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Resource heterogeneity in oldfields

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Abstract. Spatial heterogeneity of photosynthetically active radiation (PAR), soil moisture and soil N mineralization in a range of oldfield communities was analyzed using semi-variograms for transect data. Percent transmittance of PAR was examined in eight communities, and soil moisture and N mineralization were examined in the two most common communities. In general, the sites with the highest resource availability had the smallest coefficients of variation. For light, 63 % of the transects showed significant non-zero spatial autocorrelation with sills at 1 - 70 cm distance intervals. Although the grass-dominated communities had the highest average PAR levels and the lowest coefficients of variation, they also were among those with the greatest percentage of transects that had non-zero spatial autocorrelation. For light, the average semivariogram range, or distance within which samples were autocorrelated, was 19 cm and different among communities at $p = 0.07$. For soil moisture, two of three shrub sites and one of three grass sites showed non-zero spatial autocorrelation with sills at 10 - 300 cm distance intervals. Average semivariance range was 249 cm for the shrub community and 170 cm for the grass community. For N-mineralization, none of the shrub and one of three grass sites showed non-zero spatial autocorrelation with a sill, with a semivariance range of 60 cm. Soil moisture and N-mineralization were higher in the shrub than in the grass communities. Overall, these results indicate that resource variability occurred within patches of uniform vegetation, and the range of resource spatial dependence was different among resources even within a single community type. Our results suggest that different seedlings invading these communities will experience very different patterns of microsite heterogeneity as a result of their specific resource requirements.

Keywords: Autocorrelation; Community; Light; Nitrogen mineralization; Semivariogram; Soil moisture; Spatial pattern.

Nomenclature: Gleason & Cronquist (1963).

Abbreviation: PAR = Photosynthetically active radiation.

Introduction

There is ample evidence that both resources and plants are often distributed in distinct microsites (e.g. Malik, Anderson & Myerscough 1983; Beatty 1984; Crozier & Boerner 1984; Sohlberg & Bliss 1984; Fowler 1986; Gibson 1986; Huenneke & Sharitz 1986; Selter, Pitts & Barbour 1986; Collins & Good 1987; Robertson et al. 1988). Such microsites are often associated with clearly identifiable physical or biological heterogeneity within a community. For example, small ridges and depressions are important for the establishment and distribution of some plant species (Zedler & Zedler 1969; Harcombe, White & Glitzenstein 1982; Pavone & Reader 1985; Dawson 1990). Likewise, desert shrubs often provide favorable sites for establishment of other species (Muller 1953; Muller & Muller 1956; Everett, Koniak & Budy 1986).

The early focus on relatively fine-scale (1 cm - 2 m) events influencing the fate of seeds and newly emerging seedlings (i.e. safe sites, Harper 1977) has been broadened to consider the effects of larger area resource patchiness on longer-term growth and survival of juveniles (Pickett & Bazzaz 1976; Parrish & Bazzaz 1982). However, most of these studies have been done in areas with clear discontinuities in either the physical substrate or the vegetation. Much less is known about the fine-scale pattern of microhabitat variability and resource heterogeneity within compositionally homogeneous patches of vegetation.

While the safe-site concept (Harper 1977) has been widely applied and is clearly useful, few studies have objectively identified the critical environmental parameters that make a microsite 'safe' for seedling establishment, or suitable for longer-term growth and survival. This is perhaps not a serious limitation where disturbances cause simultaneous improvement in a number of environmental parameters. However, a predominantly phenomenological approach has led to a lack of attention to physical patterns of fine-scale heterogeneity in critical environmental resources (Palmer 1990a; 1990b; Palmer & Dixon 1990). For example, while it is a fundamental assumption of most forest gap-phase studies that gaps represent sites of high resource availability within an otherwise unfavorable matrix, there is very little evidence that light, soil moisture and soil nutrients show congruent patterns of spatial and temporal variability beneath gaps (Collins & Pickett 1987; Vitousek & Denslow 1986; Canham 1988).

