RESEARCH ARTICLE

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Effects of Prescribed Fire and Thinning on the Spatial Heterogeneity of the Seed Bank in a Mixed Oak Forest

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ABSTRACT: Prescribed fire and thinning are commonly employed management practices in mixed-oak forests of the central Appalachians. The effects of these practices on the soil seed bank are important to consider in order to evaluate the full impact of these treatments on plant community dynamics in the understory. Species composition of the soil seed bank was examined under three treatments: thin, burn, and thin followed by burning, and an untreated control. Thinning was conducted in Fall 2000, and burns were conducted in Spring 2001. Soil samples were collected in March 2004, three years following treatment. Species composition was assessed by seedling emergence. Seventy total species were found in the seed bank. Ruderal species such as *Erechtites hieraciifolia*, *Carex* spp., and *Rubus* spp. were the most commonly occurring species across all treatments. No significant difference in species composition or proportion of functional groups was found between any of the treatment groups. However, as found in previous studies, species composition of the seed bank and aboveground vegetation were significantly different in all treatments. Species composition and canopy cover were each significantly spatially autocorrelated in the thinned and burned treatment. While thinning and burning did not produce detectable changes in the species composition of the soil seed bank at these sites, they may influence the spatial heterogeneity of the soil seed bank.

Index terms: forest management, Moran's *I*, prescribed fire, soil seed bank, spatial heterogeneity

INTRODUCTION

The soil seed bank consists of viable, ungerminated seeds that are stored in the soil (Bigwood and Inouye 1988). The soil seed bank is an important component of the forest, which may impact several aspects of ecological functioning, including genetic (Nunney 2002; Levin 1990), population (Cohen 1966; Levin 1990), and community-level dynamics (Hyatt and Casper 2000; Wilson et al. 1993). The species composition of the soil seed bank depends on the current aboveground species composition and historical vegetation and land use of an area. Old-growth forests, old fields, and second-growth forests (both post-agricultural forests and those regenerating after non-agricultural disturbance, such as logging or fire) each have a typical complement of life form types present in the soil seed bank (Scheiner 1988; Pickett and McDonnell 1989; Schiffman and Johnson 1992; Hyatt and Casper 2000; Leckie et al. 2000).

Clear differences between the species composition of the aboveground vegetation and the soil seed bank have been found in a number of systems, including disturbed and undisturbed pine and hardwood second-growth forests, and marshes (Olmsted and Curtis 1947; Harper 1977; Morgan and Neuenschwander 1988; Scheiner 1988; Wilson et al. 1993; Carter and Ungar 2002). When the seed bank is divergent from the aboveground vegetation, disturbances that trigger a release of germination from the seed bank may result in a change in the aboveground species composition (Wilson et al. 1993).

Just as patterns can be observed in the arrangement of plants on the landscape, pattern is found in the spatial arrangement of seeds in the soil. Spatial heterogeneity – the tendency of things to be unevenly distributed in space (Dutilleul 1993) – is of critical importance to population dynamics in forested ecosystems. Studies of soil seed banks have revealed spatial heterogeneity at many scales (Major and Pyott 1966; Thompson 1986; Benoit et al. 1989; Matlack and Good 1990; Dessaint et al. 1991; Olano et al. 2002). Fine-scale heterogeneity may result from physical variability, microtopography, or population processes such as seed dispersal patterns that leave seeds more or less concentrated around the parent plant (Harper 1977). The movement and deposition of seeds across the landscape is also dependent on spatially heterogeneous factors, such as roughness of the soil surface, surface depressions, and the presence of bird roosts (Silvertown and Lovett-Doust 1993; Russell and Schupp 1998). Coarse-scale heterogeneity can result from environmental factors such as slope or moisture gradients.

Large-scale disturbances, such as forest management, can impact heterogeneity

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at many scales by creating coarse-scale heterogeneity across the landscape, while also driving finer scales of heterogeneity through impacts on canopy cover and other environmental variables, or on population processes (Walters and Stiles 1996; Brosofske et al. 2001). Patterns of spatial heterogeneity in oak forests are not well understood – in either the understory or the soil seed bank. If we are to understand the ecology of these forests, it is important to understand the plant-relevant scales of variation and to base our studies on such scales (Wiens 1989).

In many eastern deciduous forests, managers have used forest thinning and fire to introduce disturbance for a variety of reasons, ranging from restoration of hypothesized prior conditions to encourage oak regeneration, to management for specific habitats (Brose et al. 2001). These disturbances have been shown to alter the species composition of aboveground vegetation, increasing graminoids, summer forbs, and seed-banking species (Hutchinson et al. 2005). However, few studies have examined the effects of these treatments on the soil seed bank in the eastern deciduous forest.

To assess the impacts of forest management treatments on the composition and heterogeneity of the soil seed bank, we addressed the following objectives: (1) determine if soil seed bank species composition varies among forest management treatments, (2) compare the species composition of the soil seed bank and the aboveground vegetation within each treatment, (3) assess the spatial structure of the soil seed bank under typical forest management regimes at fine scales, and (4) examine environmental variables at fine scales to better understand the relationship of these spatial patterns to those of the soil seed bank.

