Temporal and Spatial Patterns of Woody Plant Establishment in Michigan Old Fields

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ABSTRACT.—We investigated temporal and spatial patterns of woody plant establishment in the first 7 y of succession in southwest Michigan old fields. From the 2nd to the 7th y following agricultural abandonment we conducted annual demographic surveys of woody plants and mapped all stems in six 10 × 20 m permanent grids to measure temporal and spatial patterns of woody stem emergence, mortality, density and species richness. Woody plant succession was characterized by increases in the emergence, density and richness of woody species over time and a shift from early dominance by wind-dispersed species to later dominance by bird-dispersed species. The increase in abundance of bird-dispersed stems reflects both clonal reproduction by the dominant bird-dispersed species, *Rhus typhina,* and establishment from seed by a variety of other bird-dispersed species. Wind and bird-dispersed species differed in spatial pattern within the grids. Wind-dispersed species were distributed at random and bird-dispersed species were aggregated. Aggregation of bird-dispersed species was due to clonal stem production by *R. typhina* and the concentration of stems of other bird-dispersed species beneath the canopy of *Rhus* clones. The results highlight the importance of dispersal mode in controlling both the rate of woody plant succession and the development of spatial structure in plant communities.

INTRODUCTION

Ecologists and land managers have long been interested in the patterns and mechanisms of woody plant establishment during secondary succession of disturbed lands such as abandoned agricultural fields, forest clearcuts and powerline rights-of-way (Niering and Egler, 1955; Buell *et al.*, 1971; Pickett, 1982; Gill and Marks, 1991; Hill *et al.*, 1995). In herb-dominated old fields invasion by woody plants imparts major structural changes to the vegetation. These changes, in turn, can influence subsequent pathways of community development and diversity by altering environmental conditions and affecting the abundance and activity of animals that consume and disperse seeds (Werner and Harbeck, 1982; McDonnell and Stiles, 1983; Archer *et al.*, 1988).

Woody plant establishment during old-field succession is highly variable, both in space and time (Bard, 1952; Buell *et al.*, 1971; Myster, 1993; Hill *et al.*, 1995). Because most woody plants do not have a persistent seed bank, establishment in abandoned agricultural fields is largely dependent upon dispersal from the surrounding landscape. As a result, the timing, rate and sequence of woody plant establishment can vary within and among fields depending upon the proximity and composition of local seed sources (Myster and Pickett, 1992; Myster, 1993; Hill *et al.*, 1995).

Wind-dispersed woody plants are often thought to be the first to invade newly abandoned fields, followed by animal-dispersed species (Buell *et al.*, 1971; Pickett, 1982). Delays in the arrival and establishment of animal-dispersed woody plants after abandonment have been attributed to the effects of increased vegetation complexity on the visitation rates of seed

dispersers (McDonnell, 1986; Myster, 1993). Several studies suggest that the first woody plants to invade old fields often become foci for bird activity and facilitate the directed dispersal of bird-dispersed species under their canopies (McDonnell and Stiles, 1983; McDonnell, 1986; Gill and Marks, 1991), thus influencing the rate of woody plant succession and facilitating the development of aggregated spatial structure in plant communities.

Although a number of studies have examined woody plant succession in old fields (Bard, 1952; Beckwith, 1954; Bazzaz, 1968; Buell *et al.,* 1971; Keever, 1979; Pickett, 1982; Myster and Pickett, 1992; Myster, 1993), most were conducted in the northeastern United States and none has provided detailed demographic information from replicated permanent plots over a relatively long time series. In this article we present data from the midwestern United States on woody plant emergence, abundance, mortality and species richness in an extensive, well-replicated permanent plot study of old-field succession in southwest Michigan. Our objectives were to examine temporal and spatial dynamics of woody plant establishment during the first 7 y following field abandonment from agriculture and assess the role of dispersal mode in affecting these patterns.

METHODS

This study was conducted at the Long-Term Ecological Research (LTER) site in agricultural ecology at W. K. Kellogg Biological Station (KBS; Michigan State University). KBS is located in southwest Michigan, USA, (Kalamazoo County; 42°24′N, 85°24′W) on an outwash plain left by the Wisconsin glaciation. Soils at the 42 ha study area are Typic Hapludalfs of moderate fertility and drainage and consist of sandy loam soils in the Kalamazoo and Oshtemo series. Mean annual temperature is 9 C and precipitation averages 860 mm/y, approximately half falling as snow (Robertson *et al.*, 1997).

The six 0.9 ha plots used in this study are replicates of one treatment in the seven treatment array of the 42 ha LTER study area. For > 20 y before the establishment of the LTER the entire 42 ha area had been used continuously for row-crop cultivation (primarily corn; Robertson *et al.,* 1997). In 1989 the study area was divided into seven different cropping treatments, each with six 0.9 ha replicates. The six plots studied here were abandoned after spring plowing in 1989 and allowed to revegetate naturally. Successional changes in herbaceous composition between 1989 and 1996 in these plots are described in Huberty *et al.* (1998).

