

Landscape interactions among nitrogen mineralization, species composition, and long-term fire frequency

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Abstract. Path analysis was used to determine the importance of long-term disturbance regime and the relative importances of correlations among vegetation patterns, disturbance history, and nitrogen (N) mineralization in old-growth forests of northwestern Minnesota. Leaf biomass (estimated by allometric equations), fire history (from fire scars on *Pinus resinosa* trees), and N mineralization rates (estimated from incubations *in situ*) were determined from sample plots dominated by

- *Betula papyrifera*, *Populus tremuloides*, and *P. grandidentata*,
- a mixture of *Acer saccharum* and *Tilia americana*, or
- *Quercus borealis* and *Ostrya virginiana*.

Results showed that topographic and soil-moisture controls on N mineralization, vegetation patterns, and disturbance are substantially stronger than is suggested by direct correlation. Indirect interactions among ecosystem variables played an important role. These interactions probably include the tendency for species that cycle large amounts of N to colonize more mesic sites that burned rarely in the past. Soil moisture was correlated both directly with N mineralization and indirectly, through its effects on vegetation pattern, and thus, litter quality. Although disturbance regime also depended on topography, the strengths of relationships between disturbance regime and other variables were relatively weak. These dependencies suggested that long-term fire regime is probably more a consequence than a cause for vegetation and fertility patterns. Topography, through its effects on soil moisture and microclimate, is an overriding influence on ecosystem properties, which in turn influence fire regime.

Introduction

Broad landscape-scale correlations among ecosystem characteristics have long been widely recognized by ecologists and foresters. Such covarying patterns of soil fertility, vegetation (Wilde 1946; Pastor et al. 1984; David et al. 1988), topography (Jenny 1980; Spurr & Barnes 1980), and disturbance (Romme 1982; Johnson 1979) suggest multiple links among biotic and physical processes (Van Cleve et al. 1983; Pastor & Post 1986; Zak et al. 1986). The relative importances of these correlations are less well understood, because the time scales describing the dynamics of each variable can be vastly different, and because variables are interrelated by way of many indirect interactions. For example, vegetation pattern may reflect soil fertility and/or disturbance patterns of past times that are unknown to the investigator (Gleason 1939). The effect of topography on soil fertility may depend on water balance, which changes with varying climate

(Clark 1990b). Disturbance influences nitrogen (N) availability in the short term through its immediate impact on organic-matter pools. Fire (Debano & Conrad 1978), treefall (Mladenoff 1987; Vitousek & Denslow 1986), and forest practice (Bormann & Likens 1979; Vitousek & Matson 1985), for example, produce patchy landscapes, and they have important immediate consequences for cycling of N as a consequence of volatilization, transfers of organic matter from aboveground biomass to the forest floor, reduced uptake by plants, altered rates of solution transport through the soil profile, and elevated mineralization with changed forest-floor temperatures and soil moisture.

Disturbance might also produce long-term changes in N cycling, and therefore availability, as an indirect consequence of the ways in which different species that colonize disturbed areas cycle N (Vitousek 1982; Tilman 1982; Nadelhoffer et al. 1985; Riggan et al. 1988). Over longer periods of time the species composition that results from disturbance might impact nutrient supply by influencing total carbon and N pools, element ratios, and pH (Zinke 1962; Wagle & Kitchen 1972; Christensen & Muller 1975; Christensen 1977; Raison 1979; Boerner 1982). For example, fire frequency may determine whether hardwoods vs. conifers dominate a site (Heinselman 1973; Christensen & Peet 1984). Substantially lower concentrations of N, P, and S (Vitousek et al. 1988), potentially higher immobilization of N (Vitousek & Matson 1985), and tighter cycling of N by gymnosperms (Melillo & Cosz 1983) suggests that chronic fire could also influence nutrient supply by maintaining the dominance of conifers. If so, we expect N cycling to depend on the long-term disturbance regime in addition to inherent soil properties that vary together with topography.

Such complex interactions make it difficult to determine the extent to which disturbance, fertility, and species composition influence one another. A weak correlation between two variables may belie a more important relationship that is masked by indirect interactions. Fire might have the direct effect of increasing N availability, while simultaneously promoting species conservative in their use of N and producing recalcitrant litter (e.g. pines). If so, the tendency of direct and indirect effects to compensate one another might result in a weak observed dependency apparently less important than actually exists (Wright 1921; Sokal & Rohlf 1981). The many and complex interactions among factors influencing vegetation pattern, disturbance regimes, and nutrient cycling must be understood and their relative importances quantified if we are to understand the composite effect of one variable on another. Because the ranges of spatial and temporal scales are broad, and because many interactions are indirect, an experimental approach to this problem is impractical in forests.

Here I analyze and compare direct and indirect interactions among soil fertility, stand type, and long-term disturbance at a landscape scale in old-growth forests of northwestern Minnesota. I establish the landscape patterns and topographic dependencies of N mineralization, forest composition, and fire history, and I use an analytical tool, path analysis, to assess the relative importances of these variables for explaining fertility patterns and disturbance history.

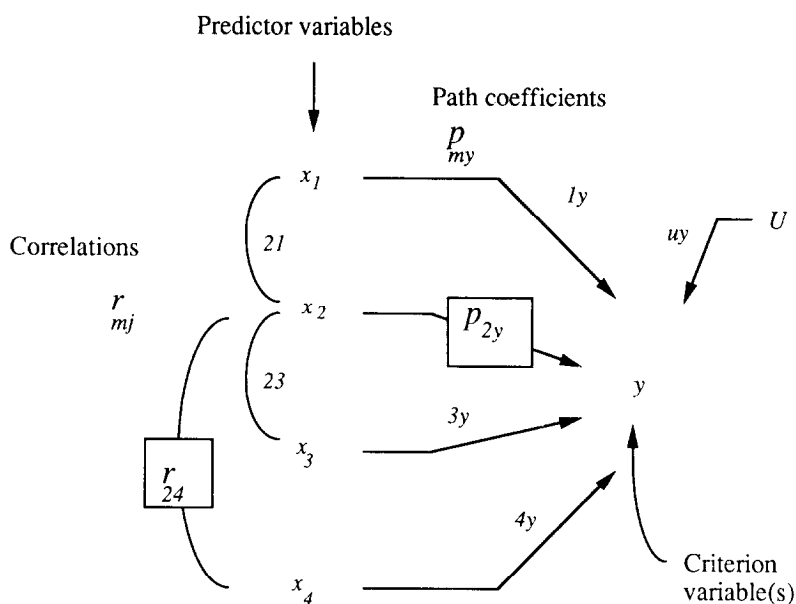


Fig. 1. Path diagram showing the correlations and path coefficients used to establish the direct and indirect contributions of x_2 on y . The direct correlation, and that which would be measured by a simple correlation analysis, is p_{2y} . But x_2 is correlated with six other predictor variables x_j that also effect y . The composite effect of x_2 on y then is the sum of the direct effect p_{2y} and all the products $r_{2m}p_{my}$ by which x_2 and y are connected.

