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Spatial patterns of mycorrhizal infectiveness of soils long a successional chronosequence

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Abstract This study quantified intersite variation and spatial pattern in arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) infectivity of soils among six sites constituting a successional chronosequence in southwestern Ohio, USA. The study sites included an active agricultural field (chronic disturbance), a site which had been stripped of its surface soil (pseudo-stripmine, acute disturbance), 5- and 10-year-old fields, a 25- to 30-year-old prairie restoration, and an undisturbed, mature forest. AM infectivity was lower in the agricultural field, successional fields, and prairie than in the mature forest, but there was no clear correlation between time since disturbance and the overall level of AM infectivity. Spatial structure in AM infectivity decreased with time since disturbance. In the pseudo-stripmine site and active soybean field, semivariance analysis attributed 44–50% of the total variance in AM infectivity among samples to spatial structure, whereas spatial dependancy accounted for only 18% of total variance in the mature forest. Kriging of AM infectiveness demonstrated small, isolated areas in the disturbed plots that were devoid of AM infectiveness, whereas the kriged AM maps of the other four sites showed AM infectiveness to become progressively more homogeneous. ECM infectiveness was lacking from 35–50% of the samples from the disturbed sites, and both overall ECM infectiveness and ECM diversity increased with time since disturbance. Approximately 44% of the variance in ECM infectiveness was related to spatial structure in the two disturbed sites, and large areas entirely devoid of ECM infectivity were present on the kriged ECM maps for these sites. There was less spatial structure in ECM in the old fields and prairie and very little in the mature forest. The results of this study emphasize the need to explicitly evaluate spatial heterogeneity in mycorrhizal infectivity in studies of the role of mycorrhizae in succession.

Key words Succession · Arbuscular mycorrhizae · Ectomycorrhizae · Infectiveness · Spatial pattern

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Introduction

Conceptual models of the role of mycorrhizae in succession emphasize nutrient availability and mycorrhizal infectiveness of soils in determining whether mycorrhizae assume an important regulatory function (e.g. Janos 1980; Allen and Allen 1990). In most mesic ecosystems, high root density and the ubiquity of long-lived mycorrhizal plants leads to a condition where inoculum (both spores and hyphae) is probably always available to newly germinated seedlings (e.g. Read et al. 1985; Janos 1984, 1992). After disturbance of the vegetation, however, the soils of such sites are more likely to have reduced and/or patchy mycorrhizal infectiveness (Janos 1992), especially for fungi that colonize new roots predominantly from hyphae rather than spores.

Most ecosystems are subject to a variety of natural and human-induced disturbances (Pickett and White 1985). The extent to which mycorrhizal infectiveness is reduced or rendered patchy following a given disturbance depends on the type, duration, and intensity of that disturbance. Thus, residual mycorrhizal infectivity could, for example, be expected to differ significantly between intense, acute disturbances such as surface mining and chronic disturbances such as row crop agriculture. Furthermore, the effect of a given disturbance may differ between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi. Before the role of mycorrhizae as regulators of succession in a given biome or ecosystem can be fully evaluated, the effect of various disturbances on both the mean level of soil infectiveness and the spatial pattern of infectiveness must be quantified. The specific objectives of this study were (1) to quantify overall levels of AM and ECM infectiveness

of soils, and (2) to determine the spatial heterogeneity in infectiveness along a successional chronosequence in southwestern Ohio.

Materials and methods

Study areas

We chose a total of six sites for this study, of which two were recently disturbed, two were successional, and two were mature communities. Five of the six were located within a 500-ha area at the Miami University Ecology Research Center in Oxford, Ohio. Site 1 was an active agricultural field which had been in soybeans (*Glycine max* L.) for the previous 5 years. This site was our chronically disturbed site and had been farmed continuously for at least 25 years. Site 2 was an area we termed a pseudo-stripmine, which had been stripped of its surface soil, leveled, compacted, and broadcast planted with the stress-tolerant grasses *Agrostis alba* L. and *Bromus commutatus* Schrad. This was our acutely disturbed site. Sites 3 and 4 were a 5-year-old field dominated by *Solidago* spp. and *Festuca eliator* L. and a 10-year-old field dominated by *Solidago* spp. and *Aster* spp. with scattered young *Juniperus virginiana* L. Site 5 was the Wilson Prairie, a 25- to 30-year-old tallgrass prairie restoration dominated by *Andropogon gerardii* Vitman and *Solidago canadensis* L. All five sites were located on Xenia silt loam (typic hapludalfs), formed on calcareous glacial till overlain by loess (Lerch et al. 1980). Xenia series soils are circumneutral (pH range 6.6–7.3) and have high water-holding capacity (Lerch et al. 1980).

The sixth study site was located in Hueston Woods State Nature Preserve, 4.5 km from the other five sites. Hueston Woods is dominated by *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., and *Fraxinus americana* L., and has remained undisturbed since Euro-American settlement (Runkle et al. 1984). The Hueston Woods site was located on Russell silt loam (typic hapludalfs) formed on calcareous glacial till (Lerch et al. 1969). Russell series soils are also circumneutral in reaction (pH range 5.6–7.3) and are high in organic matter and water-holding capacity (Lerch et al. 1969).

Sampling design

In each of the six study areas, we established three random 5×5 m sample plots within an area of 900 m^2 in mid-June 1992. Although most studies of spatial pattern in soil properties and processes focus on a single plot (e.g. Robertson 1987; Robertson and Freckman 1995), we analyzed three plots in each study area to gain insight into the variation in spatial dependence within study areas. In each sample plot, we established 32 sample points in a regular grid. A regular sampling design within random plots was used in order to facilitate later interpolation and mapping of infectiveness within each plot. The minimum and maximum distances between sample points in each sample plot were 100 cm and 707 cm, respectively.

At each sample point we cleared the surface litter or debris by hand, then extracted two A-horizon soil cores (2 cm diameter and 8–12 cm length) as close to each other as possible. Typically, the two cores came from an area of no more than 15 cm^2. The intact soil cores were transported to the greenhouse under refrigeration.

Infectiveness analysis

In the greenhouse, we packed the soil cores from each sample point into "fir-size Cone-tainers" (Cone-tainer Nursery, Canby, Ore). For mycorrhizal infectiveness bioassays, one of each pair was planted with two seeds of *Panicum virgatum* L. (switchgrass), a perennial grass with strong AM dependency and responsiveness (Boerner 1992), and the other with two seeds of *Pinus rigida* Mill. (pitch pine), an ECM-dependent species. The *Panicum* seedlings emerged in 2–3 days and the *Pinus* seedlings in 6–8 days. Cone-tainers in which seedlings did not appear by day 8, or in which seedlings had emerged prior to day 8 and subsequently died, were replanted on day 9. To control for mycorrhizal inoculum dispersing into the Cone-tainers via air or water, control *Panicum* and *Pinus* seeds were also planted in sterile sand + peat; all controls were free of infection at harvest.

The plants were then grown for 8 additional weeks (i.e. July and August) in a glasshouse at ambient light and temperature, and fed weekly with low-P Ruakura solution (Smith et al. 1983). After harvest, the root systems of the *Panicum* plants were cleared and stained with trypan blue (Phillips and Hayman 1970) and infection of 10 randomly chosen 2.0-cm root sections per seedling was assessed (Giovanetti and Mosse 1980). Any root segment in which we could observe vesicles or arbuscules was considered to be infected, regardless of the proportion of that segment with AM structures. We used this relatively rapid procedure to assess infection because prior studies of AM infection in *Panicum virgatum* in our laboratory (e.g. Boerner 1992) had established that this procedure produces estimates not significantly different from those obtained by counting entire *Panicum virgatum* root systems using a gridline intercept system.