In this paper we characterize fine-scale heterogeneity of light, soil moisture and nitrogen mineralization within a number of compositionally and structurally distinct oldfield communities. Our objectives were to determine whether resources exhibited heterogeneity within spatial areas that could be exploited by tree seedlings invading oldfield communities, and whether the different resources showed congruent patterns of spatial heterogeneity. We also examined the relationship between the availability of specific resources and the heterogeneity of those resources.

Material and Methods

Study sites

Light transmittance was determined at 21 sites in the Hudson Valley of New York. Eight of the sites were located in oldfield vegetation along powerline corridors in Dutchess and Ulster Counties (41° 45' - 42° 00' N, 73° 35' - 74° 26' W), and 13 of the sites were located on ca. 50-yr old abandoned fields located within the Mary Flagler Cary Arboretum in Dutchess County (41° 50' N, 73° 45' W). Measurements of soil moisture and nitrogen mineralization were done at a subset of six of these sites. We examined light transmittance through eight distinct community types: two shrub-dominated communities (*Cornus*, *Kalmia*), two grass-dominated communities (*Schizachyrium*, *Schizachyrium*/moss), two communities dominated by herbaceous perennials (*Dennstaedtia*, *Lythrum*), and two communities representing transitions between shrub and grass dominance (mixed grass/*Cornus*, *Rubus*/*Schizachyrium*) (Table 1). Soil moisture and nitrogen mineralization were measured in the two most common communities: *Schizachyrium scoparium* meadows and *Cornus racemosa* shrub thickets. The areas sampled for each community type were uniform in both topography and vegetation structure.

Table 1. Oldfield community types, and the number of sites (S) and transects (T) used for PAR measurements.

Category	Dominant species / Community description	S	T
SHRUB	*Cornus racemosa* / Gray dogwood shrub thickets	5	40
	Kalmia latifolia / Mountain laurel shrub thickets	2	15
GRASS/SHRUB			
	Poaceae - *Cornus racemosa* / Grasses with scattered gray dogwood	2	16
	Rubus flagellaris - Schizachyrium scoparium / Creeping raspberry and little bluestem	1	8
GRASS			
	Schizachyrium scoparium / Little bluestem bunchgrass meadows	6	45
	Schizachyrium scoparium - Polytrichum sp. / Little bluestem meadows with a moss understory	2	16
PERENNIAL HERB			
	Lythrum salicaria / Purple loosestrife wetlands	1	7
	Dennstaedtia punctilobula / Hayscented fern on a rocky substrate	2	15

Percent transmittance of PAR

Percent transmittance data were collected using an 80 cm Sunfleck Ceptometer (Decagon, Inc.) under bright sky conditions (full sun PAR > 1100 $\mu E\, m^{-2}\, s^{-1}$ between 1100 and 1400 h EDT). The sunfleck ceptometer is a small datalogger connected to a wand, which has 80 light sensors spaced 1 cm apart from one another. Full sun measurements were taken by placing the ceptometer above or along side the vegetation and taking one integrated 80 cm reading. The ceptometer was then placed at 5 cm height within the vegetation and the PAR at each sensor was recorded so that a transect of 80 cm, with readings at 1 cm distance intervals, was obtained. Each PAR reading was subsequently divided by the full sun reading to obtain percent transmittance. Four transects from each of two randomly located 4-m^2 quadrats at each site were used for the analysis. The transects ran diagonally toward the center of the quadrats from each of the four corners. The number of sites used for each community are given in Table 1.

As a result of our decision to use instantaneous light readings under full-sun conditions, our analysis is largely focused on the spatial patterns of sunflecks, rather than longer-term integrated light levels. Instantaneous, full-sun readings generally show much higher spatial variability than integrated measurements.