Survey design.—From 1991 (2 y following abandonment) to 1996 we conducted annual surveys of woody plants during May within each of the six 0.9 ha plots. In May 1991 we established a 10 m × 20 m grid that was divided into 200, 1 m² grid cells near the center of each 0.9 ha plot. In the initial survey all woody plant stems within each grid cell of each grid were identified to species, marked with aluminum tags, and mapped. Each year thereafter all newly emerged stems were marked and mapped, and stems marked in previous years were accounted for as dead or alive. After 1993 several vine species (*e.g., Rubus* sp, *Vitus* sp, *Celastrus orbiculatus, Parthenocissus quinquefolia*) were no longer marked due to difficulty in isolating the origin of individual stems. During the second survey (1992) we examined seedling bud scars to determine ages of all surviving seedlings of *Populus deltoides* that were marked in the first survey (1991). This was done to distinguish the initially unsurveyed *Populus* cohort that established between 1989 and 1990 from the second cohort that established between 1990 and 1991.

Demography.—We used our survey data to examine temporal patterns of woody stem emergence, density, mortality and species richness. Stem emergence is defined as the number of new stems marked in a grid during a given survey. Stem density, defined as the total number of stems present in a grid at the time of a given survey, includes newly emerged

stems and all surviving stems from previous years. Mortality rates were calculated for each annual interval for each grid and are expressed as the proportion of all stems present in a given survey that were missing in the following survey. We also calculated proportional emergence rates for each grid to compare with mortality rates. Proportional emergence was calculated for each annual interval as the number of newly emerged stems in a given survey expressed as a proportion of the total number of stems present in the previous survey. Species richness is the total number of species in each grid.

We used repeated measures analysis of variance (ANOVA) to examine variation in emergence, mortality, density and richness with respect to species dispersal mode and time (year of survey, or years postabandonment). Because mammal dispersed species were rare in this study, only wind- and bird-dispersed species were included in the statistical analyses that used dispersal mode as a categorical variable. Data for mammal-dispersed species are included in the figures. For ANOVA it was necessary to log-transform emergence and density data to reduce heteroscedasticity. Untransformed data are presented in the figures.

Spatial pattern analyses.—To examine spatial pattern of woody plants within each of the six grids, we first tested for spatial randomness in stem density using chi-square analyses to compare the observed distribution of woody stems among grid cells to that predicted by a Poisson distribution with the same mean. In addition, we calculated the Morisita index of aggregation (I_M: Morisita, 1962) to assess whether observed departures from random expectation were more likely due to aggregation or to over-dispersion of stems. The Morisita index is calculated as:

$$I_M = \left(\frac{N}{N-1}\right)\left(\frac{1}{\mu}\right)\left(\frac{\sigma^2}{\mu} + \mu - 1\right)$$

where N is the total number of individual stems, σ^2 and μ are respectively the variance and mean of the observed distribution of stems among grid cells. The value of I_M indicates the number of times it is more likely that two randomly drawn individuals from the observed population will originate from the same cell than would be expected if all individuals were distributed randomly. $I_M < 1$ indicates over-dispersion (evenness) and $I_M > 1$ indicates aggregation. To test the hypothesis that spatial patterns differed with respect to dispersal mode we conducted these analyses separately for species grouped as wind- and bird-dispersed. Because measures of spatial distribution are generally sensitive to the scale of observation (Ludwig and Reynolds, 1988), we carried out these analyses at both 1 m^2 and 4 m^2 grid cell scales for each grid.

We also investigated among-grid patterns in stem density. Because distance from a seed source is likely to influence the rate of dispersal and establishment into a habitat, we related total stem density in each grid in each survey year to distances from nearby forest edges using Spearman rank correlation analysis (r_s). There were three small forest fragments adjacent to the 42 ha study area, one each on the northern, southeast and west boundaries. We measured distances on an aerial photo from grid centers to the edge of the wooded area closest to each grid. In addition, we related among-grid variability in woody stem density to herbaceous composition of the grids. In 1993 we visually estimated and mapped percent of herbaceous cover by functional group (grasses and forbs) in all of the grid cells within each grid. With these data we used correlation analysis to examine the among-grid relationship between woody stem density in each survey year and mean relative cover of grasses for each grid measured in 1993. All statistical analyses were performed using SYSTAT software (version 5.2.1: Wilkinson, 1992).

<center>RESULTS</center>

Stem emergence.—Woody plants rapidly emerged in the grids following abandonment from agriculture. In the initial survey, in 1991 (2 y after abandonment), we marked an average of 25.8 stems per grid, including eight different species (Table 1). *Populus deltoides* (wind-dispersed) and *Prunus serotina* (bird-dispersed) were the most abundant species observed in the initial survey. For all species combined emergence of new stems varied significantly over time ($F_{5,25}$ = 4.5, P < 0.01) and increased from the 2nd (1991) to the 7th y (1996) following abandonment (Fig. 1A). Stem emergence of bird-dispersed species rapidly increased over time, whereas that of wind-dispersed species declined to near zero by year 5 (Fig. 1B)resulting in a significant interaction between dispersal mode and year (Table 2).

The decline in stem emergence for wind-dispersed species over time largely reflects the recruitment dynamics of the dominant wind-dispersed species, *Populus deltoides* (Fig. 2). Examination of bud scars in the second survey (1992) revealed that a large number of the *Populus* stems marked in the initial survey (1991) had established the year before (1990). As a result, we have a minimum estimate of the number of stems in the first *Populus* cohort that emerged in the initial year of abandonment. Although this is likely an underestimate, due to mortality that undoubtedly occurred before 1991, the data suggest that *Populus* had its highest emergence in the first year following abandonment and then declined to zero emergence by year 5 (Fig. 2).

