

Long-term spatial dynamics in an old-growth deciduous forest

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Abstract

In 1926, 1976, and 1986 stems (≥ 10 cm diameter at 1.37 m (dbh)) were measured and mapped in a 4 ha interior study area on the Davis–Purdue Research Forest in east-central Indiana. Spatial pattern type was determined using the Clark and Evans's index, and Ripley's L function. The G function was used to examine spatial dispersion at intertree distances (< 20 m). Spatial pattern of combined size classes shifted from weakly non-random in 1926 to uniform in 1976 and 1986. Neighborhood density was depressed for 2 m in 1976 and 5 m in 1986. Peak in neighborhood density at 6 m suggested trees were spaced 6 m apart. Subcanopy (10–25 cm dbh) tree spatial pattern shifted from aggregated in 1926 to uniform in 1976. The spatial pattern of canopy (> 25 cm dbh) trees was uniform between 1926 and 1986. Density-dependent mortality and ingrowth processes are maintaining uniform spatial distributions. Initial neighborhood tree distribution was higher around trees which died in the periods 1926–1976 and 1976–1986 than for contemporary survivors, i.e. trees which survived this period had fewer neighboring trees within 6 m at the beginning of the period than did trees which died. The higher initial neighborhood densities around mortality trees than survivors supports density-dependent mortality. Ingrowth was inhibited in a 6 m zone proximate to established trees for both the 1926–1976 and 1976–1986 periods.

Keywords: Clark and Evans's index; Density-dependent mortality ; G function; Ripley's L function; Spatial dynamics

1. Introduction

It has been well established that plants are aggregated, or clumped, at macro scales due to edaphic factors, recruitment, and other factors (Richards and Williamson, 1975; Hubbell, 1979; Whipple, 1980; Abbott, 1984; Tilman, 1984; Burdon et al., 1994). Less well understood is how plants are spatially

arranged at smaller scales. Studies of gross spatial distributions have shown that there is often a shift from aggregated distributions for smaller size classes to uniform distributions for larger size classes (Cooper, 1961; Laessle, 1965; Christensen, 1977; Ghent and Franson, 1986; Stewart, 1986; Moer, 1993). This shift implies density-dependent processes with higher mortality on high density areas and/or increased ingrowth on low density areas. Plants should become uniformly dispersed in communities without disturbance as competition for limiting resources causes density-dependent mortality (Lepš and Kindl-

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mann, 1987; Kendel, 1988; Faber, 1991; Walker and Dowling, 1991; Biging and Dobbartin, 1992).

Distance-dependent models are a subset of density-dependent models which incorporate the spatial distribution of density, instead of the absolute density for a fixed area. Density-dependent models use one parameter, an absolute measure of competition (density, basal area, etc.) in a given area. Distance-dependent models commonly utilize two parameters, a measure of the competitive status of neighboring trees (e.g. density, bole diameter, crown size), and a function of the distances to the neighboring trees.

A major restriction in developing distance-dependent models of growth and survival is limited knowledge of intertree spatial distributions and dynamics. Studies of actual neighborhood density distributions, changes over time, and density-dependent processes are mostly limited to conifers (Franklin et al., 1985; Getis and Franklin, 1987; Kendel, 1988; Duncan and Stewart, 1991; Liu and Burkhardt, 1994; Moeur, 1993). This information is crucial for development of distance-dependent models with a biological rationale (Pukkala, 1989; Walker and Dowling, 1991).

The objective of this research was to examine the 60 year spatial dynamics at inter-tree scales in a transitional (*sensu* Bormann and Likens, 1981) old-growth deciduous forest. Clark and Evans's index (Clark and Evans, 1954), Ripley's L , and the G function were used to examine spatial patterns in 1926, 1976, and 1986 at the Davis–Purdue Research Forest. Spatial patterns in 1976 and 1986 were compared against patterns resulting from random mortality and ingrowth. We compared initial neighborhood density distributions around mortality trees and survivors in the periods 1926–76 and 1976–86 for evidence of distance-dependent mortality. We examined neighborhood density distributions of trees which survived and died around ingrowth in the periods 1926–76 and 1976–86 for evidence of distance-dependent ingrowth. We conclude by discussing ramifications of these findings on development of distance-dependent models for hardwoods.

1.1. Spatial distributions

There are three general types of spatial distribution (or pattern): random, uniform (overdispersed), and aggregated (underdispersed). For this paper a

random distribution of points (trees) was defined as a two-dimensional, spatially homogeneous Poisson distribution; i.e. the probability of a point (tree) or a number of points (trees) being found in an area is proportional to the size of the area (Stiteler and Patil, 1969). This distribution assumes that individual trees do not affect the establishment or survival of other trees, i.e. the location of each tree is independent of all other trees. Random spatial distribution also assumes site homogeneity (Pielou, 1974).

A uniform distribution is an arrangement of points with the probability of finding two points (trees) in close proximity lower than expected for a random distribution. Points in a uniform distribution are regularly spaced, e.g. trees in a plantation or centers of a honeycomb. A uniform distribution, or a shift towards a uniform distribution, implies distance-dependent mechanisms which negatively affects survival, establishment, or both in close proximity to other trees.