Soil moisture and nitrogen availability

At each of six sites (three *Schizachyrium* sites and three *Cornus* sites) soil samples were collected to 15 cm depth at 10-cm intervals along a 4-m transect using a soil corer. The cross-sectional area of each sample was 17.3 cm^2. Samples were immediately processed after transport to the lab in a cooler over ice. Each soil sample was sifted through an 8-mm sieve to remove stones and clumps of roots and then was thoroughly mixed to obtain a homogeneous subsample. From the mixed soil, 20 g were used for immediate KCl extraction of NH_4^+ and NO_3^- (described below), 20 g were placed in polypropylene cups and covered with polyethylene plastic for incubation, and 50 g were placed in a soil tin for oven drying (1 week at 70 °C) to determine gravimetric moisture content. Soil samples were incubated for 58 d at 20 °C in the dark. Very little water was lost during the incubation. The cups were weighed after 35 d and deionized water was added (no more than 0.5 g) so that the samples were their original weight. No water was added to the soils initially.

Ammonium and nitrate concentrations were obtained by extracting the intital and post-incubation 20 g samples of soil with 200 ml of 2N KCl solution (Keeney & Nelson 1982). Samples were shaken several times by hand and then allowed to stand overnight (approximately 15 h). The KCl extract was then decanted into sample bottles and stored at 4 °C for analysis. The extracts were analysed within 7 d for NH_4^+ and NO_3^- using standard Technicon autoanalyser methods. Nitrogen mineralization is the net amount of NH_4^+-N plus NO_3^--N produced over the 58-d incubation period. These values represent mineralization under ambient field moisture conditions at the start of the incubation, but at constant temperatures. There may be additional variation in N mineralization under field conditions due to spatial variation in soil temperature.

Spatial statistics

We used semivariograms (Robertson 1987) to examine the size of spatial areas of resource heterogeneity. Semivariograms are plots of the spatial dissimilarity (measured by semivariance) between points separated by known distances, plotted against those distances. Normally, points in close proximity are more similar than points farther apart, so that semivariance among points increases with distance until a maximum semivariance, called the sill is reached. The distance at which the semivariance stops increasing is called the range, and the point where the semivariance begins (distance equals zero) is called the nugget. Samples separated by distances closer than the range are statistically dependent, while those separated by distances greater than the range are not, because at distances greater than the range the semivariance equals the sample variance, implying zero spatial correlation (Trangmar, Yost & Uehara 1985).

Using a program developed by Robertson (1987), we calculated and analysed semivariograms of the transects for percent transmittance of PAR, gravimetric soil moisture and nitrogen mineralization. Semivariances were calculated up to within 10 pairs of the maximum distance between all points, (i.e. 70 cm for light transects and 300 cm for soil moisture and nitrogen transects) in order to get an adequate number of paired samples representing large distance intervals. If the semivariograms exhibited several sills (periodicity or nested variation; Trangmar, Yost & Uehara 1985; Burrough 1987), only the pairs up to the first sill were used in the model-fitting analysis. This focuses interest on the smallest area of spatial autocorrelation. For transects that exhibited spatial autocorrelation, semivariogram models for range, nugget semivariance and sill semi-variance were fit using a non-linear least squares technique (Anon. 1987; Robertson 1987). These models included linear with a sill, spherical, exponential and Gaussian curves. We chose the best fitting of these four curves based on the following criteria: 1) convergence of the residuals with the partial derivatives of the model, 2) R^2 value greater than 0.40, and 3) best fit of the residuals about the curve, particularly at the sill and nugget ends of the curve. For % transmittance of PAR, estimated mean nugget semivariance, mean sill semivariance and mean range for each community type, using transects as replicates, were compared with a nonparametric analysis of variance (Anon. 1987). If a transect exhibited zero autocorrelation, the sample variance was used for sill and nugget semivariances and zero was used for the range. If a transect exhibited spatial autocorrelation with no sill it was considered to have a nonstationary mean (Trangmar, Yost & Uehara 1985) and was excluded from the analysis.

