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Forest Ecology and Management 180 (2003) 475–491

Forest Ecology and Management

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# Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession

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Received 2 September 2002; accepted 2 December 2002

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## Abstract

An analysis of spatial dispersion was conducted for individual tree species in the old-growth forest at the Davis-Purdue Research Forest in Indiana. This 20.6 ha stand has been left largely undisturbed by exogenous factors since its acquisition by Purdue in 1917. It is the only long-term study plot of its size for a temperate hardwood forest with *x*–*y* coordinates (rectangular plot) for all species above 10 cm diameter. Full censuses have been conducted spanning 60 years (1926, 1976 and 1986).

Ripley's $L(t)$ function revealed that most species are characterized by some form of aggregation, agreeing with a prior evaluation from 1981. Heterogeneity of spatial structure was evident between two large plots, indicating that differences in site quality and history had influenced spatial structure. Shade-intolerant species were numerically dominant and spatially aggregated in 1926 but have declined over the 60-year interval and become more random in spatial dispersion. Shade-tolerant species have increased in number and become more aggregated over time, or they exhibit little change in spatial structure. Examples of the latter include *Acer saccharum* and *Ulmus americana*, species that experienced explosive population growth. These contrasting patterns are masked by stand-level patterns that show a trend toward uniformity over the same time frame.

These data reveal that changes in dispersion accompany the demographic failure experienced by numerous tree species in Central Hardwood old-growth stands, and these changes may feed back into a negative population cycle and further impede regeneration. The simultaneous manipulation of dispersion and density should be considered as a tool for influencing forest succession and promoting regeneration of desired tree species.

Published by Elsevier B.V.

*Keywords:* Aggregation; Disturbance; Ripley's; Shade-tolerance; Uniformity

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## 1. Introduction

The Central Hardwood Region in the eastern United States is the world's largest contiguous assemblage of deciduous tree species, extending from the Great Plains east to the Appalachians and from Minnesota

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0378-1127/02/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/S0378-1127(02)00612-6

and Wisconsin south to Tennessee (Clark, 1989; Parker, 1989; Hicks, 1998). The region includes the present-day natural range of prized timber species such as black walnut (*Juglans nigra* L.), black cherry (*Prunus serotina* Ehrh.), and northern red oak (*Quercus rubra* L.). Of the 40 million hectare of forest in the region, less than 1% can be classified as old-growth (Parker, 1989). Old-growth acreage exists as small woodlots that have all experienced some anthropogenic disturbance through fire (or its exclusion), limited timber harvest, or livestock grazing (Merritt, 1980).

An unintentional side effect of protecting Central Hardwood forests from disturbance has been the alteration of their successional trajectories (Russell, 1983; Lorimer, 1993; Dey, 2002; Johnson et al., 2002). It is thought that much of the Central Hardwood range was maintained in a sub-climax condition prior to European settlement, in part through the repeated setting of fires and tree girdling by Native Americans. By the 1700s and 1800s, European settlers were perpetuating this disturbance through extensive cutting, grazing, and burning (Den Uyl, 1954). Later in the 1900s, disturbance was largely suppressed and late successional, shade-tolerant species (e.g., *Acer* spp.) became established as advanced regeneration in the closed understory of forests, despite the continued dominance of shade-intolerant species (e.g., *Quercus* spp.) in the canopy (Lorimer, 1993; Lorimer et al., 1994). This pattern has been observed at numerous sites throughout the Central Hardwood range, including Illinois (Boggess and Bailey, 1964; Weaver and Ashby, 1971; Fralish et al., 1991; Shotola et al., 1992), Indiana (Schmelz et al., 1975; Abrell and Jackson, 1977; Parker et al., 1985), Ohio (Boerner and Cho, 1987; McCarthy et al., 1987, 2001; Goebel and Hix, 1996), Maryland (McCarthy and Bailey, 1996), North Carolina (Christensen, 1977), Pennsylvania (Abrams and Nowacki, 1992), West Virginia (Abrams et al., 1995), and Wisconsin (McCune and Cottam, 1985).

Despite this rich body of evidence regarding species composition of old-growth temperate hardwood forests, reports of their spatial structure are uncommon, especially compared to temperate pine or mixed pine-hardwoods (e.g., Cooper, 1961; Laessle, 1965; Williamson, 1975; Whipple, 1980) or tropical forests (e.g., Hubbell, 1979; Armesto et al., 1986; Lieberman and Lieberman, 1994; Condit et al., 2000). The spatial pattern of plants is a critical determinant of habitat structure in many ecosystems, as well as food distribution (leaves, pollen, nectar, and fruits). These factors can affect the local intensity of intra- and inter-specific plant competition, the distribution of herbivores and their predators and parasitoids, and the movements of pollinators and seed dispersers (Doak et al., 1992; Dale, 1999). Though it is difficult to directly relate pattern to process, the description of spatial pattern can be useful in developing hypotheses regarding the roles that certain biological processes may have played in the history of any given assemblage (Dale, 1999). For example, in an old-growth temperate beech-maple forest, Williamson (1975) found that early seral species exhibited aggregation at the same spatial scale as the size of light gaps in the stand, whereas later seral species were largely distributed at random for all of the scales examined. Even fewer studies, temperate or tropical, have explored changes in spatial dispersion over time. At the Duke Forest, Christensen (1977) reported on changes in spatial pattern in a 140 m × 140 m mapped stand of immature climax oak-hickory. Over a 23-year period of observation, the stand-level stem pattern shifted from random to uniform, likely due to density-dependent mortality in the smaller, aggregated size classes. Long-term plots in Connecticut oak-mixed hardwood stands (Ward and Stephens, 1993, 1994; Ward et al., 1999) provide 70 years of perspective on plant demography, though changes in spatial structure have not been addressed in part because data has been collected along transects.

The 20.6 ha Davis-Purdue Research Forest (DPRF) is a temperate old-growth hardwood stand where spatial structure has been examined. To our knowledge, it is the only stand of old-growth hardwood in which all stems ≥10 cm diameter have been mapped with *x*–*y* coordinates (rectangular plot, not transects) and followed for over 60 years (initial census 1926, last fully-mapped census 1986). An evaluation of size-class distributions over this period indicates that late seral species are replacing early and mid-seral species (Parker et al., 1985). To a large extent this change at the DPRF is due to a low rate of canopy gap formation (Ward and Parker, 1989). Leopold et al. (1985) examined the spatial dispersion of individual tree species at the DPRF using census information from a single sampling period in 1981. They found that most were aggregated; only *Q. rubra* was uniform. They attributed the aggregation to gap colonization, soil drainage patterns, vegetative reproduction, and disturbance (cutting and grazing). Spetich and Parker (1998) concluded that grazing had been the primary factor influencing tree regeneration at the DPRF. The forest understory was characterized as open and park-like in 1926 shortly after the cessation of grazing in 1917 (Parker and Leopold, 1983), whereas it is now closed and dense. Although there is no information on change in spatial dispersion of individual species, the stand as a whole has shifted from a weakly non-random spatial distribution in 1926 to a uniform distribution in 1976 and 1986 (Ward et al., 1996). The authors concluded that uniformity resulted from density-dependent mortality and ingrowth.

Here, we characterize the change in spatial dispersion of individual species at the DPRF over the 60-year interval from 1926 to 1986, and address the following specific questions: (a) Is there a dominant spatial pattern revealed by Ripley's analysis, and how do our results compare with the prior evaluation of 1981 data using four different statistics? (b) Is there heterogeneity of spatial pattern between large plots within the study area? (c) Most central to this study, does the spatial pattern of individual species change over time, and if so, are populations becoming more aggregated, random, or uniform? (d) Does the interaction between shade-tolerance and disturbance regimes explain the observed patterns? (e) How can this information be used to better manage temperate hardwood forests?