Aggregated distributions can be visualized as patches of high density surrounded by areas of low density. Aggregated distributions occur when nearest neighbors are closer together than expected for a random distribution. Causal mechanisms for aggregated dispersions include edaphic patterns (Whipple, 1980; Tilman, 1984; Leopold et al., 1985), seed dispersal patterns (Abbott, 1984; Hubbell, 1979), gap colonization (Richards and Williamson, 1975), and other factors (Smith and Cottam, 1967).

2. Material and methods

2.1. Study area

The 20.6 ha Davis–Purdue Research Forest (DPRF) is located in Randolph County in east-central Indiana. The tract has been classified as a lowland depressional forest due to high numbers of wet site species (Lindsey and Schmelz, 1970). While individuals of bur oak (*Quercus macrocarpa* Michx.) are over 300 years old, most dominant and codominant oaks were estimated to be 150–200 years old (Parker et al., 1985). Disturbances have been limited to livestock grazing and possible annual burning prior to Purdue University's acquisition of the property in 1917, and removal of a few dead and dying trees in the 1940s and 1950s.

Topographic relief over the study area is less than 3.5 m. An intermittent stream running northwest to southeast connects two upland depressional areas. Vernal ponds are scattered throughout the depressional areas on Brookston and Pewano silty clays (mesic Typic Argiaquols). Blount silt loam (mesic Aeric Ochraqualf) is found on the level higher positions. Morley silt loam (mesic Typic Hapludalf) is located on the better drained slopes. More detailed descriptions of the forest can be found in Leopold et al. (1985); Parker et al. (1985) and Ward and Parker (1989).

2.2. Field measurements

In 1926 all trees > 10 cm dbh (diameter at 1.37 m) were measured, mapped, and tagged (Prentice, 1927). In 1976 surviving trees were relocated, measured, and mapped using the remaining 1926 tags, or map locations and tree descriptions (Leopold et al., 1985). Concurrently, the location, dbh, and species of ingrowth trees was recorded. A 4 ha (200 m × 200 m) interior study area was located in the eastern section of the forest in 1986. Because 1926 and 1976 data were collected using a grid system laid out using English measurements, the grid was 200 m × 189 m for those surveys. All English measurements were converted to metric units prior to analysis. The study area was located in the interior of the forest to minimize edge effects. All trees ≥ 10 cm dbh were measured and mapped.

A stratified sample of 90 trees was selected for crown measurements in 1987. Fifteen trees were randomly selected within six diameter classes (10–20, 21–30, 31–40, 41–50, 51–75, > 75 cm dbh). Horizontal crown extensions in each cardinal direction were measured to the nearest meter. The crowns of trees which were completely offset from bole center were measured along their major and minor axes.

We used the following definitions: neighborhood density (relative density at close proximity to average tree); subcanopy trees (10.0–25.0 cm dbh), canopy trees (> 25.0 cm dbh), 1926–76 mortality (trees alive in 1926 which were dead in 1976), 1926–76 survivors (trees alive in 1926 which survived into 1976), 1926–76 ingrowth (trees which were too small to measure in 1926 and were ≥ 10

cm dbh in 1976). 1976–86 mortality, survivors, and ingrowth are similarly defined.

3. Spatial pattern analysis

3.1. Clark and Evan's index

Clark and Evans's (1954) index, R_{CE} , is one of the oldest and mostly widely used methods of determining spatial pattern type and defined as:

$$R_{CE} = \frac{\bar{r}_A}{\bar{r}_E}, \text{ where } \bar{r}_A = \frac{\sum r}{n} \quad (1)$$

where $\sum r$ is the summation of nearest neighbor distances, n is the number of trees, r_E is defined below. R_{CE} values significantly < 1 indicate aggregated spatial patterns and R_{CE} > 1 indicate uniform patterns. Donnelly (1978) determined the correction factors to edge-effect bias:

$$E(\bar{r}_E) = 0.5 \sqrt{\frac{A}{n}} + \left(\frac{L}{n} \right) \left(0.0514 + \frac{0.041}{\sqrt{n}} \right) \quad (2)$$

$$SE(\bar{r}_E) = \left[\left(0.0703 A + 0.037 L \sqrt{\frac{A}{n}} \right) / n \right]^{0.5} \quad (3)$$

where A is plot area, and L is length of plot perimeter.

3.2. Ripley's L statistic

Ripley (1981) defines the estimator of $K(d_i)$ for distance d_i as:

$$\hat{K}(d_i) = \left(\frac{A}{n^2} \right) \sum_i^n \sum_j^n \omega_{ij} \quad (4)$$

The weighting factor for edge effects, ω_{ij} , is equal to the inverse of the proportion of the circumference of the circle with center on point i and radius (ij) lying within the plot (Ripley, 1977). For pairs ≤ distance d_i apart, ω_{ij} can range from 1 to 4 in rectangular areas. For pairs > distance d_i apart, ω_{ij} = 0.