METHODS

Study Sites

The study sites were located in Vinton County, Ohio, with one replicate at Zaleski State Forest and one at Vinton Furnace Experimental Forest in the Raccoon Ecological Management Area (REMA). Both sites are located in southeastern Ohio, in the Low Hills Belt of the Unglaciated Allegheny Plateau, which is located within the Mixed Mesophytic Forest Region (Braun 1950). This area, with low hills and valleys with moist bottoms, is characterized by deeply dissected topography (Braun 1950). The underlying bedrock is primarily sandstone, overlain by shale (Forsyth 1970). The vegetation consists of mixed oak forest, with *Quercus* spp. and *Carya* spp. as typical forest dominants on the ridgetops and *Acer saccharum* and *Liriodendron tulipifera* more prevalent in the valleys (Braun 1950). The herbaceous layer consists of both herbaceous and woody species, and is highly species-rich, as is common in eastern deciduous forests (Small and McCarthy 2002; Gilliam and Roberts 2003; McCarthy 2003). The average annual temperature is 11.3 °C, with average annual precipitation of 1024 mm (Hutchinson et al. 2005). The forests of this area were clearcut to produce charcoal for local iron furnaces in the mid to late 1800s, but were not cleared for row cropping (Braun 1950; Hutchinson et al. 2005).

Experimental Treatments

The study sites are part of the Ohio Hills unit of the USDA Forest Service's Fire and Fire Surrogate (FFS) study (Yaussy 2001). The FFS Study was designed to investigate the effects of forest management treatments (specifically, thinning and burning) on various aspects of forest functioning. The experimental sites are set up in a randomized complete block design, with four ± 20 ha units in each forest replicate. Each unit was subjected to a different forest management regime: (1) burning, (2) thinning, (3) thinning followed by burning, and (4) an untreated control area (Yaussy 2001). All thinning was conducted in Fall-Winter 2000-2001, and all burns were conducted in Spring 2001 (Yaussy 2001). Thinned areas were commercially thinned from below to ~13.75 $m^2 \cdot ha^{-1}$ of basal area (Yaussy 2001). Burning was introduced to restore what are believed to be historical ecosystem processes by returning frequent, low-intensity fires to the area (Brose et al. 2001). Thinning was introduced to restore what is believed to be historical ecosystem structure (i.e., density and spatial pattern of trees) (Yaussy 2001).

Field Methods

Ten 20-m × 50-m permanent plots were established within each treatment unit. The permanent plots were situated using a random stratified design to place plots evenly across the topographic gradients of our study site. Each 20-m × 50-m plot was divided into ten 10-m × 10-m subplots. Circular 1 m^2 vegetation plots were placed in two opposing corners of each of these subplots (thus, 20 circular plots per permanent rectangular plot). Presence/absence data was collected for the understory layer in these circular plots in the summer of 2004, generating the aboveground data used in this study (Todd F. Hutchinson, U.S. Forest Service, unpubl. data). Soil samples were taken immediately outside the two vegetation plots located in four of the 10 subplots in each 20-m × 50-m plot. The leaf litter layer was removed, and a 10-cm × 10-cm × 5-cm soil sample was collected from the mineral and organic soil. These two soil samples were combined for each subplot to produce one 1000 cm^3 sample, which was used to determine the seed bank. Four such combined soil samples represent each 20-m × 50-m plot ($N = 320$). The soil samples were collected 13-18 March 2004. Collection of samples in the early spring allowed for natural cold-stratification over the winter, thus breaking some seed dormancy (Schiffman and Johnson 1992; Thompson et al. 1997; Bossuyt et al. 2002).

To assess spatial pattern in the seed bank, additional soil samples were collected. Two parallel 20 m transects were laid 50 m apart in both the Control and the Thin & Burn units (the latter assumed to exhibit the greatest heterogeneity) at Zaleski State Forest. Transects were run perpendicular to the slope (along the contour) to avoid picking up possible effects of elevation or moisture gradients. A 10-cm × 10-cm × 5-cm soil sample was collected every 0.5 m along the transects, for $N = 40$ samples per transect. Leaf litter was removed, and the organic and mineral soil layers were collected. Soil samples were collected 14-15 March 2005.

Micro-environmental data (canopy cover, leaf litter depth (cm), and percent cover of bare ground and leaf litter) were collected at each sampling point (40 per transect). Canopy cover was scored on a 1-4 scale, with 1 = 0-25% cover, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%. As percent cover of bare ground was 0 across all transects and treatments and percent cover of leaf litter was 100 across all transects and treatments, no further analysis was performed on these data.

Greenhouse Procedures

Soil samples were collected, placed in Ziploc bags and stored in the cold room at approximately 4 °C until all were collected. A 400 ml subsample of soil from each subplot was sieved and examined to remove any stones and any roots large enough to resprout, and then spread in a 19.8-cm × 19.8-cm × 4.5-cm square aluminum foil cake pan over a 1-cm layer of fine vermiculite.

The pans were placed in the greenhouse, with a 16-hour day, 8-hour night light regime. Temperatures were approximately 25 °C during the day and 15 °C at night. Pans were watered as needed – approximately every other day. Pan location was randomized regularly (approximately once every two weeks) to reduce any effects from microclimatic variations within the greenhouse. Newly germinated seedlings were marked, monitored until large enough to record species, and then removed. Germination was monitored for 450 days (9 April 2004 – 2 July 2005). No new germination occurred after 18 March (day 344). Botanical nomenclature follows Gleason and Cronquist (1991). To detect possible contamination by seeds of greenhouse weeds, pans with greenhouse potting mixture were placed among the sample pans. No greenhouse weeds were detected in this way.