The root systems of the *Pinus* plants were preserved in formalin : acetic acid : ethyl alcohol, and the number of root tips with visible ECM infections was determined under a dissecting microscope. We considered any short roots with visible mantle development and morphology/color different from the long, narrow, white appearance of uninfected roots from our controls to be ECM infected. We performed checks on questionable root tips by trypan blue staining and microscopic inspection. No attempt was made to trap culture and identify the AM fungi in the bioassays, and ECM identification was limited to differentiation of ECM types based on color, morphology, and mantle characteristics.

Statistical analysis

Because the proportion of root segments exhibiting AM infections varied from 0% to 100% and was normally distributed (mean of 61%), we utilized this metric as our measure of AM infectiveness. We could not, however, use the proportion of root tips exhibiting ECM infections as a metric for infection intensity because the distribution was strongly bimodal; *Pinus* bioassay seedlings exhibited either 0% or 98–100% of root tips infected. This distribution was so strongly bimodal that we could not transform the data to a normal distribution using standard transformation techniques, and normality is a requirement for subsequent semivariance analysis. Thus, instead of percent ECM infection, we utilized the number of root tips with ECM infections as our index of infectiveness, as this parameter was both normally distributed (mean of 253 infected tips/seedling) and well correlated with above-ground seedling mass ($r = 0.897$, $P < 0.01$).

Levels of AM and ECM infectiveness were first tested for normality and homogeneity of variances, then subjected to analysis of variance, with sample plots nested within study areas (SAS 1985). All significant differences were at $P < 0.05$ unless otherwise indicated.

In any system structured by nonrandom processes, samples taken from locations close together are more likely to be positively correlated with each other than are samples taken farther apart. To quantify the degree of spatial autocorrelation existing among our samples, to determine the maximum distance at which infectiveness levels were significantly correlated, and to facilitate subsequent mapping of infectiveness patterns, we used semivariance analysis (GS^+ Version 2.0, Gamma Design Software, Plainwell, Mich.). Semivariance analysis calculates an autocorrelation index (the semivariance) among groups of pairs of samples separated by a given distance, and then produces a composite graph of the relationship between the semivariance among samples and the distance between samples (the semivariogram). GS^+ then fits

a range of models to the semivariogram by unweighted least-squares analysis. From the best fit model for the semivariogram, the total model variance can be divided into one component related to spatial pattern or structure in the data set (the structural variance, C) and a second component which combines variance due to spatially dependent properties operating at scales larger or smaller than those encompassed by the sampling design and sampling/analysis error (the nugget variance, C_0). We used the proportion of total model variance ($C+C_0$) represented by structural variance as a measure of spatial dependence (cf. Robertson and Freckman 1995). In a system that is strongly spatially structured, the proportion of total variance accounted for by the structural variance component will approach 1; in contrast, in systems with little spatial structure, or where the actual scale of the spatial structure is either larger or smaller than that defined by the sampling design, the proportion of total variance accounted for by structural variance will be small. After the best-fit semivariogram model was constructed, it was used to map infectiveness patterns for each plot by kriging (a form of nonlinear interpolation for mapping) using SURFER (Golden Software, Golden, Colo.).

Results

Chronosequence patterns

Over all study sites, >97% of the AM bioassays with *Panicum* developed an AM infection (Fig. 1). Although none of the 192 bioassays from Hueston Woods or the Wilson Prairie failed to develop an AM infection, the AM bioassay failure percentage was significantly greater than 0 in the two disturbed sites (soybean field and pseudo-stripmine) and the two successional sites (5- and 10-year-old fields).

The percent of total root segments with AM infections varied significantly among sites, but not in a consistent temporal pattern (Fig. 1). The highest levels of AM infection were present in seedlings grown in soils from Hueston Woods and the pseudo-stripmine and the lowest in soils from the soybean field, 5-year-old field and the Wilson Prairie. Thus, sufficient AM infectiveness existed in these sites for 95–100% of seedlings to establish an AM relationship within 8 weeks, and variation in infectiveness among sites was not correlated with time since last disturbance.

The temporal patterns of ECM infectiveness were quite different from those of AM. The proportion of *Pinus* bioassays that failed to develop any discernable ECM infection decreased with time since disturbance, from 38–48% in the disturbed sites to 1–3% in the mature sites (Fig. 2). Furthermore, the number of ECM root tips per *Pinus* seedling increased from a mean of <100 ECM tips/seedling in bioassays from the soybean field to >450 ECM tips/seedling in bioassays from Hueston Woods. The number of distinct ECM types also increased with time since last disturbance, and the number of rare ECM types (defined as those present on <5% of the root tips) was three-fold higher in the bioassays from Hueston Woods, Wilson Prairie and the 10-year-old field than in the three younger sites (Fig. 3). Thus, both ECM infectiveness and diversity both increased with time since last disturbance.

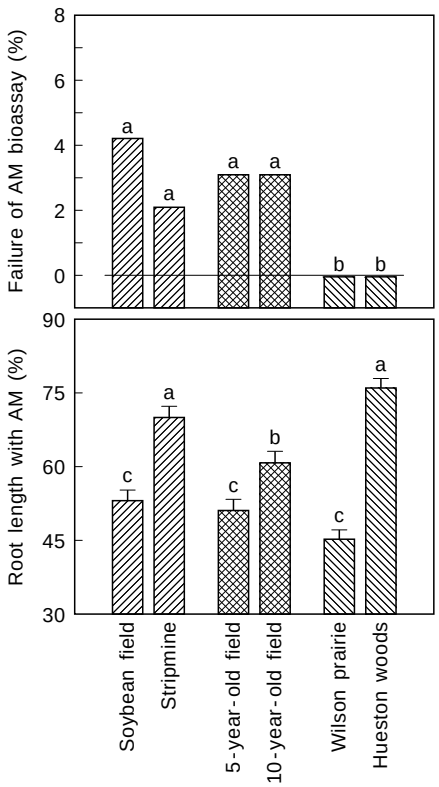


Fig. 1 Two measures of arbuscular mycorrhizal (AM) infectiveness of soils based on *Panicum virgatum* bioassays. Each histogram bar represents the mean of 96 bioassays, with standard errors of the means also indicated. Within a row, histogram bars labelled with the same lower case letter were not significantly different at $P<0.05$ following analysis of variance

Spatial patterns

To evaluate spatial heterogeneity at a coarse level of resolution, we performed an analysis of variance for each study site using the sample plots as the main effect. These analyses indicated no significant spatial differences in AM infectiveness within any site, and no significant spatial differences in ECM infectiveness in the pseudo-stripmine, Hueston Woods, or Wilson Prairie sites. There were, however, significant differences in ECM infectiveness among plots in the soybean field and the two successional fields.