Path analysis was developed by Sewall Wright (1921; Provine 1971) to establish the components of correlations where causes are interdependent and many indirect interactions exist. It has been widely applied in some biological disciplines (Sokal & Rohlf 1981), but not to ecosystem questions, where the problems of complex interactions and correlated causes are widespread. Here I use path analysis

- to describe the underlying structure of the system that effects N availability at a landscape scale,
- to compare competing structural models to explain N availability, and
- to assess the composite effects of predictor variables on soil fertility.

These results are then used to address the broader question of whether fertility and vegetation patterns are better viewed as a cause vs. a consequence of long-term disturbance history.

Path analysis

Path analysis is based on linear correlation analysis. The analysis is represented graphically by a path diagram (Fig. 1) that illustrates the system structure, including direct and indirect interactions among predictor variables x_m and

criterion variables y_i . The analysis assumes that y_i are completely determined, an assumption that is satisfied by including the unknown contribution U , a composite of effects from factors not included in the model.

The effect of a predictor variable x_i on criterion variable y_i includes the direct effect of x_i on y_i and the contribution of x_i to all other $x_{j \neq m}$ that effect y_i . The direct effect of x_i on y_i is given by the standard partial regression coefficient (standardized to permit comparison across scales), which is termed the path coefficient p_{iy} . The composite correlation between two variables is the sum of the products of path coefficients and correlations along all paths connecting them (Wright 1921). Thus, the contribution of x_i to y_i , where x_i interacts with k other x_j that also effect y_i , is given by

$$\begin{aligned} r_{iy_i} &= p_{iy_i} + r_{12}p_{2y_i} + \cdots + r_{ik}p_{ky_i} \\ &= p_{iy_i} + \sum_{j=2}^k r_{ij}p_{jy_i}. \end{aligned} \quad (1)$$

The total determination of y by k predictor variables is given as the sum of these k direct and indirect contributions

$$r_{ky} = \sum_{m=1}^k \left[p_{my} + \sum_{j \neq m}^k r_{jm}p_{jy} \right]. \quad (2)$$

The composite unknown contribution U to variance in y_i is given by the coefficient of nondetermination

$$r_{Uy_i}^2 = 1 - r_{ky_i}^2. \quad (3)$$

This coefficient of nondetermination is used to compare competing structural models, because the model structure having the lowest coefficient of nondetermination explains the most variance in y_i and thus is the best candidate for the ways in which variables are linked in the real world (Sokal & Rohlf 1981). Because known and unknown contributions can be positive or negative, it is possible to obtain $|r_{ky_i}| > 1$. This eventually can occur when r_{ky_i} and r_{Uy_i} are opposite in sign. For the analysis of structural models, probabilities are generally ignored (Sokal & Rohlf 1981). I report them here for purposes of assessing confidence of direct correlations. Sokal & Rohlf (1981) provide several clear examples of how the models are constructed and analyzed.

Study area

My study area includes one km² of forested landscape in northwestern Minnesota (Fig. 2). Soils are entisols and inceptisols in sandy moraine. Soil surveys do not exist for the study area. Webb (1986) analyzed soil texture across a

ridgetop that marks one of the abrupt transitions between stand types in the study area and found only minor differences in percent sand, silt, and clay on east vs. west aspects. Climate is continental, with mean January and July temperatures of -14.2 and 21.7°C , respectively. Total annual precipitation and potential evapotranspiration are 600–650 mm, with most precipitation falling during the growing season (Clark 1989).

Vegetation is patchy, with scattered large *Pinus resinosa* and *P. strobus* trees 200–400 yr old that emerge above a largely hardwood canopy or dense thickets of *Corylus cornuta* and *C. americana*. The hardwood canopy consists of

- *Betula papyrifera*, *Populus tremuloides*, and *P. grandidentata*,
- a mixture of *Acer saccharum* and *Tilia americana*, or
- *Quercus borealis* and *Ostrya virginiana*.

Less abundant hardwoods include *Quercus macrocarpa* and *Acer rubrum*. Several *Abies balsamea* and *Picea mariana* stands are also present. Areas not supporting a *Corylus* understory may include *Acer spicatum*, *A. saccharum*, or *Ostrya* in the shrub layer. Fire-history data showed that past burns were patchy, and fires were most frequent on southwest aspects (Clark 1990a, b). Botanical nomenclature follows Gleason (1952).

Methods

This study is part of a larger investigation of long-term dynamics of an old-growth forest. Here I focus on landscape patterns in leaf-biomass, N mineralization, fire history, soil moisture, forest-floor organic matter, and topographic variables on sample plots within each of several stand types as a basis for the analysis of direct and indirect correlations by path analysis. Because I am interested in chronic effects of the disturbance regime, rather than in individual disturbances, I determined the long-term history of fire from fire scars on *Pinus resinosa* trees and from stratigraphic charcoal analysis of annually laminated sediments of three lakes (Clark, 1990a). These methods established burn patterns since A.D. 1700.

