the gradient scale only occurred in a few of the sample periods, and the two soil horizons did not coincide on the dates on which such patterning occurred (Table 3). In the O horizon, patterning at a scale greater than the metre scale was only observed in 1992, and curvilinear gradient-scale patterning was observed only in the north set of blocks; on the south side, patterning occurred only at the patch scale. In the E horizon, soil moisture varied on a patch scale more frequently than in the O horizon, but again, variation at this scale was not constant over time. Gradient-scale patterning was also variable; it occurred on the south sample area during May (1991), and in the north area in December.
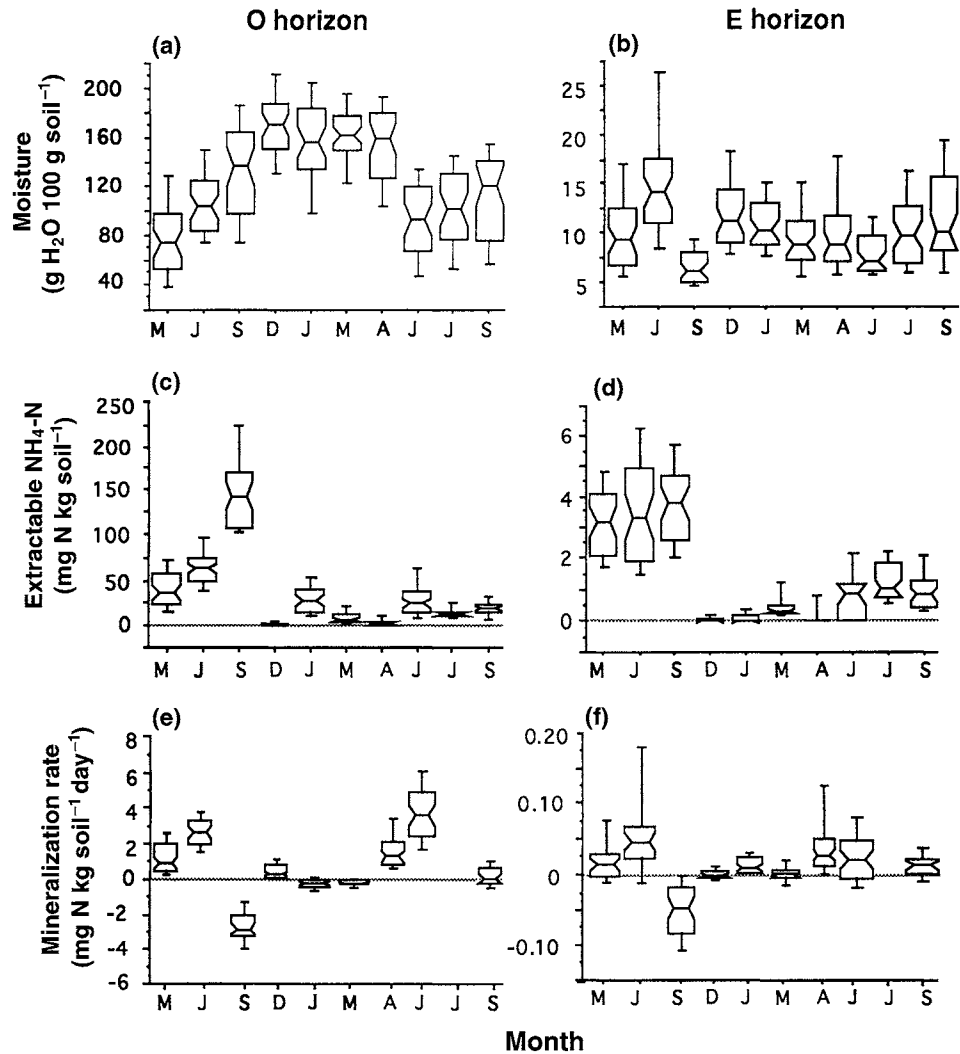
Fig. 4 Temporal patterns of soil properties in O and E soil horizons over the sample period. $n = 40$ for each value. Each sample is shown as a box plot showing the median (central horizontal line), the 25th and 75th percentiles (top and bottom lines of the closed figure), and the 10th and 90th percentiles (top and bottom bars on each figure).

Although there was no gradient-scale variation observed during most months, annual mean soil moisture showed marked curvilinear gradients in both O and E horizons (Table 2). Plots in the centre of both transects had wetter organic horizons, on average, than did the plots at the ends of the transects. In the mineral soil, however, this pattern was only found in the north set of blocks.