Though this emergence method is widely practiced (Gross 1990; Brown 1992), its main drawback is the potential failure to detect seeds which do not have their dormancy broken or germination conditions met by the conditions provided (in this case, cold-stratification, followed by regular regimes of light and watering). Some have suggested that a combination of emergence and visual inspection is best for optimal detection of seeds and a more accurate representation of the soil seed bank, as the use of either method alone is likely to lead to an underestimation of the seed bank (Schneider and Sharitz 1986; Ishikawa-Goto and Tsuyuaki 2004). Considering these recommendations, a subsample of pans was selected following assessment of the seed bank composition by the emergence method and visually inspected with the aid of a dissecting microscope to determine if any ungerminated viable seeds remained in the soil. Two pans were randomly selected to represent each treatment unit and forest replicate combination for a total of 16 samples. After drying and thoroughly mixing, a 50 mL subsample was drawn from each of the 16 pans and passed through a series of sieves (2.00, 1.40, 1.00, and 0.25 mm). Each fraction was then visually examined with a dissecting microscope. This provided a volume of soil and percentage of total plots and sites examined that was comparable to those used in previous studies that used visual inspection following emergence (Moore and Wein 1977; Matlack and Good 1990; Schiffman and Johnson 1992). This subsampling was not intended to provide quantitative data, but rather to assess the efficacy of the emergence method in this forest type and to determine if some species in the soil seed bank were undetected by the emergence method.

Analytical Methods

Species richness (*S*) of the soil seed bank was compared across the four forest management treatments (10 plots in 2 forest replicates, $n = 20$ for each treatment), and the species richness of the aboveground vegetation was compared with that of the soil seed bank within each treatment. The Shannon-Weiner diversity index (α diversity) was calculated for each treatment area (10 plots in 2 forest replicates, $n = 20$ for each treatment; $H' = -\sum p_i \ln p_i$; Shannon and Weaver 1949). The mean species richness and mean Shannon-Weiner diversity index, and standard errors for each, were also calculated for each treatment. These values were compared with an ANOVA (10 plots in 4 treatments in 2 forest replicates, $n = 80$) using Number Cruncher Statistical Systems (NCSS; Hintze 2001). The use of plots as replicates does raise issues of pseudoreplication because plots located in the same forest may not be truly independent. Moreover, there are only two replicate forests (random effect), which results in decreased power. These problems are typical of most ecosystem scale forest understory studies and cannot be easily rectified. Nevertheless, results provided here may still provide useful insight into patterns of variation.

Because the data were non-normal (and, as is typical of seed bank data, not able to be normalized through transformation (Hyatt 1999)) and not truly independent (as they were collected from only two forests), multivariate analysis techniques were deemed most appropriate (Legendre and Legendre 1998). Sørensen's distance measure was applied to the presence-absence data from the soil seed bank, and the similarity between the soil seed bank composition in the various treatment areas was assessed with cluster analysis using PC-ORD (McCune and Medford 1999). This method was also used to assess the similarity between aboveground and seed bank species composition. In both cases, the flexible beta linkage method was used ($\beta = -0.25$). This combination of distance measure and linkage method was chosen because: (1) the Sørensen distance measure and flexible beta linkage method are compatible, (2) the flexible beta linkage method with $\beta = -0.25$ is space conserving, and therefore performs well while reducing distortion, and (3) this combination of distance and linkage methods minimizes chaining (McCune and Grace 2002). The use of other distance measures or linkage methods (farthest neighbor and group average) did not change the structure of clustering.

A multiple response permutation procedure (MRPP) was also performed using PC-ORD (McCune and Medford 1999).

This nonparametric procedure tests the hypothesis of no difference between two or more groups (McCune and Grace 2002). Sørensen's distance was used. Comparisons were made between each possible pairwise combination of treatment groups. All groups were the same size, consisting of 20 plots. An MRPP was also performed to compare the species composition of the soil seed bank and aboveground vegetation in each treatment area. Again, each group contained 20 plots.

A principal coordinates analysis (PCO) was conducted using the Multi-Variate Statistical Package, Version 3.00 (MVSP) (Kovach 1998). This procedure uses a similarity or distance measure to place plots in multi-dimensional species space, such that plots with more similar composition are located closer to one another and plots with greater compositional differences are placed further apart (Legendre and Legendre 1998).

For data generated by the spatial transects, spatial autocorrelation was used to assess species and environment data. The most commonly used measure of spatial autocorrelation in ecological studies is Moran's I (Moran 1950). This measure essentially provides a single value that summarizes the degree of correlation between two data sets at a given distance of separation. It is analogous to Pearson's correlation coefficient, r (Legendre and Legendre 1998).

Assessment of spatial autocorrelation (Moran's I) was conducted using GS+ (Gamma Design Software 2004). Spatial autocorrelation values were calculated based on species richness (S) and Principal Coordinates analysis (PCO) scores. PCO scores provided a single value that represented the unique species composition of each sample and was appropriate to enter into spatial assessment software. Micro-environmental data (canopy cover and litter depth) were also analyzed using GS+ software to assess spatial autocorrelation. Statistical significance of Moran's I values was tested for every distance class with a Monte Carlo randomization approach using 1000 permutations. Monte Carlo randomization was performed using Rookcase software (Sawada 1999).

RESULTS

Soil Seed Bank Effects

Seventy taxa were recorded across all treatments. Forty-five taxa were identified to species level, 9 taxa were identified to genus, 2 were identified to family, and an additional 14 taxa were recognized as morphologically distinct but not identifiable to taxon – all will hereafter be referred to as "species" (Table 1). Of these taxa, there were 9 annual forbs, 23 perennial forbs, 12 forbs that could not be identified as annual or perennial (44 total forbs), 20 graminoids, 4 shrubs/lianas, and 2 trees. Only three identified species were not native (*Digitaria ischaemum*, *Polygonum convolvulus*, and *Verbascum thapsus*), and none were found frequently. An individual of *Typha* was not identified to species; if *Typha angustifolia*, the total number of non-native species would then be four.

