

Effects of Tree Size, Shade Tolerance, and Spatial Pattern on the Mortality of Woody Plants in a Seminatural Forest in Central Kentucky

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Previous biogeographical research has investigated the mortality of woody plants, emphasizing tree size, shade tolerance, and competition individually as critical factors. Few researchers, though, have empirically evaluated the simultaneous and relative importance of these three factors in a single study. Based on a thirty-five-year study within the University of Kentucky Arboretum, we report that none of the factors exerted an overriding influence on the tree survivorship alone. Rather, they were tightly intertwined in a complex way. Our study indicates that the three factors have contributed perhaps equally or at least simultaneously to the overall demographic processes in the woodland. **Key Words:** competition, plant survivorship, Ripley's *K*-function, spatial point pattern analysis.

过往的生物地理学研究, 已探讨了木本植物的死亡率, 并强调树木大小、耐阴性与竞争各别作为关键因素。但却鲜少有研究者在单一研究中, 就经验评估这三项因素同时发生且相对的重要性。我们根据一个在肯塔基大学植物园为期三十五年的研究, 记录这三项因素中, 没有任何一项对树木的存活率单独产生压倒性的影响。反之, 它们是以复杂的方式紧密地相互交织。我们的研究显示, 这三项因素大约均等地、或至少是同时地导致了林地的总体统计过程。 **关键词:** 竞争, 植物存活率, 雷普利的*K*函数, 空间点分佈形态分析。

La investigación biogeográfica previa ha estudiado la mortalidad de plantas leñosas, haciendo énfasis en la talla del árbol, tolerancia a la sombra y competencia individual como factores críticos. No obstante, pocos investigadores han evaluado empíricamente la simultaneidad e importancia relativa de estos tres factores en un solo estudio. Basados en un estudio de treinta y cinco años dentro del Arboretum de la Universidad de Kentucky, podemos informar que ninguno de los factores ejerció de manera individual una influencia predominante para la supervivencia del árbol. Mejor, esos factores estuvieron firmemente entrelazados de modo complejo. Nuestro estudio indica que los tres factores han contribuido quizás equitativamente, o por lo menos simultáneamente, en los procesos demográficos generales en el arbolado. **Palabras clave:** competencia, supervivencia de la planta, función *K* de Ripley, análisis espacial de patrones de puntos.

The long-term survivorship of individual plants is a central topic in both biogeographical theory and forest management (Vale 1982; Veblen et al. 1994; van Mantgem et al. 2009; Rigg et al. 2010). Within a forest stand, tree mortality often results in newly available habitats and resources that facilitate the recruitment of herbaceous plants and saplings, whereas living trees might inhibit such opportunities (Goldblum 1997; Hart and Kupfer 2011). This contrast between living and dead plants exerts profound influences on the spatial variations in various biotic and abiotic components, including species turnover, biodiversity, succession, nutrient cycling, and biomass productivity (Peet and Christensen 1980; Runkle 2000; Lutz and Halpern 2006). These components, in turn, are spatially and temporally intertwined and determine the overall forest community structure. Therefore, understanding how survival is maintained

and how mortality occurs is a fundamental springboard both for developing predictive models of forest dynamics (Malanson 2002) and for ensuring informed management of forest resources (Gray and He 2009; Larson and Churchill 2012).

Numerous physical and biological factors could significantly affect the mortality of forest plants across temporal scales (Botkin 1993; Lafon, Hoss, and Grisino-Mayer 2005; Sherriff, Berg, and Miller 2011). The physical drivers are broadly characterized as environmental conditions (e.g., soil, microclimate, landforms, etc.) and disturbance events (e.g., fire, landslide, flooding, storms, etc.). Some biological influences, such as pathogens and herbivory, are extrinsic to the vegetation. Although recognizing the importance of these factors, in this research, we focus primarily on the following three intrinsic biological aspects: shade tolerance, size, and competition.

The concept of tolerance to light limitation belongs to the broad realm of ecological life histories, which have underlain vegetation succession theories (Smith and Huston 1989; Grime 2001; Valladares and Niinemets 2008). At its simplest, individuals of a light-demanding plant species often exhibit limited longevity, because they are likely to be outcompeted by taller canopy trees. Hence, all other things being equal, those plants with greater tolerance to shade are expected to show lower mortality rates than their shade-intolerant counterparts (Burns and Honkala 1990; Kobe et al. 1995).

