Effects of Palatability and Dispersal Mode on Spatial Patterns of Trees in Oldfields

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Effects of palatability and dispersal mode on spatial patterns of trees in oldfields[1]

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ABSTRACT

MYSTER, R. W. (Terrestrial Ecology Division, University of Puerto Rico, San Juan, PR 00936), AND S. T. A. PICKETT (Institute of Ecosystem Studies, Mary Flagler Cary Arboretum, Millbrook, NY 12545). Effects of palatability and dispersal mode on spatial patterns of trees in oldfields. Bull. Torrey Bot. Club 119: 145–151. 1992.—The spatial patterns of tree stems in 480 plots were examined on a series of ten experimental oldfields adjacent to an old growth forest over a 31-year period. Tree stem density decreased exponentially with distance from the forest edge early in succession. Later in succession the predictive power of the negative exponential model decreased, suggesting that processes such as animal seed dispersal within a field become important. Species palatable to herbivores were denser than unpalatable species close to the forest edge which implies that consumer pressure originates in the field rather than in the forest. Stems of all species were clumped on the scale of the 1 m² plots. However, stems of bird-dispersed species showed the highest degree of clumping as expected if perches serve as recruitment foci. Results suggest that spatial patterns of tree seedlings in oldfields are significantly influenced by successional age, herbivory, dispersal vector and proximity to forest edge.

Key words: dispersal, spatial pattern, plant succession, tree invasion, oldfield, New Jersey USA.

Tree establishment initiates profound structural changes in oldfields abandoned from agriculture. In addition, trees may influence plant-plant interactions to either favor or inhibit further invaders (Werner and Harbeck 1982; Pickett *et al.* 1987). The spatial pattern of trees in oldfields can determine where subsequent invasion will occur, where certain other species persist or decline, and where herbivores and predators are most active (Hughes and Fahey 1981). In this paper, we examine the relationship of whole-field spatial patterns of tree establishment to species adaptations for seed dispersal and palatability to mammalian herbivores in the first three decades of oldfield succession. Specifically we test four independent hypotheses, each derived from at least one empirical or theoretical source. We briefly present some of the data or theoretical conclusions that generate each hypothesis to indicate the plausibility of these hypotheses about pattern. It is not possible with this data set, nor is it our intention, to discriminate among different mechanisms that might generate the hypothesized patterns. Complete testing of mechanistic hypotheses can only occur in field experiments which unambiguously distinguish among alternative causes for the patterns discovered here.

Hypothesis 1. Tree stem density decreases exponentially from the forest edge early in succession (Hughes and Fahey 1988). Seed dispersal is a critical determinant of tree invasion in many post-agricultural successions (Bard 1952). Seeds of common tree species at the study site have short viability or dormancy (Schopmeyer 1974) and no persistent seed bank in oldfields (Oosting and Humphreys 1940; Livingston and Allessio 1968). In addition, no tree seedlings are present at abandonment of the oldfields at the study site and therefore spatial pattern of tree invasion should be determined by dispersal strategy of the species. Density of seeds is normally greatest next to parent trees (Janzen 1971; Debussche *et al.* 1980) and seed density decreases exponentially

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with distance from parent trees (Boyer 1958; Jemison and Korstian 1944; Roe 1967; Ronco 1970).

Hypothesis 2. The exponential pattern deteriorates later in succession. Many mechanisms could produce a shift away from an exponential tree stem distribution, and they cannot be definitively discriminated with this dataset. We identify several factors that might reduce an exponential spatial pattern through succession. Animal dispersal, which is expected to be leptokurtic or generally exponential (Howe 1986) and patchy (McDonnell and Stiles 1983), may become increasingly important in older, more structurally complex oldfields (McDonnell and Stiles 1983; Reynolds 1958). Also later in succession, mammalian predation may be greater (Mittelbach and Gross 1984) and the reduced light environment next to the forest may reduce tree seedling survival by shading (Brand 1986). Finally, tree seedlings may self-thin with time, leading to convergent densities across the field (Yoda *et al.* 1963; Harper 1977).