Extractable N was dominated by NH_4^+ in both horizons, and throughout the study. Nitrate concentrations were negligible in 91% of the samples (< 0.002 mg N kg^{-1}), and even when present in detectable amounts ($0.015–1.027$ mg N kg^{-1}) were $< 5\%$ of the NH_4^+ concentrations. Therefore, analyses of spatial and temporal patterning were carried out only for NH_4^+.

Extractable NH_4-N in the O horizon was one to two orders of magnitude higher than the E horizon throughout the study (Fig. 4c,d). In both horizons, concentrations were much higher in the late spring to autumn samples of 1991 than in the samples from the same seasons in 1992. As was observed for soil

moisture, spatial patterning of available NH_4^+ at patch or gradient scales occurred sporadically (Table 3). The occurrence of patterning in one horizon was not necessarily accompanied by patterning at the same scale in the adjoining horizon, and the patterning on a gradient scale could occur in one set of blocks while the parallel set showed no such trend. In general, there was little evidence of a gradient in extractable N. As with the results for soil moisture, extractable N in the O horizon showed a stronger gradient pattern (as indexed by the r^2 of the regression) in mean annual values than for any particular month (Tables 2 and 3). However, the annual mean extractable N in the E horizon did not show a significant gradient pattern.

Nitrogen mineralization rates (Fig. 4e,f) were accounted for almost entirely by ammonification, as nitrification was observed only in the O horizon, only during the June 1991 incubation period, and even then at the low rate of 0.13 ± 0.05 mg N kg^{-1} day^{-1}. In both horizons, net N mineralization during the spring and summer of 1991 was followed by a period

Table 3 Spatial variation for time-varying properties. The data were tested for patch-scale variation with Kruskal–Wallis tests for each sample period (May 1991 to October 1992), and gradient-scale variation was tested using regression analysis. For each property, only those sample dates with significant patch- and/or gradient-scale variation are listed. All regression results are for a second-order polynomial equation (d.f. = 2,17), except as noted

Property	Date	Patch scale Kruskal–Wallis H	Side	Gradient scale F	P	r^2
% moisture, O horizon	April 1992	16.82*	N	10.810†	0.004	0.325
			S	NS		
	July 1992	16.22*	N	13.229	0.0003	0.609
			S	NS		
	October 1992	16.45*	N	6.963	0.006	0.647
		S	NS			
% moisture, E horizon	May 1991	20.59**	N	NS		
			S	8.934	0.0022	0.512
	July 1991	14.37*	N	5.240	0.0169	0.381
			S	NS		
	December 1991	18.41*		NS		
	July 1992	15.71*		NS		
	Oct 1992	24.09**	N	15.595	0.0001	0.647
			S	NS		
Extractable NH_4-N (mg kg^{-1}) O horizon	May 1991	14.43*	N,S	NS		
	September 1991	14.58*	N	6.558	0.019	0.267
			S	NS		
	December 1991	18.14*	N,S	NS		
	January 1992	15.71*	N,S	NS		
	April 1992	21.04**	N	5.412	0.0319	0.231
			S	NS		
Extractable NH_4-N (mg kg^{-1}) E horizon	December 1991	15.96*	N,S	NS		
	January 1992	28.24***	N,S	NS		
	July 1992	17.60*	N	11.646	0.0031	0.393
			S	NS		
Mineralization rate (mg N kg^{-1} d^{-1}) O horizon	May 1991	15.39*	N,S	NS		
	April 1992	16.80*	N	4.951	0.0391	0.216
			S	NS		
Mineralization rate (mg N kg^{-1} d^{-1}) E horizon	December 1991	16.40*	N	NS		
			S	7.722	0.0124	0.300
	March 1992	17.88*	N,S	NS		

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
†Linear regression (d.f. = 1,18).

of immobilization in early autumn; the pulse of mineralization observed during the spring and summer of 1992 was not followed, however, by a similar period of immobilization during the late autumn of 1992. During the winter, there were negligible rates of both mineralization and immobilization.

Spatial patterning of mineralization rates at a scale greater than a metre scale was rarely found in either horizon (Table 3). As with soil moisture and extractable N, evidence of patterning at a gradient scale occurred even more rarely, and in just one of the two transects on each date. The annual mean mineralization rates similarly did not vary at the gradient scale.

TEMPORAL VARIATION

The coefficients of variation of soil moisture showed the least amount of annual variation among samples

(Fig. 5), with coefficients of variation < 0.50. In contrast, extractable N, and especially the N mineralization rate, were highly variable, with coefficients of variation exceeding 1.0 in both horizons and for both variables. Variability in moisture among samples did not change over time, whereas the variability in both measures of N availability was greater during the winter and early spring than during the growing season.