Besag (discussion in Ripley, 1977) suggested us-

ing the square root of $K(d)/\pi$ to linearize $K(d)$ and stabilize the variance:

$$L(d_i) = \left[\hat{K}(d_i)/\pi \right]^{0.5} \quad (5)$$

Subtracting d_i from $L(d_i)$ sets the expected value of $L(d_i)$ for all d_i to zero and facilitates interpretation pattern type (Kendel, 1988; Moeur, 1993).

$$\hat{L}(d_i) = \left[\hat{K}(d_i)/\pi \right]^{0.5} - d_i \quad (5a)$$

3.3. *G statistic*

Ripley L has proven to be a powerful tool for examining the type and approximate scale of spatial patterns. However, the cumulative nature of L obscures the underlying density distribution, $G(d_i)$:

$$G(d_i) = \hat{L}(d_i) - \hat{L}(d_{(i-1)}) \quad (6)$$

$G(d_i)$ corresponds with the relative mean density (observed density/stand density) at distance d_i from all points. We interpreted $G(d_i)$ distributions with low values at small d_i as indicating uniform spatial patterns. Distributions with high values at small d_i were interpreted as aggregated spatial patterns. This is similar to the interpretation of similar relative density functions (Galiano, 1982; Franklin et al., 1985).

3.4. *Random mortality and ingrowth*

Monte-Carlo (MC) simulations were used to estimate confidence envelopes and expected L values assuming mortality and ingrowth. For each simulation, mortality was randomly assigned among trees and ingrowth was randomly placed. Tree mortality and ingrowth rates for both the 1926–76 and 1976–86 periods were used (Table 1). Ripley L values were determined for each d_i . One thousand simulations were run for each period. L values for each d_i were ranked and the 50th and 950th values were used to define the confidence envelope. Expected L for each d_i , $L_{MC}(d_i)$, was the mean of the 1000 simulations. The actual 1976 and 1986 L values for each d_i , $L_{OB}(d_i)$, were compared with the confidence intervals to determine whether the 1976 and 1986 patterns were significantly different from expected for a random mortality and ingrowth (RMI) realization.

Table 1

Density of stems by size class and year, and density of ingrowth and mortality by size class and period in an old-growth deciduous forest in Indiana, USA

Year/period	Stems ha ⁻¹		
	Subcanopy	Canopy	Combined
1926	52	120	172
1976	259	101	360
1986	235	105	340
Ingrowth (upgrowth ^a) during period			
1926–1976	254	12 (18)	266
1976–1986	41	0 (20)	41
Mortality during period (%)			
1926–1976	56.9	40.8	45.7
1976–1986	17.6	14.7	16.8

^a Upgrowth is ascension from subcanopy to canopy size class.

$G_{RMI}(d_i)$ values were found by defining $L_{RMI}(d_i)$ as:

$$L_{RMI}(d_i) = L_{OB}(d_i) - L_{MC}(d_i) \quad (7)$$

and

$$G_{RMI}(d_i) = L_{RMI}(d_i) - L_{RMI}(d_{(i-1)}) \quad (8)$$

$G_{RMI}(d_i)$ distributions with low values at small d_i were interpreted as indicating strengthening of uniform spatial patterns because the number of pairs at short distances was lower than expected for random processes. This would follow from inhibition of short distance pair formation (distance-dependent ingrowth inhibition), short distance pair repulsion (distance-dependent mortality), or both.

3.5. *Neighborhood effects on mortality and ingrowth*

We used an extension of Ripley's L analysis for interactions among populations, $L_{ab}(d_i)$, (Ripley, 1977; Kendel, 1988; Szwagrzyk, 1992; Moeur, 1993) to determine whether mortality and survival was a distance-dependent process.

$$L_{ab}(d_i) = \left[\frac{\left(\frac{A}{n_a} \right) \sum_j \sum_k^{n_b} \omega_{jk} + \left(\frac{A}{n_b} \right) \sum_k \sum_j^{n_a} \omega_{kj}}{\pi(n_a + n_b)} \right]^{0.5} \quad (9)$$

where n_a is the number of mortality or surviving trees, n_b is the initial number of trees, and other terms as defined above. The underlying density function $G_{ab}(d_i)$ was defined as

$$G_{ab}(d_i) = L_{ab}(d_i) - L_{ab}(d_{i-1}) \quad (10)$$

$G_{ab}(d_i)$ distributions with low values at small d_i reveal that mortality/survival were associated with low neighborhood density, and high $G_{ab}(d_i)$ values at small d_i reveal that mortality/survival was associated with high neighborhood density. $G_{ab}(d_i)$ values were similarly determined for 1926–76 and 1976–86 ingrowth. Ingrowth $G_{ab}(d_i)$ distributions with low values at small d_i were interpreted as indicating inhibition of ingrowth near established trees, i.e. distance-dependent ingrowth.

This study choose not to contrast ingrowth densities within gaps and under extant canopy for three reasons. (1) Overall sapling density in this forest was independent of canopy structure (Ward and Parker, 1989). (2) Eighty percent of canopy gaps in the DPRF were $< 50 \text{ m}^2$. Small gaps are often closed by lateral branch extension of surrounding survivor trees (Frelich and Martin, 1988). Unless the gap is large, pre-gap reproduction may be too small to exploit the canopy opening successfully and may require several successive gap episodes (Runkle and Yetter, 1987). The importance of gaps for ingrowth into the subcanopy size class would be obscured by including the large number of small gaps closed by branch extension. (3) Because of gap closure it would be difficult to identify the locations of older gaps, especially those which opened and closed between 1926 and 1976.