Hypothesis 3. With increasing distance from the forest, stems of palatable tree species will be denser compared to relatively unpalatable species. Mammalian herbivores and predators may affect the spatial patterns of woody plants by causing mortality of seeds and seedlings (Crawley 1983) and the principal seedling predator in fields at the study site, the eastern cottontail rabbit *Sylvilagus floridanus,* prefers woody patches (Hanson *et al.* 1969) and perhaps areas where forest and field meet (Myster and McCarthy 1989). Consumers may be affected by the cover of large woody plants which protect them from predators and so reduce stem densities closer to the forest (Pearson 1959; Hanson *et al.* 1969; Newman *et al.* 1988). Regardless of whether mammalian consumers are more active at the forest edge or in the open field, we expect palatable vs. unpalatable species to differ in spatial distribution.

Hypothesis 4. Stems of bird-dispersed species are more clumped than stems of mammal-dispersed species. Bird-dispersed species have been shown to have clumped seed input in oldfields because existing woody plants serve as perches (McDonnell and Stiles 1983). However, mammal-dispersed species early in oldfield succession are absent (Bard 1952; Beckwith 1954), perhaps because the small mammals that disperse tree seeds need the cover of large woody plants (Reynolds 1958; Newman *et al.* 1988) which are more common later in succession (Pickett 1982). When mammal-dispersed tree stems do invade they may have a clumped distribution if their seeds were dispersed as larder caches (Reynolds 1958; West 1968; Price and Jenkins 1986) or be randomly distributed if dispersed as scatterhoards (Smith and Reichman 1984) or ingested and defecated (Howe 1986). Mammals, which act as both seed dispersers and seed predators, are likely to be less effective than birds in causing clumping of seed input because they eat many of the seeds they disperse.

Methods and Materials. The study site, Hutcheson Memorial Forest Center (HMF), is located in Somerset County, New Jersey USA (40°30'N, 74°34'W). The old-growth forest at HMF has a *Quercus-Carya* canopy and a *Cornus florida* understory (Bard 1952). We analyzed the pattern of tree species in the ten oldfields adjacent to the old growth forest or established hedgerow (see maps in Monte 1973; McDonnell 1986) that comprise the Buell-Small Successional Study (BSS; Buell *et al.* 1971; Pickett 1982; Myster and Pickett 1988, 1989). The BSS oldfields were abandoned in pairs every other year starting in 1958. All had been under continuous production agriculture before abandonment and therefore lacked trees when succession began. These oldfields differ in season of abandonment (spring vs. fall), mode of abandonment (plowed vs. unplowed) and last crop (soybeans vs. soybeans and sorghum vs. orchard grass [*Dactylis glomerata*]; Myster and Pickett 1990). Forty-eight permanent plots (2.0 × 0.5 m) were arranged in a grid in each oldfield at the time of its abandonment. The dimensions of the grid were determined by the size and shape of each field. Every year since abandonment, these plots have been sampled in late July for species and density of tree stems. Because stems were not tagged and followed through time, our data do not discriminate individuals. In addition, stem sizes were not recorded (but see Rankin and Pickett 1989) and there was no upper or lower limit of stem size included in the sample.

Eight tree taxa (*Acer* spp., *Ailanthus altissima, Fraxinus americana, Prunus* spp., *Cornus florida, Juniperus virginiana, Carya* spp., *Quercus* spp., Gleason and Cronquist 1963) were common enough to calculate spatial pattern in each time period of succession. These species had at least 10 stems in at least one oldfield in each of the five time periods. Eleven additional tree species occur in the BSS but contribute less than 10% of the total tree stems in these oldfields: *Betula* spp., *Celtis occidentalis, Fagus grandifolia, Juglans nigra, Morus* spp., *Nyssa sylvatica, Pinus strobus, Platanus occidentalis, Pyrus* spp., *Sassafras albidum* and *Ulmus* spp. The tree stems are mainly seedlings, some saplings or, in a few cases, small trees. Although identification to genus is unambiguous, very young individuals of some genera cannot always be identified to species. Therefore, genus is the lowest taxon used in such cases. According to published reports, the species in each genus have the same dispersal mode and palatability to mammals (Davison 1981; Schopmeyer 1974).