Sample plots

Twenty 400 m² plots were selected to represent the range of stand types in the study area (Fig. 2). Slope, aspect, and position-on-slope were determined for each study plot from digitized relief maps. DBH and height estimates were obtained for all trees > 1 m tall on these plots. Forty soil cores 10 cm deep were obtained from each plot for soil-moisture, organic-matter, and N-mineralization (see below) estimates. Cores were sealed in plastic and placed in a cooler in the field. Samples were transferred to a refrigerator at 3°C within 3 h. Moisture content was determined gravimetrically, and it is expressed as percent of oven-dry weight. Organic matter was determined by loss-on-ignition at 500°C . All aboveground standing crop < 2 m tall was harvested in the last week

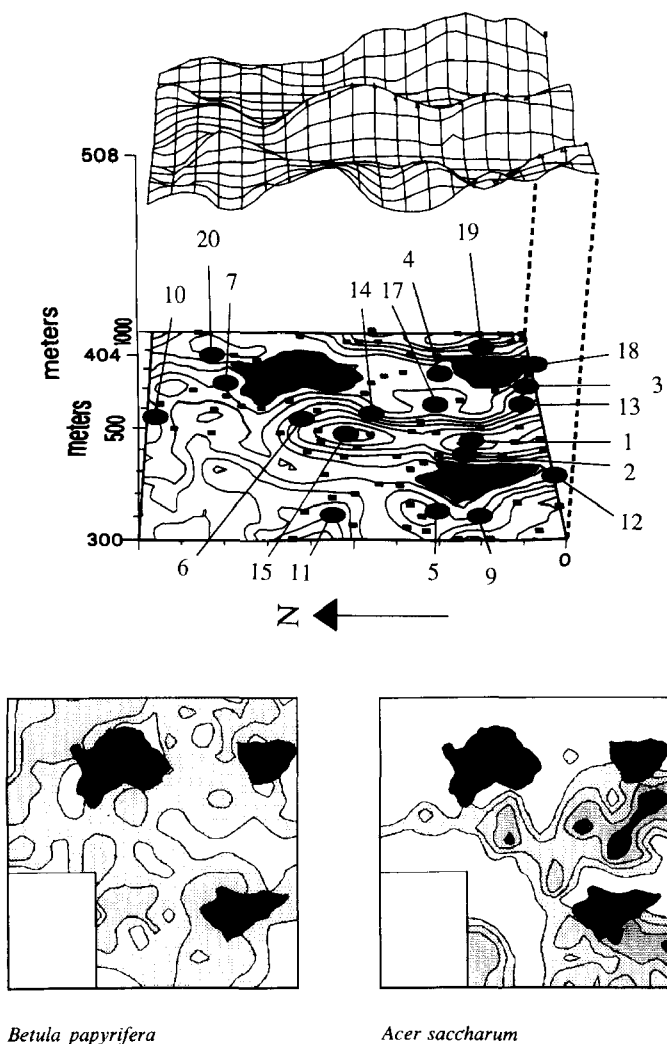


Fig. 2. Study area showing locations of the 18 plots analyzed here (elliptical symbols). Contours are 5 m. Three lakes are shown (shaded black), as are locations of variable-radius plots (rectangular symbols) used for contouring of basal-areas of *Acer saccharum* and *Betula papyrifera* (below). Basal-area maps illustrate the strong topographic effect on composition, with *Acer* on northeast aspects (southwest of lakes) and *Betula* on southwest aspects (northeast of lakes). Contours are $0.5 \times \ln(\text{basal area} + 1)$ in $\text{m}^2 \text{m}^{-2}$ for *Acer* and $1 \times \ln(\text{basal area} + 1)$ for *Betula*.

of July from each of four randomly located 1 m^2 subplots within each plot. These samples were returned to the lab, sorted by species, counted, dried to constant mass at 70°C , and weighed.

Leaf biomass of each tree species and of shrubs were used as indices of type and amount of litter on each plot. Overstory standing crop and leaf biomass

were predicted from allometric equations that relate total biomass or leaf biomass Y to diameter d , $Y = Ad^B$ (Whittaker & Woodwell 1968; Whittaker & Marks 1975), where A and B are coefficients of Ohmann & Grigal (1985a, 1985b). Leaf biomass estimates were then summed within categories reflecting different litter qualities: pine, hardwood, and spruce/fir.

Nitrogen mineralization

I used incubations *in situ* to estimate net N mineralization over a growing season (Eno 1960; Pastor et al. 1984). The method incorporates soil-moisture conditions at the time when incubations are initiated, and temperatures over the course of the incubations (Ellenberg 1977; Pastor et al. 1984; Vitousek & Matson 1985). Ten PVC pipes 3 cm in diameter were inserted to a depth of 10 cm below the surface litter layer at random locations within each of the 20 stands at each of five dates from 10 May to 9 September, 1987. Five samples were returned immediately to the lab to serve as estimates of initial nitrate (NO_3^-) and ammonium (NH_4^+) pools. A paired tube was fitted with a plastic lid that was not air-tight and left until the next sample date as an estimate of net N mineralization (calculated as initial values minus final values of NO_3^- and NH_4^+ (see below)) and nitrification (estimated from net NO_3^- production over the same interval). The forest floor was included intact in incubations.

Fifty g of each sample was shaken 30 min in 2 M KCl and extracted overnight at 5°C. Samples were then filtered, and extractable NH_4^+ and NO_3^- were determined with a Technicon Autoanalyzer (Technicon 1976). Net N mineralization and NO_3^- production are expressed as $\mu\text{g N g}^{-1}$ oven-dry soil. In all cases the bulk densities of these samples that contained the litter layer were near unity, and thus $\mu\text{g g}^{-1}$ values are similar to values for kg ha^{-1} .

Because mineralization depends on the water and heat balances, I used water-balance models of Clark (1989) to assess the extent to which the sample year might differ from 'typical' years. Methods are those of Thorntwaite & Mather (1957; Willmott et al. 1985). Temperature and precipitation data were obtained from the University of Minnesota Forestry and Biological Station located 3 km from the study area.

Data analysis

The relationships among variables were examined by principal components analysis (PCA), by multiple regression with topographic variables, and by path analysis. The variables included in analyses were forest-floor organic matter (t ha^{-1}), soil moisture (g g^{-1}), net N mineralization ($\mu\text{g g}^{-1}$), leaf biomass of pine, hardwood, and spruce/fir trees (t ha^{-1}), total biomass of shrubs (t ha^{-1}), and mean elapsed time between fires (yr). PCA was used because quadratic correlations computed for all pairs of variables included here did not reveal significant dependencies among variables of degree > 1 . Statistical analyses were completed with SAS procedures (SAS 1985).