4. Results and discussion

4.1. Tree and crown dimensions

Mean tree height was 28.8 m for canopy trees and 15.8 m for subcanopy trees. Crown diameters ranged from 3.5 to 21.0 m with a mean of 9.3 m. Mean crown diameter in 1986 was 10.7 m for canopy trees and 5.9 m for subcanopy trees. In developing a predictor of crown diameter using dbh we examined dbh, dbh^2 , $\text{dbh}^{1/2}$, and partitioned trees by size class and species groups. The best relationship ($r^2 = 0.75$,

$P < 0.001$) was: Crown diameter (m) = $3.60 + 0.128 \cdot \text{DBH (cm)}$. Partitioning trees by size class or species groups gave no significant improvement. A similar relationship was found for Appalachian hardwoods (Lamson, 1987). Most crowns were asymmetrical and somewhat offset from bole centers. Only three of the 90 sample trees had crowns centered over bole center. The crowns of four sample trees were completely offset from bole center. Mean deflection of crown center from bole center was 3.8 m and was independent of cardinal direction. Mean deflection of crown center from bole center was greater for canopy trees (4.3 m) than for subcanopy trees (2.6 m). Hardwood crowns are often asymmetric (Burns, 1929; Lorimer, 1983), even when open-grown (von der Heide-Spravka and Watson, 1990).

4.2. Spatial distributions of combined size classes

Tree density more than doubled from 172 trees ha^{-1} in 1926, to 360 trees ha^{-1} in 1976 (Table 1). In 1986 there were 340 trees ha^{-1} . Annual mortality rates increased from 1.21% for the 1926–76 period to 1.82% for the 1976–86 period. The uniform spatial distribution of trees strengthened over the 60 year period (Table 2, Fig. 1). The strong peak at 2 m observed in 1926 had weakened by 1976. G values in 1986 were depressed through 5 m. Lower than expected values at short distances (i.e. near tree centers) suggest trees have been uniformly distributed since at least 1926. G values peaked at 6 m and 8 + m from tree centers in 1986. The lower than expected values at short distances, loss of the 2 m peak, and strengthening of the peak at scales corresponding to tree spacing indicate one or more factors were operating to impose a uniform spatial distribution upon the forest.

These results are consistent with earlier research on monotypic stands (Cooper, 1961; Laessle, 1965; Ford, 1975; Ghent and Franson, 1986). The spatial distribution of trees in an upland oak stand in North Carolina shifted from random to uniform distribution after 23 years (Christensen, 1977). In contrast, Payandeh (1974) indicated that natural mixed hardwood–conifer stands in Ontario displayed aggregated or random spatial distributions. In the absence of exogenous disturbance (fire, cutting, grazing, etc.)

Table 2
Clark and Evans index values and spatial pattern types by size class and status in an old-growth deciduous forest in Indiana, USA

Status	Subcanopy (10–25 cm dbh)		Canopy (> 25 cm)		Combined	
	Clark and Evans index	Spatial pattern type	Clark and Evans index	Spatial pattern type	Clark and Evans index	Spatial pattern type
Alive in 1926	0.75	Agg	1.08	Uni	1.06	Uni
Alive in 1976	1.07	Uni	1.14	Uni	1.07	Uni
Alive in 1986	1.10	Uni	1.13	Uni	1.09	Uni
1926–1976 mortality	0.78	Agg	0.98	Ran	0.99	Ran
1926–1976 survivors	0.82	Agg	1.11	Uni	1.09	Uni
1926–1976 ingrowth					1.07	Uni
1976–1986 mortality	1.01	Ran	1.17	Uni	0.99	Ran
1976–1986 survivors	1.09	Uni	1.12	Uni	1.10	Uni
1976–1986 ingrowth					1.07	Ran

there has been a strong trend towards the maintenance and strengthening of a uniform spatial distribution at the DPRF over the past 60 years.

4.3. Spatial distributions of subcanopy trees

Subcanopy (10.0–25.0 cm dbh) density increased from 52 trees ha^{-1} in 1926 to 259 trees ha^{-1} in 1976 (Table 1). The large increase in the subcanopy density from 1926–76 is believed to be due to the exclusion of grazing from the forest after 1917 (Parker et al., 1985). Between 1976 and 1986 subcanopy density decreased 9% to 235 trees ha^{-1} . There has been a continuous change in subcanopy tree spatial patterns. Clark and Evans's index indicates the pattern has changed from strongly aggregated in 1926 to uniform in 1976 and 1986 (Table 2). G values for subcanopy trees in 1926 were much higher than expected in the ≈ 12 m circular zone proximate to subcanopy tree centers (Fig. 2), i.e. the 1926 subcanopy was aggregated into small scale clumps. Den Uyl (1961) noted regeneration in grazed Indiana forests was usually found in small clumps. Subcanopy trees in 1926 were predominantly moist site species such as *Ulmus americana* and *Fraxinus americana* (Ward and Parker, 1987). The combina-

tion of small-scale clumps and moist site species suggests development into the subcanopy size class prior to 1926 was limited to those areas which were too wet for grazing and for carrying periodic surface fires.