We summed the data (10 oldfields with 48 plots each, defining 480 total data points) into five, 6-yr time periods spanning the 31 years of the study. These time periods reflect the dominance patterns of plant species with different life histories (Pickett 1982; Myster and Pickett 1988). We attempted to fit a regression line on the nonzero data (stem density vs. distance to nearest forest edge) after log-transformation to realize an exponential model (Hughes and Fahey 1988). We used the same analysis without a transformation to realize a linear model. Tree stems and plots were not closer than 5 meters to the original forest edge and were not farther away than 40 meters from an edge. The spatial patterns for each time period were summarized using the regression parameters, i.e., p, slope, Y-intercept and R^2 values. Patterns with p values up to 0.10 were interpreted as they can be used for descriptive purposes (Hughes and Fahey 1988).

We next divided the data points used in the regressions into groups for each of the eight tree taxa in each of the ten oldfields and repeated the exponential regression analysis on the groups. The Scheffe-box test for homogeneity of variance (Sokal and Rohf 1981) was first preformed on the groups. Then, unbalanced analysis of variance (ANOVA), on slopes from these regressions using stem data of individual species in each oldfield, discriminated among patterns. Classification variables defining groups for the ANOVAs were: (1) dispersal vector (wind vs. bird vs. mammal), (2) palatability of seedlings to mammalian herbivores (high vs. medium vs. low) defined by relative number of seedlings eaten, and (3) ability to resprout after herbivory (does vs. does not).

The species were divided among the classification variables as follows. Wind-dispersed taxa include *Acer, Ailanthus,* and *Fraxinus.* Bird-dispersed taxa include *Prunus, Cornus,* and *Juniperus.* Mammal-dispersed taxa include *Carya* and *Quercus* (Schopmeyer 1974). The eastern cottontail rabbit, *Sylvilagus floridanus,* is the major seedling predator at HMF (Buell *et al.* 1971; Meadows 1988) and other herbivores may include white-tailed deer (*Odocoileus virginianus*) and meadow vole (*Microtus pennsylvanica,* Burton 1989). Experiments at HMF (Davison 1981) have determined the foliage of *Prunus, Cornus* and *Quercus* to be most palatable, *Juniperus* least palatable and all other species to be of moderate palatability to local herbivores. Insect herbivory has been shown to reduce leaf area of tree seedlings but does not usually contribute to seedling mortality in HMF oldfields although mammalian herbivores greatly affect seedling mortality (Davison 1981; Myster and McCarthy 1989). In addition, *Carya, Quercus,* and *Acer* resprout after browsing (Hutnik and Yawney 1961; Fowells 1965; Myster and McCarthy 1989). There were no correlations among species traits used for the ANOVA's.

We investigated clumping of stems grouped by dispersal vectors. We used Poisson and negative binomial functions to test our data for departure from these defined random and clumped distributions, respectively. Using Chi-square analysis, we tested hypotheses (alpha = 0.05) of random or clumped spatial pattern of tree stem groups defined by dispersal vector (Ludwig and Reynolds 1988). If stems were clumped, we computed Green's index (Green 1966), which is based on the variance to mean ratio, to assess the degree of clumping.

Results and Discussion. HYPOTHESES 1 AND 2. There was a higher stem density adjacent to the forest and hedgerow than elsewhere in abandoned fields early in succession for all species in all ten oldfields (Table 1). As succession proceeded, stem number became more evenly spread throughout entire oldfields, leading to less significant regressions and less variance explained by the regressions (Table 1). Regressions using three dimensions (stem density vs. grid location of plot in oldfield) rather than two dimensions (stem density vs. distance to nearest forest edge) revealed very low R^2 values and nonsignificant P values ($P > 0.50$), therefore the two-dimensional regression parameters were used for analysis and interpretation. R^2 values for exponential regressions began at 0.90 (Table 1, $P < 0.01$) and decreased monotonically during succession. Exponential regressions remained significant with $P < 0.10$ (Hughes and Fahey 1988) past the mid-

Table 1. R^2, slope, Y-intercept and p values from regressions of stem density vs. distance to closest forest edge for five six-year time periods. Number of data points used to define each regression line = 480 for each time period.