To better resolve finer scale spatial patterns of infectiveness within and among sample plots, we subjected the AM and ECM infectiveness patterns to semivariance analysis and generated interpolated maps of infectiveness in each study plot from the best-fit models for the semivariograms by kriging. Semivariograms with both a sill and fit of $r^2 \geq 0.200$ could be fit to the AM infectiveness levels for 13 of the 18 study plots, including all three plots from the soybean field, the 5-year-old field, and the Wilson prairie, but only one of three plots in Hueston Woods (Table 1). The proportion of total model variance attributable to spatial structure was greatest in the pseudo-stripmine

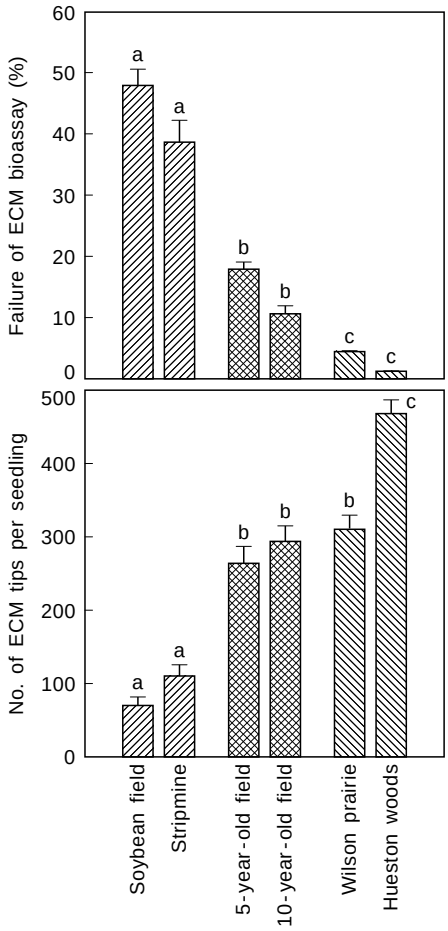


Fig. 2 Two measures of ectomycorrhizal (ECM) infectiveness of soils based on *Pinus rigida* bioassays. Format follows Fig. 1

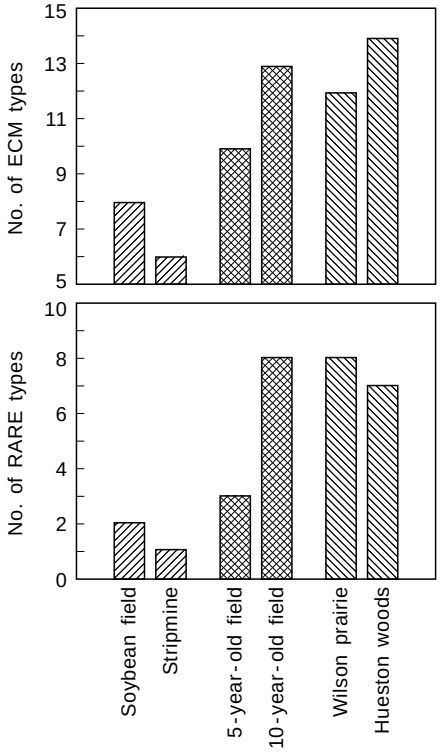


Fig. 3 Ectomycorrhizal diversity in *Pinus rigida* bioassays from six southwestern Ohio study site. The total number of ECM types (defined by color, morphology, and mantle characteristics on short roots) and the number of rare ECM types (defined as being present on $<5\%$ of the root tips in any study site) are given. Each histogram bar represents 96 bioassays

(mean = .501) and soybean field (mean = .438) and lowest at Hueston Woods (mean = .179). Overall, spatial structure in AM infectiveness decreased with time since disturbance.

The kriged maps for the pseudo-stripmine and soybean field plots exhibited spatial gradients from distinct areas of low to high AM infectivity (Fig. 4). As a result, samples taken close together would be more likely to be highly correlated than samples from farther apart on the gradients, and the plots appeared to be strongly structured spatially. This pattern was particularly striking in plots 2 and 3 of the active soybean field, where areas of low and high infectivity were separated by distances of 100 and 212 cm, respectively. These were the only plots in which significant directionality (anisotropy) in AM infectivity was present, with spatial patterns of AM infectivity correlating well with plowing patterns.

The AM infectiveness plots for the 5- and 10-year-old fields (Fig. 5) showed small, isolated areas of either very high or very low AM infectiveness within a larger matrix of intermediate infectiveness. Most of the isolated points with low infectiveness were associated with sites of concentration of typically nonmycotrophic plant species [e.g. *Juncus tenuis* Willd., *Carex complanata* Torr. & Hook., and *Lepidium campestre* (L.) R. Br.]. The presence of these isolated patches, especially in the 10-year-old field, was the reason that the semivariance analysis attributed a minor proportion of the total variance in AM infectiveness in these sites to spatial structure. The kriged maps for the plots in the mature sites showed them to be fairly uniform, with moderate infectiveness in the Wilson Prairie plots and high infectiveness in the Hueston Woods plots (Fig. 6). Thus, we observed the greatest spatial structure in AM infectiveness in the soybean field and pseudo-stripmine site, and the least in the mature prairie and forest sites.

The pattern for ECM infectiveness differed markedly from the AM pattern. Semivariance analysis produced significant ($r^2 \geq 0.200$) semivariograms with a detectable sill for only nine of the 18 plots sampled, including all three in the soybean field, two in each of the old fields, and none in Hueston Woods (Table 1). In the two disturbed sites, spatial structure accounted for 33.3–50.5% of the total variance in ECM infectiveness among samples within a plot, and the kriged maps generated from the semivariograms showed small, distinct patches of moderate ECM infectiveness surrounded by

Table 1 Semivariance analysis of spatial structure in arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) infectiveness of soil in six sites in southwestern Ohio ($N=96$ for each site). Structural variance is expressed as the proportion of structural + nugget variance represented by structure, and range is the lag distance at which the semivariogram asymptotes to the sill

Site	Plot	Nugget variance (C_0)	Total model variance ($C+C_0$)	Structural variance $C/(C+C_0)$	Model form	Model fit r^2	Range (cm)
AM infectiveness							
Pseudo-stripmine	1	3.82	7.83	0.512	Gaussian	0.879	646
	2	1.98	3.14	0.369	Spherical	0.157	268
	3	3.64	9.65	0.623	Gaussian	0.578	1127
	Mean			0.501			
Soybean field	1	4.09	9.92	0.588	Linear/sill	0.485	647
	2	2.23	3.23	0.310	Linear/sill	0.315	100
	3	2.37	4.06	0.416	Exponential	0.367	212
	Mean			0.438			
Five-year-old field	1	2.07	3.11	0.334	Linear/sill	0.787	212
	2	2.91	4.66	0.376	Linear/sill	0.623	445
	3	1.79	3.83	0.533	Linear/sill	0.666	158
	Mean			0.414			
Ten-year-old field	1	3.26	5.16	0.328	Exponential	0.161	212
	2	2.94	>2.94	0.000	Linear	0.498	>707
	3	2.52	3.79	0.335	Spherical	0.136	212
	Mean			0.221			
Prairie	1	1.70	5.71	0.703	Gaussian	0.788	1069
	2	2.72	>2.72	0.000	Linear	0.310	>707
	3	2.42	3.72	0.353	Gaussian	0.558	521
	Mean			0.352			
Hueston Woods	1	2.27	3.77	0.398	Spherical	0.186	212
	2	3.01	3.02	0.003	Exponential	0.186	30
	3	3.06	3.55	0.138	Linear/sill	0.444	349
	Mean			0.179			
ECM infectiveness							
Pseudo-stripmine	1	5584	11190	0.501	Linear/sill	0.024	212
	2	3560	7233	0.508	Exponential	0.592	393
	3	15450	31430	0.508	Exponential	0.152	1799
	Mean			0.506			
Soybean field	1	7305	10960	0.333	Spherical	0.454	212
	2	10140	15220	0.334	Spherical	0.361	212
	3	17100	29630	0.423	Linear/sill	0.210	158
	Mean			0.363			
Five-year-old field	1	7260	13000	0.442	Exponential	0.215	212
	2	35710	65290	0.453	Exponential	0.414	212
	3	31100	45480	0.316	Linear/sill	0.135	157
	Mean			0.404			
Ten-year-old field	1	20830	27570	0.244	Linear/sill	0.566	641
	2	23020	38620	0.404	Exponential	0.436	212
	3	37300	43290	0.138	Gaussian	0.024	250
	Mean			0.262			
Prairie	1	26400	47980	0.450	Linear/sill	0.139	157
	2	34800	>34800	0.000	Linear	0.248	nd
	3	23900	35850	0.333	Spherical	0.352	212
	Mean			0.261			
Hueston Woods	1	41900	41920	0.001	Linear	0.389	nd
	2	36400	50950	0.286	Exponential	0.069	773
	3	39220	40510	0.032	Linear	0.293	nd
	Mean			0.106			