Species richness was determined for each treatment unit, both for each forest replicate and for both sites combined. In combined totals, the Burn unit contained 43 species, the Thin unit contained 37, the Thin & Burn unit had 48, and the Control unit contained 38 species. The mean species richness was not significantly different ($P < 0.05$) among the treatments. The Shannon-Weiner diversity index (H') was calculated for each treatment unit (Burn = 3.23, Thin = 3.03, Thin & Burn = 3.33, Control = 3.11). Mean Shannon-Weiner index values were not significantly different ($P < 0.05$) among the treatments. Visual inspection of the soil at the conclusion of the emergence period revealed seeds of only three species – occurring at low numbers (0-16 seeds per sample) across the treatments. Thus, the emergence method appears to have effectively captured the species composition present in the soil seed bank of these sites.

As revealed by cluster analysis, species composition of the forest management treatment units was not distinct. A multiple response permutation procedure (MRPP) showed largely the same result. Most pairs of treatment groups were not significantly different, but the Control and the Thin & Burn units were significantly different from one another ($T = -1.868$, $P = 0.0497$; Table 2a). The relatively small magnitude of the test statistic (T) values indicates that the groups were only weakly separated. Low chance-corrected within-group agreement (A) values are common for community data. The overall comparison (an analysis of all treatments) showed no significant difference between the groups ($T = -0.935$, $P = 0.1609$).

Separate analysis of the two forest replicate blocks essentially confirmed the results obtained by the combined analysis (Tables 2b and 2c). No overall patterns of treatment differences emerged, though differences between treatments were found within sites. In Zaleski, the Thin & Burn unit was significantly different from both the Thin unit and the Burn unit. In REMA, the Control unit was significantly different from the Thin unit and the Burn unit. Additionally, the Thin & Burn unit was significantly different from the Thin unit. These differences between sites indicate a treatment by site interaction. Such differences could be based in existing biological differences between the treatment units at a given site.

The lack of clear differences in species composition among the treatments was also apparent in the principal coordinates analysis (PCO). Here we see all four treatments overlapping, with no clear trend of separation. One group of plots did fall out separately from all the others – those belonging to the REMA Thin & Burn unit. This unit appears to be compositionally different from not only the other treatments but also from the Zaleski Thin & Burn unit.

Soil Seed Bank vs. Aboveground Vegetation

Aboveground vegetation and soil seed bank composition were distinct, as shown by cluster analysis (Figure 1). All aboveground vegetation plots separated into one cluster, and all the soil seed bank plots grouped into a separate cluster; thus, composition was quite different between the two strata. A significant difference

Table 1. List of species found in the soil seed bank at Zaleski State Forest and Raccoon Ecological Management Area, Vinton County, Ohio. A (v) following the species name indicates that species was also found in the aboveground vegetation. Values in the treatment columns indicate the number of plots species were found in (of 80 overall, and 20 per treatment). Group indicates functional group type: annual forb, AF; perennial forb, PF; other forb, F; graminoid, G; shrub/liana, S; tree, T.

	Total	Burn	Control	Thin	Thin & Burn	Native	Group
Erechtites hieraciifolia (v)	63	12	14	18	19	Y	AF
Carex sp. (*C. pensylvanica* or *C. muhlenbergii*) (v)	60	13	17	15	15	Y	G
Rubus sp. (*R.. occidentalis* or *R. allegheniensis*) (v)	56	16	17	13	10	Y	S
Panicum dichotomum (v)	34	5	7	12	10	Y	G
Carex sp. Wide (*C. platyphylla* or *C. laxiculmis*) (v)	33	8	7	7	11	Y	G
Eupatorium rugosum (v)	30	8	8	7	7	Y	PF
Viola blanda (v)	29	5	6	7	11	Y	F
Panicum sp.	28	10	4	8	6		G
Juncus tenuis	25	7	5	3	10	Y	G
Liriodendron tulipifera (v)	19	2	8	5	4	Y	T
Panicum commutatum (v)	18	7	3	4	4	Y	G
Asteraceae*	17	1	4	5	7		F
Oxalis stricta (v)	17	5	1	8	3	Y	PF
Potentilla sp. (*P. Canadensis* or *P. simplex*) (v)	17	3	4	2	8	Y	PF
Antennaria neglecta (v)	14	2	5	1	6	Y	PF
Hedyotis caerulea (v)	13	2	2	3	6	Y	PF
Phytolacca americana (v)	13	5	1	5	2	Y	PF
Pilea pumila (v)	12	3	5		4	Y	AF
Vitis sp. (*V. riparia* or *V. vulpina*) (v)	11	1	5	2	3	Y	S
Unknown dicot 2	11	1	3	4	3		F
Galium triflorum (v)	10	3	1	3	3	Y	PF
Lysimachia quadrifolia (v)	9	3		2	4	Y	PF
Saxifragaceae (*Heuchera americana* or *Tiarella cordifolia*) (v)	9	1	3	2	3	Y	F
Rhus glabra (v)	8	4	3		1	Y	S
Lobelia inflata	6		1	1	4	Y	PF
Unknown grass 1	6		5	1			G
Acalypha virginica (v)	5	1		2	2	Y	AF
Arisaema triphyllum (v)	4	1			3	Y	PF
Conyza canadensis	4	2			2	Y	AF
Hypericum punctatum (v)	4	1		1	2	Y	PF
Rhus copallina (v)	4		2	1	1	Y	S
Verbascum thapsus	4				4	N	PF
Unknown dicot 5	4	1		3			F
Amphicarpaea bracteata (v)	3			1	2	Y	AF

continued

* presumed to be one species

Table 1. Continued.