Topographic effects

I used a modified version of the topographic model presented by Clark (1990a) to test for slope, aspect, and position-on-slope effects,

$$y = f(\beta, \mathbf{u}), \quad (4)$$

where \mathbf{u} is a vector of covariates

$$\mathbf{u} = \begin{bmatrix} \cos \theta \sin \phi \\ \sin \theta \sin \phi \\ \cos \phi \end{bmatrix}$$

having slope ϕ and aspect θ , and β is a vector of regression parameters. This model is here termed the ' u_3 model'. An extended version that includes a covariate u_4 , representing proportionate distance from the base of the slope, is termed the ' u_4 model'. The u_3 variables are discussed in Clark (1990a).

Structural models

Four different structural models are explored here by path analysis. Model I takes N mineralization to represent a single criterion variable that is explained by the direct action of seven predictor variables and all of their indirect effects (Fig. 3a). Model II differs from Model I in treating fire interval as a second criterion variable, rather than as a predictor of mineralization rate (Fig. 3b). Model II then views both N mineralization rate and fire interval as results of soil moisture and litter types. Model III contains a further modification, suggesting that soil moisture is best viewed as both a cause for vegetation pattern (and thus, litter types) that, in turn, effects both mineralization and fire interval, while having additional direct effects on N mineralization and fire interval (Fig. 3c). Model IV represents a combination of topography and measured variables (Fig. 3d). This model implies that topography exerts an overriding control on many of the measured variables, but that correlations among variables might be improved by considering not only the direct topographic correlations, but also the indirect correlations among variables. These results are compared with the multiple regression model (4).

Correlations were computed among all measured variables, and path coefficients for Model IV were taken from standard partial regression coefficients determined by multiple regression.

Results

Of the 20 original plots, two were abandoned. Plot 8 was disturbed when a trail was widened, and incubation tubes on plot 16 were destroyed by animals. All analyses therefore include data from 18 plots.

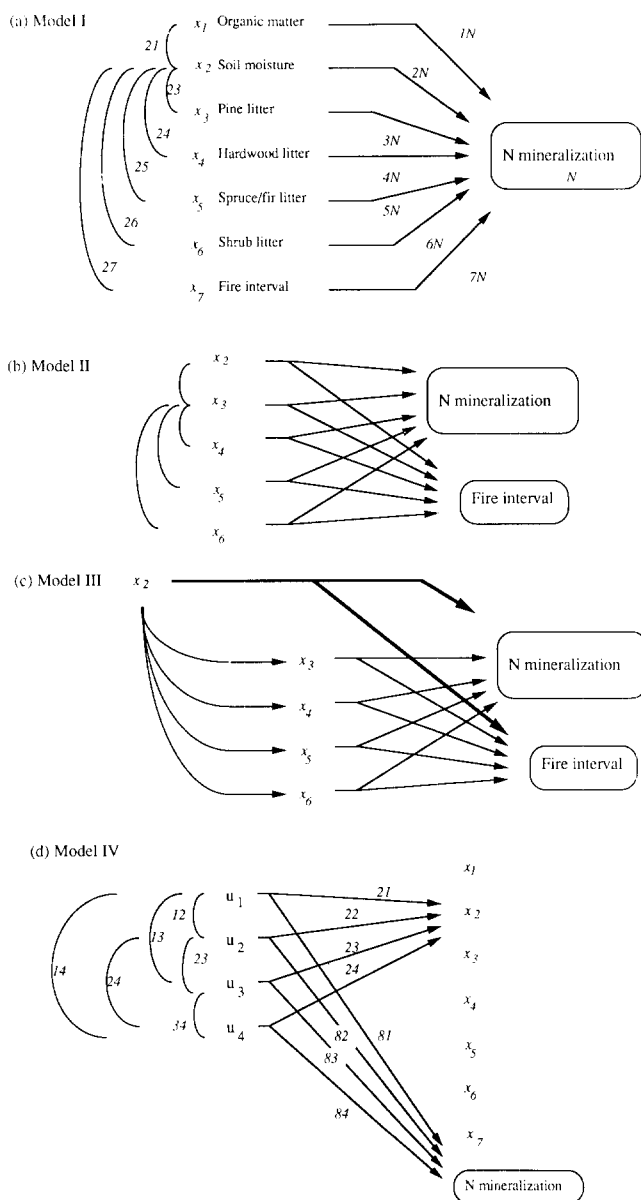


Fig. 3. Path diagrams for the four models discussed in the text. Predictor variables x_m are given in (a), and u_j are from Eq. (4).

The water balance during the sampling season suggests a rather dry growing season, with larger than average deficits in effective precipitation (precipitation minus potential evapotranspiration) and soil storage during July and August and an unusually wet autumn (Fig. 4).