Results

Percent transmittance of PAR

Light levels at 5 cm height were highest in the grass-dominated communities (*Schizachyrium*, *Schizachyrium*/moss) and in the communities that represent transitions from grass dominance to shrub dominance: grass / *Cornus*, *Rubus* / *Schizachyrium* (Table 2). %-transmittance of PAR varied substantially along individual 80 cm transects in all eight community types - the lowest average coefficient of variation was 73 % (Table 2). Overall, community types with the highest average percent transmittance had the lowest average coefficient of variation among transects, even though these communities had the highest standard deviations and sill and nugget semivariances (Table 2).

Table 2. Characteristics of light transmittance through canopies of eight oldfield community types. '% autocorr.' is the % of transects from each community that showed non-zero autocorrelation with a sill. The community types are arranged from highest to lowest mean % T (% transmittance of PAR). Mean S.D. (standard deviation) and C.V. (coefficient of variation) were determined by using the S.D. or C.V. (%) for each transect as a sample and calculating the mean of these samples (n = the number of transects listed in Table 1). Sample sizes for the mean nugget semivariances (C_0), mean sill semivariances (C_A) and mean ranges (cm) (A) are in the last column and standard errors are in parentheses.

Comm. Types	Mean % T	Mean S.D.	Mean C.V. (%)	% autocorr.	Mean C_0	Mean C_A	Mean A	n
Schizachyrium / moss	37.3	19.93	72.9	75	279.4 (67.0)	583.6 (85.0)	26.1 (4.5)	14
Schizachyrium	34.9	21.91	84.4	69	298.8 (27.2)	657.2 (50.0)	24.1 (2.5)	34
grass / *Cornus*	19.8	17.04	92.6	50	182.6 (35.7)	501.4 (126.0)	25.1 (6.4)	11
Rubus / *Schizachyrium*	16.6	14.88	97.4	50	101.8 (29.5)	184.5 (64.3)	9.8 (3.4)	6
Kalmia	16.0	9.46	155.6	67	125.3 (42.2)	211.0 (74.3)	18.8 (3.9)	12
Dennstaedtia	6.6	9.29	128.6	80	75.2 (24.9)	167.2 (52.9)	19.3 (3.8)	13
Cornus	5.7	6.26	102.2	55	27.3 (6.6)	80.0 (26.1)	15.5 (2.5)	32
Lythrum	5.5	9.51	176.2	43	82.6 (23.8)	175.3 (58.9)	11.5 (4.9)	5

The communities varied greatly in the percentage of transects that showed non-zero autocorrelation with a sill, ranging from 80 % of the transects for *Dennstaedtia* to 43 % for *Lythrum* (Table 2). Communities dominated by the grass *Schizachyrium* had a greater proportion of the transects showing non-zero autocorrelation (75 %, 69 %) than communities containing shrubs (*Cornus*, *Kalmia*, *Rubus* / *Schizachyrium*, grass / *Cornus*) (55 %, 67 %, 50 %, 50 %) (Table 2). Overall, 63 % of the transects showed non-zero autocorrelation with a sill in percent transmittance within areas of 1 - 70 cm.

The average range was 19 cm for the 63 % of the transects that showed distinct spatial autocorrelation, and semivariance ranges were different among communities at $p = 0.07$, $F = 1.92$ (Table 2). The sill and nugget semivariances were significantly different among community types (Table 2) (sill semivariance: $F = 16.2$, $p < 0.0001$; nugget semivariance: $F = 12.2$, $p < 0.0001$).

Soil moisture and nitrogen availability

Mean soil moisture and N mineralization values were generally higher in the *Cornus* thickets than in the *Schizachyrium* meadows, although two of the *Schizachyrium* and two of the *Cornus* sites had overlapping soil moisture values (Table 3). The difference between *Schizachyrium* and *Cornus* was greater for N-mineralization than for soil moisture. Our mean N-mineralization values were similar to those of Matson & Vitousek (1981) for samples of low soil moisture, but were lower than for other oldfield communities (Pastor et al. 1984; Pastor, Stilwell & Tilman1987; Robertson et al. 1988).