large areas without ECM inoculum (Fig. 7). As was the case for AM infectiveness, the range of spatial variation in ECM infectiveness in the soybean plots (158–212 cm) was correlated well with the plowing pattern, whereas in the pseudo-stripmine site the range of spatial variation varied almost tenfold among the three plots (Table 1). In only one of the six plots in these two sites (soybean no. 3) did areas with moderate infectivity cover ≥25% of the plot area. Seeds of ECM-dependent plants entering these two study areas stood a con-

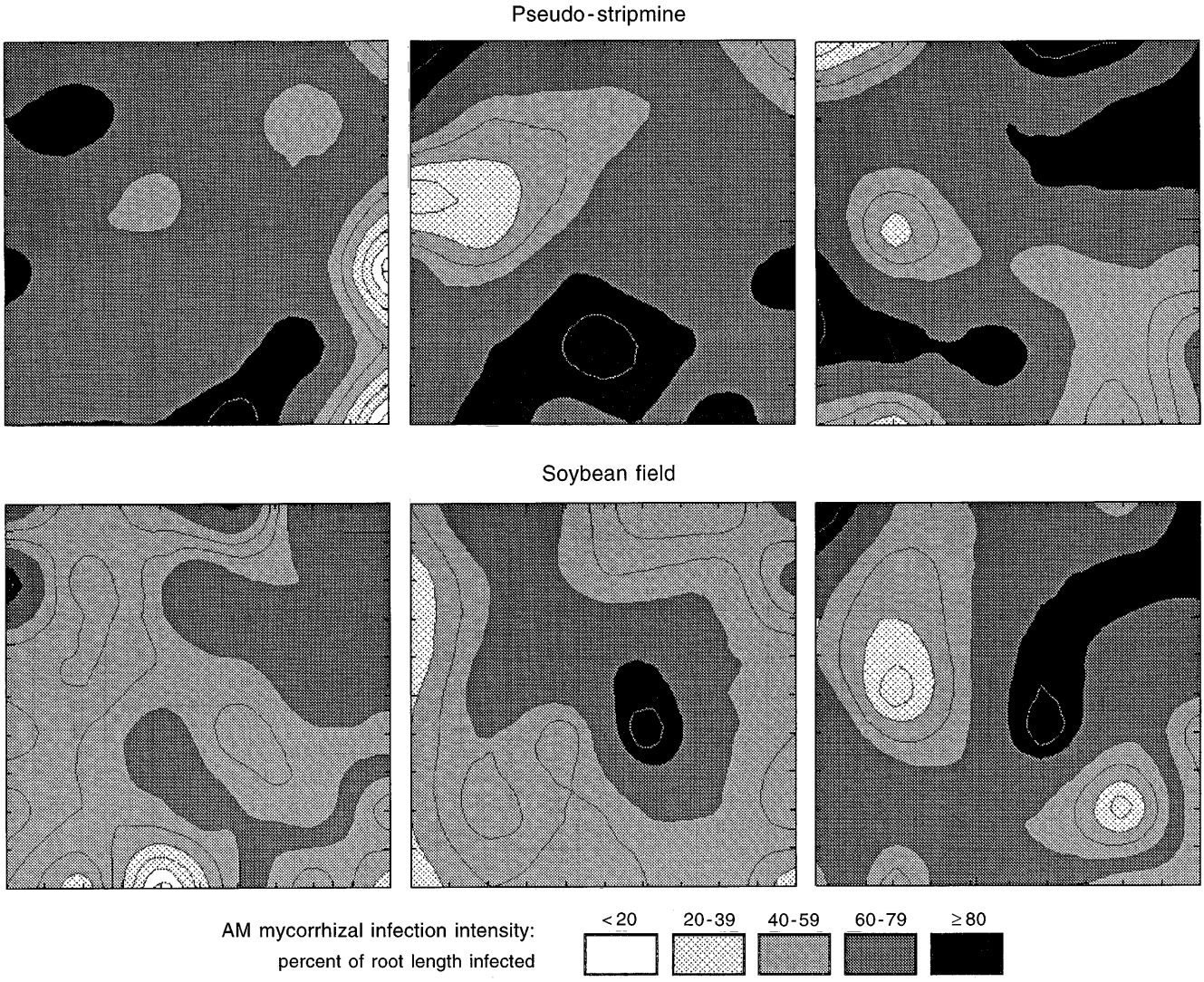


Fig. 4 Arbuscular mycorrhizal infectiveness of soil, as measured by the percent of root length infected in *Panicum virgatum* bioassays, in 5 × 5 m study plots in a pseudo-stripmine and active soybean field in southwestern Ohio. The maps were generated by kriging from 32 sample points using the best-fit semivariogram. Tick marks on the axes indicate 50-cm intervals

siderable chance of not encountering ECM inoculum in the volume of soil into which their roots could initially grow.

In the 5- and 10-year-old successional sites, spatial structure accounted for 13.8–45.3% of total variance among samples within a plot (Table 1). Overall, the proportion of total ECM infectiveness model variance attributable to spatial structure in the 5-year-old was similar to the mean for the six disturbed plots. However, the proportion of spatial variance in ECM infectiveness in the plots in the 10-year-old field was approximately 35% lower than that of the 5-year-old field and 41% lower than the mean for the two disturbed sites. The kriged plots for the successional sites (Fig. 8) showed an intermixing of areas of low, intermediate, and high ECM infectiveness, particularly in plot 2 in each site (Fig. 8). Although the areas of low ECM infectiveness were smaller and more isolated than in the disturbed plots, there were still distinct patches without significant ECM inoculum in the successional sites.

As was the case for the overall level of ECM infectiveness, the spatial dependency and pattern of ECM infectivity in the Wilson Prairie were similar to those of the two successional sites (Table 1 and Fig. 9). In contrast, semivariance analysis detected little spatial structure in ECM infectiveness in soils from Hueston Woods within the range that could be detected by our sampling design (Table 1). Most of the area within the kriged plots in Hueston Woods had moderate-to-high ECM infectivity, and the kriged plots in the mature forest showed the soils in this site to be virtually an unbroken matrix of high ECM infectiveness (Fig. 9).