The Friedman's tests of temporal concordance of the sample blocks showed that in the E horizon, only moisture had consistent patterns over time; the other variables all showed significant variation in the ranking of the blocks over time (extractable NH_4-N: $\chi^2 = 117.77$, $P = 0.0003$; N mineralization rate: $\chi^2 = 78.59$, $P = 0.025$). In the O horizon, both moisture and extractable N were consistent over time, but the N mineralization rate varied in its spatial pattern over time ($\chi^2 = 82.25$, $P = 0.013$).
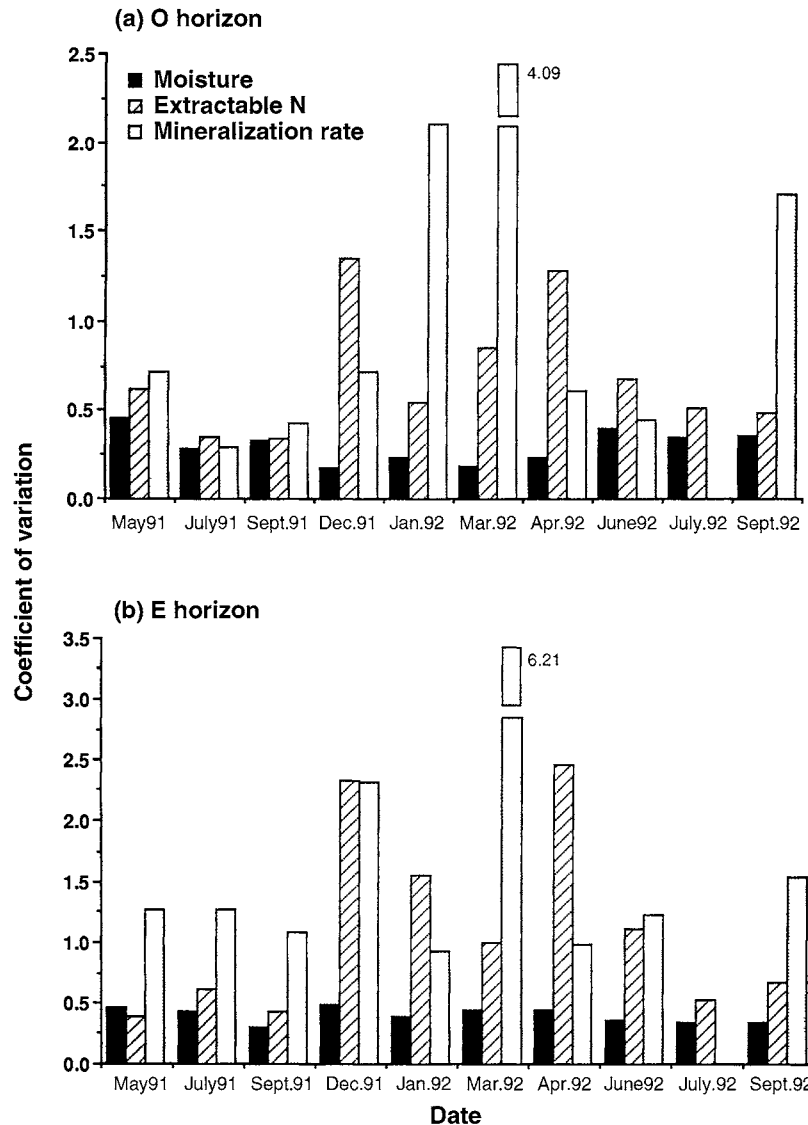
These results are consistent with the analyses of

(a) O horizon

(b) E horizon

Fig. 5 Coefficients of variation for each sample time for the temporally varying soil properties ($n = 40$).

spatial pattern described above. Moisture and extractable N in the O horizon vary in their spatial patterning from month to month, but over long periods of time (1+ years) trends are evident either as significant concordance of block ranking, or as a significant gradient-scale spatial pattern. Similarly, the results of the Friedman's tests are consistent with the finding that annual means of extractable N in the E horizon and N mineralization rate did not show a gradient-scale pattern. Thus, spatial differences in moisture throughout the profile, and in the extractable N of the O horizon, are reliable over long periods of time, whereas mineralization rates, and the N content of the E horizon, show no such reliability.

Seasonal patterning, indexed by significant correlations between consecutive samples, was apparent only for organic horizon moisture content (Table 4). For the nitrogen variables, values for most sample periods were uncorrelated with values for the subsequent period. Thus, nitrogen availability, as indexed by both the extractable amounts and the rate of min-

eralization, varied mostly over short periods of time (weeks), with little consistency over seasonal periods of time.