Exponential model

	Time period (years)				
	1–6	7–12	13–18	19–24	25–31
R^2	0.90	0.83	0.72	0.66	0.52
Slope	−0.04	−0.03	−0.03	0.01	0.02
Y-intercept	1.58	1.49	1.42	1.33	1.11
P value	0.01	0.06	0.09	0.12	0.20

Linear model

	Time period (years)				
	1–6	7–12	13–18	19–24	25–31
R^2	0.78	0.72	0.70	0.60	0.55
Slope	−0.40	−0.31	−0.22	−0.01	0.06
Y-intercept	11.45	10.88	8.10	5.03	4.95
P value	0.08	0.10	0.11	0.15	0.19

point of the successional sequence (Table 1). A linear model fitted the data less well than the exponential model early in succession, as shown by higher P values, and did not remain significant for as long (Table 1). During the early periods of succession when the regressions are significant, the slope of the exponential and linear regression lines becomes more positive and the Y-intercept value decreases (Table 1) which also point to a reduction of positive association between stem density and the original forest edge as succession proceeds.

The well known pattern of exponential decline of seed density with distance from seed trees (Boyer 1958; Jemison and Korstian 1944; Roe 1967; Ronco 1970) may explain hypothesis 1 (Hughes and Fahey 1988). There are at least four explanations for hypothesis 2, the declining negative exponential distribution relative to the forest edge ($P > 0.10$, Table 1; Hughes and Fahey 1981), which cannot be discriminated with this data set. First, the tree seed dispersal pattern may change with time as perches for birds become available in an oldfield (McDonnell and Stiles 1983). Second, shade may increase as plant cover increases with time in HMF oldfields (Pickett 1982) and reduce the growth rate and survival of tree seedlings (Jarvis and Jarvis 1964; Grime and Hunt 1975; Brand 1986). Third, density-dependent mortality or self-thinning (Harper 1977; Yoda *et al.* 1963) may increase with the decrease in light intensity with time (Hiroi and Monsi 1966). Finally, herbivory may increase with successional time (Watt 1981) and be greater under woody patches compared to herbaceous patches (Hanson *et al.* 1969). Because woody plant cover increases with time in HMF oldfields (Pickett 1982), this also could explain the decline in exponential pattern of stem density.

HYPOTHESIS 3. Variance between slopes in classification groups were homogeneous (Sokal and Rohf 1981). ANOVA's on slopes from the individual species regressions in each oldfield

Table 2. ANOVA results on slope values from exponential regressions of tree taxa in each oldfield divided into groups by species characteristics. Statistical significance is denoted by "*" ($0.05 < P < 0.01$). Sample size = 80, 8 tree taxa by 10 oldfields. Slopes were divided into three groups by dispersal vector (sample size for wind dispersed species = 30, sample size for bird dispersed species = 30, sample size for mammal dispersed species = 20), into three groups by palatability (sample size for high = 30, sample size for medium = 40, sample size for low = 10) and into two groups by resprouting ability (sample size for sprouters = 30, sample size for non sprouters = 50).

			Time period (years)				
Grouping	df	Error	1–6	7–12	13–18	19–24	25–31
Dispersal vector	2	158	ns	ns	ns	ns	ns
Palatability	2	158	ns	ns	ns	*	*
Resprouting	1	79	ns	ns	ns	ns	ns

Table 3. Green's index. Relative degree of stem clumping is expressed as a percentage. The index ranges from 0 for no clumping and 100 for clumping of all stems in the same plot. There were no stems of mammal-dispersed tree species present in any plot during the first two time periods.