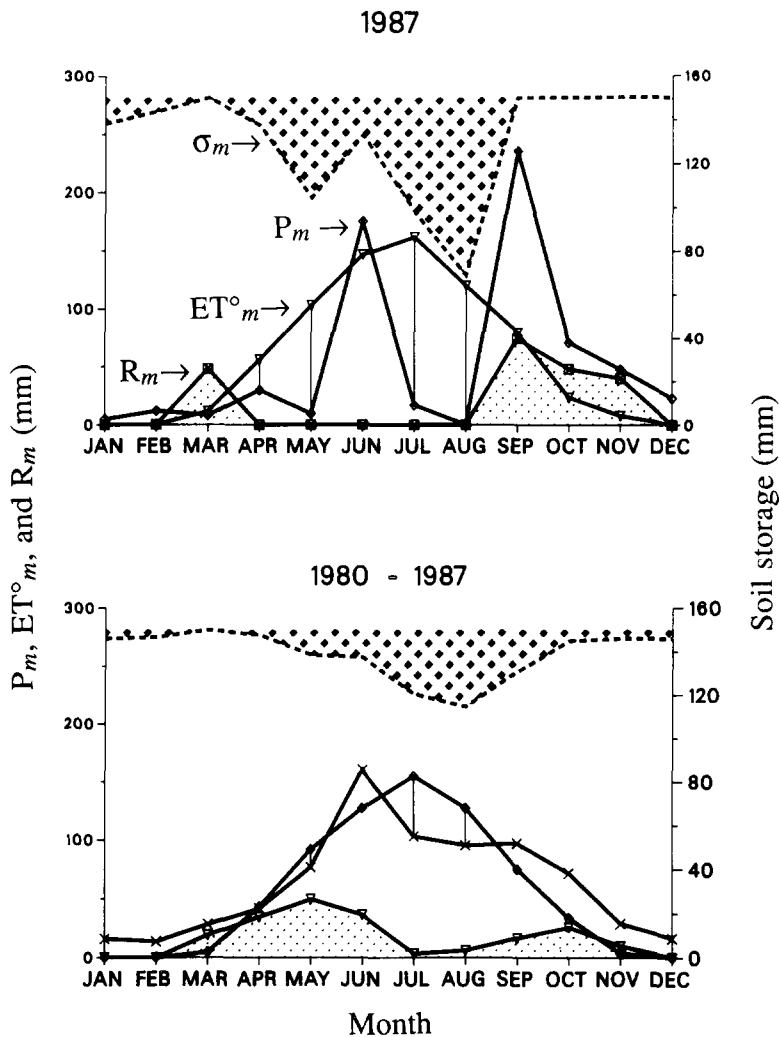


Fig. 4. Water balance for sampling year (1987) compared with average for the 1980's calculated by the model of Clark (1989) for Itasca State Park. P_m = total monthly precipitation, ET_m^0 = total monthly potential evapotranspiration, σ_m = soil storage, R_m = total runoff.

Direct relationships among variables

The direct relationships among variables at a landscape scale is demonstrated by linear correlations (Table 1), topographic dependencies (Table 2, Fig. 5), and PCA (Fig. 6). There were no significant topographic patterns in forest-floor organic matter or soil-moisture pool sizes (Fig. 5), although soil moisture was somewhat higher on northeast aspects. Organic matter had the lowest coefficient of variation (CV) of all measured variables (16%).

Table 1. Correlations of topographic and ecosystem variables. Pearson correlation coefficients (r) (upper value for each entry) and probability of a value $> |r|$ (lower value). Probabilities are presented only for comparisons having $P < 0.10$. Those values < 0.05 are indicated by * and those < 0.01 by **.

	Organic matter	Soil moisture	Leaf biomass				Fire interval
			Pine	Hardwood	Spruce/fir	Shrub	
x_1 Organic matter	0.618						
x_2 Soil moisture	0.182	-0.368					
x_3 Leaf biomass: Pine	0.088	0.488	-0.407				
x_4 Leaf biomass: Hardwood		0.040*	0.094				
x_5 Leaf biomass: Spruce/fir	-0.400	-0.145	0.060	-0.353			
	0.10						
x_6 Shrub biomass:	0.383	-0.025	0.467	-0.396	-0.283		
x_7 Fire Interval	-0.499	-0.053	-0.204	0.488	-0.159	-0.335	
	0.035*			0.040*			
N	0.111	0.525	-0.279	0.723	-0.174	-0.281	0.380
Mineralization		0.025*		0.0007**			

Table 2. Fitted topographic models u_3 (left) and u_4 (right). Covariates u_1 and u_2 contain slope and aspect, u_3 contains slope alone, and u_4 contains position-on-slope (see text). Probabilities (P) for the full models and r^2 estimates are given. Probabilities for full models < 0.1 are indicated by NS.

Variable	Without position-on-slope (u_3 model) r^2 P	With position-on-slope (u_4 model) r^2 P
x_1 Organic matter	NS	NS
x_2 Soil moisture	NS	NS
x_3 Leaf biomass:	NS	NS
Pine		
x_4 Leaf biomass:	0.38	0.63
Hardwood	0.07	0.0075**
x_5 Leaf biomass:	0.88	0.93
Spruce/fir	$< 0.0001^{**}$	$< 0.0001^{**}$
x_6 Leaf biomass:	NS	NS
Shrub		
x_7 Fire Interval	NS	0.44
		0.091
N	NS	0.79
Mineralization		0.0003**

Although pine leaf biomass did not show a clear topographic trend, leaf biomass of hardwood species and spruce/fir was greatest on north and northeast aspects (Fig. 5). Position-on-slope was particularly important for hardwoods (Table 2), with biomass increasing toward slope bases. Southwest aspects supported large shrub biomass, primarily *Corylus*. A second mode on northeast aspects (plots 9 and 6 on Fig. 5) results from *Acer spicatum*, *A. saccharum*, and *Ostrya virginiana* in the understory.

North and east aspects and slope bases supported the highest mineralization rates (Table 2, Fig. 5). Despite this general trend of higher mineralization rates on north and northeast aspect plots, those that were either very steep (plots 3, 6, 10, 18) or near ridgetops (plots 1, 15) had low mineralization rates. Net N mineralization was positively correlated with hardwood leaf biomass (Table 1). Correlations of N mineralization with pine, shrub, and spruce/fir biomass were all weak and negative (Table 1). Although spruce/fir biomass did not yield a significant correlation with N mineralization rate (Table 1), the northeast aspects supporting spruce/fir (plots 3, 10, 18) had unusually low mineralization rates relative to other northeast aspects that supported more hardwoods (Fig. 5). NO_3^- production (Fig. 5) was positively correlated with net mineralization (linear: $r = 0.85$; quadratic: $r = 0.96$).

The average interval between fires over all plots was 33 ± 13 yr, with a range of 20 (plot 2) to 60 (plot 3) years. Forty-four percent of the variance in fire frequency was explained with the u_4 model, although this model was not significant at the 0.05 level ($P = 0.091$, Table 2). Fires occurred more frequently on southwest aspects, where *Corylus* was most abundant, hardwood trees