Concurrent with the five-fold increase in subcanopy density between 1926 and 1976, the spatial pattern of subcanopy trees shifted to uniform (Table 2). Unlike the distribution of subcanopy trees in 1926, G values in 1976 were lower than expected at 1 m and 5 m (Fig. 2). There was a strong peak at 6 m, suggesting tree spacing of 6 m. If trees were planted on a grid with 6 m spacing, the peak at 8 m would correspond to trees separated by the diagonal. The weak peak at 14 m also supports tree spacing of approximately 6 m. The annual mortality rate of subcanopy trees was 1.67% between 1926 and 1976 and increased to 1.91% between 1976 and 1986. After 1976 subcanopy tree distribution became further depressed through 3 m. The peaks at 6 m, 8 m, and 14 m strengthened in 1986, again suggesting a tree spacing of about 6 m. This is close to the observed 5.9 m mean crown diameter for subcanopy trees in 1986.

The combination of decreasing density and increasing annual mortality rates, tree spacing corre-

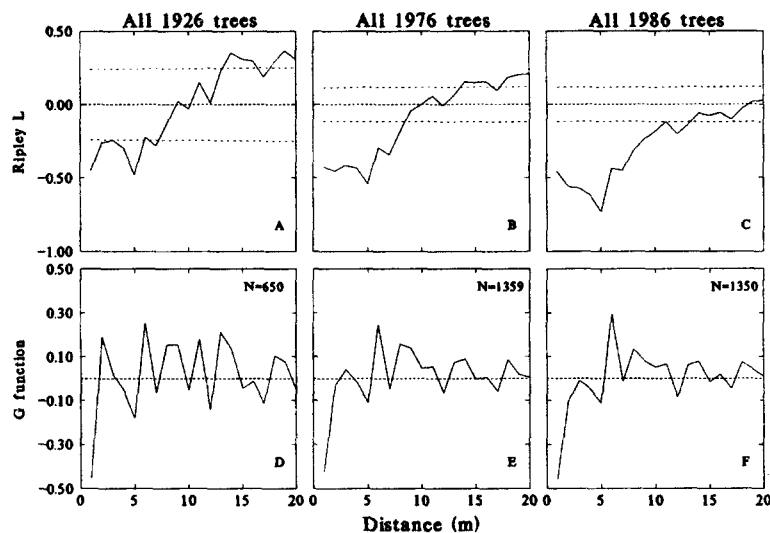


Fig. 1. G function and Ripley's L index by intertree distance and survey year for all stems ≥ 10 cm dbh for an old-growth deciduous forest in Indiana, USA. Solid lines, observed values; dashed lines, expected values for random realizations; dotted lines, upper and lower 5% confidence envelope.

sponding to crown diameter, and development of a uniform tree distribution after 1926, suggests that this stratum was approaching, or had achieved, full site occupancy with utilization of most of the available growing space by 1976. The shift of subcanopy spatial distribution from aggregated to uniform parallels the observations of Ghent and Franson (1986) with red pine (*Pinus resinosa*). They reported aggregations formed in the interval between planting and canopy closure due to edaphic factors. Following crown closure and subsequent natural thinning, they found trees became more uniformly dispersed. Likewise, Sitka spruce (*Picea sitchensis*) plantations became more uniformly dispersed over a 35 year period (Ford, 1975).

4.4. Spatial distributions of canopy trees

Canopy (> 25.0 cm dbh) density decreased from 120 trees ha⁻¹ in 1926 to 101 trees ha⁻¹ in 1976, and then increased to 105 trees ha⁻¹ in 1986. The increase in canopy density from 1976 to 1986 was due to increased ingrowth into the canopy and not decreased annual mortality rates. Annual mortality rates for canopy trees increased from 1.04% between 1926 and 1976 to 1.58% between 1976 and 1986.

During the 1926–76 period 0.6 tree ha⁻¹ year⁻¹ grew into the canopy size class and survived through 1976. Trees entered the canopy size class at a higher rate between 1976 and 1986, 2.0 tree ha⁻¹ year⁻¹.

In contrast to subcanopy trees, canopy trees have maintained a uniform spatial distribution since 1926 (Table 2). Other research has reported more uniform spatial distributions for larger size classes than for smaller size classes (Cooper, 1961; Laessle, 1965; Yeaton and Cody, 1976; Christensen, 1977; Phillips and MacMahon, 1981; Turner and Franz, 1985; Stewart, 1986). *G* values of canopy trees in 1926 were lower than expected at 1 m, 3 m, and 5 m (Fig. 3). The peaks at 2 m and 6 m suggest a pattern of tree pairs separated by approximately 6 m. The uniform spatial pattern strengthened through 1976 as the depression of canopy tree neighborhood density was observed at 1, 3–5 m. The peak at 2 m weakened and the highest values were observed at 6 m and 8 m. The canopy tree distribution dramatically changed between 1976–1986. The peak at 2 m disappeared and values were lower than expected through 7 m. A very strong peak was noted at 8 m with weaker peaks at 11 and 13 m. This brackets the mean observed crown diameter of canopy trees in 1986, 10.7 m.