## 2. Study site and methods

### 2.1. Study site

We conducted research at the DPRF located in Randolph county, east-central Indiana. Parker and Leopold (1983) and Parker et al. (1985) provide detailed site descriptions. The forest is one of the largest (20.6 ha) and oldest remaining tracts of mature deciduous forest on the Tipton Till Plain, covering central Illinois, Indiana, and Ohio. Tree coring at the site in 1980 (The Lamont-Doherty Geological Observatory of Columbia University, Pallisades, NY, unpublished data) revealed ages for *Quercus macrocarpa* Michx. ranging from 195 to 300 years, which antedates the major wave of European settlement in this area around 1810–1870 (Den Uyl, 1954). Historical records note recent exogenous disturbances, mainly a period of heavy livestock grazing from the mid-1800s until 1917, a surface fire in the western portion of the stand in 1972, removal of <50 dead and dying trees in the 1940s and 1950s, theft of 3–4 adult *J. nigra*, and the persistent effects of Dutch elm disease and phloem necrosis on *Ulmus americana* L. and *Ulmus rubra* Muhl. Two seasonal ponds (0.4–0.8 ha) accumulate in the spring, and a drainage ditch was established between them in the 1940s; smaller wet depressions are scattered about the stand. Lindsey and Schmelz (1970) classified the site as lowland depressional forest because of the large numbers of wet site species present.

### 2.2. Censuses

We examined dispersion in the central portion of the 20.6 ha stand (Fig. 1). In 1926, Professor Burr N. Prentice (Purdue Department of Forestry) mapped, measured, and tagged all stems ≥4.0 in. (10.2 cm) diameter at breast height (dbh, 1.37 m above ground) in the full stand (Prentice, 1927). In 1976 and again in 1986, the censuses was repeated for all stems ≥10 cm dbh in the central 8.5 ha (approximately 440 m × 200 m), including recording new stems entering the ≥10 cm class (ingrowth) and dead stems. The spatial (*x*–*y*) coordinates of all stems were mapped to the

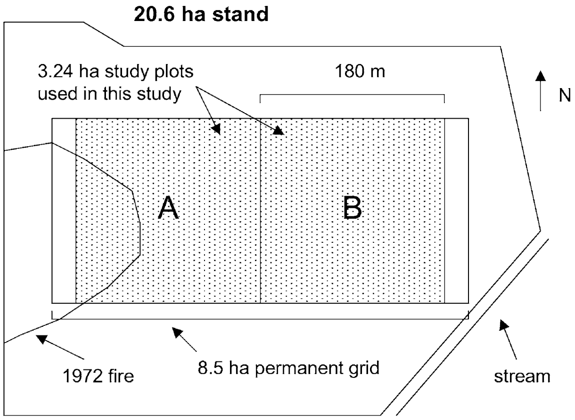

Fig. 1. Compartment 1 at the DPRF. Plots A and B were established within the central 8.5 ha *x*–*y* coordinate grid.

nearest meter. In this study, we restrict our attention to spatial patterns in two adjacent square 3.24 ha plots (180 m on a side) (Fig. 1; plot A on the west side and plot B on the east). Together, these two plots covered most of the internal 8.5 ha mapped plot. We used square plots to minimize edge effects with this formulation of $L(t)$, and the split plot design permitted spatial replication (e.g., Hubbell and Foster, 1986).

### 2.3. Species

We examined dispersion in 23 tree species from nine families (Tables 1 and 2). These species were present at densities $\geq 10$ stems in at least one plot from at least one census; 12 species were excluded because they were too rare. Leopold et al. (1985) also required that species be present at densities $\geq 10$ stems. Sutherland et al. (2000) reviewed 20 life history characteristics of these, and other, tree taxa throughout the Central Hardwood Region. A cursory examination indicated that shade-tolerance at the seedling stage was most clearly associated with our observed changes in spatial dispersion, and we report shade-tolerance in Table 2, wherein "INT" indicates shade-intolerance (see categories 2 (= intolerant) and 3 (= intermediate or mid-tolerant) of Sutherland et al. (2000)) and "TOL" indicates shade-tolerance [see categories 4 (= tolerant) and 5 (= very tolerant)].

### 2.4. Spatial analyses

We examined stem dispersion using a modification of Ripley's $K(t)$ function (Ripley, 1977, 1981; see also Berg and Hamrick, 1994). $K(t)$ measures stem abundance within a radius $t$ from a focal stem, evaluated over all $n$ stems in the plot of area A. Thus, dispersion

Table 1
Spatial scales at which any significant spatial structure appeared based on 95% CIs from Ripley's tests at 18 distance radii (0–90 m) for individual species in plots A and B in three census periods[a]

| Species | 1926 A/B | 1976 A/B | 1986 A/B |
|---|---|---|---|
| *Acer negundo* L. | N/N | C:5–90/N | C:5–90/N |
| *A. saccharum* Marsh. | C:10–70/C:5–85 | C:10–45/C:5–90 | C:10–40/C:5–90 |
| *Aesculus glabra* Willd. | N/N | C:5,15,25–30,45–65,75–90/C:5–40 | C:5,25–30,45,60–65,75–90/ C:5–50 |
| *Carpinus caroliniana* Walt. | N/N | C:5–90/C:5–70 | C:5–90/C:5–70 |
| *Carya cordiformis* (Wangenh.) K. Koch | N/N | N/C:15,45 | N/R |
| *Carya ovata* (P. Mill.) K. Koch | R/C:40,60–65 | C:10–45/C:5–70 | C:5–55/C:5–60,70 |
| *Celtis occidentalis* L. | N/N | C:5–90/N | C:5–90/R |
| *Crataegus* spp. | N/N | C:5–25,60–65/C:10–90 | C:5–55/C:10–90 |
| *F. grandifolia* (Ehrh.) Little | N/N | R/R | R/C:15–20,30–35 |
| *F. americana* L. | C:10–75/C:10–50 | C:10,45,55–60,70–85/U:65,90 | C:65/U:70–90 |
| *Fraxinus nigra* Marsh. | C:5–90/C:40–75,85–90 | N/N | N/N |
| *G. triacanthos* L. | N/C:5–85 | N/N | N/N |
| *J. nigra* L. | C:10–70/C:30 | C:65,85/R | R/C:40 |
| *O. virginiana* (Mill.) K. Koch | N/N | C:5–50/U:65–85 | C:5–35/N |
| *P. serotina* Ehrh. | N/N | C:10–15/C:5,20–25,35–40 | C:15/C:20–25,35–40 |
| *Q. alba* L. | C:10–50/R | C:10–55 U:90/R | C:5–10,20–50 U:90/R |
| *Quercus bicolor* Willd. | C:5–30/R | C:5–10/R | C:5–15/N |
| *Q. macrocarpa* Michx. | C:20–35/C:20,35–90 | C:25/C:15–25,35–90 | C:25/C:15–25,35–90 |
| *Q. muehlenbergii* Engelm. | N/R | N/C:5 | N/R |
| *Quercus palustris* Muenchh. | C:10–25,35,45–90/R | N/R | N/N |
| *Q. rubra* L. (and *Quercus shumardii* Buckl.) | U:70–90/C:10–15,25–90 | C:15 U:65–70/C:40 | C:15 U:55–70/C:45 |
| *U. americana* L. | C:5–90/C:5–90 | C:5–90/C:5–90 | C:5–90/C:5–90 |
| *U. rubra* Muhl. | N/N | C:5–45/C:5–55 | C:5–50/C:5–55 |

[a] C (clustered = aggregated) or U (uniform) is followed by the radial distance classes (5 m intervals) at which the structure was observed; distances not listed indicate spatial pattern that was essentially random. R indicates randomness across the entire interval (0–90 m), and N represents the null state of rarity (<10 stems in the plot). Data for plot A is followed by that for plot B within each census (A/B).