CONCORDANCE BETWEEN SOIL HORIZONS

Environmental heterogeneity could result not only from varying spatial and temporal patterns of soil properties, but also from differences in the behaviour of the adjoining O and E horizons. If the two horizons are tightly linked, then variation in one horizon should be mirrored by changes of a similar magnitude and direction in the other horizon. Soil moisture levels in the O and E horizons are significantly correlated most of the time (significant correlation coefficients for all but one sample period; Table 5). However, the correlation coefficients are often low (0.3–0.5), indicating that there is considerable residual variation between horizons. Unlike soil moisture, there was little correspondence in either extractable NH_4-N or the N mineralization rate between horizons (Table 5).

Table 4 Pearson product-moment correlations between consecutive soil measurements. $n = 40$ for each analysis. Only periods with significant correlations are shown

Horizon	Variable	Correlated periods	r
Organic	Moisture	September 1991– December 1991	0.36*
		January 1992–March 1992	0.52***
		March 1992–April 1992	0.47**
		June 1992–July 1992	0.45**
	Extractable NH₄-N	May 1991–July 1991	0.39*
	Mineralization rate	September 1991–December 1991	−0.38*
Mineral	Moisture	March 1991–April 1992	0.76***
	Extractable NH₄-N	September 1991–December 1991	0.38**
	Mineralization rate	December 1991–January 1992	0.35*

$*P < 0.05; **P < 0.01; ***P < 0.001.$

Table 5 Spearman rank correlation coeffficients for correspondence of moisture (g H_2O 100 g^{-1} soil), extractable NH₄-N (mg kg^{-1}), and N mineralization rate (mg kg^{-1} day^{-1}) between horizons for each sample period. $n = 40$ for each analysis, and the significance level is given in parentheses

Date	% moisture	Extractable NH₄-N	N mineralization rate
May 1991	0.583	0.329	−0.148
	(< 0.0001)	(0.0399)	NS
July 1991	0.103	0.189	0.049
	NS	NS	NS
September 1991	0.406	−0.029	−0.348
	(0.0184)	NS	(0.0298)
December 1991	0.323	0.212	−0.375
	(0.0435)	NS	(0.0193)
January 1992	0.351	0.136	−0.020
	(0.0285)	NS	NS
March 1992	0.590	0.184	0.173
	(0.0002)	NS	NS
April 1992	0.394	0.162	0.268
	(0.0138)	NS	NS
June 1992	0.311	−0.317	0.046
	(0.0520)	(0.0478)	NS
July 1992	0.532	0.097	Not done
	(0.0009)	NS	
October 1992	0.452	−0.024	−0.253
	(0.0048)	NS	NS

Moreover, the significant interhorizon correlations occurred at different sample times for the two variables.

The changes in moisture, extractable N and ammonification rate between consecutive sample periods in each horizon were rarely correlated with each other. In only one case for each variable was the change in magnitude of a soil resource in one horizon correlated with the change in the adjacent horizon (moisture: June–July 1992, $r = 0.430$, $P = 0.0073$; extractable NH4-N: June–July 1992, $r = -0.326$, $P = 0.0418$; ammonification rate: September– December 1991, $r = -0.405$, $P = 0.0113$). Thus, only moisture content covaries in the two horizons, and this linkage is not sufficiently close that the magnitude of change in one horizon over time is paralleled by a similar magnitude of change in the other horizon.

RELATIONSHIP OF SOIL PROPERTIES TO VEGETATION

In the PCA of the soils data (10 measurements for each of six soil properties, at each of 40 sample points,

for each horizon), we found that only one component was significant (using the criteria of Franklin *et al.* 1995) at $P = 0.05$ for soil moisture and extractable N in each horizon, and the ammonification rate in the mineral horizon; no component was significant for the ordination of ammonification in the organic horizon. In all cases, the first eigenvalue explained only 20% and 30% of the variance. Because the PCA analyses did not effectively reduce the complexity of the data, we also carried out multiple regression analyses using annual means of each of the soil variables. These could be interpreted as long-term indices of resource availability that integrate the month-to-month variability.

Few soil variables were useful in explaining the two vegetation axes, either as environmental ordination axes or as annual means (Table 6). Only moisture in the mineral horizon and extractable N in the organic horizon were selected by the regression procedure; the ammonification rate was not important in explaining any aspect of the vegetation. Furthermore, the coefficients of determination for all equations were

Table 6 Step-wise multiple regression analysis relating environmental axes to the vegetation axes. Time-varying soil properties were summarized using separate principal components ordinations of each dataset (moisture (MOIST.), extractable NH_4-N and N (EXTRN.) mineralization rate) in each horizon. Annual means were also used as alternative, time-invariant descriptors of the sample points

Vegetation axis	F	P	r^2	Equation
PCA-based analyses:				
1	4.593	0.040	0.122	$0.016 + 0.341$MOIST.E
2		None significant		
Annual means				
1	5.859	0.020	0.134	$-1.782 + 0.169$MOIST.E
2	4.642	0.0376	0.109	$1.262 - 0.029$EXTRN.O

very low (< 0.14), reinforcing the implication that the soil variables provided little explanation for the plant community composition.