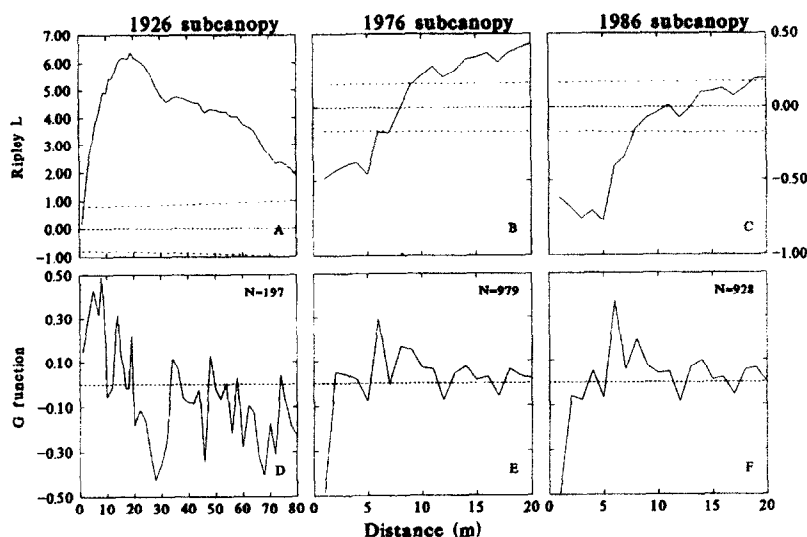


Fig. 2. *G* function and Ripley's *L* index by intertree distance and survey year for subcanopy size class (10 cm ≥ dbh ≤ 25 cm) for an old-growth deciduous forest in Indiana, USA. Solid lines, observed values; dashed lines, expected values for random realizations; dotted lines, upper and lower 5% confidence envelope.

Canopy trees averaged 44.5 cm dbh in 1926 and 54.7 cm dbh in 1986. Using the crown diameter to dbh relationship described above and assuming the crown diameter to dbh relationship was similar in 1926, the 10.2 cm dbh increase for canopy trees from 1926 to 1986 would indicate mean crown diameter increased from 9.3 m in 1926 to 10.6 m in 1986. This approximates the observed 2 m extension of canopy tree neighborhood density depression from 1926 to 1986.

The strengthening uniform spatial distribution of canopy trees between 1926 and 1986 supports the conclusions of Ghent and Franson (1986). They postulated that self-thinning by the largest trees tends to form a uniform distribution of these trees in the absence of exogenous disturbance. Let us assume light competition is the primary factor driving mortality and ingrowth, or that root distributions are as asymmetrical and offset from boles as crowns. Unless trees with offset, asymmetrical crowns are all offset in the same direction, trees with offset boles will decrease the intensity of a uniform bole spatial distribution in a fully stocked stand by increasing the number of boles in close proximity. The increased uniformity of canopy tree spatial distribution in this stand suggests that trees with large deflections of crown to bole centers were at a competitive disadvantage,

perhaps due to increased allocation of photosynthate to support structures to offset mechanical instability.

4.5. Distance-dependent mortality and ingrowth

Simulation studies have demonstrated that, in the absence of ingrowth and when mortality is independent of density, random spatial distributions are maintained and uniform spatial distributions converge toward a random distribution (Lepš and Kindlmann, 1987; Kent and Dress, 1979; Kent and Dress, 1980). Using the same assumptions, aggregated spatial distributions converged towards random (Lepš and Kindlmann, 1987), or remained stable (Kent and Dress, 1980).

In the above sections, we reported that there was not a trend from a uniform towards a random spatial distribution of trees at the DPRF. Rather, uniform distributions strengthened over the 60 year period (Table 2, Figs. 1–3). We also found that the initial aggregated subcanopy spatial distribution had shifted towards a uniform spatial distribution (Fig. 2). These observations, coupled with the simulations and work of Kent and Dress (1979) and Kent and Dress (1980) indicate that either mortality, ingrowth, or both were not random processes in this forest.

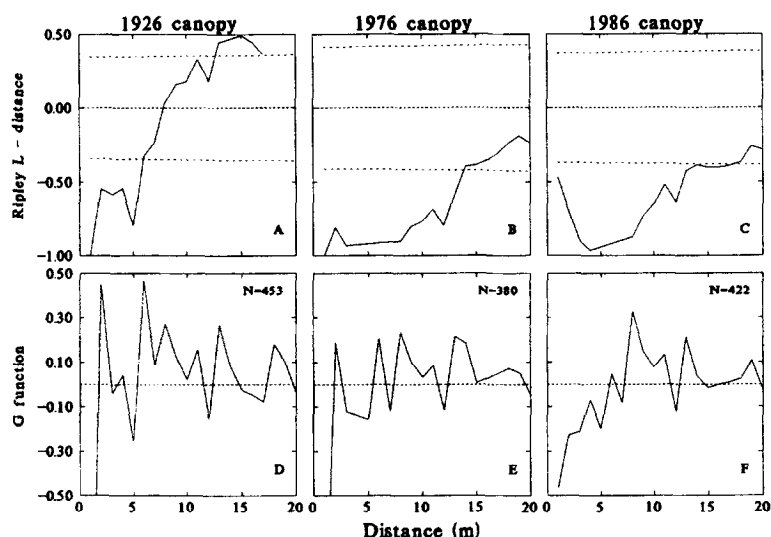


Fig. 3. *G* function and Ripley's *L* index by intertree distance and survey year for canopy size class (dbh > 25 cm) for an old-growth deciduous forest in Indiana, USA. Solid lines, observed values; dashed lines, expected values for random realizations; dotted lines, upper and lower 5% confidence envelope.