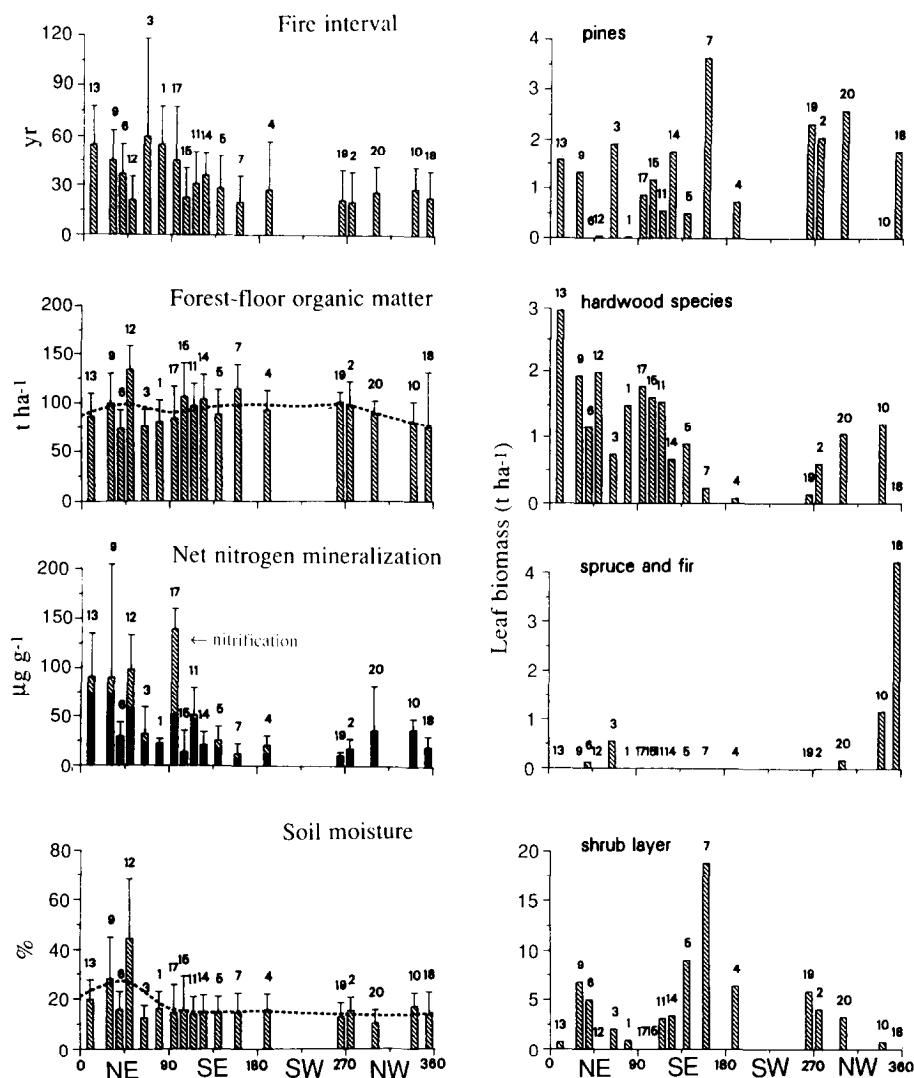


Fig. 5. Relationships of ecosystem variables to aspect. N mineralization shows NO_3^- (hatched) and NH_4^+ (solid). Error bars are one standard deviation. Dashed lines for soil moisture and organic matter are smoothed curves.

infrequent, and mineralization rates low (Fig. 5). Forest-floor organic matter was correlated with fire interval ($y = 112.8 - 0.586x$, $r = -0.50$, $P = 0.035$), but mineralization was not ($r = 0.38$, $P = 0.12$). However, plot 12 was unusual in having a high fire frequency, despite being a wet site and having a high mineralization rate (Fig. 5), probably as a result of its close proximity to drier ground (20 m from the plot edge) that would be expected to burn more frequently. Removing plot 12 from the analysis resulted in a dependency of

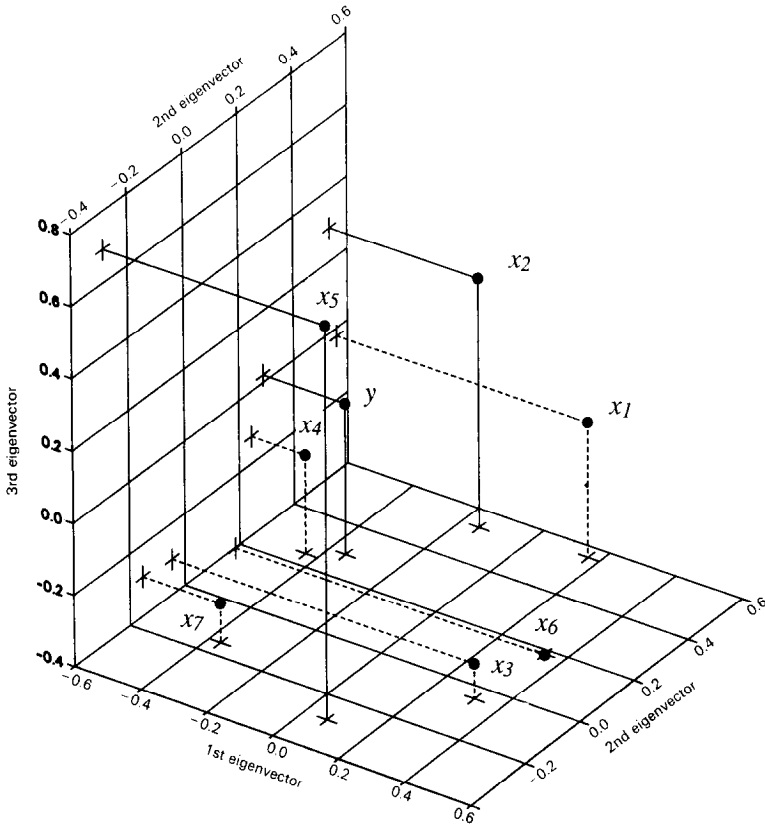


Fig. 6. Principal components analysis of ecosystem variables. Numbers are (x_1) forest-floor organic matter, (x_2) soil moisture, (x_3) leaf biomass of pines, (x_4) leaf biomass of hardwoods, (x_5) leaf biomass of spruce/fir, (x_6) leaf biomass of shrubs, and (x_7) mean interval between fires, and (y) net N mineralization. Units for these variables are given in Fig. 5.

mineralization rate on fire frequency ($y = -12.3 + 1.57x, r = 0.57, P = 0.013$).

Results of PCA reflect these correlations (Fig. 6). The first eigenvector accounted for 37% of the variance in the data set and displayed high positive loadings for pine and shrub-leaf biomass. Highly negative loadings were observed for hardwood-leaf biomass and net N mineralization. The second eigenvector explained 25% of the total variance, with high loadings for forest-floor organic matter and soil moisture. Together the first two eigenvectors separated mesic, northeast aspects from southwest aspects. The third eigenvector explained 13% of the variance and separated spruce/fir stands on north aspects from pines and shrubs on southwest aspects.