To express the combined spatial and successional variations in AM and ECM infectiveness from the perspective of colonizing seedlings, we classified each of our 576 sample points into "unsuitability classes" based on which types of mycorrhizal infectiveness they

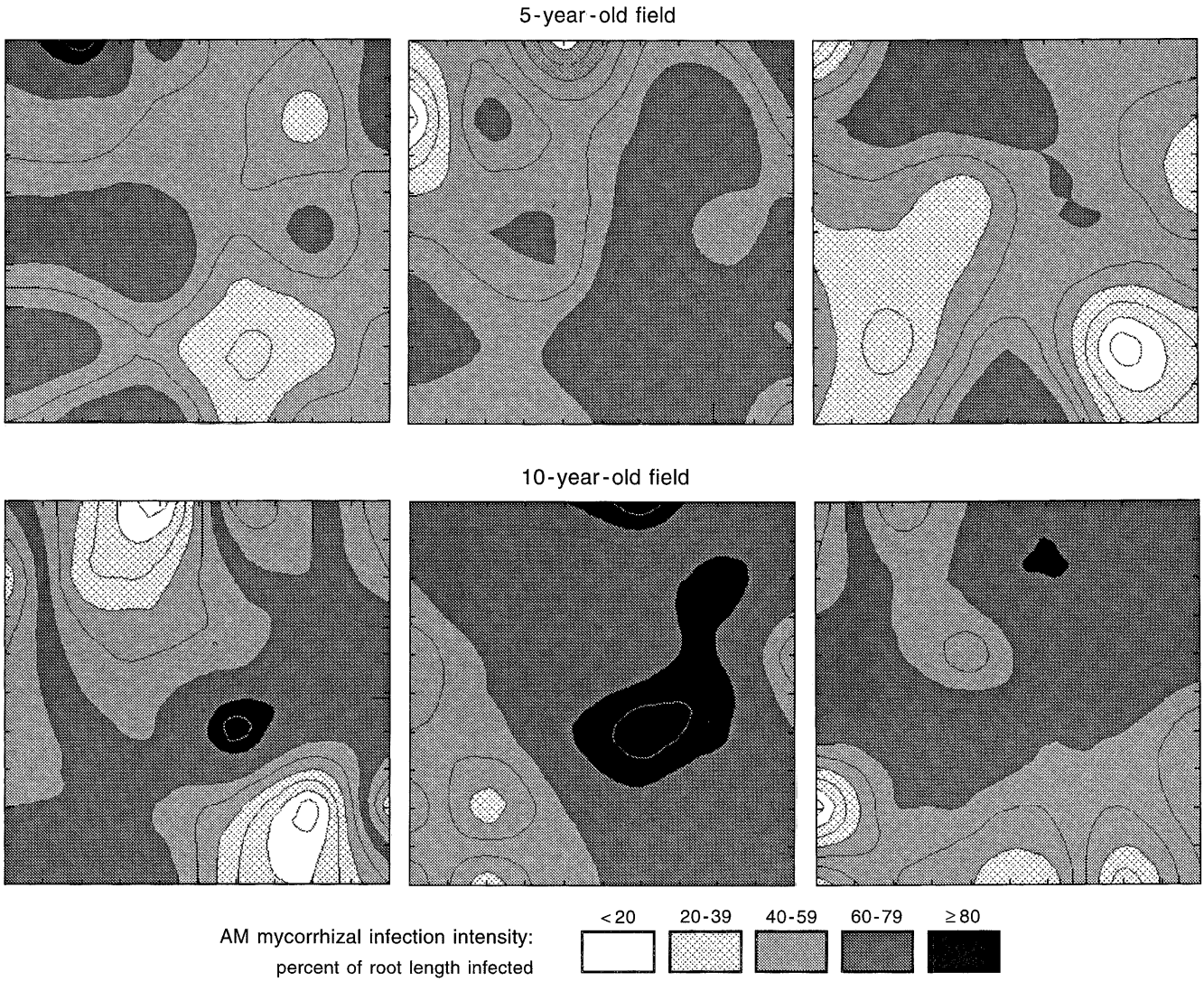


Fig. 5 Arbuscular mycorrhizal infectiveness of soil in 5- and 10-year-old fields in southwestern Ohio. Format follows Fig. 4

lacked. The frequency of sites unsuitable for the establishment and growth of ECM-dependent species (i.e. sample points without ECM infectiveness but with significant AM infectiveness) decreased from 57–67% of sample points in the two disturbed sites to <20% in the 10-year-old field and prairie, and to 3% in the Hueston Woods plots (Table 2). In contrast, the frequency of sample points unsuitable for establishment and growth of AM-dependent species (i.e. sample points with no AM infectivity but significant ECM infectivity) ranged from 0–6% and did not vary consistently with time since last disturbance. In five of the six study areas there was a single sample point in which both AM and ECM infectivity were lacking.

Discussion

Our bioassays of mycorrhizal infectiveness confirmed that conventional row crop agriculture reduced AM infectiveness of soils relative to the levels in an undisturbed forest, a result consistent with others from a variety of temperate ecosystems (review by Douds 1994). Excluding for the moment the pseudo-stripmine site, there was no indication from our chronosequence that predisturbance levels of AM infectiveness would be reestablished during the first 25–30 years of succession following abandonment from agriculture (i.e. up through the age of the Wilson Prairie since conversion from agriculture to grassland vegetation), despite dominance of the two successional sites and the Wilson Prairie by perennial, AM-dependent plants. Waalend and Allen (1987) reported a similar pattern in a cold desert ecosystem: no differences in mycorrhizal activity in sites of 1–30 years since disturbance, but levels consistently lower than those found in mature areas.

ECM infectiveness of the active soybean field was reduced by agricultural practices to an even greater extent than was the AM infectivity. The soils from almost half of the points we sampled in the soybean field failed to produce ECM infections on pitch pine seedlings, and those seedlings that did acquire some ECM infection