Soil moisture and nitrogen mineralization varied substantially among sites for each community type. Mean soil moisture varied little within sites (coefficients of variation ranged from 7 to 13 %) (Table 3), whereas variation in N mineralization was much higher (C.V. values from 28 - 135 %). *Schizachyrium* sites were more variable relative to mean mineralization rates (C.V. 110 - 135 %) than *Cornus* sites (C.V. 28 -48 %).

Nitrogen mineralization was significantly correlated with soil moisture in the two *Cornus* thickets, but not in the *Schizachyrium* meadows (Fig. 1). Within site regressions were significant for *Cornus* sites 1 ($p < 0.0001$, $R^2 = 0.44$) and 3 ($p < 0.0001$, $R^2 = 0.36$). As was the case with coefficients of variation in light levels within a community type, sites with high mean N mineralization or soil moisture also had the lowest coefficients of variation (Table 3). Thus, the highest quality sites were also the least variable in soil moisture and nitrogen

Table 3. Soil moisture (% by weight) and nitrogen mineralization (µg N/g dry soil over a 58-d incubation) in little bluestem meadows (*Schizachyrium*) and gray dogwood thickets (*Cornus*).

Comm.	Site	Mean	S.D.	C.V. (%)
Soil Moisture (% by weight)				
Cornus	1	46.2	3.9	8.4
	2	22.8	2.7	11.6
	3	27.4	2.7	9.9
Schizachyrium	1	15.4	2.0	12.7
	2	23.5	2.3	9.7
	3	30.0	2.1	7.2
Nitrogen Mineralization (µg N / g dry soil)				
Cornus	1	68.9	19.6	28.5
	2	20.5	9.8	47.9
	3	41.9	15.2	36.3
Schizachyrium	1	11.5	12.6	110.0
	2	1.3	1.7	134.6
	3	8.3	10.4	125.4

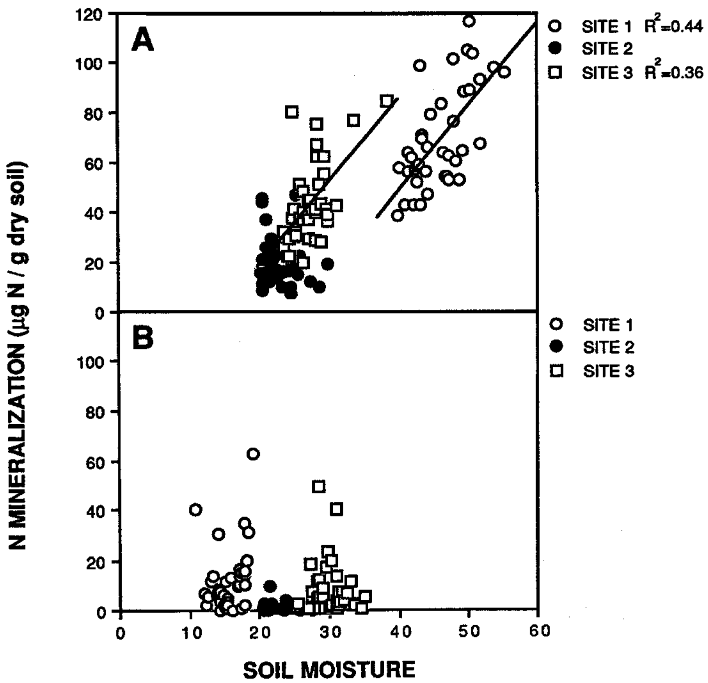

Fig. 1. N mineralization as a function of soil moisture for *Cornus* (A) and *Schizachyrium* (B) assemblages. Each point represents a sample and different symbols represent different sites. Within site regressions are significant only for *Cornus* Sites 1 ($p < 0.0001$, $R^2 = 0.44$) and 3 ($p < 0.0001$, $R^2 = 0.36$).

mineralization.