Discussion

We have demonstrated that the spatial scales at which environmental properties vary can be very different, even for properties that are normally thought to be functionally linked. Furthermore, we have found that the scale of spatial patterning of an environmental property is itself variable over time. Other studies have documented a high degree of spatial variation in soil properties at scales of centimetres to 10s of metres (Quesnel & Lavkulich 1980; Grigal *et al.* 1991; Goovaerts & Chiang 1993; Robertson *et al.* 1988, 1997), and a few studies have shown that different nutrients can have different temporal patterns of availability in the same soil (Gupta & Rorison 1975; Federer 1983), but there has been no demonstration that the spatial patterns themselves change over time. Our data suggest that environmental variation is best conceptualized as four-dimensional, in which patterns extending over horizontal planes and simultaneously over depth in the soil profile are continuously changing in time. While this study targeted the variation associated with soil properties, a similar result could be expected with such above-ground properties as light intensity, spectral distribution or air temperature.

Despite a large amount of variation in the soil properties, there was little correlation with vegetation patterns. The multiple regression analyses suggested that a moisture gradient, primarily that of the mineral soil horizon, contributes to an explanation of the variation in some species (*G. baccata* and *L. racemosa*, which were those significantly associated with the first PCA axis). Similarly, a gradient in extractable NH_4-N in the organic horizon explains, in part, the variation of two other species (*G. procumbens* and *L. mariana*). The distributions of the other species, however, are not related to either moisture or nitrogen availability in a simple or obvious way. As our data are based on correlations among observed properties, we cannot distinguish environmental control of plant distributions from the equally plausible plant influ-

ence on soil properties (Ehrenfeld *et al.* 1997; van den Putten 1997). However, either direction of causality should result in an observable association between plant abundance and soil properties, if a causal relationship exists.

The lack of relationship of either individual species patterns, or groups of correlated species, as captured by principal components ordination, to the variation in soil resources is surprising; yet it is similar to other studies of soil variability and vegetation. For example, Robertson *et al.* (1997) found much lower correlation between soil properties and net production in a homogeneous soybean field than was expected. Even for a monospecific crop grown on a level field with uniform land-use history, only 46% of the variation in peak plant biomass could be explained using a much larger number of soil properties than were included here. Their suggestion that the lack of clear relationship could be due to temporal variability in the soil is strongly supported by our study. We observed a high degree of variability in water and N availability over time. This included month-to-month differences at individual sample points, variation at patch scales (i.e. lack of temporal consistency among blocks of points), lack of consistency between adjoining horizons, and lack of consistency in the amount of change from month to month between adjoining horizons. In other words, different points on the landscape had different amounts and patterns of variation with time. The caution expressed by Goovaerts & Chiang (1993) in interpreting the spatial patterning of several soil properties, including moisture and mineralizable N, as consistent on the basis of only two sample dates appears justified. Our data suggest that temporal consistency should be measured over multiple time intervals.

The degree to which variation in environmental properties affects the structure of vegetation may thus reflect the consistency of spatial patterns over both space and time. The first axis of the ordination of the shrub community was associated with the moisture content of the mineral horizon, while the second axis was associated with extractable NH_4-N. These two variables were among the most predictable, in terms of their spatial patterning (Table 3) and their temporal consistency among sample blocks.

The moisture content at any point in time or even over a season was not necessarily a good indicator of the patterning evident over annual or longer periods of time. The same result was observed for O-horizon extractable N: patterns clearly evident at yearly time scales were not always discernible at shorter time scales. These results suggest that single measurements of soil properties, or even short-term, seasonal measurements, may give a misleading picture of the scale of environmental variation, and its predictability over time.

Environmental gradients are commonly and often implicitly assumed to control the distribution of plant species and plant associations (Kent & Coker 1992). The assumption is that each species maximizes its abundance at some value of each environmental property, but is capable of surviving over some range of values. Species' abundances should therefore approximate Gaussian distributions (Jongman *et al.* 1987), and this assumption underlies both direct and indirect gradient analyses. It is further generally assumed that environmental properties vary at scales that permit different groupings of species to occur, that such variation is constant over time, and that it increases or decreases monotonically across a landscape (Phillips 1985). Therefore, the various methods for explaining spatial differentiation of plant communities, which are based on species' occurrences in an array of sample plots, depend on the spatial variation of environmental properties.