Table 2

Taxa and their respective density and large-pattern dispersion at three census periods evaluated in plots A and B at the DPRF[a]

| Change in aggregation | Species | Family | Density (stems per plot) | | | | Spatial dispersion ($S$) | | | | Shade-tolerance |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1926 A/B | 1976 A/B | 1986 A/B | $\Delta_D$ A/B | 1926 A/B | 1976 A/B | 1986 A/B | $\Delta_S$ A/B | |
| Diminished | *F. americana* | Oleaceae | 76/148 | 48/61 | 42/47 | −34/−101 | +/+ | +/0 | 0/0 | −1/−1 | INT (3) |
| | *Fraxinus nigra* | Oleaceae | 27/12 | 3/9 | 2/8 | −25/−4 | +/+ | $\phi/\phi$ | $\phi/\phi$ | −1/−1 | INT (2) |
| | *G. triacanthos* | Fabaceae | 2/11 | 0/5 | 0/2 | −2/−9 | $\phi$/+ | $\phi/\phi$ | $\phi/\phi$ | /−1 | INT (2) |
| | *J. nigra* | Juglandaceae | 23/23 | 18/25 | 16/23 | −7/0 | +/0 | 0/0 | 0/0 | −1/0 | INT (2) |
| | *Quercus bicolor* | Fagaceae | 28/14 | 25/10 | 22/8 | −6/−6 | +/0 | 0/0 | 0/$\phi$ | −1/0 | INT (3) |
| | *Quercus palustris* | Fagaceae | 10/12 | 9/10 | 8/9 | −2/−3 | +/0 | $\phi$/0 | $\phi/\phi$ | −1/0 | INT (3) |
| | *Q. rubra*[b] | Fagaceae | 130/125 | 75/82 | 64/65 | −66/−60 | 0/+ | 0/0 | 0/0 | 0/−1 | INT (3) |
| No change | *A. saccharum* | Aceraceae | 31/24 | 250/155 | 306/190 | +275/+166 | +/+ | +/+ | +/+ | 0/0 | TOL (5) |
| | *Carya cordiformis* | Juglandaceae | 1/1 | 3/16 | 4/16 | +3/+15 | $\phi/\phi$ | $\phi$/0 | $\phi$/0 | /0 | INT (3) |
| | *F. grandifolia* | Fagaceae | 5/3 | 23/46 | 23/48 | +18/+45 | $\phi/\phi$ | 0/0 | 0/0 | 0/0 | TOL (5) |
| | *P. serotina* | Rosaceae | 3/1 | 17/16 | 14/12 | +11/+11 | $\phi/\phi$ | 0/0 | 0/0 | 0/0 | INT (3) |
| | *Q. alba* | Fagaceae | 59/27 | 48/23 | 42/22 | −17/−5 | +/0 | +/0 | +/0 | 0/0 | INT (3) |
| | *Q. macrocarpa* | Fagaceae | 25/39 | 21/33 | 21/33 | −4/−6 | 0/+ | 0/+ | 0/+ | 0/0 | INT (3) |
| | *Q. muehlenbergii* | Fagaceae | 8/19 | 8/15 | 8/14 | 0/−5 | $\phi$/0 | $\phi$/0 | $\phi$/0 | /0 | – |
| | *U. americana* | Ulmaceae | 79/43 | 194/236 | 161/204 | +82/+161 | +/+ | +/+ | +/+ | 0/0 | INT (3) |
| Increased | *Acer negundo* | Aceraceae | 0/0 | 13/1 | 15/1 | +15/+1 | $\phi/\phi$ | +/$\phi$ | +/$\phi$ | +1/ | TOL (4) |
| | *Aesculus glabra* | Hippocastenaceae | 2/3 | 50/48 | 50/53 | +48/+50 | $\phi/\phi$ | +/+ | +/+ | +1/+1 | TOL (4) |
| | *Carpinus caroliniana* | Betulaceae | 0/0 | 38/54 | 26/42 | +26/+42 | $\phi/\phi$ | +/+ | +/+ | +1/+1 | TOL (5) |
| | *Carya ovata* | Juglandaceae | 20/36 | 56/67 | 60/60 | +40/+24 | 0/0 | +/+ | +/+ | +1/+1 | TOL (4) |
| | *Celtis occidentalis* | Ulmaceae | 6/0 | 43/8 | 50/10 | +44/+10 | $\phi/\phi$ | +/$\phi$ | +/0 | +1/0 | TOL (4) |
| | *Crataegus spp.* | Rosaceae | 0/0 | 12/20 | 12/20 | +12/+20 | $\phi/\phi$ | +/+ | +/+ | +1/+1 | – |
| | *O. virginiana* | Betulaceae | 1/0 | 20/14 | 18/9 | +17/+9 | $\phi/\phi$ | +/0 | +/$\phi$ | +1/ | TOL (5) |
| | *U. rubra* | Ulmaceae | 5/2 | 43/71 | 49/70 | +44/+68 | $\phi/\phi$ | +/+ | +/+ | +1/+1 | TOL (4) |

[a] Census data are shown for each 3.24 ha plot in each census; $\Delta_D$ represents change in density between 1926 and 1986. Dispersion indices ($S$) from the Ripley's analyses indicate significant aggregation ("+") or uniformity ("−") only if the null model of randomness ("0") was rejected at ≥6 distance radii out of 18 (large-pattern); a null state of no spatial structure ($\phi$) was assigned if there were <10 stems per plot in any given census. $\Delta_S$ represents large-pattern change in spatial dispersion between 1926 and 1986. Shade-tolerance: INT, intolerant; TOL, tolerant ((2, intolerant; 3, mid-tolerant; 4, tolerant; 5, very tolerant) follows Sutherland et al. (2000)).

[b] The 1926 census includes a few *Q. shumardii*.

is considered across a variety of spatial scales simultaneously, calculated as

$$K(t) = \frac{A^2 I_{ij}}{n^2 W_{ij}} \tag{1}$$

where $I_{ij}$ is the number of stems within radius $t$. $W_{ij}$ is an edge correction that weights $K(t)$ by the probability that radius $t$ extends off the plot, measured as the plot area outside of the rectangle defined by stems $i$ and $j$. In order to limit edge effects, $t$ was constrained to take only values $\leq$half the length (here, 90 m) of the shortest plot side. The following transformation stabilizes the variance and is a linear function of $t$ centered at zero:

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t \tag{2}$$

Ward and Ferrandino (1999) showed that the variance is not stabilized for low expected densities, and they provide an improved estimator for such circumstances; our approach is therefore conservative and may under-estimate the amount of spatial structure.

We tested for significant departures from a null model of complete spatial randomness using bootstrap analyses (Efron and Tibshirani, 1993). Replicate stem populations ($N = 999$) were produced by distributing individuals along the $x$-axis as a Poisson process, wherein the mean density equaled the density in the observed data (Lewis and Shedler, 1979). We then randomly assigned $y$-coordinates and reshuffled them relative to the $x$-axis. Independent random data sets were generated at each of 18 distances ($t$) up to 90 m (5 m radial increments), and the resultant values of $L(t)$ were used to construct confidence intervals (CIs; two-tail, 95 and 99%) around each of the 18 observed data points. Observed data values that fall above the CI indicate pattern that is significantly aggregated whereas those that fall below are significantly uniform.