For soil moisture, two of the three *Cornus* sites and one of the three *Schizachyrium* sites showed non-zero autocorrelation among sample locations (Fig. 2). The average semivariance range for soil moisture was 249 cm for *Cornus* and 170 cm for *Schizachyrium* (Table 4). The range of sill and nugget semivariances for *Cornus* was about 3 x that for *Schizachyrium*. For nitrogen, none of the *Cornus* sites and only Site 2 of the three *Schizachyrium* sites showed spatial autocorrelation within 10 - 300 cm areas (Fig. 3). *Schizachyrium* Site 2 had the lowest mean N mineralized and the highest C.V. of all sites (Table 3). The semivariances for this site were about 30 x less than for the other *Schizachyrium* sites, and about 30 - 100 x less than for *Cornus* sites (Fig. 3). The range for nitrogen mineralization in *Schizachyrium* Site 2 was 60 cm. The models that best fit the soil moisture and nitrogen mineralization semivariogram data were linear with a sill (Figs. 2 and 3).

Discussion

Many studies indicate that safe sites can be clearly associated with physical and biological heterogeneity such as depressions and ridges or desert shrubs. Our results indicate that relatively small, structurally and topographically homogeneous patches of oldfield communities also exhibit fine-scale resource heterogeneity, and that the variability in resources may, but does not necessarily, show significant spatial autocorrelation. This significant autocorrelation suggests that resources can be patchy within structurally and topographically homogeneous vegetation and within areas small enough to be relevant to seedling invasion. We expect that additional structured variability in resources occurs in much larger areas (e.g. several meters) corresponding with changes in underlying topography and vegetation structure (Robertson 1987; Robertson et al. 1988), or with specific soil characteristics (Palmer 1990a). Structured variability in soil chemical characteristics could have subsequent effects on species distribution and richness

Table 4. Estimates of nugget semivariance, C_0, sill semivariance, C_A, range, A (cm) and R^2 values from regression models fit using programs from Robertson (1987). 'Lag' is the maximum lag distance used for fitting the semivariogram curves. All models chosen were linear with a sill. Results are only given for transects for which there was significant non-zero autocorrelation with a sill.

Comm. type	Site	Lag	R^2	C_0	C_A	A
Soil moisture						
Cornus	1	30	0.97	2.49	30.4	265
	2	30	0.89	3.00	10.7	233
Schizachyrium	1	20	0.94	0.85	6.4	170
Nitrogen mineralization						
Schizachyrium	2	15	0.84	1.7	4.2	60