Thus, four of eight ecosystem-level variables were correlated with topographic variability (Table 2). The strongest dependencies were for spruce/fir leaf biomass ($r^2 = 0.93$), net N mineralization ($r^2 = 0.79$), hardwood leaf biomass

Table 3. Direct and composite correlations r_{my} of variables with N mineralization rate in each of the three models. Table entries in boxes are those contributing to the coefficient of nondetermination.

	Direct correlation	Model		
		I	II	III
x_1 Organic matter	0.11	0.15		
x_7 Soil moisture	0.52	0.80	0.75	1.0
x_3 Lead biomass: Pine	-0.28	-0.20	-0.14	-0.14
x_4 Lead biomass: Hardwood	0.73	0.66	0.47	0.47
x_5 Lead biomass: Spruce/fir	-0.17	0.049	0.15	0.15
x_6 Shrub biomass	-0.28	-0.23	-0.15	-0.15
x_7 Fire interval	0.38	-0.09	0.49	1.1
Coefficient of nondeterminations:				
$r^2_{U_{yi}}$		-0.72	-0.17	-0.094

($r^2 = 0.63$) and fire interval ($r^2 = 0.44$) (Table 2). Several plots deviated from these general trends. Plot 12 was mentioned above as a northeast aspect that was unusual in having burned often. Like other northeast aspects it was characterized by high mineralization rates, it had high soil moisture as a result of its location at a slope base, and it supported high hardwood leaf biomass. Thus, despite the high frequency of fire, plot 12 displayed the characteristics of most other plots having its topographic characteristics. Nonetheless, although shrub biomass was low on plot 12, the most important shrub species there was *Corylus*, a species common on southwest aspects, where fire was frequent. Plot 18 also deviated from the expected trend in having burned frequently despite its north aspect. Like plot 10, it supported mostly *Abies balsamea*; slopes were steep and mineralization low.

Underlying structure

The simplest Model I is substantially overdetermined ($r^2_{U_{yi}} = -0.72$), while Models II and III are more or less fully determined (i.e. $r^2_{U_{yi}}$'s are near zero) by the measured variables and all of their indirect interactions (Table 3). This overdetermination implies that the model leaves a large negative component of N mineralization unexplained. This overdetermination can occur either because an important predictor variable has been overlooked, or because the structure of the models do not reflect the linkages that exist in the real world. The signs of correlations with N mineralization are mostly consistent across models. Only spruce/fir leaf biomass changes sign from the direct negative to the composite positive effect of the path models, but these values are too low to interpret. All models predict a substantially stronger composite correlation between soil moisture and N than is given by direct correlation. Indeed, Model III, which had the lowest $r^2_{U_{yi}}$, indicates that soil moisture, both directly and as a consequence of its indirect effects on litter quality and disturbance regime, accounts for a large amount of the variance in

Table 4. Comparison of correlations determined by multiple regression on topographic variables alone vs. Model IV, which includes both topography and the indirect effects of all other measured variables.

	Topography plus indirect correlations (Model IV)	Topography alone (Multiple regression)
x_1 Organic matter	-0.015	0.47
x_2 Soil moisture	0.85	0.62
x_3 Leaf biomass: Pine	-0.58	-0.44
x_4 Leaf biomass: Hardwood	1.14	0.79
x_5 Leaf biomass: Spruce/fir	-0.31	-0.96
x_6 Shrub biomass	-0.39	-0.48
x_7 Fire interval	0.92	0.66
N Mineralization	1.15	0.89

mineralization rate. So much so that it is likely that most of the important variables are probably contained in the model, and the model structure is probably a reasonable caricature of the actual linkages. The correlation between fire interval and N was lower in Model I than was the direct correlation, while the same correlation was substantially greater in Models II and III.

With three exceptions, the topographic model that included indirect correlations displayed correlations stronger than were those obtained for topography alone (Table 4). The correlations that declined were those for organic matter, for which there was little variance to be explained ($CV = 16\%$), shrub biomass, which was bimodal as a result of different species being abundant on different aspects, and spruce/fir leaf biomass.

Discussion

In this paper I determined fire histories, vegetation patterns, and N mineralization rates from stands in an old-growth forest, and I analyzed their direct and indirect relationships using path analysis. Previous studies have demonstrated interactive effects of litter type and topography (Van Cleve et al. 1983) and parent material (Pastor et al. 1984) on fertility. Simulation models also suggest the importance of these higher-order interactions (Pastor & Post 1986). Here I consider these variables together with long-term disturbance data, and I use path analysis to accommodate these indirect interactions for purposes of analysis.

Landscape patterns of stand types and nitrogen supply

Although it has long been known that fertility varies with topography (Wilde 1946; Spurr & Barnes 1980) and that topographic effects on soil moisture (Sartz 1972; Petch 1988) are among the important controls on site fertility (Jenny 1980; Van Cleve et al. 1983), this analysis indicates that dependencies among fertility, litter type and quantity, soil moisture, and disturbance history at a landscape

scale (Table 3) are substantially stronger than is suggested by direct correlation (Table 1). Although the direct correlation between soil moisture and N mineralization was only 0.53, path analysis indicates that the soil-moisture effect is actually much greater. The many variables that influence N mineralization, including litter quality and quantity (represented here by leaf biomass estimates) also depend on soil moisture. When these indirect effects of soil moisture on vegetation patterns are included in a path analysis, the composite correlation increases. Working at a finer spatial scale, Robertson et al. (1988) observed a direct correlation between soil moisture and potential mineralization rate of $r = 0.33$. Their study represents another example of a direct correlation that may underestimate the importance of soil moisture on fertility.