Tree size is also an important intrinsic property. Forest ecologists have both theoretically and empirically demonstrated a decrease in the probability of mortality as plants get larger (Uriarte et al. 2004; Coomes and Allen 2007; Ma et al. 2014). This is because large individuals are generally better able to withstand environmental stresses than smaller ones. Moreover, larger plants are superior to smaller plants with regard to competition for light, water, and nutrients (Peet and Christensen 1987; Weiner 1990). There are two caveats associated with this widely accepted negative relationship between size and mortality. Very large trees are not considered if they are in the phase of imminent death due to their old age. Also, wind disturbance is not accounted for in this relationship because taller canopy trees might be more subjected to the impact of tornadoes or hurricanes than shorter subcanopy trees (Everham and Brokaw 1996; Comita et al. 2009).

Competition, whether it occurs at a population or community level, is essentially a spatial process because an individual plant's fate is influenced by the size and proximity of its neighbors (Ford and Diggle 1981; Kenkel, Hendrie, and Bella 1997). Woody plants are generally long-lived and the competitive interaction among them is a very slow phenomenon; hence, measuring the type, intensity, and effects of competition has been a major challenge in biogeography, and empirical studies of tree mortality directly driven by competition at multidecadal scales are limited (Šebková et al. 2011; Ma et al. 2014). One alternative approach is to infer processes from spatial patterns (Watt 1947; Dale 1999; Mast and Veblen 1999; McIntire and Fajardo 2009). For example, spatial aggregation (or clumping) of individual plants likely indicates clonal connections, cooperative interactions among them, or the preferential establishment of seedlings at favorable microsites. Conversely, spatial uniformity (or regularity) is often associated with the process of self-thinning as individual trees get larger, intensifying competitive exclusion. In between these two extremes, random patterns exist, potentially implying independent spatial relationships among plants. Some ecologists, however, suggest that even under observed spatial randomness, significant nonrandom biological interactions might still be in operation; the strength of such interactions is simply not enough to induce either visible clustering or regularity of stems (e.g., Szwagrzak and Czerwczak 1993).

Inferential investigations of spatial patterns have long contributed to understanding the survivorship of individual plants through their interactions. Most of these studies have one important limitation, though: They often rely on a single snapshot pattern of plants' spatial distribution. Reflecting the integration and accumulation of numerous confounding physical and biological factors over time, spatial patterns at a moment in time indeed cannot be true representations of forest dynamics (Kenkel, Hendrie, and Bella 1997; Larson and Churchill 2012). As Shackleton (2002) acknowledged, characterizing the nature of biological interactions is highly dependent on "the temporal timing of the potential pairings at that time only" (74). Overall, the snapshot option might be useful for generating hypotheses or for exploratory data analysis but not for testing hypotheses with enough confidence. Although modeling or chronosequence methods are available as alternatives (Busing and Maily 2004; Getzin et al. 2006; Gray and He 2009), an ideal approach is composed of spatial positioning and the long-term monitoring of each individual woody plant, such that tree-by-tree comparisons become possible in the long run (Ward, Parker, and Ferrandino 1996; Condit et al. 2000; McDonald, Peet, and Urban 2003; Cowell, Hoalst-Pullen, and Jackson 2010). Such an approach is still limited, but the associated efforts are being increasingly reported (e.g., Smithsonian Tropical Research Institute; www.ctfs.si.edu).

The purpose of this article is to investigate the simultaneous and relative importance of tree size, shade tolerance, and competition to the mortality of individual woody plants over thirty-five years in a seminatural, managed woodlot at the University of Kentucky Arboretum. We have the advantage of possessing long-term data that were fully mapped and inventoried in 1977, 1986, and 2012. Thus, all woody individuals are classified into three categories based on their survivorship: present in 1977 but died before 1986 (Y1); present in both 1977 and 1986 but died before 2012 (Y2); and present in 1977, 1986 and 2012 (Y3). We broadly hypothesize that these three groups are composed of woody individuals, which possessed the following initial characteristics in 1977 when we started this project:

1. Y1: Generally small, light-demanding, and crowded at a fine spatial scale.
2. Y2: Traits in between those of Y1 and Y3.
3. Y3: Generally large, shade tolerant, and uncrowded at a fine spatial scale.