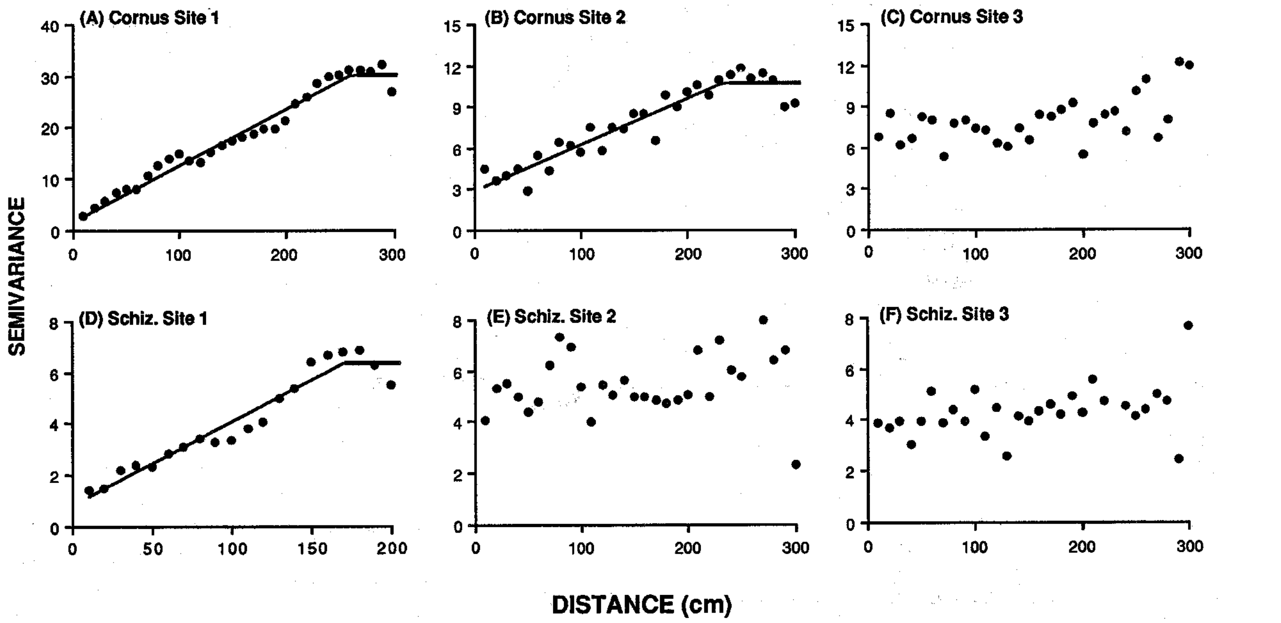

Fig. 2. Soil moisture semivariograms for each of the *Cornus* (A-C) and *Schizachyrium* (D-F) sites. Curves are presented for only the semivariograms with non-zero autocorrelation with a sill. Note differences in y-axis scales and difference in x-axis scale for (D) *Schizachyrium* Site 1.

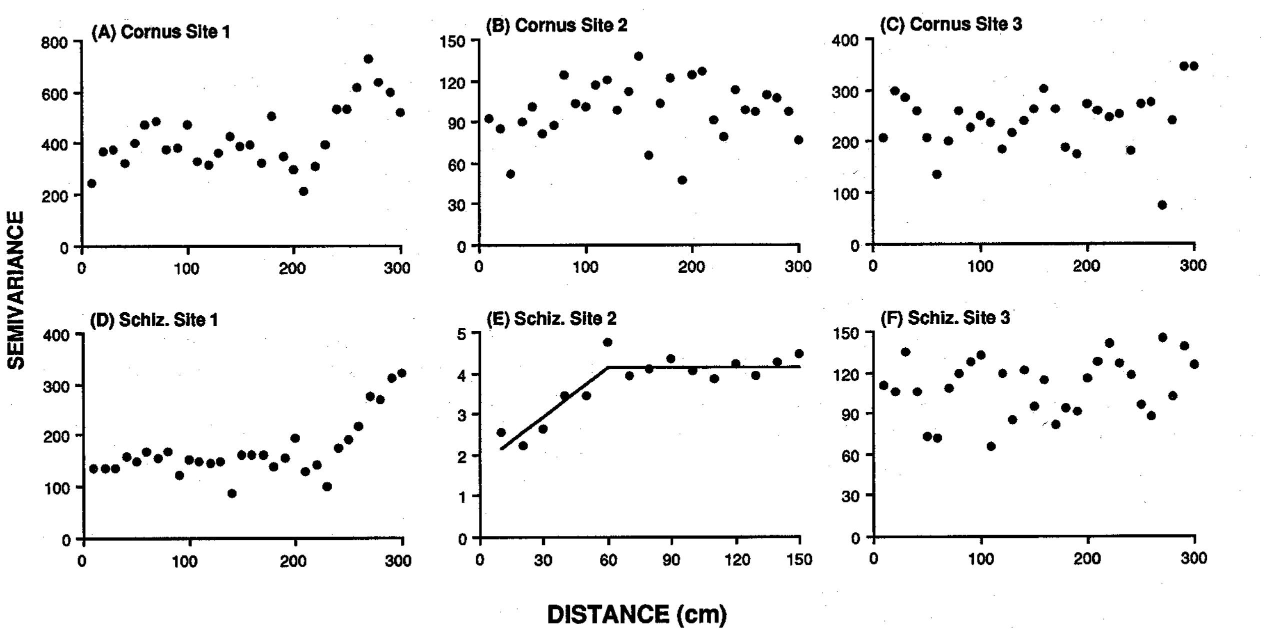

Fig. 3. Nitrogen mineralization semivariograms for each of the *Cornus* (A-C) and *Schizachyrium* (D-F) sites. Curves are presented for only the semivariograms with non-zero autocorrelation with a sill. Note differences in y-axis scale and difference in x-axis scale for (E) *Schizachyrium* Site 2.