The observed increase in stem emergence over time for all species combined was strongly influenced by the clonal stem production of *Rhus typhina*, hereafter referred to as *Rhus* only; (Fig. 1, Table 1). Because *Rhus* was the only species showing strong clonal expansion in this study, we reanalyzed the data excluding *Rhus* in order to examine the emergence dynamics of stems that arose primarily by seedling establishment. After excluding *Rhus*, total woody stem emergence rates no longer varied significantly with time ($F_{5,25}$ = 1.5, P = 0.24; Fig. 1C). However, an increase in the emergence of bird-dispersed species with time was still evident (Fig. 1D) and the significant interaction between dispersal mode and year was retained (Table 2).

Stem mortality.—Mean stem mortality ranged from a low of 12% in the interval between 1992 and 1993 to a high of 22% in the interval between 1993 and 1994 (Table 3), but did not differ significantly among intervals ($F_{4,25}$ = 0.83, P > 0.05). The mortality rate was significantly lower than the emergence rate across all intervals ($F_{4, 25}$ = 24.06, P < 0.01).

Stem density.—The total density of woody stems differed significantly among years ($F_{5,25}$ = 8.6, p < 0.001) and increased from year 2 (1991) to year 7 (1996) after abandonment (Fig. 3A). The significant interaction between dispersal mode and year (Table 2) reflects initial dominance by wind-dispersed species in year 2, followed by a shift to dominance by bird-dispersed species after year 4 (Fig. 3B). Stem density of bird-dispersed species increased over time while that of wind-dispersed species remained relatively constant. Mammal-dispersed species (*i.e.*, *Quercus, Carya* species) were rare in this study and did not become apparent in the grids until after year 5 (Table 1).

When we excluded *Rhus* data from the analyses, the total density of woody stems still differed among years ($F_{5,25}$ = 10.5, P < 0.0001) and increased from year 2 to year 7 (Fig. 3C). ANOVA revealed a significant interaction between dispersal mode and year (Table 2), again reflecting an increase in stem density of bird-dispersed species with time and a shift in dominance by wind-dispersed species early on to dominance by bird-dispersed species by year 7 (Fig. 3D).

Species richness.—Total woody plant species richness differed significantly among years ($F_{5,25}$ = 26.9, P < 0.0001) and increased over time (Fig. 4A). This was due to the accu-

TABLE 1.—Mean number of new woody stems (emergence: Em.) and mean total stem density (Den.). Both are No./200 m². The mode of dispersal for each species is indicated (W = wind-dispersed; B = bird-dispersed; M = mammal-dispersed). Taxonomy follows Gleason and Cronquist 1991

Species	1991		1992		1993		1994		1995		1996	
	Em.	Den.	Em.	Den.	Em.	Den.	Em.	Den.	Em.	Den.	Em.	Den.
Acer saccharinum (W)	0.17	0.17	—	0.17	0.17	0.33	—	0.17	—	0.17	—	0.17
Crataegus sp. (B)	0.33	0.33	0.17	0.33	0.50	0.67	0.17	0.83	1.00	1.50	0.17	1.50
Morus rubra (B)	0.83	0.83	0.33	0.83	0.33	1.00	—	1.00	0.33	1.33	0.33	1.50
Populus deltoides (W)	4.67*	17.33*	5.17	20.50	2.83	21.67	—	18.17	—	16.67	—	15.83
Populus grandidentata (W)	0.17	0.17	0.17	0.33	—	0.33	—	0.33	—	—	—	—
Prunus serotina (B)	4.50	4.50	1.17	4.00	4.50	7.83	3.50	10.00	2.67	10.17	4.67	14.67
Rhus typhina (B)	1.83	1.83	2.00	3.67	11.50	14.83	8.50	16.33	24.33	37.00	32.17	66.50
Salix sp. (W)	0.67	0.67	—	0.50	0.33	0.83	—	0.83	—	0.83	—	0.83
Acer negundo (W)	—	—	0.17	0.17	—	0.17	0.33	0.50	0.17	0.67	0.33	0.67
Elaeagnus angustifolia (B)	—	—	0.17	0.17	—	0.17	—	0.17	—	0.17	0.83	1.00
Lonicera tatarica (B)	—	—	0.33	0.33	—	0.33	1.17	1.50	1.33	2.17	2.67	4.50
Rhamnus frangula (B)	—	—	0.17	0.17	—	0.17	0.33	0.50	2.00	2.33	0.17	2.50
Rosa multiflora (B)	—	—	0.17	0.17	0.33	0.50	0.50	1.00	0.67	1.50	0.50	2.00
Sassafras albidum (B)	—	—	—	—	0.17	0.17	0.50	0.50	0.17	0.33	0.50	0.83
Catalpa speciosa (W)	—	—	—	—	—	—	0.17	0.17	0.67	0.83	—	0.83
Cornus florida (B)	—	—	—	—	—	—	0.33	0.33	0.17	0.50	0.17	0.67
Fraxinus americana (W)	—	—	—	—	—	—	0.17	0.17	0.17	0.17	0.17	0.33
Carya glabra (M)	—	—	—	—	—	—	0.17	0.17	0.50	0.67	—	0.17
Juniperus virginiana (B)	—	—	—	—	—	—	0.33	0.33	0.17	0.33	1.00	1.33
Morus alba (B)	—	—	—	—	—	—	0.17	0.17	0.17	0.17	—	0.17
Quercus rubra (M)	—	—	—	—	—	—	0.17	0.17	3.17	3.33	0.50	1.50
Ptelea trifoliata (W)	—	—	—	—	—	—	0.17	0.17	—	—	0.17	0.17
Acer rubrum (W)	—	—	—	—	—	—	—	—	0.17	0.17	—	—
Rhamnus cathartica (B)	—	—	—	—	—	—	—	—	0.17	0.17	3.00	3.17
Acer saccharum (W)	—	—	—	—	—	—	—	—	—	—	0.17	0.17
Ligustrum vulgare (B)	—	—	—	—	—	—	—	—	—	—	0.17	0.17
Lonicera maackii (B)	—	—	—	—	—	—	—	—	—	—	0.33	0.33
Malus coronaria (B)	—	—	—	—	—	—	—	—	—	—	0.17	0.17
Prunus americana (B)	—	—	—	—	—	—	—	—	—	—	0.50	0.50
Rhus copallina (B)	—	—	—	—	—	—	—	—	—	—	0.17	0.17