Landscape patterns of N mineralization and species composition suggest direct and indirect influences of topography and soil-moisture on fertility patterns. Despite the fact that relief is rather subdued on this landscape, topographic control on vegetation pattern is reflected in hardwood leaf biomass (Fig. 5). The high-quality litter produced by *Acer saccharum* (Gosz et al. 1973; McClaugherty et al. 1985) on northeast aspects was probably responsible in part for high mineralization rates there (Fig. 5). This interpretation is supported by the fact that stands dominated by spruce/fir (plots 3, 10, 18), which have higher lignin:N, displayed low mineralization rates despite north aspects (Fig. 5). Position-on-slope was important on north and east aspects, for steep slopes and ridgetops having these aspects (plots 1, 3, 6, 10, 14, 15, 18) had low mineralization rates compared to sites having shallower slopes. On north aspects with spruce/fir, low temperatures may have combined with poor litter quality to produce low mineralization rates (e.g. Van Cleve et al. 1983). The litter from *Corylus*, *Betula papyrifera*, and pines, all of which occur on southwest aspects, contains a high lignin:N (Gosz et al. 1973; McClaugherty et al. 1985; Pastor & Post 1986). Water may also limit decomposition rates during much of the summer (Clarholm et al. 1981; Matson & Vitousek 1981; Vitousek & Matson 1985; White et al. 1988) on these southwest aspects. The strong correlation between NO_3^- production and net N mineralization is in accord with a number of other studies (Robertson & Vitousek 1981; Robertson 1982; Pastor et al. 1984; Mladenoff 1987; Zak et al. 1986) and suggests that nitrification is substrate-limited.

The topographic control over all of these variables results from its effects on microclimate and soils. Topographic variables can serve as a surrogate for local water balance, as frequency of soil saturation and runoff is highly correlated with distance from tops of slopes and slope angle (height/distance) (Petch 1988). Slope aspect also influences water balance; southwest aspects are generally drier in north temperate latitudes, because they receive more solar radiation late in the day when moisture levels are lower, and they are exposed to prevailing westerlies (Sartz 1972; Rosenberg et al. 1983). These topographic effects on microclimate can be intensified by soil textural properties, because fines collect at slope bases allowing for greater moisture-holding capacity. Studies of soil moisture in my region have demonstrated strong correlations between local

water balance and topographic variables (Stoeckler & Curtis 1960; Sartz 1972). Such effects might also be enhanced during dry years such as 1987 (Fig. 4).

The role of long-term fire regime

To what extent can the observed landscape patterns of N mineralization and stand type be explained by topography versus different disturbance regimes? The frequency of fire has varied markedly among stands (Clark 1990a), and these differences have had important effects on species composition (Clark, in review). In many ways my study area provides the other end of the disturbance spectrum from Pastor et al. (1984) in upper midwestern forests. Here the existing patterns in vegetation depend on disturbance frequency, with standing crop of hardwoods (particularly *Acer saccharum* and *Tilia americana*) being correlated with the average time between fires. *Corylus* thickets occur almost exclusively on sites that burned frequently in the past (Clark, in prep.). This pattern is also true, albeit less strong, for *Betula papyrifera* and *Pinus resinosa* (Clark, in prep., Fig. 3). Because these species cycle less N than do *Acer saccharum* and *Tilia americana*, which dominate sites that burned rarely, it may be that past fire regimes have had persistent effects on N-cycling regimes through their influences on species composition.

If so, then continued fire suppression might lead to invasion of southeast aspects by northern hardwood species, and mineralization rates might eventually increase. Litter quality might generally be higher with less frequent disturbance as a result of species replacement during succession. The extent to which this pattern might occur would also depend on the timing of bole and branch litter production with time since the last disturbance (Vitousek 1985; Pastor & Post 1986). Lower mineralization rates might also be expected if losses during fire from volatilization and/or leaching exceed atmospheric inputs over the interoccurrence interval. Frequent disturbance might then promote species more efficient in their use of N.

Comparisons of strengths of dependencies and correlations among variables, however, suggest that topography has a stronger direct control over N mineralization than it does on fire regime (Table 2). Path analysis suggests that both fertility and fire regime are primarily determined by soil moisture at this site. Topographic effects on N mineralization and hardwood and spruce/fir leaf biomass (Table 2), and the importance of litter type for N mineralization rate (Table 1, Fig. 5) caused the composite effect of topography on N mineralization to be greater than was the direct effect (Table 4). The relatively weak direct correlation between fire interval and N mineralization increases when the indirect correlations between them are considered in Model III. This determination is stronger than one would gather from direct comparisons, because of the many indirect effects through vegetation type tend to mask the strong soil-moisture influence.

The rather low correlations between fire interval and most other variables (Table 1), however, reflects the spatial and temporal stochasticity that makes fire

prediction so difficult and the stochastic nature of vegetation establishment patterns on past burns. Although fire depended on topography, that dependency was substantially weaker than were the topographic dependencies of hardwoods, spruce/fir, and N mineralization. It is unlikely that the measurement errors associated with fire-history data were greater than were those associated with other measurements. Fires dated by fire scars are precise to ± 1 yr, and all chronologies derive from within 20 m of the sample plots. In contrast, mineralization rates are variable over scales of meters (e.g. Robertson et al. 1988). An overriding effect of topography on stand type and mineralization rate is further suggested by plot 12, where a northeast aspect experiencing frequent fire still had N mineralization rates and biomass characteristics like other northeast stands (Fig. 5).

The ability to explain fire regime from a knowledge of soil moisture improves substantially, however, when the many indirect effects of other variables influenced by soil moisture (Fig. 3) and topography are considered (Table 4). The improved explanatory power provided by path analysis results from the strong topographic dependencies contained in vegetation data that are affected by and that influence fire regime (Fig. 1, Clark, in review). Many fires burned south and west aspects, stopping at ridgetops. There are today abrupt changes in understory and overstory composition across many of these ridgetops that result in strong gradients between *Pinus resinosa*/*Betula papyrifera* stands on southwest aspects vs. northern hardwoods stands on northeast aspects. These patterns hold throughout the study area, and they are reflected in the leaf-biomass data of Fig. 5.

Conclusions

Results of this study indicate that topographic and soil-moisture controls on soil fertility and disturbance regime are stronger than has been suggested by the direct correlations that are usually reported in previous studies. Although long-term differences in fire frequency certainly affect fertility and species composition, topography had stronger direct and composite effects on the distribution and amount of litter types (Table 2) than it did on fire regime. As a result, topographic effects on fertility appear to represent a stronger interaction than does the relationship between fire history and fertility. It therefore appears that fire regime is more a result than a cause of fertility patterns, as mediated through the indirect influence of soil moisture on species composition (Fig. 3c), and topography provides an overriding influence on all of these variables through its effects on microclimate and drainage patterns.

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