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Spatio-temporal patterns of soil available nutrients following experimental disturbance in a pine forest

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Abstract Although disturbance is known to alter soil nutrient heterogeneity, it remains unclear whether spatial patterns in soil nutrients after disturbance follow predictable temporal changes that reflect underlying processes. This study examined the effects of tree harvesting and girdling on overall variability, geostatistical patterns, and resource congruence of soil available nutrients in a mature *Pinus elliottii* Engelm. forest. The two disturbances led to different patterns of vegetation removal, forest floor redistribution, and revegetation, but showed similar post-disturbance changes in overall soil nutrient variability. Soil nutrient variability increased after both disturbances by more than 5-fold, and then decreased, returning to the undisturbed level in 4 years. Spatial structures assessed using geostatistics did not show predictable temporal trends. However, girdled plots showed more persistent spatial structures in soil nutrients than harvested plots, and had semivariogram ranges mostly equal to or less than 10 m, reflecting effects of persistent and spatially stable patches of undisturbed hardwoods that had an average patch size of 10 m. Resource congruence examined with Spearman rank correlations was nil before disturbance, increased after disturbance and then became nil again by the 4th year post-disturbance. The timing of the increase was related to treatment, occurring in the 1st year after disturbance in the girdled plots, but not until the 2nd year in the harvested plots. These two patterns of congruence were potentially caused by different rates of nutrient patch formation and resource uptake by plants during early succession. Although temporal changes in soil heterogeneity have been documented previously, the present study indicates that temporal trends in nutrient variability after disturbance may be predictable, and that the marked changes in spatio-temporal patterns of soil nutrients as a result of disturbance are ephemeral.

Keywords Geostatistics · Nitrogen and phosphorus · Resource congruence · Spatio-temporal variation · Trees

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Introduction

Heterogeneity in soil resources influences seedling recruitment (Mou et al. 1993), species coexistence and competition (Grime 1979; Fransen et al. 2001; Bliss et al. 2002), community composition and structure (Tilman 1988), and succession (Armesto et al. 1991; Gross et al. 1995). The recognition of the importance of the soil resource heterogeneity has resulted in research designed to characterize soil heterogeneity in terrestrial ecosystems. This research has clearly shown that soil resource heterogeneity is substantial, highly structured at different spatial scales (Bell et al. 1993; Jackson and Caldwell 1993a, 1993b; Halvorson et al. 1994; Ehrenfeld et al. 1997; Kleb and Wilson 1997), and changing over time (Ryel et al. 1996; Cain et al. 1999; Farley and Fitter 1999; Guo et al. 2002). However, ecological agents and processes governing spatio-temporal patterns of soil heterogeneity are not well understood (Pickett et al. 2000).

Disturbance is a major ecological agent that may profoundly alter patterns of soil resource heterogeneity (Pickett and White 1985; Pickett et al. 2000). By removing dominant vegetation, disturbance events increase light levels, produce a flush of nutrients, and create root gaps and nutrient release zones (Silver and Vogt 1993; Parsons et al. 1994; Schroeer et al. 1999). By redistributing plant litter and mixing it with the mineral soil (Beatty 1984), disturbances increase patchiness in the litter layer and soil, thereby increasing spatial variability in soil moisture and temperature (Clinton and Baker 2000; Guo et al. 2002), and influencing nutrient mineralization and transport in the soil (Stark 1994). When disturbances create highly contrasted microsites within a site, resource congruence, i.e., spatial correspondence of different plant resources, may increase (Carlton and Bazzaz 1998). Post-disturbance patchiness in forest floor can also influence spatial patterns of re-vegetation (Mou et al. 1993; Carlton and Bazzaz 1998). Regenerated vegetation patches interact with soil nutrient distributions altered by disturbances. Such interactions may lead to a dynamic process in which the growth of individual plants and the interactions among plants of different species not only respond to soil nutrient heterogeneity (Einsmann et al. 1999; Fransen et al. 2001; Wijesinghe et al. 2001), but also modify soil nutrient distributions (Ryel et al. 1996; Cui and Caldwell 1997).

Despite the potentially large effects of disturbance on soil resource heterogeneity and congruence, remarkably little quantitative information exists on post-disturbance patterns of soil heterogeneity (Carlton and Bazzaz 1998). Even less is known about the spatially explicit patterns of soil heterogeneity after different types of disturbances at the same site (Guo et al. 2002). Here we examine spatio-temporal patterns of soil available nutrients (e.g., NH_4^+, NO_3^-, and $H_2PO_4^-$) following two different types of disturbance in a 40-year-old slash pine (*Pinus elliottii* Engelm.) forest. Adopting an approach proposed by Armesto et al. (1991), we experimentally simulated disturbances and then repeatedly quantified soil resource spatial patterns through time. The disturbances used in this study were whole-tree harvesting, and tree girdling, which was employed to simulate a southern pine beetle (*Dendroctonus frontalis* Zimm.; Coleoptera: Scolytidae) outbreak. Effects of the two disturbances are similar in that they result in total mortality of the overstorey pines, but differ greatly in their post-disturbance patterns of forest floor and plant regeneration. While harvesting removes all vegetation cover and disturbs forest floor and soil (Pritchett and Fisher 1987), girdling leaves patches of hardwoods and does not disturb forest floor immediately (Schroeer et al. 1999; Guo et al. 2002). As a result, vegetation regeneration follows different patterns after the two disturbances. Our choice of disturbances therefore provided us an opportunity to determine the overall effects of disturbance type, as well as the effects of forest floor patchiness and re-vegetation process on soil nutrient patterns by testing the following hypotheses:

1. Overall variability in soil nutrients increases after disturbance because variability in plant cover and forest floor distributions increases after disturbance. Soil nutrient variability then rapidly decreases as vegetation quickly reestablishes and the impact of forest floor disturbance fades. This temporal trend was described for soil moisture in our previous report (Guo et al. 2002). If soil nutrients show the same trends, a pattern of a general increase followed by a rapid recovery can be predicted for all four key plant resources (soil NH_4^+, NO_3^-, $H_2PO_4^-$, and moisture).
2. The scale at which soil nutrient variability is spatially structured becomes finer, and the degree of the spatially structured variability in soil nutrients increases immediately after disturbance, mainly because patches in forest floor and vegetation become smaller in size and more contrasted after the disturbances. As vegetation fully recovers and the impact of forest floor disturbance weakens, the scale of the spatially structured variability in soil nutrients becomes coarser.
3. Soil resources (i.e., nutrients and moisture) are spatially congruent immediately after disturbance due to the increased contrast among vegetation and among forest floor patches. However, within 4 years after disturbance, spatial congruence will re-approximate pre-disturbance conditions due to the rapid recovery in plant cover during early succession in forests.

To test these hypotheses, we spatially sampled soil nutrients, forest floor, and plant cover. We recognized that heterogeneity is a complex and scale-dependent property and that a single measure at a single scale may generate a biased quantification for heterogeneity (Li and Reynolds 1995; Guo et al. 2002). We therefore used multiple sampling scales and several analyses including overall variability, geostatistical patterns, and spatio-temporal correlations, to provide more robust results.

Materials and methods

Study site, spatial sampling regime, disturbance treatments

This study was conducted in a 40-year-old *Pinus elliottii* plantation located at the Savannah River Site near Aiken, South Carolina, USA. The mean annual precipitation is 1,130 mm and is relatively evenly distributed throughout the year (South Carolina State Climatology Office 1998). The soils are of well-drained Dothan sandy loam with a low nutrient-holding capacity and low organic matter content (Rogers 1988). Slash pine, planted in the 1950s, comprised 82.5% of the average total stand basal area of 37.3 m^2 ha^{-1}. The remaining basal area was dominated by *Quercus* spp., *Myrica cerifera* L., and *Prunus serotina* Ehrh. (Lister et al. 2000). Detailed site information can be found in Guo et al. (2002).

Five 1-ha plots were randomly placed within a 20-ha portion of the plantation. In March 1997, a 50×50 m survey plot was established in the center of each plot with a 25 m buffer zone on each side. Each survey plot was divided into 100 5×5 m grid cells. Coarse-scale sampling locations were set at 41 grid intersections following Halvorson et al. (1994) (Fig. 1). For fine-scale sampling, we randomly selected two 5×5 m grid cells in each survey plot and divided each into 100 micro-grid cells of 0.5×0.5 m. Forty-one additional sampling points were arranged in each fine-scale (i.e., 5×5 m) cell using the 0.5×0.5 m micro grid and the same pattern of sample locations chosen for whole survey plots (Fig. 1). The total number of coarse- plus fine-scale sample locations was 615. Coarse-scale sampling locations were unchanged throughout the study. Fine-scale plots were randomly relocated each year to minimize the impact of sampling disturbance.

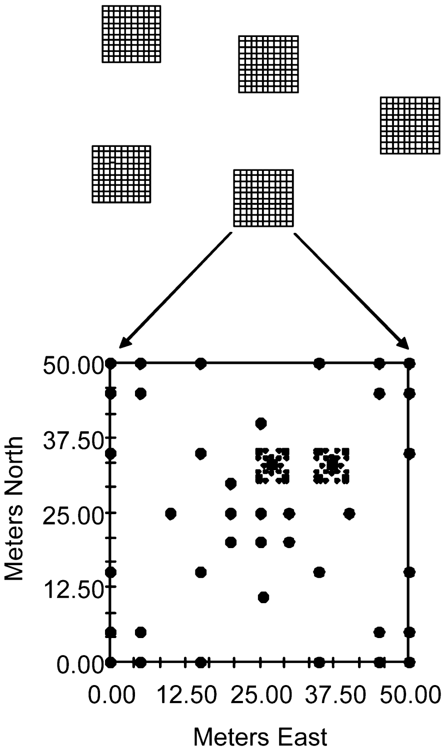

Fig. 1 Sampling design for measuring soil nutrient heterogeneity. In each of the five plots, 41 points were located on the intersections of a 5×5 m grid to optimize semivariogram analysis with a minimum sampling interval of 5 m. The same sampling layout was also applied to each of two randomly chosen cells, but with a minimum sampling interval of 0.5 m

In late May 1997, we applied whole-tree harvesting to two randomly selected survey plots (H1 and H2 hereafter), and girdling to two other randomly selected survey plots (G1 and G2 hereafter). One survey plot remained undisturbed. In H1 and H2, all trees with diameter at breast height (DBH) ≥10 cm were felled and removed from the site. Smaller trees were cut and left in the place along with the slash. In G1 and G2, all pines ≥25 cm in DBH were girdled with chain saws, and the herbicide triclopyr amine (44% active ingredient in water; Garlon 3A, Dow Chemical, Midland, Mich., USA) was applied to the chain saw cuts. The understory pine seedlings and saplings were felled and left in place. All hardwoods were left undisturbed.