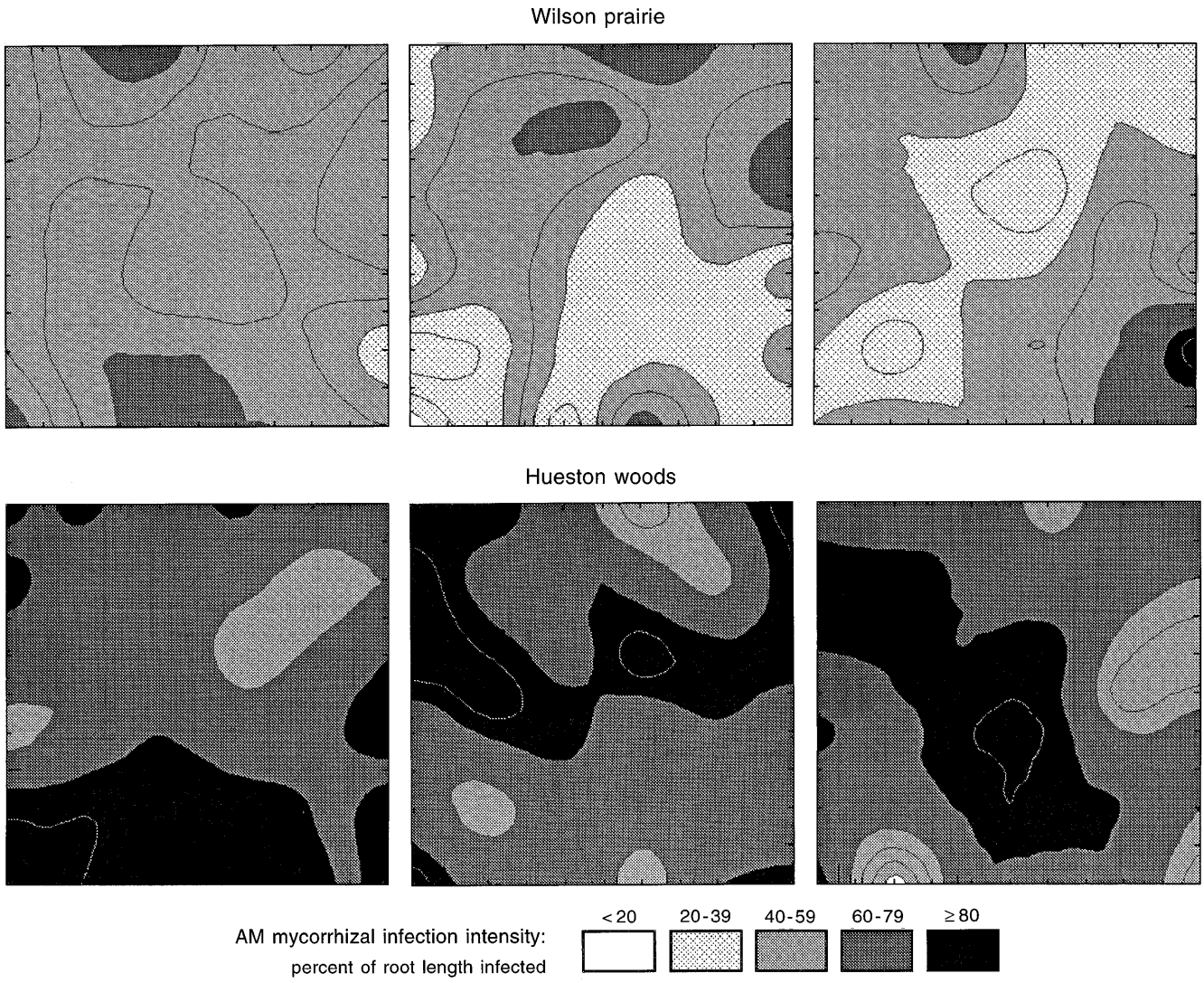


Fig. 6 Arbuscular mycorrhizal infectiveness of soil in the Wilson Prairie and Hueston Woods in southwestern Ohio. Format follows Fig. 4

were very sparsely colonized. ECM infectiveness and diversity increased steadily through our chronosequence, and this result was consistent with similar studies in birch plantations in the UK (Deacon and Fleming 1992). In contrast to what we observed for AM infectivity, our ECM data suggest that predisturbance levels of ECM infectiveness could be reestablished in 25–30 years after abandonment of agriculture.

ECM infectiveness was also reduced by the removal of the surface soil and subsequent leveling and compaction of our pseudo-stripmine site, but AM infectiveness was not reduced significantly. It was not surprising to us that some AM infectiveness remained in this site, because previous studies of mining practices (e.g. Bondini et al. 1985) have shown that removing the vegetation and the top 30 cm of soil in preparation for mining reduces but does not eliminate AM infectiveness.

Three factors may have contributed to the greater disruption in the ECM infectiveness of the site. First, there may have been relatively little ECM infectiveness present prior to surface soil removal. The pseudo-stripmine site had been farmed until approximately 6 months prior to treatment, and may have had low and patchy ECM infectiveness similar to that observed in the active soybean field. Second, the vertical distribution of ECM and AM inocula in the soil profile may have differed prior to disturbance such that the removal of the surface soil affected ECM fungi that were localized in the surface soils. Finally, differences in dispersal into the pseudo-stripmine during the two growing seasons after the initial disturbance may have produced or augmented these differences. Winter erosion of surface soil from neighboring farm fields is common in this region, and both wind erosion (Warner et al. 1987) and water erosion (Friese 1984) can be effective dispersal mechanisms for AM fungi. In contrast, wind velocities near the forest floor of nearby forest patches may not be sufficient for significant long-distance dispersal of spores of epigeous ECM fungi, leaving disper-

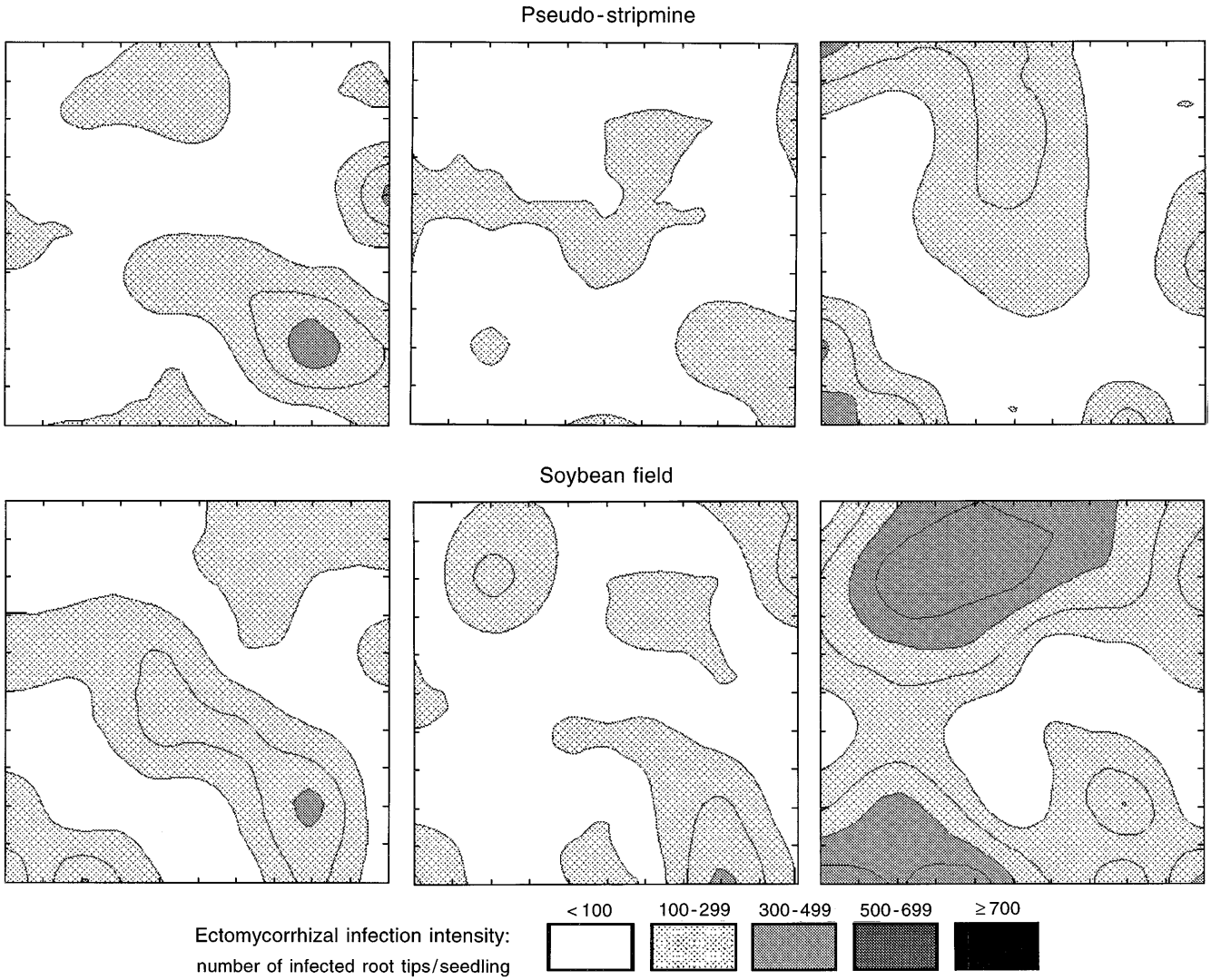


Fig. 7 Ectomycorrhizal infectiveness of soil, as measured by the number of infected root tips per seedling in *Pinus rigida* bioassays, in 5 × 5 m study plots in a pseudo-stripmine and active soybean field in southwestern Ohio. The maps were generated by kriging from 32 sample points using the best-fit semivariogram. Tick marks on the axes indicate 50-cm intervals