	Total	Burn	Control	Thin	Thin & Burn	Native	Group
Anemonella thalictroides (v)	3	1	1		1	Y	PF
Chamaecrista nictitans	3	1	1		1	Y	AF
Hedeoma pulegioides (v)	3		1	1	1	Y	AF
Juncus sp. 2	3		2		1	Y	G
Panicum boscii (v)	3		1	1	1	Y	G
Unknown grass 3	3	1	1		1		G
Acer rubrum (v)	2			2		Y	T
Helianthus divaricatus (v)	2		1	1		Y	PF
Polygonum convolvulus (v)	2	2				N	F
Solidago caesia (v)	2	1		1		Y	PF
Unknown dicot 4	2		2				F
Unknown grass 6	2	1			1		G
Aster lanceolatus	1		1			Y	PF
Cunila origanoides (v)	1	1				Y	PF
Digitaria ischaemum	1				1	N	G
Lespedeza hirta (v)	1		1			Y	PF
Ludwigia alternifolia	1	1				Y	PF
Ludwigia palustris	1				1	Y	F
Muhlenbergia schreberi	1				1	Y	G
Plantago rugelii (v)	1	1				Y	PF
Polygonum punctatum (v)	1			1		Y	AF
Ranunculus sp.	1				1		F
Schizachyrium scoparium	1		1			Y	G
Sisyrinchium angustifolium	1				1	Y	PF
Solanum carolinense	1		1			Y	PF
Solanum nigrum	1			1		Y	AF
Typha sp. (*T. latifolia* or *T. angustifolia*)	1	1				Y/N	PF
*Viola villosa***	1	1				Y	F
Unknown dicot 1	1				1		F
Unknown dicot 3	1				1		F
Unknown grass 2	1			1			G
Unknown grass 4	1	1					G
Unknown grass 5	1				1		G
Unknown grass 7	1	1					G
Unknown grass 8	1	1					G
Unknown grass 9	1				1		G

***Viola hirsutula* (Cooperrider 1995)

Table 2. Multiple response permutation procedure (MRPP) for soil seed bank species composition in four treatments. Comparisons are made for: a) both forest replicates combined, b) Zaleski State Forest, and c) Raccoon Ecological Management Area. *P*-values for Zaleski and REMA have been Bonferroni corrected to account for multiple comparisons. δ_{obs} = observed weighted mean within-group distance, δ_{exp} = expected weighted mean within-group distance, *T* = test statistic, *A* = chance-corrected within-group agreement.

a.	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control vs. Thin	0.661	0.668	-1.517	0.0785	0.010
Control vs. Thin & Burn	0.631	0.639	-1.868	0.0497	0.013
Control vs. Burn	0.661	0.668	-1.517	0.0785	0.010
Thin vs. Thin & Burn	0.622	0.628	-1.211	0.1176	0.009
Thin vs. Burn	0.652	0.657	-0.891	0.1756	0.006
Thin & Burn vs. Burn	0.661	0.668	-1.553	0.0762	0.011

b.	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control vs. Thin	0.612	0.622	-1.092	0.2727	0.016
Control vs. Thin & Burn	0.588	0.596	-0.998	0.3090	0.013
Control vs. Burn	0.647	0.650	-0.382	0.6213	0.005
Thin vs. Thin & Burn	0.547	0.569	-2.636	0.0291	0.038
Thin vs. Burn	0.606	0.622	-1.812	0.1026	0.026
Thin & Burn vs. Burn	0.583	0.607	-2.678	0.0308	0.040

c.	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control vs. Thin	0.578	0.612	-3.448	0.0124	0.055
Control vs. Thin & Burn	0.620	0.635	-1.597	0.1440	0.024
Control vs. Burn	0.646	0.675	-2.987	0.0158	0.044
Thin vs. Thin & Burn	0.629	0.666	-3.235	0.0173	0.056
Thin vs. Burn	0.655	0.658	-0.281	0.7040	0.005
Thin & Burn vs. Burn	0.697	0.715	-1.518	0.1611	0.026

between the aboveground vegetation and the soil seed bank within each treatment area, as well as overall ($T = -95.273$, $P < 0.0001$), was also determined by MRPP analysis (Table 3a). The large magnitude of these *T* values indicates that there is very strong separation between the seed bank and the aboveground vegetation in each treatment. The values of *A* ($A = 0.187 - 0.225$) are within the expected range for community data ($A < 0.3$).

Similar results were found when the same data were analyzed for each forest replicate separately (Tables 3b and 3c). Because factors cannot be nested in an MRPP, separate analyses and tables were generated for each forest to allow site differences to be explicitly examined. As the results were the same (composition of the soil seed bank and aboveground vegetation were significantly different in all treatments), no site difference was found.

The aboveground vegetation was found to contain 253 species (Todd F. Hutchinson, U.S. Forest Service, unpubl. data), and 70 species were found in the seed bank. If unknown species are excluded, there are 244 species in the aboveground vegetation and 56 species in the soil seed bank. Of those, 36 species are held in common. This means that 51.4% (64.3% of identified species) of species in the soil seed bank were found in the aboveground vegetation, but only 14.2% (14.8% of identified species) of aboveground species held seed in the soil seed bank.

Spatial Pattern of the Soil Seed Bank

Species richness exhibited no consistent spatial pattern in either the Control unit or the Thin & Burn unit. In the Control unit, community composition (represented by PCO scores) had no spatial pattern on the scale examined (0-20 m). In the Thin & Burn unit, community composition was significantly spatially autocorrelated along one of the two transects. On that transect, significant positive autocorrelation was discovered at distances of 0.5-4.0 m, and significant negative autocorrelation was found at distances from 10.0-13.5 m (Figure 2). The difference in spatial patterning between the two transects in the Thin & Burn unit indicate a patchy treatment effect or other variability in spatial ordering on the scale of 50 m.