(Palmer 1990b; Palmer & Dixon 1990).

Even though specific microsites, such as ridges or depressions, can be associated with seedling presence, it is not always clear which environmental parameters make such a microsite 'safe'. In addition, it is not clear if resources show congruent patterns of spatial and temporal variability. Our results demonstrate that light, water and nitrogen did not vary within areas of the same size. For light, the average range, or distance within which light levels were spatially autocorrelated, was different among community types (Table 2) and was much smaller than for nitrogen or soil moisture. Similarly, nitrogen and soil moisture varied within areas of different size (20 cm for light, 60 cm for nitrogen and 220 cm for soil moisture). In addition, sites within which nitrogen levels were spatially autocorrelated did not necessarily have soil moisture spatially autocorrelated. This was unexpected given the significant correlations between nitrogen and soil moisture, especially for the *Cornus* Site 1 (Figs. 1, 2 and 3). Because the three resources we examined varied within different-sized areas, invading seedlings could potentially experience different-sized patches of light, water and nitrogen in these oldfield communities. Similarly, a community may have nonrandom spatial distribution of one resource but not other resources. Thus, a seedling may occur in a patch of high light, but spatially random levels of nitrogen and soil moisture.

One of our objectives was to determine whether the availability of resources affected the level of heterogeneity and the presence of autocorrelation in those resources. Our results indicate that sites with low mean values of light, soil moisture or nitrogen were more relatively heterogeneous than sites with high mean values of light, soil moisture or nitrogen (Tables 2 and 3). Also, three of the four sites that showed significant spatial autocorrelation in soil moisture or nitrogen (*Cornus* Site 2 and *Schizachyrium* Site 1 for soil moisture; *Schizachyrium* Site 2 for nitrogen) were the sites with low mean values of soil moisture and nitrogen (Table 4, Figs. 2 & 3). This was not necessarily true among community types for light. Some of the community types with high light levels had a high percentage of transects with spatial autocorrelation, as did some of the low light community types (Table 2). Thus, the relative heterogeneity seems to be greater in low-quality sites or community types (i.e. sites with low average levels of resources) for all of the resources examined here, and autocorrelation tended to be associated with the low-quality sites for nitrogen and soil moisture, but was not necessarily related to mean light levels in the community types we examined. These results suggest that invading seedlings may have to tolerate more relative variation in a resource in a site that has a low average availability of that resource, but the variation in that resource at that site may not necessarily be random and thus may occur in distinct patches. The implications here are that what may be important for an individual tree seedling in an oldfield along a powerline corridor, is not the average resource availability in that community, but the heterogeneity and the size of the area in which the resources are spatially autocorrelated if they are not spatially random. Thus, even though the average quality of a community may be low, and the community may seem relatively homogeneous, a seedling may by chance land in a small microsite of high resource availability and thus may be able to become established in that community. It is important to remember, however, that the average availability of a resource may become important as the seedling becomes larger, and may also be important in determining the number of seedlings that can invade that community (Hill, Canham & Wood, submitted).

Conclusions

Most previous studies of microsite requirements have focused on heterogeneity associated with clear discontinuities that are often created by topographic variation or disturbances within vegetation. Our results demonstrate that distinct heterogeneity of resource availability can occur in small areas within relatively homogeneous patches of oldfield vegetation having little topographic relief. Also, the three resources varied incongruently. As a result, species with different resource requirements would 'perceive' very different patterns of resource heterogeneity in a given community.

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