sal by rodents as the primary mode of transport of ECM inoculum to the pseudo-stripmine site (cf. Maser et al. 1978). The high degree of spatial heterogeneity in ECM infectiveness in both the soybean field and the pseudo-stripmine site are also consistent with the notion that inoculum was brought into those sites in discrete bundles of high infectiveness potential, such as sporocarps in faeces.

In addition to the significant effect of row crop agricultural practices on the mean level of AM infectivity, this chronic source of disturbance produced an increase in spatial heterogeneity and structure in AM infectiveness. In both the active soybean field and the pseudo-stripmine, we were we able to resolve significant spatial structure in AM infectiveness within the range limits of our sampling design. Thus, for a newly germinated seedling, the lag time prior to the initial establishment of an AM infection and the rate at which that infection developed may have differed as a function of both the differences in mean infectiveness (Wilson and Tommerup 1992), and the likelihood that a germinating seedling would encounter AM inoculum in the volume of soil its root could explore. Furthermore, the actual spatial distribution of AM fungal spores (Anderson et al. 1983; Friese 1984; Sylvia 1986; St. John and Koske 1988) and AM hyphae (Allen and MacMahon 1985) may well have been strongly aggregated or clumped at spatial scales below what could be resolved by our sampling design, and this may have been reflected in the large nugget variances in the semivariance analyses of AM infectivity.

There were also indications of a high degree of spatial structure in ECM infectiveness in the recently disturbed sites. Approximately half of the variance in ECM infectiveness among samples within plots in the soybean field and the pseudo-stripmine was related to the spatial position of those samples relative to each

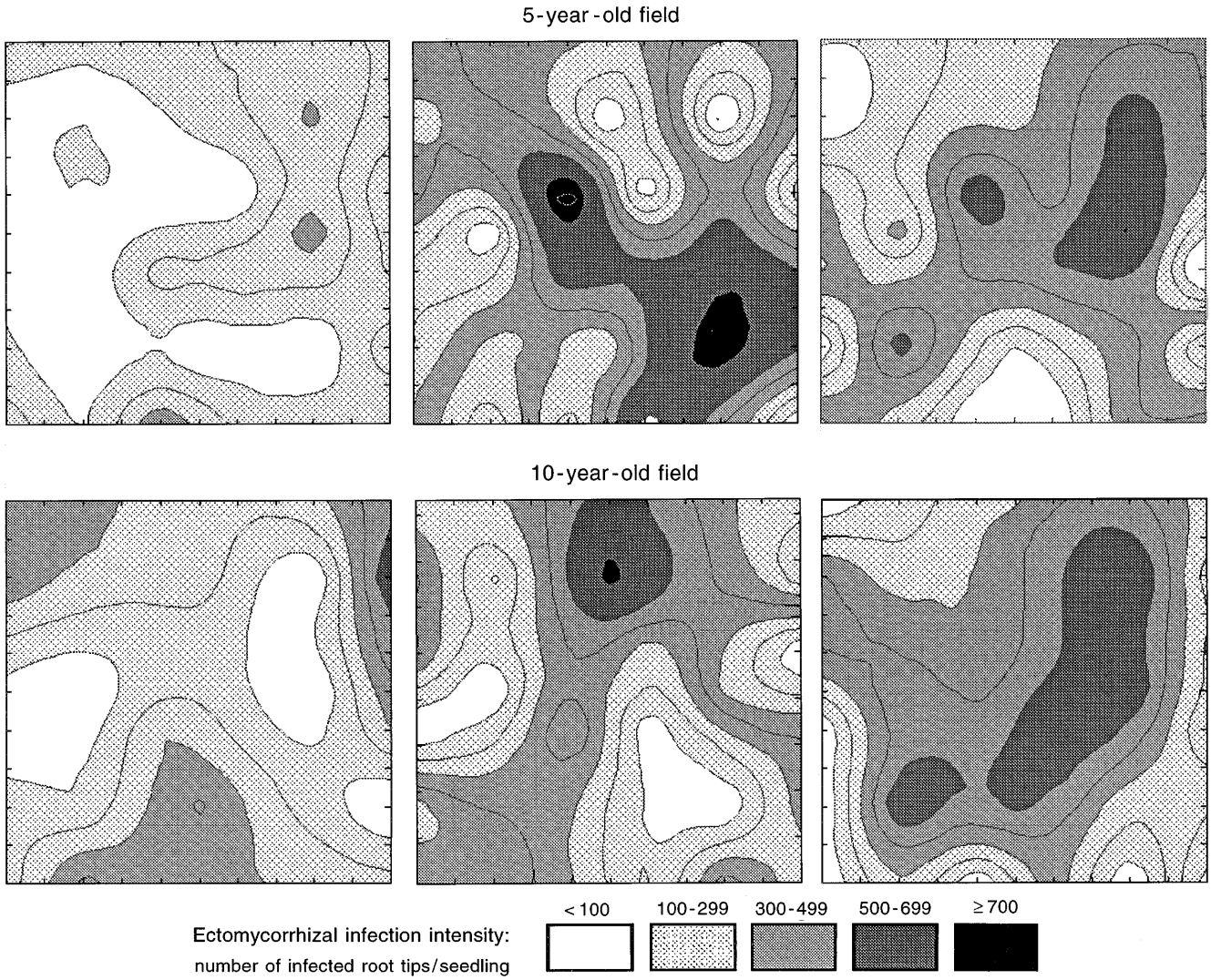
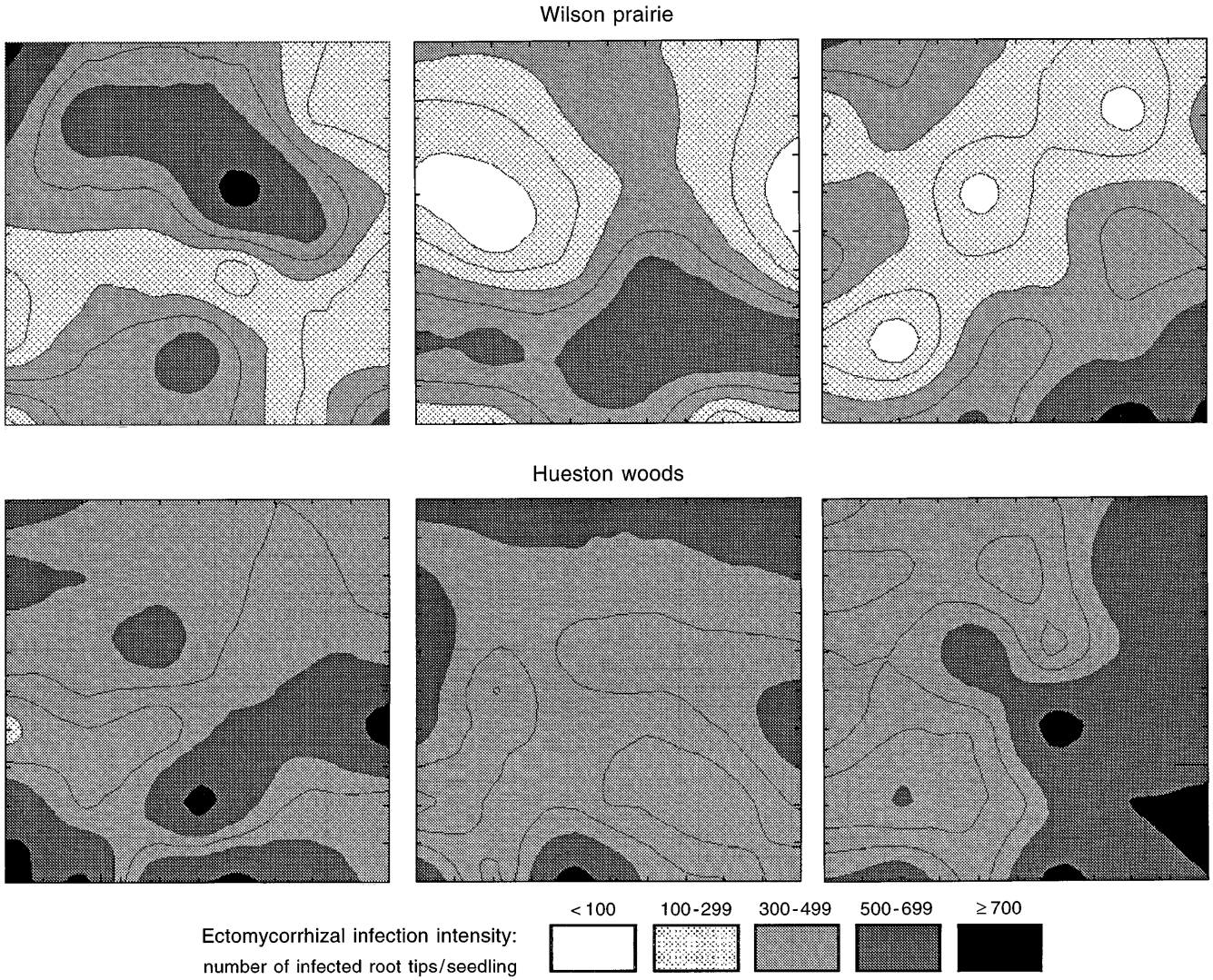