	Time period (years)				
	1–6	7–12	13–18	19–24	25–31
Wind-dispersed	11.19	8.12	9.79	15.53	10.23
Bird-dispersed	6.62	10.67	10.62	24.21	29.12
Mammal-dispersed	—	—	4.42	7.73	3.84

(Table 2) indicated that some spatial patterns differed among species having different characteristics. During 5 time periods through the 31 years of succession examined, there were significant differences among species grouped by palatability in years 19–24 and 25–31 (Table 2). In these later years the general exponential regressions are no longer significant (Table 1). This is due mainly to the species of lowest palatability which have the largest mean slope in the last time period. The low palatability species show increasing stem density with distance into oldfields later in succession. In contrast, later in succession species of high and moderate palatability are more dense close to the forest, less dense away from the forest and maintain some significant exponential regressions ($0.05 < P < 0.10$). Because many oldfield herbivores prefer woody patches (Pearson 1959; Hanson *et al.* 1969; Newman *et al.* 1988) and woody cover increases during oldfield succession (Pickett 1982), herbivore density and activity may be greater in or around these patches. This is consistent with the pattern of decreasing density of the more palatable tree species away from the forest edge and out in the oldfield later in succession.

As expected, stems of mammal-dispersed species are not present until later in succession, compared to wind- and bird-dispersed species (Table 3; Bard 1952). However, in the first six years after invasion (years 13–18), the stem density of mammal-dispersed species is highly correlated (exponential regression parameters: $R^2 > 0.90$, $P < 0.01$) with distance to the forest edge as were wind- and bird-dispersed species (Table 1). Species having different dispersal vectors differ in time of entry into succession rather than in the spatial pattern of invasion.

HYPOTHESIS 4. Comparison to a Poisson distribution reveals the spatial patterns are not random (χ^2: $18.112 > 12.592$, df = 6, $P < 0.01$). Further comparison with a negative binomial distribution reveals all species patterns are clumped (χ^2: $17.521 > 12.592$, df = 6, $P < 0.01$). In addition, the greatest degree of clumping occurs with bird-dispersed species in time periods 4 and 5 (Table 3). Wind-dispersed species show less variability in degree of clumping through time than bird-dispersed species (Table 3). This may be the result of a more uniform wind-dispersed seed rain not dependent on animal behavior or population sizes that change with time. Mammal-dispersed species have the lowest degree of clumping (Table 3), indicating little effect of caching of seeds on the clumping of established tree stems (contra West 1968; Howe 1986) or the preference of squirrels of the genus *Sciurus* for scatterhoarding only one or a few seeds (Smith and Reichman 1984).

To summarize, three of the four hypotheses tested were supported by these data. (1) Stem density decreased exponentially from the forest edge early in succession. (2) This exponential pattern was significant only in the first six years of time period 1. (3) Starting with the 19–24 year time period, patterns of established tree stems were different for species having different palatabilities to HMF herbivores. Species that are most palatable had relatively more stems close to the forest compared to unpalatable stems. (4) Stems of bird-dispersed species were clumped, but stems of mammal-dispersed species were much less clumped. Stems of mammal-dispersed species were absent during the first 12 years of succession.

Analysis of a long-term permanent plot successional data set is extremely rare. Instead of relying on chronosequences or short-term data, we have explored a long-term establishment pattern that may be used in refining future demographic studies and other more detailed experiments. Our pattern analysis does not definitively answer questions concerning mechanism but, rather, presents hypotheses for future experiments. Regardless of the mechanism (or suite of mechanisms) that might produce the significant spatial patterns we described, an important generalization is suggested by the patterns. Early in succession, the stems of plants are statistically associated with the nearest forest or hedgerow. Such a pattern implies that control of the invasion and establishment of tree species is influenced most strongly by factors and interactions associated with the adjacent landscape elements (Naveh and Lieberman 1984) rather than the field itself. As succession proceeds, the statistical association with the forest diminishes, suggesting that factors and interactions associated with the field itself become dominant.

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