The first step was to determine what spatial dispersions could be expected if both mortality and ingrowth had been randomly distributed across the study area. This was accomplished by running MC simulations with random mortality and ingrowth (see Section 2). Spatial dispersions in both 1976 and 1986 were not realizations of random mortality and ingrowth of the 1926 and 1976 dispersions, respectively. G function graphs illustrate that tree densities were lower than expected at short distances in both 1976 and 1986 (Fig. 4). This provides evidence that one or more mechanisms had inhibited trees occurring in close proximity. The peaks at 8 m (1976) and 6 m (1986) further support the notion that trees were more uniformly dispersed than would be expected for a realization of random mortality and ingrowth.

Clark and Evans's index indicate that canopy and combined mortality between 1926 and 1976 were randomly dispersed and 1926–76 survivors were uniformly dispersed (Table 2). These results support Kendel's (1988) speculation that development of a uniform pattern among survivors was caused by competition for light. The aggregated spatial pattern of subcanopy mortality and survival between 1926 and 1976 was not unexpected, given the highly aggregated initial dispersions (Kendel, 1988). Subsequent mortality (1976–86) of subcanopy and combined size classes was randomly dispersed. That lack of evidence for mortality being aggregated contraindicates some abiotic (edaphic, windstorm), and biotic (insect and disease clusters) factors.

The initial distribution of trees around mortality

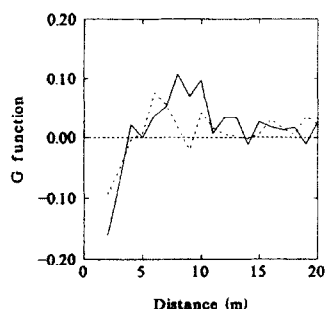


Fig. 4. G function by intertree distance of observed values in 1976 (solid line) and 1986 (dashed line) vs. mean of 1000 Monte-Carlo simulations of random interperiod mortality and ingrowth. Horizontal dashed line is expected value for random mortality and ingrowth realization. See text for details.

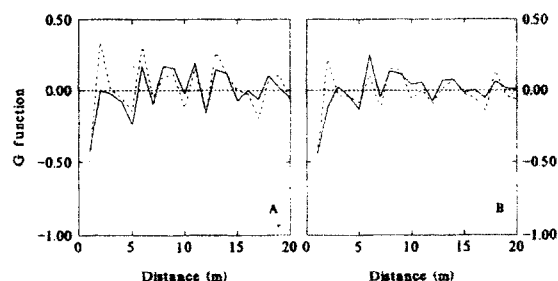


Fig. 5. (a) G function values by intertree distance of neighborhood tree density in 1926 around by 1926–76 survivors (solid line) and mortality (dashed line), (b) G function values of neighborhood tree density in 1976 around by 1976–86 survivors (solid line) and mortality (dashed line).

was different from the initial distribution of trees around survivors for both the 1926–76 and 1976–86 periods (Fig. 5). Trees which were dead at the end of each period had higher neighborhood densities at the beginning of the period, especially at 2 m, than did trees which survived. This highlights the importance of examining not only the spatial pattern of mortality and survivors but also examining the spatial distribution of neighborhood density when studying density-dependent mortality. There was little difference in neighborhood densities beyond 9 m for the 1926–76 period and 3 m for the 1976–86 period. Inclusion of zones where the neighborhood density of survivors and mortality are similar, whether by large plot sizes or non-tree centered plots, reduces the relative neighborhood density differences around mortality and survivors. Using plot sizes larger than 28 m² (3 m radius) to examine density-dependent mortality between 1976 and 1986 at DPRF would have obscured the differences of neighborhood densities between mortality and survivors.

Ingrowth for both periods was mostly suppressed within 1 m of a pre-existing tree (Fig. 6). The peak in ingrowth density at ≈ 6 m suggest the inhibition zone extends about the distance corresponding to crown diameter of established trees. The weaker inhibition zone and 6 m peak for the 1926–76 ingrowth was not unexpected because much of the available growing space was underutilized due to abiotic factors (grazing, fire) not directly related to intertree competition. Ingrowth densities were higher near mortality than survivors for both periods (Fig. 7). Several mechanisms could explain the low in-

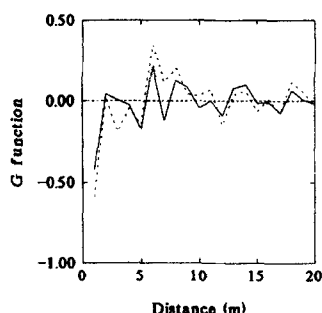


Fig. 6. G function values by intertree distance of neighborhood tree density in 1926 around 1926–76 ingrowth (solid line) and neighborhood tree density in 1976 around 1976–86 ingrowth (dashed line). Horizontal dashed line is expected value for random initial neighborhood distribution.

growth density in the 1 m proximate to mortality: physical damage from falling branches and boles, growth suppression prior to mortality, disease (*Armillaria* spp.) on dead root systems, and nitrogen sequestering by decay organisms.

Not surprisingly, these results indicate that ingrowth in a fully stocked stand is strongly controlled by established trees and by patterns of mortality and survival. Growth from the seedling and sapling size classes into the subcanopy size class requires availability of adequate amounts of limiting resources, such as light, which are usually restricted near established trees. Depression of ingrowth near established trees provides evidence that growth into larger size classes is dependent on antecedent spatial distributions.