* Emergence and density of *Populus* in 1991 are not equivalent because a subset of the *Populus* seedlings marked in 1991 were determined by bud scale analyses to have emerged prior to the first survey
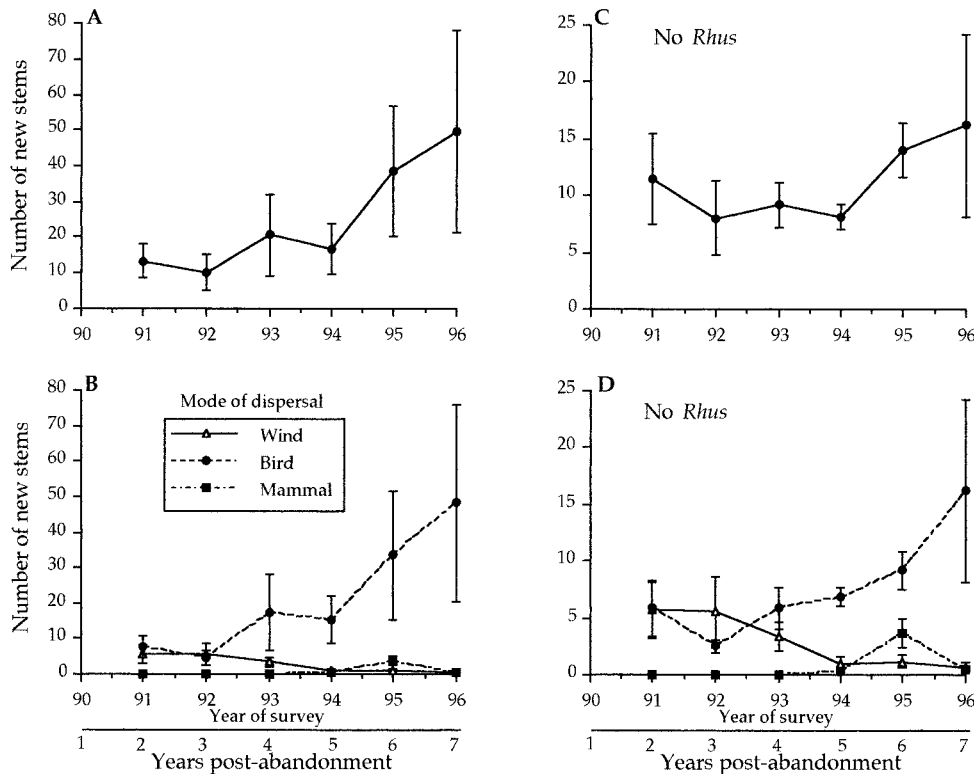
FIG. 1.—Number of newly emerged stems (mean ± 1 SE) in relation to years following abandonment: (A) total stem emergence; (B) stem emergence for species grouped by mode of dispersal; (C) total stem emergence with *Rhus* data excluded; (D) stem emergence by dispersal mode with *Rhus* data excluded. The horizontal axis is labeled with both the year of the survey and the number of years postabandonment

mulation of both wind- and bird-dispersed species (Fig. 4B, Table 1). Wind and bird-dispersed species richness were similar in year 2, and both increased over time. However, bird-dispersed species richness increased at a faster rate than that of wind-dispersed species, as shown by the significant interaction between dispersal mode and year (Table 2, Fig. 4B).

Within-grid spatial patterns.—In the final year of the study (1996) we examined within-grid spatial distributions of stems of wind- and bird-dispersed species. Three of the six grids (grids 1, 2 and 4) contained sufficient numbers of stems to permit a test for spatial patterning of wind-dispersed species. In these three grids the stem distributions of wind-dispersed species did not differ significantly from random expectation at either the 1 m² or 4 m² scales (Table 4). In contrast, the stem distributions of bird-dispersed species differed significantly from random at both spatial scales in four of the six grids. Values of the Morisita aggregation index (I_M) exceeded 1 for wind- and bird-dispersed species in all cases, suggesting that stems were aggregated in space. However, I_M values for bird-dispersed species indicated much stronger aggregation for this group compared to wind-dispersed species at both spatial scales. This pattern was especially apparent in grids 1, 2,