Spatial Pattern of Environmental Variables

Environmental variables were assessed for spatial autocorrelation. Canopy cover was spatially autocorrelated in the Thin & Burn treatment, with significantly positive autocorrelation from 0.5 to 2.0 m and significant negative autocorrelation from 5.0 to 10.0 m on one transect and 8.5 to 10.0 m on the other. This scale of autocorrelation is close to that found for species composition in the Thin & Burn unit, suggesting that canopy cover may drive or contribute to spatial variation in species composition at a fine scale. By contrast, the canopy cover in the Control unit was spatially autocorrelated only from 0.5 to 1.0 m – at very fine scale (Figure 2). Again, this lack of spatial organization in the canopy cover matches the lack of spatial organization in the species richness and composition of the soil seed bank in the Control unit. Litter depth was not spatially autocorrelated at any lag distance over a 20 m scale. This absence of spatial patterning in litter depth was found in both the Control and the Thin & Burn units.

DISCUSSION

Three years following forest management treatments, the species composition of the soil seed bank of treated areas was not strongly altered relative to the Control. This indicates that thinning and burning do not produce a wholesale change in the species composition of the soil seed bank in the short-term (three years following one fire).

Contrasts in species composition between aboveground vegetation and the soil seed bank have been widely reported in the literature from many forest types, including pine and hardwood forests and old-growth and second-growth forests (Scheiner 1988; Schiffman and Johnson 1992; Bossuyt *et al.* 2002; Decocq et al. 2004; Leary and Howes-Keiffer 2004). Here, we found that 51% of species occurring in the soil seed bank were also found aboveground, but only 14% of species in the aboveground vegetation were found in the soil seed bank. This is largely because many of the aboveground species are woodland herbs, which do not generally maintain a persistent soil seed bank (Leckie et al. 2000). Bossuyt et al. (2002) report that in Belgian forests of varying age, the species most frequently found in the aboveground vegetation are absent in the soil seed bank and vice versa. Our findings are quite the opposite – nine of the 10 most frequent species in the soil seed bank were found in the aboveground vegetation, both in the control and the treated units. Thus, it is unlikely that disturbance in these areas would result in a widespread change to the aboveground vegetation due to germination from the seed bank. Other studies in managed deciduous forests (oak and pine-hardwood) have also found species in common between the two strata (Scheiner 1988; Decocq et al. 2004).

Several common seed bank species are prevalent in the aboveground vegetation following disturbance, including *Carex* spp., *Rubus* spp., *Erechtites hieraciifolia*, and *Liriodendron tulipifera*. The majority of the species that are frequent aboveground but not found in the soil seed bank are tree and shrub species (seedlings of canopy and subcanopy species such as *Carya* spp., *Quercus* spp., *Nyssa sylvatica*, *Sassafras albidum*, and shrubs or vines such as *Smilax* spp., *Viburnum acerifolium*, *Toxicodendron radicans*, and *Vaccinium* spp.). Our findings agreed with other studies that have found very few tree species maintaining a soil seed bank (Pickett and McDonnell 1989), with only two tree species (*Acer rubrum* and *Liriodendron tulipifera*) and four shrub (woody) species found in the