However, many studies of vegetation–environment relationships utilize environmental properties such as soil moisture and extractable nutrient concentraions that themselves vary over time (examples in Kent & Coker 1992). The use of both single measurements and seasonal means are of limited value, since our results demonstrate that the explanatory value of an environmental property may vary. A gradient present at some time(s) may not be present at other time(s), or may even be reversed in direction. Also, different environmental properties thought to be important to plant distributions within a community may show different spatial patterns at the same time. Finally, a soil property may display one spatial pattern in a surface horizon, and a different pattern in the sub-surface horizon at the same point in time. Rather than ignoring this temporal and spatial variability, this variability and four-dimensional nature of environmental gradients should be incorporated into conceptual models of vegetation–environment relationships.

The plant species were also patterned at different scales, with five patterned only at the metre scale, five patterned at the patch scale, and only two patterned at the gradient scale (Table 1). These results suggest that the species are responding differently to environmental variables. Some species, for example *L. mariana*, are patterned at patch and gradient scales, as is moisture, while others, like *G. baccata*, show no

patterning at the same scales as the environmental variables. A species whose patterning is congruent with the pattern of a soil resource probably has a tolerance (range of environmental conditions under which it can survive) similar in magnitude to the range of variation of the resource. Conversely, the pattern of a species that has a tolerance that is greater than the range of variation of the resource would not be expected to show a relationship with resource patterning.

The cumulative N mineralized per year per unit area (59.3 ± 8.4 kg N ha^{-1} year^{-1} for the O horizon and 7.4 ± 1.9 kg N ha^{-1} year^{-1} for the E horizon) differs somewhat from a previously reported value for the Lakehurst soil. Poovarodom *et al.* (1988) documented 38.4 kg N ha^{-1} year^{-1} mineralization. but this was for a combination of O and E horizon soils, with no indication of the relative thickness of the two horizons. The range of values observed in our samples (9.1–127.0 kg N ha^{-1} year^{-1} in the O horizon; 2.4–28.7 kg N ha^{-1} year^{-1} in the E horizon) suggests that differences among studies could simply be a result of spatial variation.

The relationship of N dynamics to plant community structure is still unclear, despite recent research on the subject (e.g. Thompson 1987; Wedin & Tilman 1990, 1993). The competitive ability of herbaceous plants has been linked to their ability to reduce extractable N concentrations (Tilman 1990a,b) and their ability to influence N mineralization rates (Wedin & Tilman 1990). Our data, however, show no relationship between individual species and either extractable N or N mineralization rates, and no relationship between the N mineralization rate and either vegetation axis. Thus, there is little evidence that N availability has as large a role in structuring this shrub community as it does in herbaceous communities. Communities of clonal plants, such as these shrub species, may be structured by different factors than non-clonal communities. Shrubs are long-lived, and the clonal growth form of many (Matlack *et al.* 1993) implies that an individual plant is spread out over a large range of soil conditions. The temporal and spatial variation documented for N cycling may be integrated by intraplant transfers of N and through storage of N in extensive rhizome systems (Laycock 1967). The roots of different species may also be found in different soil horizons, as documented for the Pinelands shrubs (Harshberger 1916; Laycock 1967). It is possible that direct uptake of organic N associated with mycorrhizal infection of the ericaceous shrubs (Kaye & Hart 1997) may uncouple plant success from the production of mineral forms of N. Models of community structure developed for herbaceous, non-clonal plants and based on N uptake and N availability may not therefore be appropriate for woody shrub communities.

Our results show that environmental gradients should be conceptualized and modelled as four-

dimensional patterns, with vertical and temporal dimensions given equal weight with the more commonly studied horizontal dimensions. Furthermore, the degree of consistency over both space and time, rather than the magnitude of variation, allows an environmental property to structure a plant community. The degree to which vegetation structure is not explained by measured environmental gradients may itself be a measure of the relative importance of biotic processes such as competition, herbivory, clonal growth patterns or mycorrhizal symbioses, compared to the direct effect of environmental properties on the physiology of the individual plants.

Acknowledgements

References

Arp, P.A. (1984) Forest floor variability and factor analysis: a case study. *Canadian Journal of Soil Science*, **64**, 457–461.

Arp, P.A. & Krause, H.H. (1984) The forest floor: spatial variability as revealed by systematic sampling. *Canadian Journal of Soil Science*, **64**, 423–437.

Bååth, E. & Söderström, B. (1982) Seasonal and spatial variation in fungal biomass in a forest floor. *Soil Biology and Biochemistry*, **14**, 353–358.

Buja, A. & Eyuboglu, N. (1992) Remarks on parallel analysis. *Multivariate Behavioral Research*, **27**, 509–540.