TABLE 2.—Repeated measures ANOVA for woody stem emergence, stem density and species richness. [NR] indicates that data for *Rhus typhina* were excluded from the analyses (*P < 0.05; ** P < 0.01; *** P < 0.001)

| Source of variation within-Plot	df	Stem emergence		Stem emergence [NR]		Stem density		Stem density [NR]		Species richness	
		MS	F	MS	F	MS	F	MS	F	MS	F
Dispersal	1	5.23	3.04	0.01	0.3	63.58	15.60*	23.64	37.55**	117.56	211.60***
Error (Disp × Plot)	5	1.72		0.41		4.08		0.63		0.56	
Year	5	25.45	9.22***	6.34	7.20***	15.45	2.67*	2.72	0.60	37.30	21.62***
Error (Year × Plot)	25	2.76		0.89		5.79		4.62		1.73	
Dispersal × Year	5	11.01	5.87**	4.41	3.19*	12.65	7.37**	4.23	4.73**	15.36	9.389***
Error (Dispersal × Year)	25	1.88		1.38		1.71		0.89		1.66	
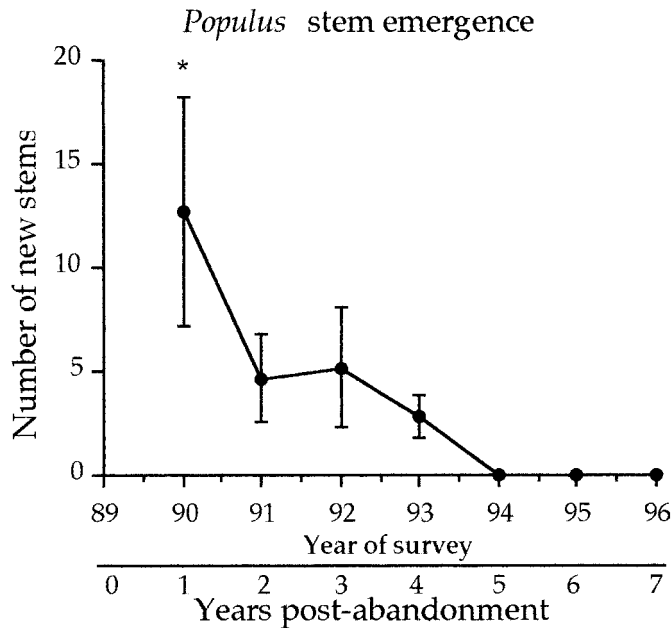
FIG. 2.—Stem emergence (mean $\pm$ 1 SE) of *Populus deltoides* in relation to years following abandonment. *Data for 1990 was estimated in 1992 by examining bud scars of established stems marked in the 1991 survey

4 and 6, where the stem distributions of bird-dispersed species departed significantly from random expectation.

Aggregation of bird-dispersed species in four of these grids was undoubtedly influenced by the clonal proliferation of *Rhus* stems. However, field observations suggested that bird-dispersed species other than *Rhus* tended to establish below the canopy of *Rhus* clones, thus contributing to aggregation. To investigate the potential spatial association between *Rhus* and other bird-dispersed species we conducted chi-square tests of association for these two groups using data from the final year of the study (1996). In two of the six grids (grids 2 and 4) stems of bird-dispersed species other than *Rhus* were highly significantly spatially associated with *Rhus* stems at the 1 m^2 scale (grid 2: $X^2_1 = 365.05$, P < 0.0001; grid 4: $X^2_1 = 92.7$, P < 0.0001).

TABLE 3.—Proportional stem mortality and emergence rates (mean $\pm$ 1 SE) calculated for each annual interval

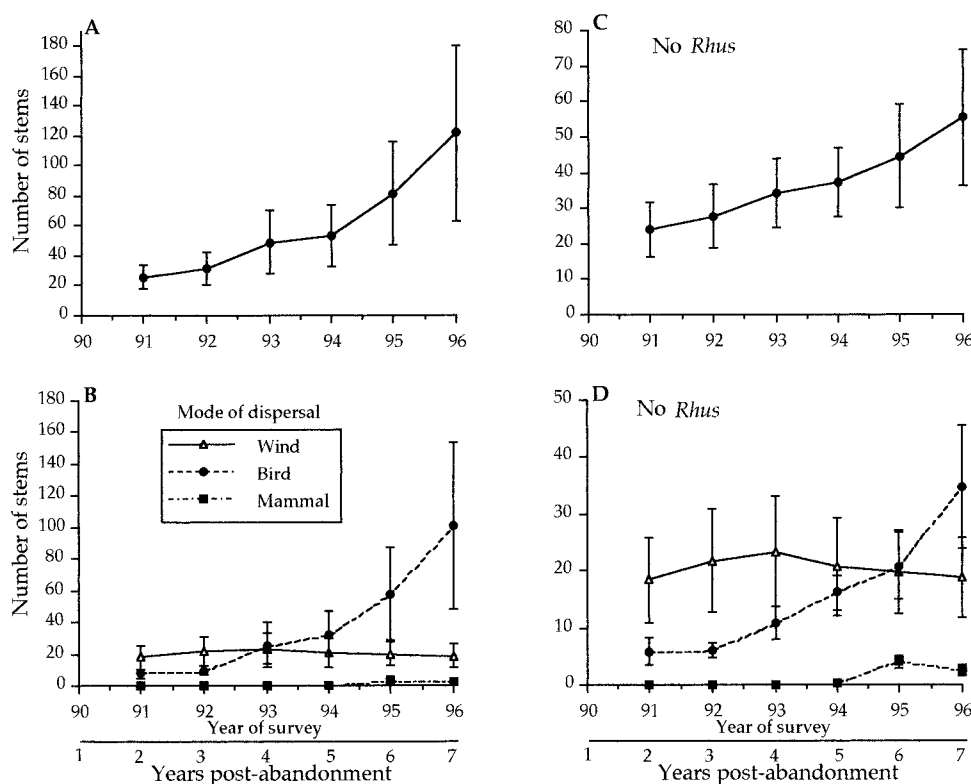| Time interval	Stem mortality rate	Stem emergence rate
1991–1992	0.193 $\pm$ 0.094	0.454 $\pm$ 0.141
1992–1993	0.120 $\pm$ 0.037	0.691 $\pm$ 0.185
1993–1994	0.218 $\pm$ 0.021	0.552 $\pm$ 0.267
1994–1995	0.211 $\pm$ 0.034	0.765 $\pm$ 0.243
1995–1996	0.132 $\pm$ 0.025	0.498 $\pm$ 0.155