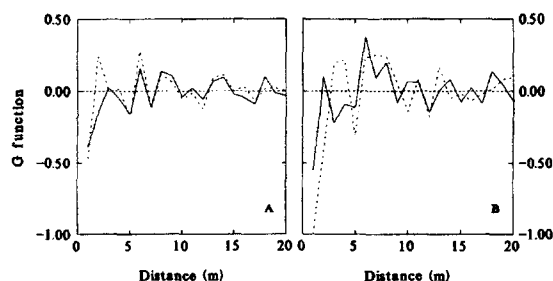


Fig. 7. G function values by intertree distance of mortality (dashed line) and survivors (solid line) around (a) 1926–76 ingrowth and (b) 1976–86 ingrowth. Horizontal dashed line is expected value for random neighborhood distribution.

5. Implications for distance-dependent modeling

Distance-dependent competition indices incorporate the influence of neighboring trees using some function of the distance between subject and neighboring trees. Therefore, it is imperative to understand the patterns and dynamics of neighborhood spatial distributions. Neighborhood tree densities were depressed near bole centers, but did not approach 0 trees ha^{-1} . In this stand, neighborhood tree densities around trees of the same size class were reduced to about 50% of stand densities in the 1 m annulus (Fig. 1). Neighborhood subcanopy densities were approximately 75% of densities in the 1 m and 2 m annuli surrounding canopy trees. The predominant influence of the larger trees on spatial distribution is consistent with previous distance-dependent modeling research (Daniels, 1976; Lorimer, 1983; Tome and Burkhart, 1989).

The peak in neighborhood density curves for both size classes roughly corresponded with the mean crown diameters. Mean crown diameter is equivalent to the sum of crown radii of two neighboring trees. Therefore, it was not surprising that the spacing between canopy trees was approximately the same as the mean crown diameter of canopy trees. The limit of neighborhood influence to approximately the scale of mean crown diameter supports research advocating smaller influence zones (Lorimer, 1983; Walker and Dowling, 1991; Biging and Dobbertin, 1992).

Most neighborhood density curves appeared to be linear rather than curvilinear (Figs. 1–3). Performance of linear distance weighted functions was superior to curvilinear functions in earlier studies (Daniels, 1976; Gutierrez and Fuentes, 1979; Gutierrez and Fuentes, 1981; Walker et al., 1989). As those studies and the present research included a variety of woody vegetation types, a linear distance function appears to be applicable for a wide range of plant communities. These results do not support models for similar forest types which have functions with strong inhibitions to near crown edge. Neighboring tree densities increased steadily from bole centers.

The 60 year record of the DPRF indicates uniform spatial distributions have been maintained or strengthened for both subcanopy and canopy size classes in this mature hardwood forest. The stability of uniform distributions reported in this study, and

earlier reports that random mortality shifts non-random distributions toward a random distribution (Lepš and Kindlmann, 1987; Kent and Dress, 1979; Kent and Dress, 1980), strongly suggests that distance-dependent processes have been influencing tree spatial distributions in the DPRF. Clearly, the dynamics of forest spatial distributions and the density-dependent mortality and ingrowth processes driving these changes should be included in distance-dependent modeling.

Considering the subtle differences in the distribution of neighborhood density around mortality and survivors (Fig. 5), the grossest measure of growth, it is not hard to understand the difficulties in developing distance-dependent growth models. This research demonstrated just how critical the distance component is for distance-dependent mortality and ingrowth modeling. Selecting too wide a search radius will include trees in zones where neighborhood density distributions are similar around the classes of interest (e.g. mortality vs. survivors). For example, neighborhood density distributions after 7 m around 1976–86 survivors and mortality were similar (Fig. 5). Including those trees beyond 7 m would obfuscate an analysis of distance-dependent effects. Selecting too narrow a search radius can also decrease the power of a distance-dependent model by excluding zones where neighborhood densities differ around the classes of interest.

Accurate distance-dependent modeling in hardwoods using ground level spatial coordinates of boles may well remain intractable. The plasticity of hardwood crowns introduces considerable random noise into any modeling system. Competition between trees is not due to bole locations, which are fixed, but is for limiting resources such as light, moisture, and nutrients. The ability of hardwoods to grow towards light and develop asymmetrical crowns, or crowns completely offset from bole centers, can lead to competition between trees which are not nearest neighbors from a bole center perspective. This increases the difficulty of producing accurate distance-dependent forest models using bole spatial coordinates.

Although not addressed in this paper, it is probable that root systems are also asymmetric. The presence of a > 25 m tall *U. americana* growing under the crown and within several meters of a 45 m tall

Q. macrocarpa suggests the root system of the oak was asymmetric. Unless the assumption is made that competition between root systems does not affect root growth, the close proximity of boles often observed in hardwoods implies asymmetric root system development.

Although the specific results of this study may be limited to old-growth stands with similar disturbance histories, the importance of distance-dependent ingrowth and mortality in stand dynamics should apply to all fully, or nearly fully, stocked stands. Distance-dependent modeling would be improved by incorporating crown spatial data along with bole spatial data. This information could be collected using aerial photographs or by developing additional models which estimate crown locations using bole locations, diameters, species, and other ground collectible information.

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