Clarholm, M. & Rosswall, T. (1980) Biomass and turnover of bacteria in a forest soil and a peat. *Soil Biology and Biochemistry*, **12**, 49–57.

Clark, J.S. (1990) Landscape interactions among nitrogen mineralization, species composition, and long-term fire frequency. *Biogeochemistry*, **11**, 1–22.

Courtin, P., Feller, M.C. & Klinka, K. (1983) Lateral variability in some properties of disturbed forest soils in southwestern British Columbia. *Canadian Journal of Soil Science*, **63**, 529–539.

Ehrenfeld, J.G., Kaldor, E. & Parmelee, R.W. (1992) Vertical distribution of roots along a soil toposequence in the New Jersey Pinelands. *Canadian Journal of Forest Research*, **22**, 1929–1936.

Ehrenfeld, J.G., Parsons, W.F.J., Han, X., Parmelee, R.W. & Zhu, W. (1997) Live and dead roots in forest soil horizons: contrasting effects on nitrogen dynamics. *Ecology*, **78**, 348–362.

Ehrenfeld, J., Zhu, W. & Parsons, W.F.J. (1995) Above- and below-ground characteristics of persistent forest openings in the New Jersey Pinelands. *Bulletin of the Torrey Botanical Club*, **122**, 298–305.

Emmer, I.M. (1994) Humus form characteristics in relation to undergrowth vegetation in a *Pinus sylvestris* forest. *Acta Oecologica*, **15**, 677–687.

Fahey, T.J., Yavitt, J.B., Pearson, J.A. & Knight, D.H.

(1985) The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. *Biogeochemistry*, **1**, 257–275.

Federer, C.A. (1983) Nitrogen mineralization and nitrification: depth variation in four New England forest soils. *Soil Science Society of America Journal*, **47**, 1008–1014.

Forman, R.T.T. (1979) *Pine Barrens: Ecosystems and Landscapes.* Academic Press, New York.

Franklin, S.B., Gibson, D.J., Roberston, P.A., Pohlman, J.T. & Fralish, J.S. (1995) Parallel analysis: a method for determining significant principal components. *Journal of Vegetation Science*, **6**, 99–106.

Garten, C.T. Jr, Huston, M.A. & Thoms, C.A. (1994) Topographic variation of soil nitrogen dynamics at Walker Branch watershed, Tennessee. *Forest Science*, **40**, 497–512.

Goovaerts, P. & Chiang, C.N. (1993) Temporal persistence of spatial patterns for mineralizable nitrogen and selected soil properties. *Soil Science Society of America Journal*, **57**, 372–381.

Grigal, D.F. & Ohmann, L.H. (1989) Spatial patterns in elemental concentrations of the forest floor across the North Central United States. *Journal of Environmental Quality*, **18**, 368–373.

Grigal, D.F., McRoberts, R.E. & Ohmann, L.H. (1991) Spatial variation in chemical properties of forest floor and surface mineral soil in the North Central United States. *Soil Science*, **151**, 282–290.

Gupta, P.L. & Rorison, I.H. (1975) Seasonal differences in the availability of nutrients down a podzolic profile. *Journal of Ecology*, **63**, 521–534.

Harshberger, J.W. (1916) *The Vegetation of the New Jersey Pine-Barrens.* Christopher Sower Co., Philadelphia, PA.

Hart, S.C. & Firestone, M.K. (1991) Forest floor–mineral soil interactions in the internal nitrogen cycle of an old-growth forest. *Biogeochemistry*, **12**, 103–127.

Hendrickson, O.Q. & Robinson, J.B. (1984) Effects of roots and litter on mineralization processes in forest soil. *Plant and Soil*, **80**, 391–405.

Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (1987) *Data analysis in Community and Landscape Ecology.* Centre for Agricultural Publishing and Documentation. Wageningen, the Netherlands.

Kaye, J.P. & Hart, S. (1997) Competition for nitrogen between plants and soil microorganisms. *Trends in Ecology and Evolution*, **12**, 139–142.

Kent, M. & Coker, P. (1992) *Vegetation Description and Analysis. A Practical Approach.* CRC Press, Boca Raton, FL.

Klinka, K., Wang, Q. & Carter, R.E. (1990) Relationships among humus forms, forest floor nutrient properties, and understorey vegetation. *Forest Science*, **36**, 564–581.

de Kroon, J. & der Laan, P. (1983) A generalisation of Friedman's rank statistic. *Statistica Neerlandica*, **37**, 1–14.

Laycock, W.A. (1967) *Distribution of Roots and Rhizomes in Different Soil Types in the Pine Barrens of New Jersey.* US Geological Survey, Professional Paper No. 563-C.