FIG. 3.—Stem density (mean ± 1 SE) in relation to years following abandonment: (A) total stem density; (B) stem density by dispersal mode; (C) total stem density with *Rhus* data excluded; (D) stem density by dispersal mode with *Rhus* data excluded

To more closely examine the association of woody species with *Rhus* in grids 2 and 4 we compared the emergence of stems of bird-dispersed species (other than *Rhus*) with respect to the presence or absence of *Rhus* stems. In each year for which sufficient data were available, we asked if stems of bird-dispersed species other than *Rhus* emerged more frequently than would be expected by chance in 1 m^2 grid cells that contained at least one previously established *Rhus* stem. For both grids 2 and 4 the emergence of bird-dispersed species other than *Rhus* was not significantly associated with the presence of *Rhus* during the first 5 y after abandonment, but became significantly associated with *Rhus* in years 6 and 7 (Table 5).

Among-grid variability.—There was considerable variation in stem density among the grids that became more pronounced over time (Fig. 5), as indicated by a significantly positive rank correlation between the coefficient of variation for total stem density and year ($r_s = 0.83$, $P < 0.05$). However, this correlation was not significant when *Rhus* data were excluded from the analyses ($r_s = -0.48$, $P > 0.05$), reflecting the important contribution of *Rhus* to among-grid variability in stem density. This divergence over time in the abundance of woody plants was primarily due to a greater rate of stem accumulation in grid 4 relative to the other grids (Fig. 5).

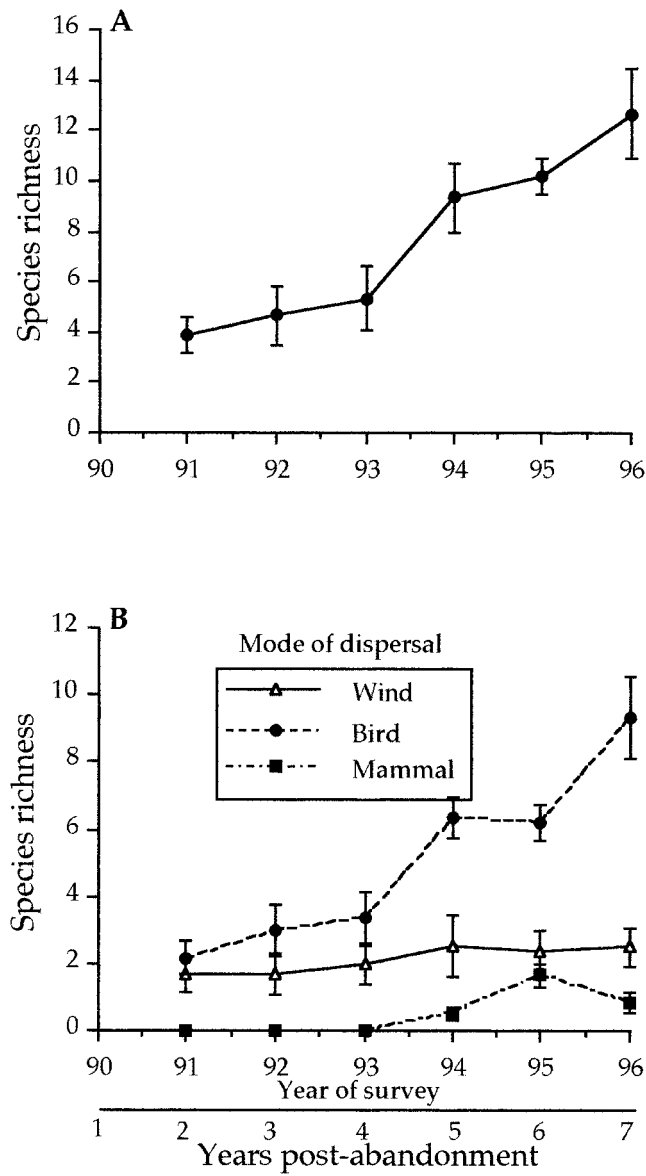Total stem density of the grids showed no significant correlation with distance from the

FIG. 4.—Species richness (mean ± 1 SE) in relation to years following abandonment: (A) total species richness; (B) species richness by dispersal mode

closest forest edge (maximum correlation in year 3; $r_s = -0.57$, $P > 0.05$), although coefficients were of the same sign in all years. Total stem density was significantly negatively correlated with 1993 grass relative cover in survey years 1–4 (maximum correlation in year 1; $r_s = -0.90$, $P < 0.01$).