## 2.5. Evaluation of changes in spatial dispersion

We examined large-pattern changes in spatial structure that involved significant departures from randomness over several distance classes. A separate Ripley's analysis was conducted for each species in both plots (A and B) at each of the census periods (1926, 1976 and 1986). We used an index of dispersion ($S$ = ‘‘ − ’’, uniform; “0”, random; or “+”, aggregated) to tabulate and evaluate changes in spatial pattern. We assigned an index of “+” only if at least 1/3rd ($N = 6$) of the 18 observed $L(t)$ values fell above the 18 independently derived 95% CIs. Similarly, we assigned a “−” if 6 of the 18 $L(t)$ values fell below the 95% CI. All other intervals were assigned a score of “0”. Just by chance, roughly one out of 18 tests (5%) should yield a false rejection of the null hypothesis of randomness, so our approach is both conservative and places emphasis on changes that extend across a wider spatial dimension. We treated species with fewer than 10 stems in any given plot and census as existing in a null state, or “$\phi$”, essentially too rare to display any significant spatial structure.

The split or paired-plot design allowed an examination of heterogeneity of spatial pattern. We judged the pattern of a species to be spatially heterogeneous if large-pattern profiles (i.e., “+”, “0”, or “−”) differed between plots within a census. For instance, *J. nigra* was aggregated in plot A but essentially random in plot B during the 1926 census (“+/0”, Table 2; Fig. 2).

We measured the temporal trend in spatial pattern ($\Delta_S$) between the 1926 and 1986 censuses, requiring the same significant pattern at six or more radii (i.e., large-pattern changes). Plots A and B were considered separately. For each taxon in each plot, the dispersion index, $S$, from census 1926 was subtracted from that for the 1986 census; we used a dispersion index of $S = 0$ to calculate the trend if a species was present at fewer than 10 stems in a plot on any given census (null state). As an example, the spatial dispersion of *Q. rubra* remained the same in plot A but became less aggregated in plot B over the 60-year interval (i.e., $[0/0]_{1986} - [0/+]_{1926} = [0/-1] = \Delta_S$, Table 2). Note that this does not imply that *Q. rubra* attained a truly uniform spatial pattern in 1986 based on the dispersion index ($S$); the Ripley's tests detected uniformity at a few distance classes in each census (Table 1), but the more conservative $S$ revealed a change from aggregation to randomness over the interval, measured by $\Delta_S$. In general, positive $\Delta_S$ values arise when spatial pattern changes from random to aggregated, uniform to random, or uniform to aggregated; negative $\Delta_S$ values indicate changes from random to uniform, aggregated to random, or aggregated to uniform.

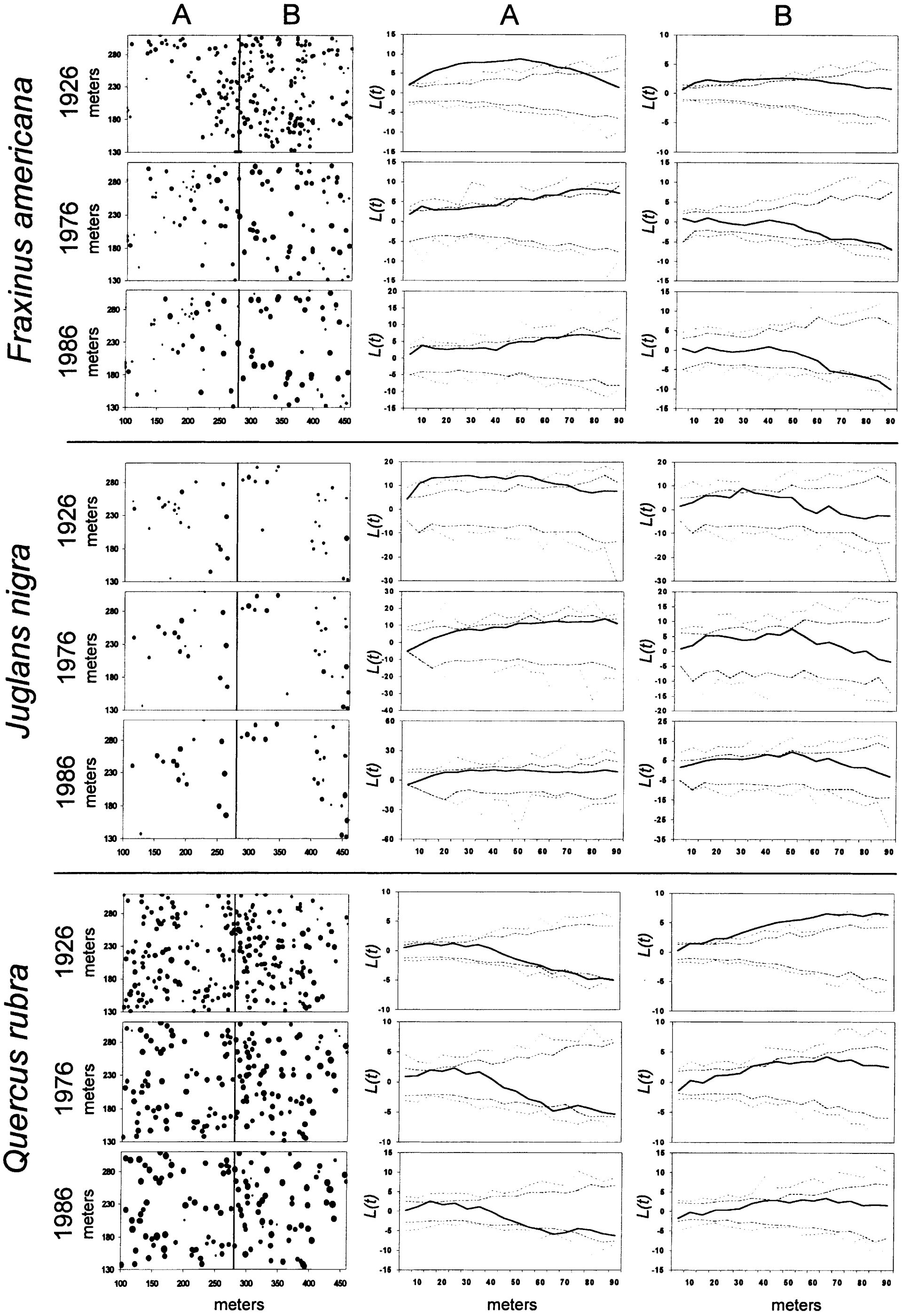

Fig. 2. Species becoming less aggregated (more random) over the 60-year interval according to $\Delta_S$. Their spatial distributions are shown for the three census periods in plots A and B. The size of each dot is proportional to stem dbh, standardized across species. We also show results of the separate Ripley's analyses for each plot: dark line, observed data; dashed lines, 95% CI; dotted lines, 99% CI. A deviation above the envelope indicates significant aggregation, below indicates uniformity.

Finally, we related change in spatial dispersion to change in the population density (stems/3.24 ha plot) between 1926 and 1986 ($\Delta_D$), and shade-tolerance of each species. We constrain our attention to censuses within plots A and B as defined in this study; see Parker et al. (1985) for a more thorough assessment of demography in this stand. We plotted $\Delta_D$ versus $\Delta_S$, referencing the shade-tolerance of each species according to Sutherland et al. (2000) as a potential source of causation for the observed pattern.

## 3. Results

### 3.1. Overall dispersion

Aggregation was the most common departure from randomness, and uniformity was very rare; we report the spatial scales at which we detected significant spatial structure with the Ripley's tests (Table 1). Only four species (*Fraxinus americana* L., *Ostrya virginiana* (Mill.) K. Koch, *Quercus alba* L., and *Q. rubra*) exhibited significant uniformity in this study. We detected uniform spatial patterns only at distances $\geq$55 m.

Much of the aggregation detected in the Ripley's tests spanned multiple distance radii; we report large-pattern spatial structure (*S*, Table 2), which required significant departures from randomness at $\geq$6 distance radii. Based on a tally of the 96 "+", "0", and "−" entries in Table 2, most observations ($N = 54$) were aggregated and the remainder were random (or null); none were uniform.