Soil available nutrients, forest floor mass, and plant cover

Indices of available nitrogen (NH_4^+ and NO_3^-), and phosphorous ($H_2PO_4^-$) were measured using ion exchange resin membranes (Ionics, Watertown, Mass., USA; Qian et al. 1992; Cain et al. 1999), once prior to and five times after disturbance treatments (i.e., twice a year in the first 2 years and once in the 4th year after the disturbances). For each sampling event, three 2.5×5 cm membranes were vertically inserted into the soil at the same depth (5–10 cm), but 2 cm apart from each other, at each of the 615 sampling locations. The membranes were collected after 14-day incubation and immediately refrigerated at 3°C until extraction. Membrane-bound NH_4^+ and NO_3^- were extracted with 25 ml of 2.0 M KCl, and $H_2PO_4^-$ was extracted with 25 ml of 0.5 M HCl. The extracts were analyzed with a Lachat 4000 autoanalyzer (Lachat Instruments, Milwaukee, Wis., USA).

Forest floor litter was collected using a 9-cm-diameter steel core once prior to disturbance and twice annually in the first 2 years after disturbance. Sampling of forest floor litter was offset 20 cm from the sampling location for soil nutrients to minimize disturbance. Litter samples were then oven dried at 65°C to constant weight and weighed. Subsamples were burned at 550°C for 5 h to determine ash-free weight.

Prior to disturbance, species and DBH for all woody stems ≥5 cm DBH were recorded and mapped in each survey plot, and reported in Lister et al. (2000). Re-vegetation of H1 and H2 was surveyed annually during summer or early fall from 1997 to 2001. Each survey plot was divided into 400 2.5×2.5 m quadrats, and the percentage plant cover in each quadrat was visually estimated to the nearest 5%. G1 and G2 had little ground re-vegetation in 1997, and were therefore not surveyed until 1998 using a quadrat size of 5×5 m. Beginning in 1999, plant cover in G1 and G2 was also surveyed with 2.5×2.5 m quadrats. We report post-disturbance total plant cover here for the purpose of inferring the processes underlying soil nutrient heterogeneity patterns. A more complete report of post-disturbance vegetation patterns will be published elsewhere (Mou et al., unpublished data).

Data analysis

Mean, variance, and coefficient of variation (CV) of soil available nutrients, forest floor litter mass, and plant cover were calculated using SAS version 8 (SAS, Cary, N.C., USA) for each survey plot sampled at the scale of 5–60 m and for each fine-scale subplot sampled at the scale of 0.5–6 m. These univariate statistics were used to evaluate overall variability in soil nutrients, forest floor mass, and plant cover.

Semivariograms were used to analyze spatial structures in soil nutrients (Robertson and Gross 1994). In a spatial data set, points located closer to each other usually have values more similar than points far apart. As a result, semivariances (half of the variances of the data points separated by a fixed distance, see Isaaks and Srivastava 1989 for details) will increase with distance, until the dissimilarity among data points is no longer distance-dependent. The relationship between semivariance and distance can be fitted with regression models (e.g., spherical, exponential, linear, nugget). The fitted curve is called a semivariogram, and several parameters can be estimated. The plateau of a semivariogram curve is called sill, the distance from zero to where the sill occurs is called range, the semivariance at zero distance is called nugget. Nuggets are often greater than zero because of sampling error or the lack of observations at very small distances. If a semivariogram does not show autocorrelation (i.e., sill equal to nugget), it is defined as a nugget effect (Isaaks and Srivastava 1989). In this study, we used range and SH% [which is defined as 100 (sill−nugget)/sill] to indicate the scale and the degree of spatially structured variability, respectively (Rossi et al. 1992; Robertson and Gross 1994; Li and Reynolds 1995).

Semivariograms were modeled using GS+ software version 5.1 (Gamma Design, Plainwell, Mich., USA). Data for soil nutrients were log-transformed prior to analysis because they were positively skewed (Webster and Oliver 1990). Plant cover data were normally distributed and not transformed. Before constructing semivariograms, we examined spatial trends as described in Davis (1986) but found no significant trends of 1st- or 2nd-order. The choice of lag distance was based on a balance between equal lag distance and equal numbers of pairs for each lag (Zheng and Silliman 2000). To ensure that variation was isotropic (i.e., direction independent), we compared isotropic semivariograms with corresponding anisotropic ones at 0, 45, 90 and 135°, and did not find any difference. Therefore, isotropic semivariograms were used in all analyses.