TABLE 4.—Analyses of within-grid spatial patterns of woody stem density using data from the final survey year (1996). Pearson's chi-square statistic (χ^2) tests for departure from Poisson (* P < 0.05; ** P < 0.01; *** P < 0.001). I_M = Morisita's index of aggregation

| | 1 m² scale | | | | 4 m² scale | | | |
| | Wind-dispersed | | Bird-dispersed | | Wind-dispersed | | Bird-dispersed | |
Grid	χ^2	I_M	χ^2	I_M	χ^2	I_M	χ^2	I_M
1	1.26	1.36	14.41***	26.14	2.22	1.26	10.14**	7.27
2	0.01	1.49	54.84***	32.7	0.75	1.43	73.94***	9.22
3	—	—	2.75	2.83	—	—	0.59	1.45
4	2.05	1.08	483.56***	16.4	6.1	1.29	681.22***	10.64
5	—	—	3.39	3.73	—	—	3.10	2.46
6	—	—	57.18***	71.23	—	—	78.80***	19.68

DISCUSSION

Temporal patterns.—In this study the first 7 y of succession following abandonment from agriculture were characterized by increases in woody plant emergence, stem density, species richness and a shift in numerical dominance from wind- to bird-dispersed species. These findings are broadly consistent with the patterns of woody plant succession previously documented in the northeastern United States (Bard, 1952; Buell *et al.,* 1971; Pickett, 1982; Myster 1993), suggesting that many of the same basic processes are responsible for driving successional change in the midwest.

The observed increase in total stem density in our study was due to an increasing rate of stem emergence and a low rate of mortality in all years. Much of the increase in density of bird-dispersed species is attributable to clonal stem production by *Rhus typhina. Rhus* often exhibits episodic proliferation of new stems from root sprouts, resulting in periodic rapid clonal spread (Gilbert, 1966; Luken, 1990). In the 1993 survey (year 4 postabandonment) we observed a large increase in the emergence of new *Rhus* stems near many of the previously established *Rhus* stems. This likely reflects a clonal sprouting response to a severe May frost in that year. Damage to *Rhus* meristems from frost can result in loss of apical dominance and stimulation of secondary meristems (Luken, 1990). However, the abun-

TABLE 5.—Chi-square tests of association between the emergence of bird-dispersed species other than *Rhus* and previously established *Rhus* stems (* P < 0.05; ** P < 0.01; *** P < 0.001)

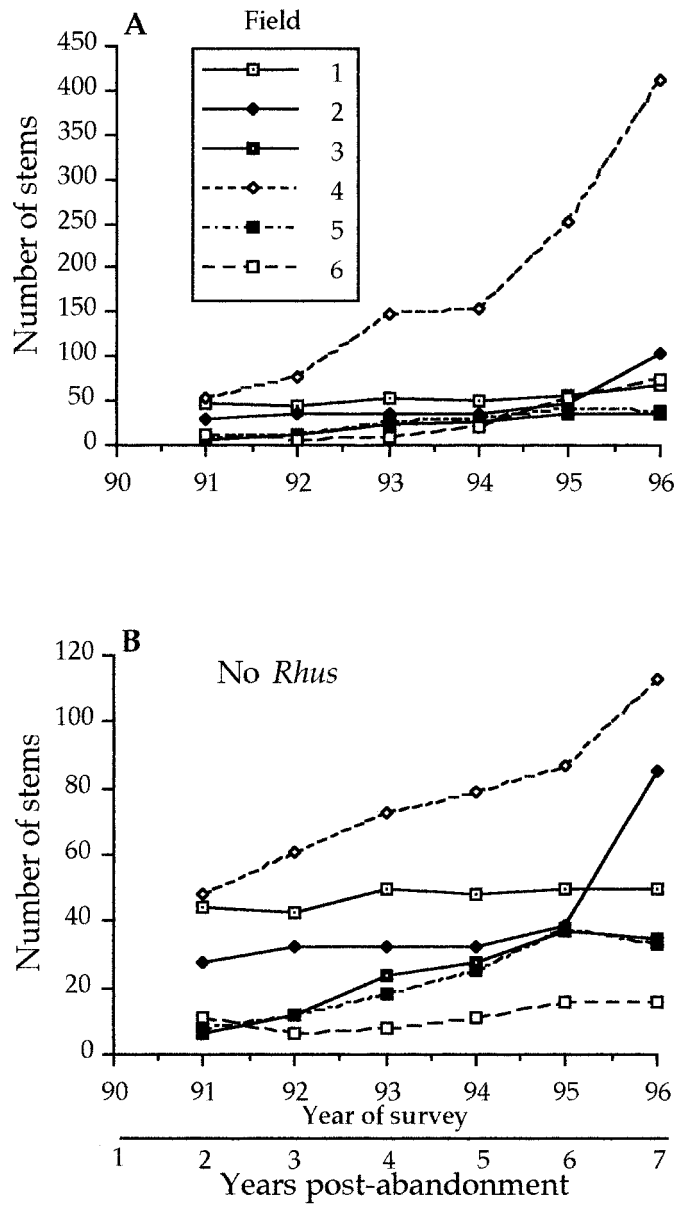| | Grid 2 | | | | Grid 4 | | | |
Year	No. of *Rhus* cells	No. of stems emerged in *Rhus* cells	No. of stems emerged in non-*Rhus* cells	χ^2	No. of *Rhus* cells	No. of stems emerged in *Rhus* cells	No. of stems emerged in non-*Rhus* cells	χ^2
3	2	0	1	—	5	0	2	—
4	3	0	1	—	12	1	8	0.81
5	3	0	7	0.11	28	1	9	0.13
6	3	4	4	127.36***	37	12	5	30.64***
7	5	28	18	642.96***	64	24	11	21.51***