Levene, H. (1960) Robust tests for equality of variances. *Contributions to Probability and Statistics* (eds I. Olkin, S. G. Ghurye, W. Hoeffding, W. G. Madow & H. B. Mann), pp. 278–292. Stanford University Press, Stanford, CA.

Marascuilo, L.A. & McSweeney, M. (1977) *Nonparametric and Distribution-Free Methods for the Social Sciences.* Brooks/Cole, Monterey, California.

Matlack, G.R., Gibson, D.J. & Good, R.E. (1993) Clonal propagation, local disturbance, and the structure of vegetation: ericaceous shrubs in the Pine Barrens of New Jersey. *Biological Conservation*, **63**, 1–8.

Mladenoff, D.J. (1987) Dynamics of nitrogen mineralization

and nitrification in hemlock and hardwood treefall gaps. *Ecology*, **68**, 1171–1180.

Parmelee, R.W., Ehrenfeld, J.G. & Tate, R.L. III (1993) Effects of pine roots on microorganisms, fauna, and nitrogen availability in two soil horizons of a coniferous forest spodosol. *Biology and Fertility of Soils*, **15**, 113–119.

Pastor, J., Aber, J.D., McClaugherty, C.A. & Melillo, J.M. (1984) Above-ground production and N and P cycling along a nitrogen-mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*, **65**, 256–268.

Phillips, J.D. (1985) Measuring complexity of environmental gradients. *Vegetatio*, **64**, 95–102.

Plymale, A.E., Boerner, R.E.J. & Logan, T.J. (1987) Relative nitrogen mineralization and nitrification in soils of two contrasting hardwood forests: effects of site microclimate and initial soil chemistry. *Forest Ecology and Management*, **21**, 21–36.

Poovarodom, S., Tate, R.L. III & Bloom, R.A. (1988) Nitrogen mineralization rates of the acidic, xeric soils of the New Jersey Pinelands: field rates. *Soil Science*, **145**, 257–263.

Quesnel, H.J. & Lavkulich, L.M. (1980) Nutrient variability of forest floors near Port Hardy, British Columbia. *Canadian Journal of Soil Science*, **60**, 565–573.

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.

Robertson, G.P., Klingensmith, K.M., Klug, M.J., Paul, E.A., Crum, J.R. & Ellis, B.G. (1997) Soil resources, microbial activity and primary production across an agricultural ecosystem. *Ecological Applications*, **7**, 158–170.

Rossi, R.E., Mulla, D.J., Journel, A.G. & Franz, E.H. (1992) Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs*, **62**, 277–314.

Schimel, D.S., Stillwell, M.A. & Woodmansee, R.G. (1985) Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology*, **66**, 276–282.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, **77**, 364–375.

Tedrow, J.C.F. (1979) Development of Pine Barrens soils. *Pine Barrens: Ecosystems and Landscapes* (ed. R. T. T. Forman), pp. 61–79. Academic Press, New York.

Thompson, K. (1987) The resource ratio hypothesis and the meaning of competition. *Functional Ecology*, **1**, 297–303.

Tilman, D. (1990a) Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. *Perspectives on Plant Competition* (eds J. Grace & D. Tilman), pp. 117–141. Academic Press, New York.

Tilman, D. (1990b) Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*, **58**, 3–15.

Turner, R.S. (1983) *Biogeochemistry of trace elements in the McDonald's Branch watershed, New Jersey Pine Barrens.* PhD thesis. University of Pennsylvania, Philadelphia, PA.

van den Putten, W.H. (1997) Plant-soil feedback as a selective force. *Trends in Ecology and Evolution*, **12**, 169–170.

Vitousek, P.M. & Denslow, J.S. (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *Journal of Ecology*, **74**, 1167–1178.

Wedin, D. & Tilman, D. (1990) Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia*, **84**, 433–441.

Wedin, D. & Tilman, D. (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs*, **63**, 199–229.

Zak, D.R. & Grigal, D.F. (1991) Nitrogen mineralization, nitrification and denitrification in upland and wetland ecosystems. *Oecologia*, **88**, 189–196.

Zak, D.R. & Pregitzer, K.S. (1990) Spatial and temporal variablity of nitrogen cycling in northern Lower Michigan. *Forest Science*, **36**, 367–380.

Zak, D.R., Hairston, A. & Grigal, D.F. (1991) Topographic influences on nitrogen cycling within an upland pin oak ecosystem. *Forest Science*, **37**, 45–53.

Zak, D.R., Pregitzer, K.S. & Host, G.E. (1986) Landscape variation in nitrogen mineralization and nitrification. *Canadian Journal of Forest Research*, **16**, 1258–1263.