The Spearman rank correlation coefficients were calculated in SAS Version 8 (SAS, Cary, N.C., USA) to quantify the congruence among soil resources. Spatial congruence was evaluated with the correlations among different soil variables sampled simultaneously, while temporal correspondence was examined with the correlations for the same soil variable between different sample periods. The significance level for correlations was adjusted with a Bonferroni correction. Correlation coefficients were calculated using pooled data from replicated plots (i.e., H1+H2 and G1+G2) because replicated plots within each treatment had similar correlation patterns. An average soil moisture value for each year was used in nutrient-moisture correlations because intra-annual temporal correlations in soil moisture were high (correlation coefficients >0.5, *P* -values<0.0001).

Results

Spatial and temporal variability in soil available nutrients

Coarse-scale mean nutrient availability was similar in all plots prior to disturbance, but increased dramatically after disturbance with a similar magnitude of increase for girdling and harvesting (Fig. 2a). Eventually nutrient availability declined in all disturbed plots and returned to the undisturbed level within 4 years (Fig. 2a). The two girdled plots had nearly identical temporal patterns, but the two harvested plots differed, with H2 having consistently higher means until 2001. The means of NH_4^+ and NO_3^- had distinct "increase and then decline" pattern regardless of the season of the sampling, while $H_2PO_4^-$ had summer peaks superimposed on the "increase and then decline" trend. Temporal changes in mean nutrient levels at the fine scale (0.5–6 m) (data not shown) were similar to those at the coarse scale (5–60 m). However, the differences between the two fine-scale subplots embedded in the same coarse-scale plot were large, particularly in G1 and G2 (data shown in Electronic Supplementary Material).

Before disturbance, variances of the three nutrients at the coarse scale were similar and low (ranging from 0.24–0.30 for NH_4^+, 0.11–0.39 for NO_3^-, and 0.09–0.21 for $H_2PO_4^-$) (Fig. 2b). Variances increased by more than five-fold after disturbance, and then rapidly declined and recovered to the undisturbed level by 2001 (Fig. 2b). After disturbance, the magnitude of variances differed between H1 and H2, though the general temporal trends were similar. The variances also differed among nutrient variables. NH_4^+ and NO_3^- were as much as 10 times more variable than $H_2PO_4^-$ (Fig. 2b). Large differences in variance were also found in the embedded fine-scale subplots (data shown in Electronic Supplementary Material). Post-disturbance CV fluctuated over time, though some of the replicate plots had comparable trends (data shown in Electronic Supplementary Material). The temporal changes in CV were difficult to use in interpreting temporal trends of spatial patterns in soil nutrients because they were driven in part by unparallel changes in mean and variance.

Spatial and temporal variability in forest floor mass and plant cover

Pre-disturbance forest floor litter mass had similar mean, variance, and CV in all five plots (Fig. 3). One year after disturbance (March 1998), mean, variance, and CV of litter mass increased in H1 and H2, and then decreased by March 1999 (Fig. 3). Means of litter mass in the harvested plots were similar to that of the undisturbed plot in 1999,