### 3.2. Spatial heterogeneity of dispersion

Roughly a quarter of the paired-plot, single census observations (Table 2) exhibited different large-pattern (*S*) signatures in plot A versus plot B (e.g., "+/0"). On a per-species basis, about half of the species exhibited a different spatial pattern in plot A versus B in at least one of the census periods. Of the eight species present at >10 stems per plot in both plots in every census, only *Acer saccharum* Marsh. and *U. americana* were homogeneously aggregated in every census (i.e., "+/+ +/++/+"). *Q. alba* always exhibited heterogeneity between plots A and B as "+/0" and *Q. macrocarpa* as "0/+".

### 3.3. Temporal heterogeneity of dispersion

Changes in dispersion over time were pronounced. Over half of the $\Delta_S$ values were non-zero on the 1926–1986 interval (Table 2), demonstrating that many of the differences in spatial structure involved large changes that included several distance classes. Slightly more observations were positive ($N = 13$) than negative ($N = 9$), which indicates that changes were biased toward a gain of aggregation. For paired-plot, single census observations, only five of the paired $\Delta_S$ values differed among plots within a census. The difference always involved a positive or negative score for one plot and no change for the adjacent plot; none of the species exhibited a positive $\Delta_S$ in one plot and a negative $\Delta_S$ in the adjacent plot within a census. In other words, the direction of change of spatial pattern in plot A always was the same as, or at least neutral to, that in plot B.

At the species level, approximately the same number of species became more aggregated as became more random based on large-pattern differences (Table 2). Seven species exhibited negative $\Delta_S$ values (e.g., Fig. 2), changing from aggregated in 1926 to random or a null state by 1986. Eight species showed no significant large-pattern change on the interval ($\Delta_S = 0$, e.g., Fig. 3). The remaining eight species became more aggregated over several distance classes ($+\Delta_S$, e.g., Fig. 4), in most cases moving from a null state in 1926 to aggregation by 1986.

### 3.4. Population demography, shade-tolerance, and changes in spatial dispersion

Species that were less tolerant to shade (INT) generally experienced reductions in population size and their spatial structure became indistinguishable from random (Table 2). Of the twelve INT species in this group, seven became less abundant and changed from aggregated in 1926 to a random or null state by 1986. Exceptions included *Q. alba*, *Q. macrocarpa*, and *U. americana* (Fig. 3), each of which maintained a level of aggregation throughout the study interval.

Species that were more shade-tolerant (TOL) generally increased in numbers and became more aggregated between 1926 and 1986 (Table 2, Fig. 4). All of these nine species increased in abundance in both plots, and seven of them became more aggregated.

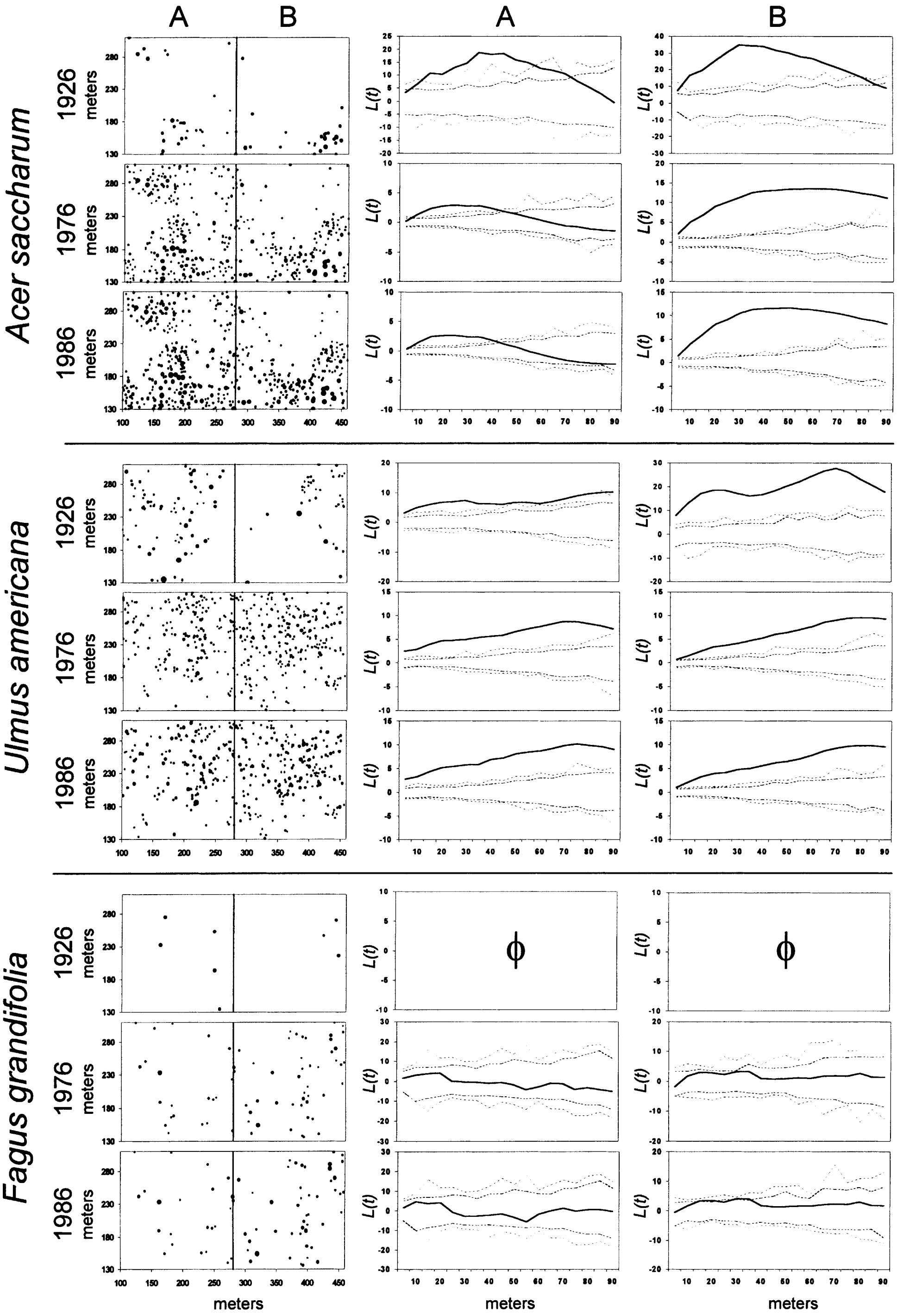

Fig. 3. Species exhibiting no change in spatial structure over the 60-year interval according to $\Delta_S$. See Fig. 2 for a description of figure details.