Fig. 8 Ectomycorrhizal infectiveness of soil in 5- and 10-year-old fields in southwestern Ohio. Format follows Fig. 7

other. In these recently disturbed sites, the probability of a germinating seedling of an ECM dependent species failing to encounter ECM inoculum approached 50%. Furthermore, the kriged maps of ECM infectivity for those two sites show clearly the presence of discrete patches of high ECM infectivity within a matrix devoid of ECM infectivity and, therefore, unsuitable for the establishment of ECM-dependent plants. As suggested earlier, this spatial pattern of ECM infectivity is consistent with the suggestion that dispersal of ECM sporocarps by animals is the primary means by which ECM infectiveness is established following disturbance.

The kriged maps of ECM infectiveness for the two successional fields suggest that the probability of successful entry of ECM-dependent species into this successional sequence increases greatly during the first 5–10 years of succession, and by 25–30 years after abandonment the network of hyphae and spores is such that the probability of a seedling of an ECM-dependent species not encountering inoculum approaches zero. Finally, our analysis of both the AM and ECM infectiveness of the soils of Hueston Woods supports the view expressed by Read et al. (1985) for ECM and Janos (1992) for AM that inoculum is ubiquitous in mature, undisturbed vegetation in mesic climates.

Classifying the suitability of our 576 sample points for various groups of plants by the types of mycorrhizal inoculum present produces some interesting parallels with studies of the vegetation dynamics in this successional chronosequence. We found the great majority of sample points to be suitable for colonization by AM-dependent plants, and such species do dominate the early successional dynamics of the area (Vankat and Carson 1991). We also found that sites lacking both AM and ECM infectiveness, and therefore perhaps the most suitable for dominance by nonmycotrophs, remained present at low frequency through at least the first 25–30 years of secondary succession. Consistent with this, studies of the vegetation dynamics of these and neighboring field plots in southwestern Ohio have



demonstrated that nonmycotrophs do remain common, although not abundant, in this area through at least the first 50 years of secondary succession (Vankat and Carson 1991).

Finally, sites with significant ECM infectiveness, which are therefore suitable for the successful establishment of ECM-dependent species such as oaks (*Quercus* spp.), beech (*Fagus grandifolia*), and pines (*Pinus* spp.), are relatively less abundant in the first years after disturbance, but become more abundant during the first decade following abandonment. Our own field observations and earlier surveys of this chronosequence (Vankat and Carson 1991) suggest, however, that establishment of these ECM-dependent species after abandonment of agriculture is sporadic and concentrated near forest-field margins. Thus, the stochastic nature of seed dispersal and the competitive interactions between seedlings of ECM species and established individuals of AM-dependent and nonmycotrophic species may interact with the patchy nature of ECM infectiveness to regulate the rate and spatial pattern of establishment of ECM-dependent species in this area. In other forested ecosystems, establishment of arbutoid mycorrhizal species after disturbance may serve as a mechanism for the maintenance of ECM infectiveness until the propagules of ECM-dependent species can reach the site in significant numbers (Molina and Trappe 1982; Molina et al. 1992). Unfortunately, the absence of arbutoid mycorrhizal species among the suite of colonizing species renders this mechanism moot in our study area. Thus, while heavy colonization by AM-dependent plants immediately following abandonment can be effective in helping the AM infectiveness to be maintained or even proliferated, the lack of early establishment of ECM-dependent species may actually retard the development of the heavily ECM, late successional vegetation (West et al. 1981; Allen 1991).

Given the wide range in mycotrophy of the plants in this region, the high volume of effective precipitation and the moderate nutrient levels of the soils, the model of Allen and Allen (1990) predicts that mycorrhizae

Table 2 Unsuitability of the soils at 96 sample points in each of six sites in southwestern Ohio fore establishment and growth species with different mycorrhizal requirements. Soils without AM or ECM infectivity are listed as unsuitable for AM- or ECM-dependent plant species, respectively, and soils without AM and ECM infectivity are indicated as unsuitable for both groups of plants

Site	No. of sites (total $n=96$) unsuitable for colonization by		
	AM-dependent species	ECM-dependent species	Both AM- and ECM-dependent species
Pseudo-stripmine	2	64	1
Soybean field	6	55	1
Five-year-old field	0	30	1
Ten-year-old field	2	17	1
Wilson Prairie	5	12	1
Hueston Woods	0	3	0

play an important role in regulating succession in our study sites. The results of this study emphasize the need for experiments designed to evaluate such mycorrhizal regulation of succession to explicitly consider both temporal changes in the mean levels of mycorrhizal infectivity of soil and the spatial structure and heterogeneity of that infectivity.

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