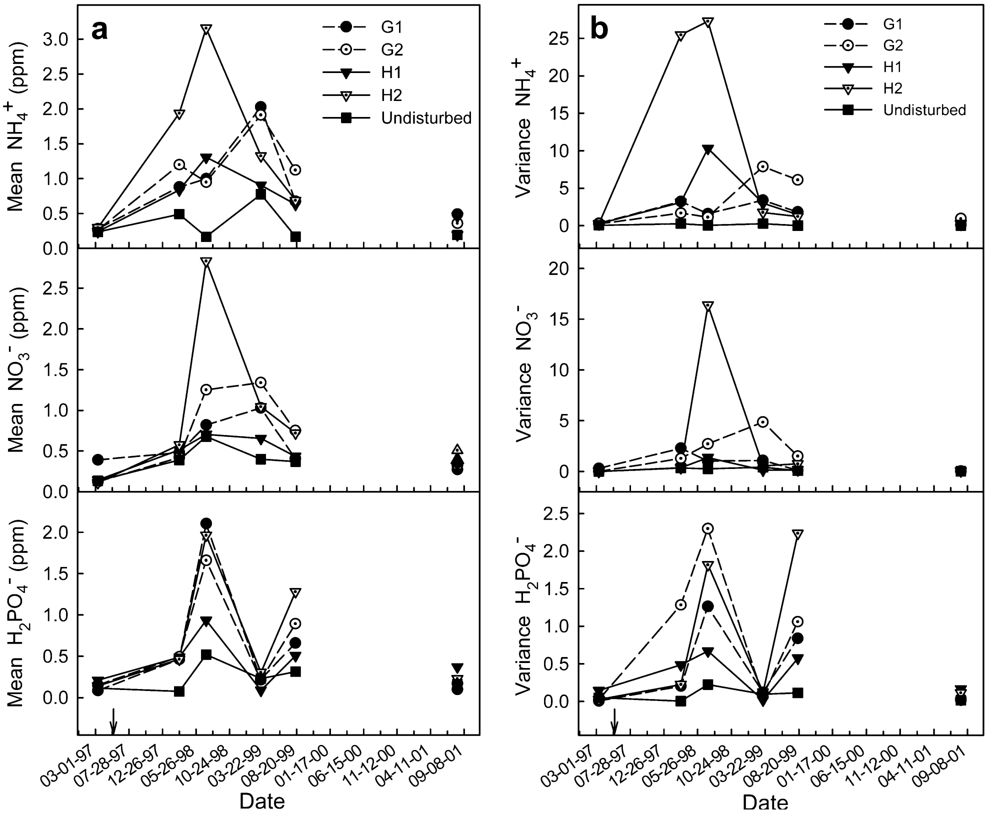

Fig. 2 Temporal changes in NH_4^+, NO_3^-, $H_2PO_4^-$ in the coarse scale (5–60 m) plots. The *arrow* indicates the date of disturbance. *n* =41 for each data point. *Panel a* means, *panel b* variances

but variances and CVs were greater. In contrast, G1 and G2 had similar means, variances, and CVs in litter mass to those found in the undisturbed plot throughout the study.

Before disturbance, all five plots had a closed canopy (Lister et al. 2000). In both treatments, nearly 100% of the pines were killed, but harvesting removed all aboveground portions of trees and large shrubs, while girdling did not remove aboveground portions of non-pines (Lister et al. 2000). Mean total plant cover increased after the treatments, but at a greater rate in the harvested than in the girdled plots (Fig. 4). By the summer of 1999, the harvested plots reached >80% total plant cover, while the girdled plots were <60%. In contrast, variance in plant cover increased at a slower rate after harvesting than girdling (Fig. 4). CV generally decreased in all disturbed plots. Temporal patterns in mean, variance, and CV were similar in the two replicated girdled plots, but differed somewhat in the two replicated harvested plots mainly due to a divergence in the year 2000.

Spatial structures in soil nutrients and plant cover

Prior to disturbance, spatial structures in soil nutrients were present in 4 out of 15 semivariogram analyses: NO_3^- in G1, and $H_2PO_4^-$ in H1, H2, and the undisturbed plot. Ranges were 17.5, 29.1, 24.7 and 46.9 m, and SH% values were 86%, 82%, 50% and 64%, respectively for these plots. After disturbance, two patterns of spatial structures emerged. First, spatial structures occurred in 20 out of 30 semivariogram analyses in the girdled plots but only in 6 out of 30 analyses in the harvested plots. Second, soil nutrient variability was mostly structured at fine scales (i.e., less than 10 m, which was the case in 21 out of 30 analyses where a spatial structure was present). Scale

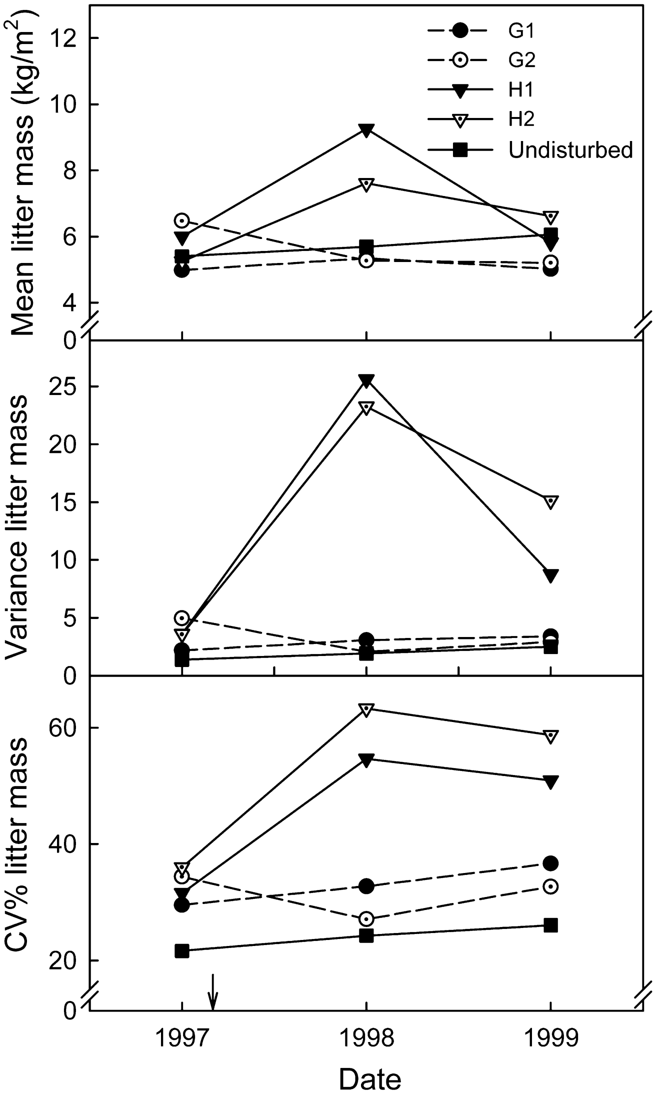

Fig. 3 Temporal changes in mean, variance, and CV of forest floor litter mass in the coarse scale (5–60 m) plots. The *arrow* indicates the date of disturbance. Litter samples were collected in March of each year. *n* =41 for each data point