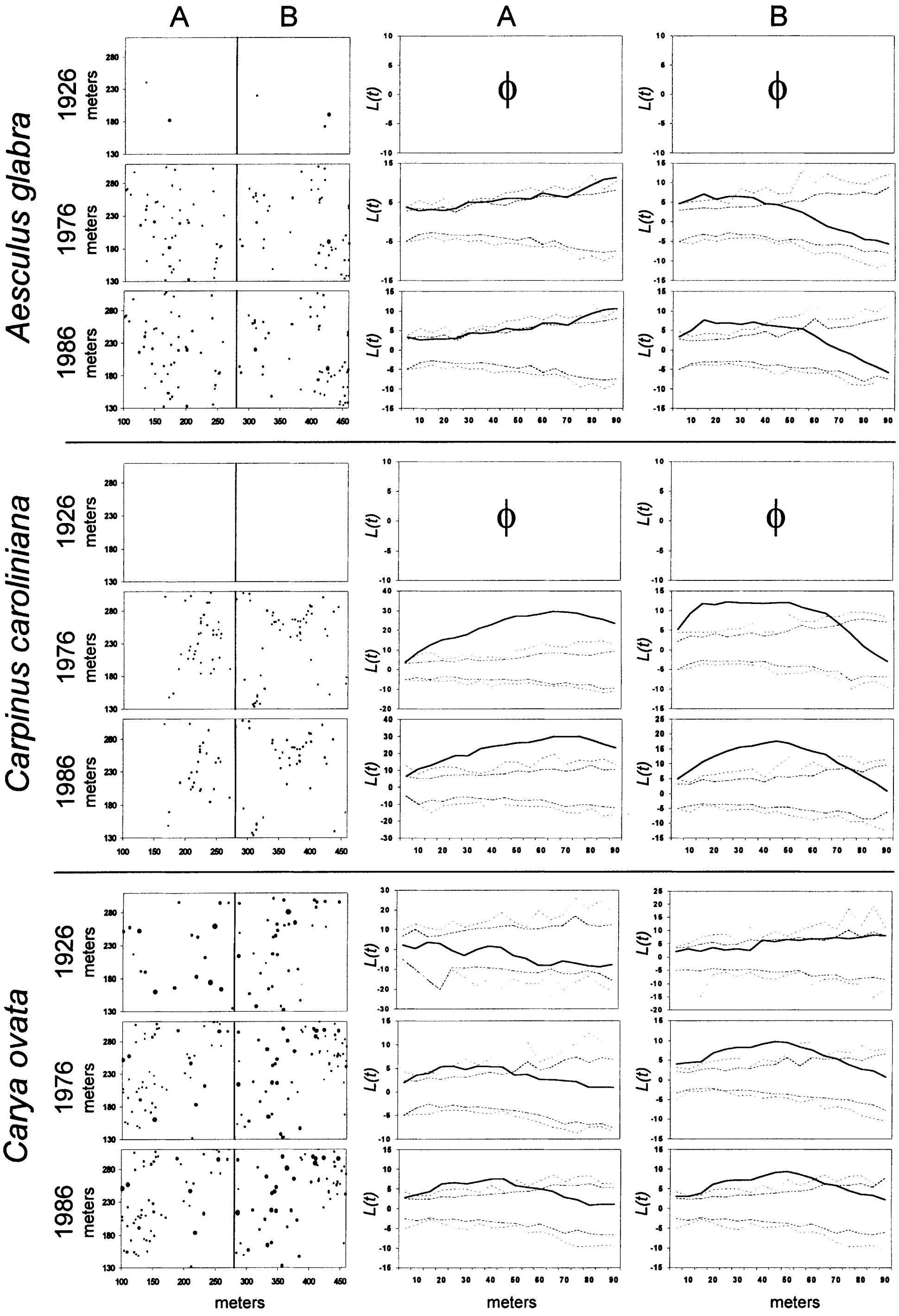

Fig. 4. Species becoming more aggregated over the 60-year interval according to $\Delta_S$. See Fig. 2 for a description of figure details.

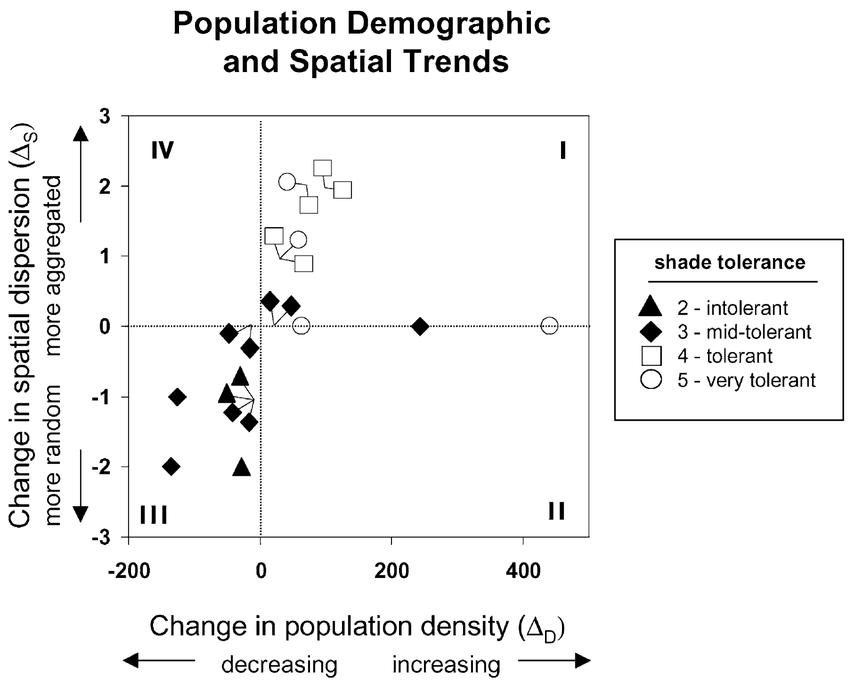

Fig. 5. Change in spatial structure ($\Delta_S$) relative to change in population size ($\Delta_D$) for individual species over the 60-year interval. Data for plots A and B are pooled for each species. Shade-tolerances follow Sutherland et al. (2000).

*A. saccharum* and *Fagus grandifolia* (Ehrh.). Little were the exceptions, exhibiting no large-pattern change in spatial structure ($\Delta_S = 0$, Fig. 3).

The strong correspondence between demography, shade-tolerance, and spatial pattern was evident as a clear trend at the community level (Fig. 5). We pooled data for plots A and B, retaining species identifications, and plotted $\Delta_D$ versus $\Delta_S$. All of the shade-tolerant (TOL) species that experienced a change in spatial structure appeared within quadrant I. All of the intolerant (INT) species that exhibited a change in spatial structure plotted within quadrant III.

## 4. Discussion

### 4.1. Tree life history strategies in undisturbed mesic old-growth

Although the DPRF stand has become more uniform over 60 years (Ward et al., 1996), it harbors at least three distinct groups of species that exhibit unique spatial profiles: species becoming less aggregated, species remaining unchanged, and species becoming more aggregated. Species within each group share at least one life history attribute critical to succession, shade-tolerance, and they display a similar demographic response to stand succession.

Species that became less aggregated also had fewer stems in 1986 than 1926, and surviving individuals were mostly large, overstory trees. There had been little ingrowth for these species, a result that agrees with the demographic evaluation of Parker et al. (1985). All of these species that declined in abundance were shade-intolerant or mid-tolerant (INT). Half of the species in this group were oaks, which have experienced widespread population declines in other old-growth stands (Johnson et al., 2002). All of the species that declined in abundance were present in 1926 at frequencies >10 stems per plot. Most of their spatial structure at that time was aggregated, possibly reflecting patchy recruitment on particular soils or in light gaps and patchy mortality due to heavy grazing pressure. Several of the species, including *F. americana*, *J. nigra*, and *Q. rubra* (Fig. 2), require well-drained soils, a characteristic that would contribute to aggregation in all of the censuses. The most dramatic population reductions were seen in *F. americana* and *Q. rubra*. Though *F. americana* is fairly tolerant of shade as a seedling, saplings and young adults require a light gap to reach the canopy (Fowells, 1965). It is likely that ash dieback (Smith, 1970; Hepting, 1971) also contributed to high mortality of *F. americana*. As for the oaks, Parker et al. (1985) showed that *Q. rubra* was the dominant species in the 1926 canopy but is likely to be the first oak to disappear from the stand because of high mortality and limited ingrowth.