FIG. 5.—Stem density for each field separately in relation to time following abandonment with (A) and without (B) *Rhus* data included

dance of stems other than *Rhus* also increased with time. This illustrates that the increase in woody stems was also influenced by the establishment of stems by germination.

The relatively invariant temporal pattern in stem density for wind-dispersed species reflects early emergence and high survivorship of the most abundant wind-dispersed species,

Populus deltoides. Emergence of this species was greatest in the initial year (1989) and then declined to insignificant levels by year 5 (Fig. 2). This early peak and rapid decline of *Populus* emergence is consistent with the regeneration ecology of this species. *Populus* produces large crops of small highly-dispersible seeds that require bare-soil microsites to germinate (White, 1979; Bradley and Smith, 1986). In alluvial systems, *Populus* often initiates even-aged stands on newly formed sand bars through synchronous seedling establishment, followed by reduced recruitment once herbaceous cover establishes (Scott *et al.*, 1997).

In these grids bare soil was abundant only during the first year after abandonment, but declined rapidly as perennial grasses and forbs became dominant within 2–3 y (Huberty *et al.*, 1998). It is likely that the decline in *Populus* emergence over time was due to an inability to establish and compete in intact vegetation. We observed abundant seed rain of *Populus* in all years at our field site. As a result, it is likely that dispersal limitation was not an important factor influencing the temporal dynamics of this species.

In contrast, bird-dispersed species established both early on when bare soil was abundant, and in later years when vegetative cover was great. Bird-dispersed species often have large well-provisioned seeds capable of germinating and establishing seedlings in intact vegetation (Myster, 1993). Therefore, it is likely that limited seed availability early in succession, rather than microsite availability, was the main factor limiting the abundance of bird-dispersed species in this study.

Spatial patterns.—Wind- and bird-dispersed species had different spatial distributions within the old field grids. Stems of wind-dispersed species were distributed randomly. In contrast, stems of bird-dispersed species were aggregated in most grids. Spatial aggregation of bird-dispersed stems was due to clonal reproduction of *Rhus* stems, and the clustering of other bird-dispersed species beneath the *Rhus* canopy. The strong spatial association between *Rhus* and other woody species is consistent with the hypothesis that *Rhus* clones act as foci to facilitate establishment and spatial aggregation of other bird-dispersed woody species. Several studies in old fields have shown that previously established woody plants can facilitate dispersal and concentrate seed input by serving as perches (*e.g.,* McDonnell and Stiles, 1983; McDonnell, 1986). *Rhus* clones may be especially attractive to birds after reaching some minimum size because they provide a broad canopy for perching and a source of edible seed.

Our data do not allow us to reject the alternative hypothesis that the observed spatial association between *Rhus* and other bird-dispersed species is merely a result of a common requirement among all bird-dispersed species for the same establishment microsites. However, facilitation is suggested by our analyses showing that emergence of new bird-dispersed stems other than *Rhus* was strongly associated with the presence of previously established *Rhus* stems in only the latter years following abandonment when *Rhus* canopies became prominent above the herbaceous layer. If *Rhus* facilitates seedling establishment by influencing bird visitation rates, we would expect to see such a delay in this effect until such time that *Rhus* clones attained sufficient size and prominence in the field to consistently attract birds. If the observed association between these species was purely driven by similar microsite requirements, we would have expected to see this association early in succession as well as in later years.

The rate of increase in woody stem density differed among the six replicate grids. In particular, grid 4 accumulated over four times the number of stems than the other grids by the final year of the study. Differences in physiognomy among these grids reflects both absolute differences in woody stem density and differences in the number of stems in larger age and size classes. Reasons for this among-grid difference are unclear. We found no significant correlations between stem density and distance from the nearest forest edge. We

did find significant negative correlations between stem density and the relative cover of grasses in some years, suggesting that interference with establishment by grasses may have influenced among-grid variability in woody plant establishment.

Our study supports the findings of other studies and suggests that the sequence of woody plant species and the rate of community change during old-field succession is strongly influenced by species differences in dispersal strategy (Bard, 1952; Buell *et al.,* 1971; Pickett, 1982; Myster, 1993). Interestingly, our data suggest that these same differences appear to have important consequences for the rate of development of spatial structure in these communities as well, by influencing the likelihood that seed arrival will be linked to the behavior of animals which move nonrandomly throughout the landscape. Although our findings are correlative, they are consistent with the view that multiple direct and indirect interactions occurring among plants and animals are important agents of successional change, including direct negative interactions between woody and herbaceous plants, and indirect, animal-mediated positive interactions among different woody plant species.

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