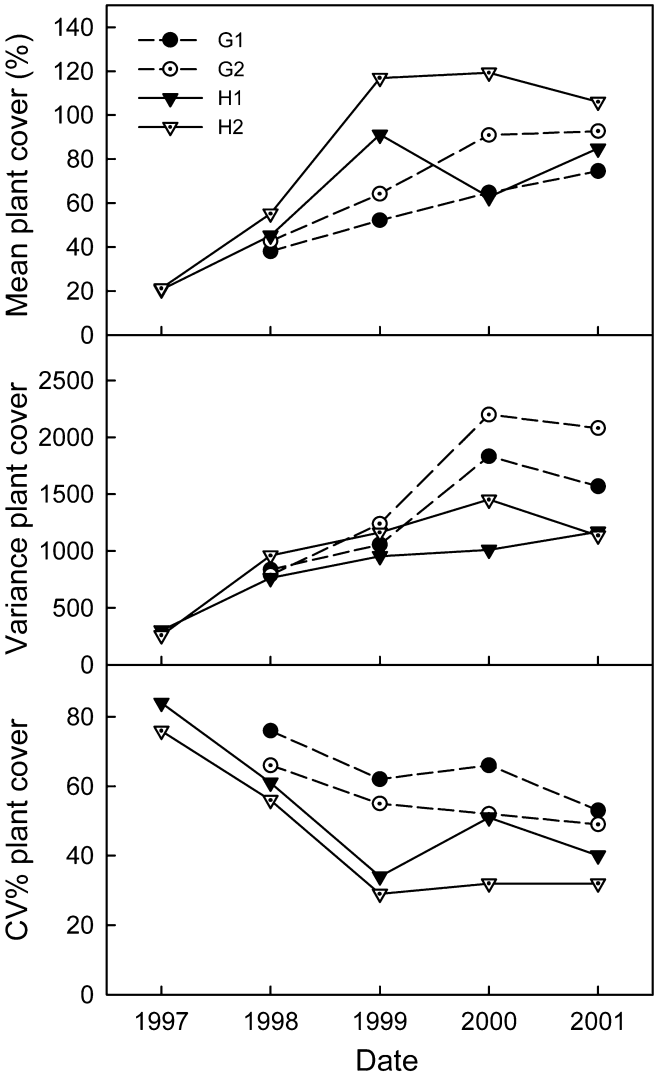

Fig. 4 Temporal changes in mean, variance, and CV of total plant cover in the disturbed plots. All data points are post-disturbance. All plots had a closed-canopy before disturbance. *n* =100 (5×5 m sampling resolution) for 1998 data points for G1 and G2, *n* =400 (2.5×2.5 m sampling resolution) for the rest of data points

(range) and the degree (SH%) of the spatial variability in soil nutrients exhibited no clear temporal trends. Spatial structures were similar between the two girdled plots but different between the two harvested plots. The three nutrients did not differ consistently, though NO_3^- was more frequently structured than NH_4^+ and $H_2PO_4^-$. (See Electronic Supplementary Material for more detail.)

Patchiness in plant cover was strong with SH% exceeding 80% in nearly all semivariograms. The size of the patches (indicated by semivariogram range) varied from 7 to 18 m in the girdled plots and 5 to 15 m in the harvested plots. In addition, patch size and SH% were relatively similar between replicate plots in both treatments. (See Electronic Supplementary Material for more detail.)

Resource congruence

Prior to disturbance, correlations among resources were weak. A number of strong, positive correlations were noted in the first 2 years after disturbance (Table 1). Moreover, correlation patterns differed between girdling and harvesting. In 1998, significant correlations were found in 13 out of 21 cases in the girdled plots, but only in 2 out of 21 in the harvested plots (Table 1). For both treatments, the highest correlations were those between NH_4^+ and NO_3^- sampled simultaneously. The pattern for 1999 was the reverse of that for 1998. Only 2 out of 21 correlations in 1999 were significant in the girdled plots, but 10 out of 21 correlations were significant in the harvested plots (Table 1). The highest correlations were also those between NH_4^+ and NO_3^- sampled simultaneously. Within-year temporal correlations for the same nutrient variable were weak, albeit a few significant temporal correlations were found for NH_4^+ (r =0.40, P <0.0001) and NO_3^- (r =0.38, P <0.0001) in the girdled plots in 1998, and for $H_2PO_4^-$ (r =0.26, P <0.001) in the harvested plots in 1999. Four years after the disturbance treatments (August 2001) no correlations were significant.

Discussion

Temporal trends in overall variability of soil nutrients

In support of our first hypothesis, overall variability in soil nutrients increased after disturbance, and then decreased, reaching the undisturbed level in a few years (Fig. 2b). A similar "increase and then decline" temporal trend was previously reported in the same sites for soil moisture (Guo et al. 2002), though soil moisture variability recovered more rapidly than soil nutrient variability. Nevertheless, all four soil variables (i.e., NH_4^+, NO_3^-, $H_2PO_4^-$, and soil moisture) followed a predictable "increase and then rapidly recover" pattern in overall variability.