Several species maintained the same spatial structure between 1926 and 1986 (Fig. 3). Notable here were *A. saccharum* and *U. americana*, which were present at densities >10 adults per plot in 1926 and experienced considerable population growth thereafter, displaying aggregation throughout. *A. saccharum* and *F. grandifolia*, the latter of which began 1926 in a null state and was essentially random by 1986, are among the most shade-tolerant of species in the Central Hardwood Region (Hicks, 1998; Sutherland et al., 2000), and their increases in old-growth forests throughout the region have been widely reported. *U. americana* is a wet soil specialist and is well-suited to the depressional topography of the DPRF. However, the species contributes little to canopy structure as the larger adults are repeatedly killed by Dutch elm disease and elm yellows (Shuder, 1955; Parker and Leopold, 1983; Parker et al., 1985). *Ulmus* spp. dominated the understory even in 1926 prior to the influx of disease, though mainly in wet areas (Ward and Parker, 1987), and it is thought that release from grazing pressures was a critical factor in its recent demographical increase at the DPRF (Parker and Leopold, 1983; Parker et al., 1985).

The large-pattern dispersion of *Q. alba*, *Q. macrocarpa*, and *Quercus muehlenbergii* Engelm. also did not change over the 60 years, but these species experienced reductions in population sizes. Some of these *Q. macrocarpa* are at least 300 years old and the modest changes in population sizes over this 60-year interval probably did not allow for any appreciable change in spatial structure. We anticipate that with time these white oaks would join the other white and red oaks in the group that is becoming less aggregated and experiencing a population decline.

Species that became more aggregated between 1926 and 1986 experienced population growth (Fig. 4), but not to the magnitude displayed by *A. saccharum* or *U. americana*. Species in this group were rare or absent in the 1926 census and then increased over time; *C. ovata* (P. Mill.) K. Koch was the exception. All of the taxa in this group were shade-tolerant (TOL). Den Uyl (1961) studied Indiana woodlands and noted that after 30 years of protection from grazing, *O. virginiana* (from this group) was among the most abundant seedlings (after *A. saccharum* and *U. americana*); *Crataegus* spp., *Carya* spp., and *Ulmus* spp. persisted through periods of grazing. Modest population growth in these fairly low-density species combined with dispersal limitation, especially for taxa that produced few large seeds (e.g., *Aesculus glabra* Willd.), would explain much of the development of aggregation in this group over the 60 years.

### 4.2. Development and change of spatial structure

Most species at the DPRF in 1926, 1976, and 1986 were either aggregated or random in their spatial pattern—results that concur with the findings of Leopold et al. (1985) for a 1981 census using different spatial statistics. There are several factors that can produce aggregation in plant populations, including vegetative reproduction, dispersal limitation, and habitat-specific recruitment. A frequently cited cause of uniformity is density-dependent mortality, which can develop through competition for space and light. Pattern that is essentially random can arise by a variety of mechanisms, including the decay of pre-existing structure and the overlap of signal from multiple sources. We consider these causative factors as they pertain to the DPRF data set.

Certain modes of reproduction can result in aggregation, especially vegetative reproduction (e.g., Peterson and Squires, 1995) and limited seed dispersal (e.g., Hamrick et al., 1993). Root-sprouting has been observed in *A. glabra*, *F. grandifolia*, and *Gleditsia triacanthos* L. (Curtis, 1959; Leopold et al., 1985), each of which was aggregated at spatial scales that might have included clumps of ramets. Limited seed dispersal also has contributed to aggregation in the DPRF, as seed shadows tend to form around parent trees if dispersal distances are small with respect to adult spacing. This may be especially true for some of the larger-seeded species such as *A. glabra* and *G. triacanthos*, both of which

Sutherland et al. (2000) identified as commonly dispersal limited.

Leopold et al. (1985) identified soil drainage and grazing as chief factors influencing species distributions at the DPRF. Although topographic relief at the site spans only ∼5 m, some species clearly have either favored or avoided the wet depressions in the stand. Perhaps most visually striking are the nearly mirror-image 1986 distributions of *A. saccharum*, established in better drained soils, and *U. americana*, which tolerated the poorly drained sites (Fig. 3). We showed that both of these species were highly aggregated in 1926 in both plots, and they remained so through 1976 and 1986. Furthermore, wet sites within the stand have been less subject to surface fires. Variation in fire intensity increased the degree of aggregation in a population of *Quercus laevis* in Florida sandhills (Rebertus et al., 1989), and some aggregation at the DPRF probably can be traced back to the 1972 fire documented in the western portion of plot A.

Livestock grazing contributed to aggregation of stems in 1926 because foraging appears to have been spatially heterogeneous, non-random, and influenced by soil drainage patterns. Grazing was pervasive in midwest woodlands during the 1800s and early 1900s, as 85% of the farm woodlots in the Indiana Corn Belt were used by livestock (Den Uyl et al., 1938). Den Uyl (1961) observed that regeneration in these grazed forests typically occurred in clumps. At the DPRF, Spetich and Parker (1998) noted that the distribution of tree biomass was very patchy in 1926 but much less so in later surveys, following the exclusion of livestock in 1917. It is likely that low, poorly drained areas experienced lower grazing pressures (Ward et al., 1996), and this would have contributed to habitat-specific survivorship and clumpiness of regeneration in the stand. In support of this view, Ward and Parker (1987) found that the 1926 subcanopy was comprised predominantly of moist site species, such as the highly aggregated *U. americana*. Livestock grazing can account for little if any of the new aggregation detected in 1976 and 1986, but we cannot rule out deer browse that is widespread in the region.

Habitat-specific survivorship in light gaps versus a closed understory represents another potentially important source of aggregation, as documented in tropical (Newbery et al., 1986; Hubbell et al., 1999) and temperate forests (Williamson, 1975). However, most canopy openings at the DPRF currently are randomly distributed, single-tree gaps that are too small ($<100\ \text{m}^2$) to allow a shade-intolerant tree to reach the canopy (Parker and Sherwood, 1986; Ward and Parker, 1989), much less a cluster of conspecifics. These small gap sizes probably contrast sharply with those present prior to 1917 when exogenous disturbances played a greater role in canopy dynamics, or compared to the 1960s when Dutch elm disease opened numerous gaps by killing large *U. americana* in the stand (Shuder, 1955; Parker and Leopold, 1983).

Evidence suggests that canopy gaps play a limited role in generating aggregation at the DPRF because gaps are small and species that require gaps are not regenerating effectively. Ward and Parker (1989) reported a 7:1 ratio of area in primary canopy relative to canopy gaps at the DPRF, and individual gaps were generally smaller ($<100\ \text{m}^2$) than the estimated area ($2000\ \text{m}^2$) required by many mid-tolerant to intolerant species such as *Quercus* spp. (Roach and Gingrich, 1968). Ward and Parker (1989) examined stems $\geq 2$ cm dbh and found only a limited association between overall regeneration density and canopy structure. In fact, most species were aggregated at scales ($>400\ \text{m}^2$) larger than that of canopy gaps, indicating that edaphic factors have played a larger role. Notably, the most shade-intolerant canopy tree species (e.g., *Quercus* spp.) were under-represented in the Ward and Parker (1989) study because of low densities; we have shown that these species declined in degree of aggregation as well as population size. As an example, *F. americana* exhibited the largest reduction in population size between 1926 and 1986 in our study, and was one of only two species (also *Q. alba*) to change from aggregated to uniform (small-pattern change) on this interval. *F. americana* also was one of only a few species to display significant aggregation at the scale of light gaps, when smaller stem sizes were considered (Ward and Parker, 1989). Thus, small light gaps may promote aggregation of small stems of shade-intolerant species over short distances, but the signal is prone to decay through thinning as the stems grow larger and through a low rate of regeneration throughout the stand due to few light gaps.

Density-dependent mortality has influenced spatial structure at the DPRF. Competition for space and light probably are intense within clumps of stems in the smaller size classes, below our cutoff of 10 cm dbh.