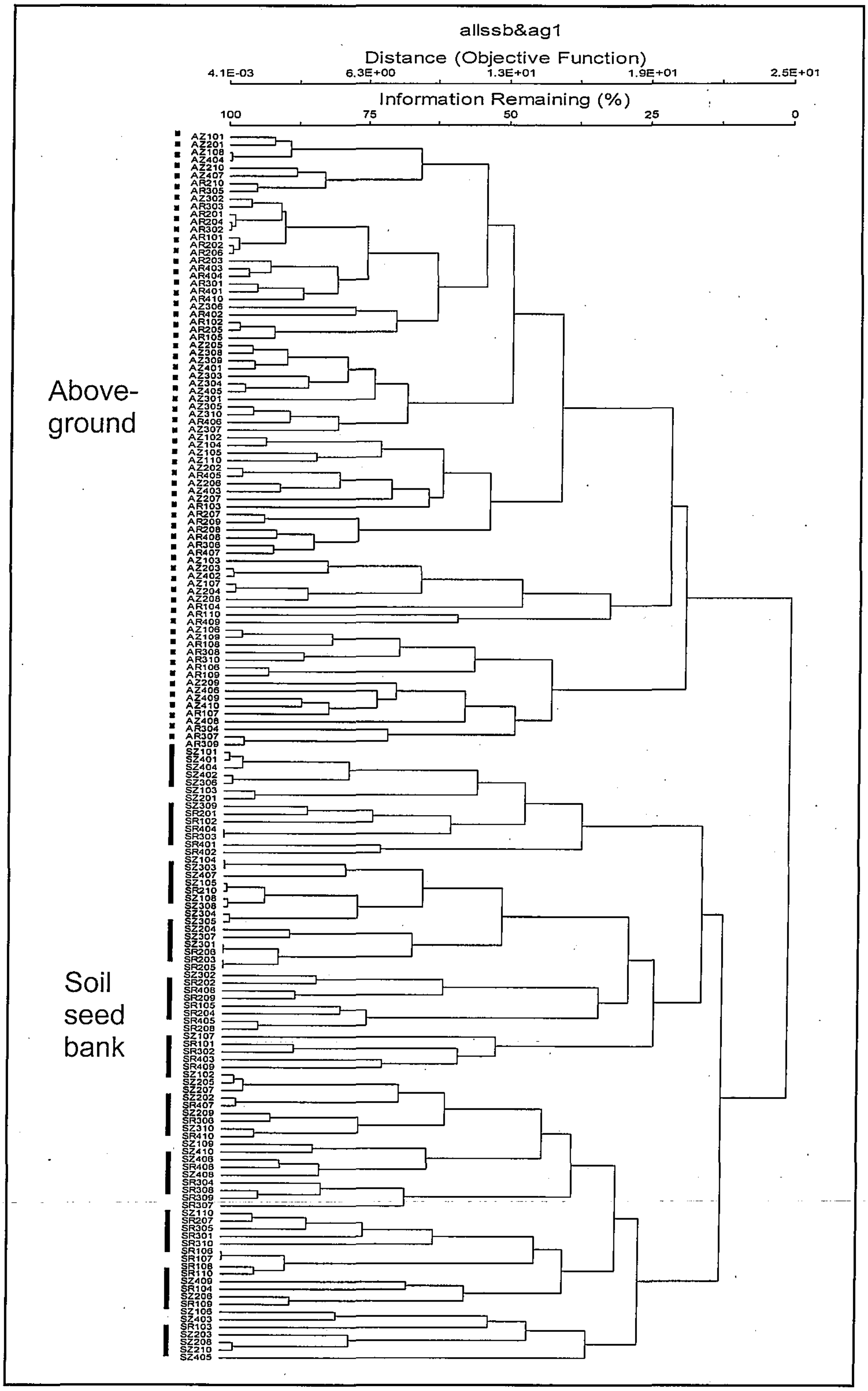

Figure 1. Cluster analysis showing separation of above-ground (dotted line) and soil seed bank plots (dashed line), based on species composition.

Table 3. Multiple response permutation procedure (MRPP) comparing composition of aboveground vegetation and soil seed bank in each treatment. Comparisons are made for: a) both forest replicates combined, b) Zaleski State Forest, and c) Raccoon Ecological Management Area. *P*-values for Zaleski and REMA have been Bonferroni corrected to account for multiple comparisons. The compositions are significantly different in all treatments ($P < 0.05$). δ_{obs} = observed weighted mean within-group distance, δ_{exp} = expected weighted mean within-group distance, *T* = test statistic, *A* = chance-corrected within-group agreement.

a.	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control	0.609	0.761	-23.259	<0.0001	0.199
Thin	0.545	0.703	-23.992	<0.0001	0.225
Thin and Burn	0.577	0.720	-23.117	<0.0001	0.199
Burn	0.611	0.751	-22.595	<0.0001	0.187
Overall	0.597	0.736	-95.273	<0.0001	0.189

b.	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control	0.605	0.766	-11.105	<0.0001	0.210
Thin	0.542	0.693	-11.352	<0.0001	0.218
Thin and Burn	0.468	0.654	-12.309	<0.0001	0.285
Burn	0.583	0.733	-10.854	<0.0001	0.204
Overall	0.570	0.718	-48.257	<0.0001	0.205

c.	δ_{obs}	δ_{exp}	*T*	*P*	*A*
Control	0.576	0.745	-11.695	<0.0001	0.227
Thin	0.499	0.698	-11.844	<0.0001	0.285
Thin and Burn	0.613	0.751	-10.412	<0.0001	0.184
Burn	0.612	0.759	-10.925	<0.0001	0.194
Overall	0.606	0.746	-46.270	<0.0001	0.187

seed bank. Though species of disturbed habitats were common in the seed bank, old-field species were not, which agrees with results from other second-growth forests on land that was never in agricultural use (Scheiner 1988; Schiffman and Johnson 1992).

While a combined MRPP analysis of species composition showed no significance between treatments, separate analyses showed inconsistently significant results. Those treatment pairs that show significant differences at one site are not significant at the other. The one exception to this is in the comparison of the Thin and the Thin & Burn units, which is significant at both sites. Other than this one pairwise comparison, no distinct differences between treatments are apparent at both sites. The inconsistency of these results creates some difficulty in interpretation. While it is possible that these differences are the result of treatment effects, it is equally possible that results found in only one of two forests are the result of individual site idiosyncrasies and not treatment effects. Without trends that appear in both forest blocks, it seems that the results found from the combined analysis (that is, no clear differences in composition between treatment units) hold.

While differences between forest management treatments were not detectable on a broad scale, at finer scales different patterns did become apparent. Differences in fine-scale spatial organization (0-20 m) were apparent in managed and undisturbed forests, both in biological variables (species composition) and physical variables (canopy cover). Though no spatial pattern was found in species composition in the Control unit, in the Thin & Burn unit, plots had more similar composition when located within 4 m of one another and more divergent composition when 10-13.5 m apart. This seems to represent a clustering of species at the scale of a single tree canopy or canopy gap. The spatial range of seed dispersal around a parent plant is also included within this distance (Harper 1977), and may be one factor that helps to structure the clustering of similar species under a canopy or gap. In the Thin & Burn unit, canopy gaps may introduce spatial structuring by encouraging the growth and flowering of certain light-responsive species. These species may then perpetuate themselves in a cluster, driven by short-distance seed dispersal and the light conditions that encouraged their growth initially.

The spatial pattern of canopy cover closely matched that of the species composition in both treatments. This suggests that canopy cover and gaps contribute to, and may be important drivers of, variability in species composition of the seed bank. Compositional differences in understory vegetation have been found to be highly correlated with differences in canopy cover (Brosofske et al. 2001). Differences in spatial pattern of composition are likely due to an interaction of environmental factors, such as canopy gap, and other factors that are spatially dependent, such as seed dispersal, ability of seeds to get to the site, and patchy burn effects (Silvertown and Lovett-Doust 1993).

On our study site, forest management appears to have generated a patchy environment that was not apparent at broad scales but was detectable at fine scales. This may have important implications for management plans and monitoring. At broad scales, physical processes (such as canopy gaps, etc.) can dominate biological effects. However, local biological interactions can create webs of indirect effects that modify the direct effects of physical patterns (Wiens 1989). At the fine, plant-relevant scales, changes in environmental (physical) conditions are detectable. These changes will generate population dynamics effects, which will in turn impact the community dynamics.