Table 1 Spearman rank correlations between nutrients and water (H_2O) at the scale of 0.5–60 m 1 year (1998) and 2 years (1999) after girdling or harvesting a 40-year-old pine forest. Significance levels: * <0.05, ** <0.001, *** <0.0001. Some non-significant portions of correlation matrices (in rows) were omitted

Disturbance/nutrient	NH_4^+ (Mar)	NO_3^- (Mar)	$H_2PO_4^-$ (Mar)	NH_4^+ (Jul)	NO_3^- (Jul)	$H_2PO_4^-$ (Jul)
1998						
Girdled						
NO_3^- (Mar)	0.29**	1.00				
$H_2PO_4^-$ (Mar)	0.35***	0.12	1.00			
NH_4^+(Jul)	0.40***	0.23*	0.27**	1.00		
NO_3^- (Jul)	0.40***	0.38***	0.30**	0.42***	1.00	
H_2O	0.30**	0.32**	0.21*	0.13	0.35***	−0.15
Harvested						
NO3$^-$(Jul)	0.08	0.08	−0.01	0.53***	1.00	
H_2O	0.11	−0.02	0.05	0.18	0.33**	0.11
Undisturbed						
$H_2PO_4^-$ (Mar)	−0.20*	0.18	1.00			
H_2O	−0.21*	−0.27**	0.13	0.09	−0.14	0.04
1999						
Girdled						
NO_3^- (Aug)	−0.07	0.03	−0.02	0.40***	1.00	
H_2O	−0.31**	−0.09	0.09	−0.09	0.09	0.12
Harvested						
NO_3^- (Mar)	0.33**	1.00				
$H_2PO_4^-$ (Mar)	0.31**	0.31**	1.00			
NO_3^- (Aug)	−0.01	0.06	−0.01	0.35***	1.00	
$H_2PO_4^-$ (Aug)	0.12	0.20*	0.26**	−0.03	0.16	1.00
H_2O	−0.35***	−0.21*	−0.41***	0.05	0.04	−0.29**
Undisturbed						
H_2O	−0.15	−0.09	−0.11	−0.14	−0.25*	−0.23*

Increases in nutrient availability and variability after disturbance were expected because disturbances tend to increase site heterogeneity (Pickett and White 1985), which in turn may lead to both increased soil resource availability and variability (Guo et al. 2002). However, we were surprised by the similarity in the pattern that the two distinctly different types of disturbance displayed. Girdling killed all overstory pines, left in place the snags and the undisturbed, patchily distributed hardwoods, and caused no immediate impact on forest floor (Figs. 3, 4). In contrast, harvesting removed all aboveground vegetation and created a highly variable forest floor (Figs. 3, 4). Despite the differences in residual vegetation and forest floor, two disturbances led to a similar degree of increase in soil nutrient availability and variability (Fig. 2). The timing and rate of subsequent recovery in soil nutrient variability to the undisturbed level were also similar between the two disturbances. Yet the two disturbances differed in the pattern of forest floor changes and in the pattern of revegetation (Figs. 3, 4), and therefore, they presumably differed in the pattern by which plant uptake capacity was reestablished. These findings suggest that care should be taken in inferring underlying processes for an observed pattern in soil resource variability, particularly when these processes are not directly examined.

The similarity between the two disturbances also points to an emerging pattern of soil nutrient variability along the successional gradient; i.e., early-successional communities have the highest variability in limiting resources such as N, P, and soil moisture. The present study shows that in this southern pine forest ecosystem nutrient variability increases strongly after disturbance and then declines rapidly. Unless the system encounters other disturbances of the similar or greater magnitude in future development, we expect that nutrient variability will remain at a level comparable to that of the undisturbed pine forest. We therefore predict that the early successional plant communities may have highest variability. This prediction is contingent upon the elevated nutrient availability, and the initially discontinuous plant cover in early successional communities. Discontinuous plant cover is an important contributor to soil nutrient variability in shortgrass steppe ecosystems where ‘islands of fertility’ are created under plants (Vinton and Burke 1995; Ryel et al. 1996). In systems where nutrient levels are high due to the removal of the previous vegetation (e.g., our system), discontinuous plant cover in early stages of secondary succession contributes to nutrient variability perhaps by creating ‘islands of nutrient depletion’. As vegetation further develops and plant roots fully exploit the soil, however, these islands of nutrient depletion may coalesce, resulting in decreases in overall nutrient variability. In this study, the pattern of vegetation development after both disturbances was apparently the primary reason for the marked increase and subsequent recovery in nutrient variability.

Consistent with previous reports, available N had much greater variability than available P. Jackson and Caldwell (1993a) found a more than 10-fold variation in NO_3^- and NH_4^+, and a 3-fold variation in $H_2PO_4^-$ over a 0.25 m^2 area around plants in a sagebrush steppe. The present study revealed that NO_3^- and NH_4^+ were as much as 10 times more variable than $H_2PO_4^-$ at the scale of 0.5–60 m (Fig. 2b). Higher variability in NO_3^- and NH_4^+ than $H_2PO_4^-$ may be related to a higher susceptibility to localized microbial transformations and immobilization for NH_4^+ and NO_3^- (Jackson and Caldwell 1993a).