Clusters of conspecific seedlings and saplings accumulate around parent trees, in light gaps, and on soil types, and subsequent thinning yields a loss of aggregation over time. High-density species such as *A. saccharum* and *U. americana* may experience intense intra-specific competition yet remain aggregated because they use only a subset of the habitat in the stand. Inter-specific competition may play a greater role in the spacing of larger size classes, which would explain the stand-level uniformity revealed by Ward et al. (1996) yet also the rarity of species-level uniformity (Leopold et al., 1985; this study). In their study of stand-level spatial pattern, Ward et al. (1996) showed that subcanopy stems (10–25 cm dbh) shifted from aggregated in 1926 to uniform in 1976, and canopy stems (>25 cm dbh) were uniform throughout 1926–1986. Research in other temperate forests shows a similar trend toward stand-level uniformity as succession proceeds (Christensen, 1977; Cooper, 1961; Laessle, 1965). Lieberman and Lieberman (1994) surveyed Costa Rican rainforest and concluded that close packing of tree crowns produced spatial uniformity within the stand. They observed that the forest canopy was uniform on level ground and in portions of the stand with high stem densities, whereas random stem distributions prevailed on low-density sites and slopes where canopies could overlap. Pielou (1960) had made a similar argument that the close packing of tree root zones would yield uniformity in an even-aged stand.

A random pattern of dispersion may arise by several means, such as if dispersal distances are large with respect to adult spacing (e.g., Hamrick et al., 1993) and if habitat quality is spatially homogeneous. Yarranton and Morrison (1974) suggested that changes in spatial structure from aggregation to randomness would occur through the coalescence of patches that increase in size as succession proceeds. In general, overlapping and conflicting spatial patterns from different sources may obscure the natural history information that otherwise is present in stem distributions. Rebertus et al. (1989) viewed randomness as an intermediate stage of succession that arises from the culling of young stems, which typically are aggregated, and culminates in a uniform spatial pattern in mature stands. Similar phenomena would explain the loss of aggregation in the shade-intolerant group at the DPRF wherein random (or density-dependent) mortality within populations that are not replacing themselves would generate random (and eventually uniform) stem patterns over time.

It is reasonable to assert that shade-intolerance in early seral species should produce aggregated spatial patterns due to obligatory associations between regeneration and light gaps. Though aggregation definitely is present in the populations of shade-intolerant species at the DPRF (Leopold et al., 1985; this study), the temporal trend that we report runs in the opposite direction toward a loss of aggregation for shade-intolerant species and increased aggregation for shade-tolerants. We submit that this difference in trends reflects a fundamental shift in the demography of tree species at the DPRF. Increased aggregation, and in some cases persistent aggregation (e.g., *A. saccharum* and *U. americana*), signifies active recruitment around parent trees and along soil drainage gradients. Loss of aggregation reflects the decay of past regeneration that had been aggregated for these and other reasons, namely a higher frequency of disturbance by timber harvest, grazing, and fire that favored shade-intolerant species. Essentially, the community has become uncoupled from its prior canopy disturbance regime and is sorting out mostly along the lines of physiological tolerances to persistently low-light conditions and to the unchanging mosaic of edaphic properties of the stand.

### 4.3. Management implications

These findings on dispersion may have applications for uneven-aged silvicultural methods such as single-tree and group selection, since judgments can be made regarding the placement of gaps relative to the population structure of tree species. Prescribed burns and the creation of canopy gaps have been used as management tools to promote the release of early seral species such as oaks in disturbance-suppressed hardwood forests albeit with mixed success (see Johnson et al., 2002). Abrams and Nowacki (1992) note that removal of adult oaks from such stands could lead to accelerated succession if the later successional species are not removed from the understory in the vicinity of the cut. Otherwise, advanced regeneration of late seral species would enter rapidly and close canopy gaps, promoting succession rather than resetting it. This can be seen at the DPRF where the majority of ingrowth stems within 5 m of a dead dominant or codominant tree were *A. saccharum* and *U. americana* (Parker et al., 1985). We propose that both loss of aggregation and low-density contribute to the difficulty of managing early seral species in old-growth hardwood forests.

The spatial proximity of available seeds and advanced regeneration (seedlings, saplings, and young adults) relative to natural or artificial openings in the canopy will affect regeneration dynamics. Consider three removal techniques with respect to management of *A. saccharum* (shade-tolerant, high-density, aggregated) and *Q. rubra* (shade-intolerant, low-density, random-uniform) at the DPRF. Though we describe single-tree selection, the relevance to group selection is similar. (a) Opening a gap anywhere in the canopy by random removal of a tree probably would benefit *A. saccharum*, or *U. americana* depending on the part of the stand, because of the species' high density in the understory as advanced recruitment. *Q. rubra*, by virtue of its low-density, probably would not be near the gap. (b) Removal of an *A. saccharum* adult is likely to benefit another *A. saccharum* due to the species' high density and the aggregated spatial structure of its population; an adult *A. saccharum* generally is surrounded by several conspecifics that could grow rapidly into the gap. (c) On the contrary, removal of a *Q. rubra* adult is unlikely to benefit another *Q. rubra* because the species occurs at low-density, but also because conspecific stems are not necessarily near the adult that was cut; other *Q. rubra* adults either bear no particular spatial association to the gap (random distribution) or they are farther away than expected by chance (uniform distribution).

A similar argument applies to seed sources, though the disparity in canopy sizes between species may mitigate some of the effects of spatial isolation for large oaks that are able to drop seeds over a wider area. This size imbalance should diminish as succession proceeds and late-seral species enter the canopy. At some point a canopy gap created by removal of an adult *Q. rubra* should be closer to a source of *A. saccharum* or *U. americana* seed than *Q. rubra* seed—for reasons of density, dispersion, and a loss of size advantage. Nevertheless, regeneration failure has been documented in forests with a high density of oaks in the canopy and so proximity of gaps to seed sources may only be a contributing factor rather than a critical determinant of old-growth demography in many cases.

## 5. Conclusion

Old-growth stands that develop canopies composed predominantly of large, late-successional tree species like *A. saccharum* are a normal, and for many a desirable, part of the landscape. This is especially true on high-quality mesic sites in the Central Hardwood Region that have experienced limited disturbance and are too small to encompass a mosaic of seral stages. By contrast, preservation of oak forests on these sites requires not only a commitment to management but also a viable strategy that will involve some form of disturbance. Our contribution is to bring into focus the possible role that spatial dispersion plays in the succession of old-growth forests of this region, and how this information may be useful to management. We have shown that a loss of aggregation accompanies reductions in population size for shade-intolerant trees of an old-growth forest in which disturbance has been suppressed. Loss of aggregation appears to be a by-product of recruitment failure, but it also may contribute directly to the rate of population decline, and to the difficulty of managing for early seral species in old-growth forests. We propose that natural or artificial canopy openings are less likely than might be expected to benefit shade-intolerant species, unless they are placed with special consideration to the population structure of the species under management. Active management may be required that includes thorough removal of shade-tolerants from the understory of a single-tree or group selection cut and replanting of advanced-regeneration shade-intolerants into the cut, assuming that the gap is large enough to support the attainment of canopy stature for the target species. These actions may be necessary at least until the demographic decline has been mitigated, which may take several years given that oaks can live for 150–350+ years. More research is warranted on management practices that manipulate both density and dispersion as this may improve the success rate of promoting regeneration of early seral tree species in old-growth temperate hardwood forests.

## Acknowledgements

We thank B. Prentice for his original census of the land and later researchers for assistance with the subsequent census periods. S.R. Shifley and an anonymous reviewer offered valuable comments on the manuscript, and E. Berg provided generous advice on the application of Ripley's tests. Research funding came from the USDA Forest Service and Purdue University, Department of Forestry and Natural Resources.

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