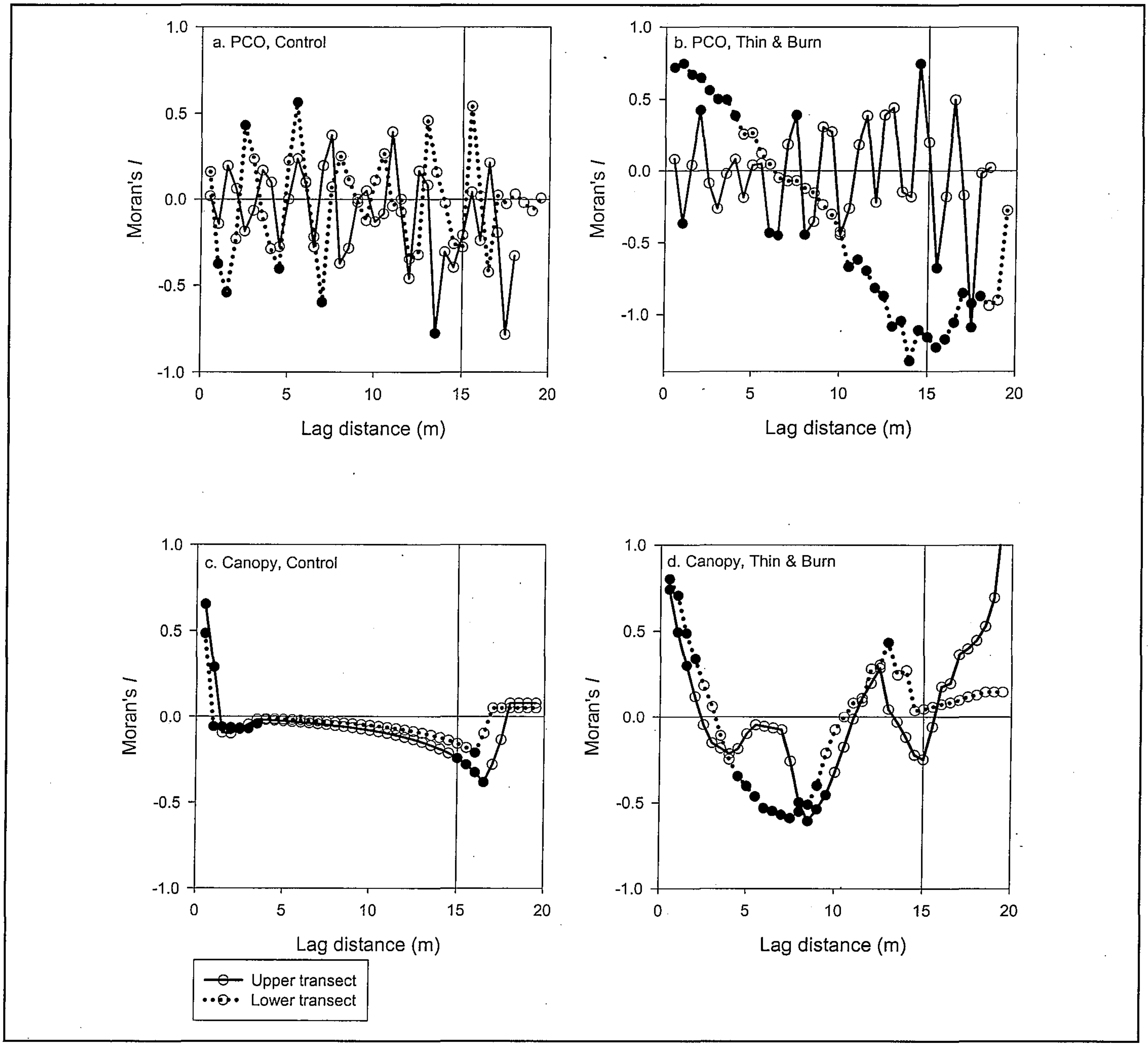

Figure 2. Moran's *I* correlograms for PCO values and canopy cover along two transects in the Control and Thin & Burn units at Zaleski State Forest, Vinton County, Ohio. Filled symbols indicate significant values ($P < 0.05$), based on Monte Carlo resampling (1000 permutations). Values to the right of the vertical line are invalid, as they are based on too few pairs of samples.

While it is widely acknowledged that prescribed fires burn in a patchy manner (Price *et al.* 2003) and that thinning or removal of trees will necessarily result in a patchy mosaic, these spatially patchy effects are generally not explicitly addressed in forest management plans or when studies of the effects of management are being carried out (Wiens 1989). The effects of these treatments may occur on a finer scale than is typically studied in monitoring efforts. This may result in a failure to detect plant-level effects of such treatments. Here, we have looked specifically at impacts on the soil seed bank, which can play a critical role in population and community dynamics. The implications for monitoring are that one must either sample at multiple scales to effectively sample an area or seriously consider the relevant scales before sampling.

The lack of significant autocorrelation in either species richness or species composition in the Control treatment at our study site suggests that, in the absence of management treatments or other disturbance, there may be no clear fine-scale spatial patterns of seed bank composition. Conversely, forest management such as thinning or burning may influence the spatial heterogeneity of both biological and environmental variables. The clear difference in spatial autocorrelation of community composition between the two transects in the Thin & Burn unit suggest a pattern of patchiness on a variety of spatial scales. This patchiness of disturbance should be more fully explored in future studies, and should inform both plans for management and assessments of the impacts of management.

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