Temporal changes in spatial structures of soil nutrients

We predicted that immediately after disturbance the scale at which soil nutrient variability is spatially structured would become finer, and the expression or visibility of spatial structures would increase. This prediction was partially supported. The girdled plots showed an increased number of spatial structures with generally smaller semivariogram ranges, and relatively high SH% values in the first year after disturbance (i.e., 1998). However, no such pattern was found in the harvested plots. We also predicted that the scale of spatially structured variability in soil nutrients would become coarser as plant cover reestablishes throughout the plot and the impact of forest floor disturbance weakens. This prediction was not supported because no consistent increases in semivariogram ranges were observed from 1st to the 2nd, and then the 4th year after both treatments, a period during which plant cover increased and forest floor disturbance impacts likely faded (Figs. 3, 4).

The size and spatial distribution of individual plants can influence the scale and the degree at which soil nutrients are spatially structured (Jackson and Caldwell 1993a, 1993b; Gross et al. 1995; Ryel et al. 1996). This may have occurred in our study. Before girdling, hardwoods were spatially structured at the 10 m scale (Lister et al. 2000), and in the 4 years after girdling, the size of hardwood trees was relatively stable, and the scale at which these hardwoods were spatially structured remained at the 10 m scale. Spatial structuring of soil nutrients after girdling was strong and occurred at a scale a little less than 10 m. In contrast, the harvested plots lacked temporally persistent and spatially well-defined vegetation patches due to the scattered pattern of initial revegetation and rapid changes in plant cover in the first 2 years after harvesting (Fig. 4). In addition, forest floor in the harvested plots was highly variable (Fig. 3) and did not exhibit strong patterning (data not shown). Accordingly, soil nutrients lacked spatial structure in the harvested plots.

The spatial structures of soil N and P differed from those of soil moisture. In this study, soil nutrients displayed spatial structures mostly at the scales less than 10 m, and structuring occurred primarily in the girdled plots. In contrast, soil moisture exhibited long-range (>40 m in most cases) spatial trends, mostly in the harvested plots (Guo et al. 2002). These patterns suggest that spatial distributions of different soil resources may be regulated by different mechanisms operating at different scales. We attributed spatial trends in soil moisture to underlying soil trends in micro-topography or soil texture that were unmasked by the removal of the vegetation (Guo et al. 2002). Here we suggest that soil nutrients are structured at the scales of individual plants or temporally stable vegetation patches because nutrient distributions in soil may be primarily controlled by plant uptake and by localized microbial transformations and immobilization (Jackson and Caldwell 1993a, 1993b; Robertson et al. 1993; Ryel et al. 1996).

Resource congruence

We hypothesized that disturbance would increase spatial congruence among soil resources. We tested two predictions from this hypothesis; i.e., that congruence should increase after disturbance and that temporal correspondence of individual resources should be poor due to marked fluctuations over time. This hypothesis was supported by stronger spatial correlations after than prior to disturbance, and by post-disturbance temporal correlations that were weak relative to spatial correlations (Table 1). However, the two disturbances showed different patterns of resource congruence. Spatial congruence was high in the girdled plots but low the harvested plots in the first year after disturbance; low in the girdled plots but high in the harvested plots in the subsequent year. These contrasting congruence patterns may reflect different rates of soil nutrient patch formation and resource uptake by plants. In the 1st year after disturbance (1998), the surviving hardwoods in the girdled plots may have created root uptake zones (Parsons et al. 1994; Schenk and Jackson 2002), and generated well-defined areas of nutrient depletion in a matrix of high nutrient availability. By the 2nd year (1999), however, the roots of surviving trees and regenerated plants in girdled plots may have colonized most of the available nutrient patches (Wilcznski and Pickett 1993; Schroeer et al. 1999; Jones et al. 2003), thereby disrupting spatial congruence of different soil resources. In the harvested plots, plant cover occupied less than 50% of the aboveground space by the summer of 1998 (Fig. 4), and the legacy of forest floor disturbance was still pronounced (Fig. 3). Therefore, probably not until 1999 did well-defined and relatively large nutrient patches and depletion zones develop to the degree that could be captured by our spatial sampling regime.

The congruence patterns found in this study were consistent with earlier reports. Carlton and Bazzaz (1998), for instance, found higher spatial congruence among soil resources in blow-down sites than in undisturbed forests, mainly due to the increased patch contrast in vegetation and forest floor after blow-down. However, temporal correspondence of the same soil variable sampled at different times within a growing season may be low, with or without the influence of site disturbance, probably due to rapid temporal changes in such factors as plant cover, soil temperature, and soil moisture over a growing season (Ryel et al. 1996; Cain et al. 1999).

Although temporal changes in overall variability, geostatistical parameters, and congruence of limiting soil resources have been shown by earlier studies, this study indicates a temporal trend in overall variability of soil resources after disturbance—a marked increase followed by a rapid recovery. The same pattern was found even when the types of soil resource and site disturbance differed, suggesting that overall variability of soil resources after disturbance may be predictable.

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