We develop these expectations based on the assumption that each individual factor—tree size, shade tolerance, and competition—has significantly contributed to the long-term survivorship of woody individuals in the study site since 1977. In particular, we assume that patterns in the spatial distribution of

plants as of 1977 have influenced the intensity of competition among them in subsequent years, thereby affecting their mortality.

Materials and Methods

Study Area

This research was performed at the 6-ha woodland within the University of Kentucky Arboretum (38°00'56" N, 84°30'18" W), located in the Inner Bluegrass region with midtemperate climate conditions (Campbell 1980). The region has four distinct seasons with monthly average temperature ranging from 0.5°C in January to 24.6°C in July. The total annual precipitation is 1,150 mm with the late spring and early summer seasons being slightly wetter than the other seasons. The woodland has been under ecological investigation since at least 1940 (Campbell 2014).

The soil within this woodland has been mapped by the Natural Resources Conservation Service of the U.S. Department of Agriculture (USDA), mostly as Maury silt loam, with slopes of 2 to 12 percent (Sims et al. 1968). This soil series is a typic paleudalf, largely derived from residuum of phosphate-rich limestone of the Middle Ordovician age, which lies at about 1.5 to 3.5 m below the surface. In recent mapping by the USDA Natural Resource Conservation Service (2014), the Maury of 1968 is now redefined as a mixture of Maury and Bluegrass, with the latter increasing on higher ground with less slope. In the south-central lowland of the woods, there is an area mapped as

Newark silt loam, which is similar to the Maury except for being somewhat poorly drained. The Newark series here was formerly mapped as an imperfectly drained variant of the Maury.

The woodland is dominated by black walnut (*Juglans nigra*) in the canopy and hackberry (*Celtis occidentalis*) in the subcanopy; other trees are listed in Table 1. These are all native wild species at this site, except for yellow poplar (*Liriodendron tulipifera*), which is native to the region but planted here. Since the beginning of the twentieth century, the woodland has undergone a variety of management actions, including mowing herbaceous plants before 1950, planting several yellow poplar individuals in the 1950s, and eliminating nonnative exotic shrubs such as *Lonicera maackii* and *Euonymus alatus* in the 1990s. Most canopy trees, especially black walnut, appear to date from about 1930 to 1940, based on ring counts and historical information (Campbell 2014). In 1950, the Forestry Department at the University of Kentucky put a fence around the western corner of the woodland (ca. 2 ha), so that undisturbed growth could be observed thereafter. The fence was woven wire, about 1.5 m high, to exclude cattle from this part of the Arboretum. There have been no deer in these woods or nearby for over a century. Today, this portion forms the best remnant of original vegetation in the whole Arboretum. Our field survey was conducted within this remnant.

Field Survey and Data Handling

In 1977, we established four square plots, each being 25 m × 25 m, within the remnant of original vegetation of the Arboretum. Plots 1, 2, 3, and 4 were linearly aligned at approximately 50-m intervals: Plot 1 lay

Table 1 Classification of woody plants at the University of Kentucky Arboretum, based on their long-term survivorship within the surveyed subplots (20 m × 20 m)

Species ^a		Number of individual stems														
		Plot 1			Plot 2			Plot 3			Plot 4			All plots combined		
		Y1 ^c	Y2 ^d	Y3 ^e	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3
<i>Acer saccharum</i>	Tol	0	0	0	0	1	2	0	0	0	0	0	0	0	1	2
<i>Aesculus glabra</i>	Tol	0	0	1	1	2	1	1	0	4	3	0	2	5	2	8
<i>Celtis occidentalis</i>	Tol	8	9	16	23	15	7	8	8	6	15	22	15	54	54	44
<i>Tilia heterophylla</i>	Tol	1	0	1	0	2	5	1	1	0	0	0	0	2	3	6
<i>Ulmus americana</i>	Tol	0	0	1	3	0	1	0	0	1	0	0	0	3	0	3
<i>Fraxinus americana</i>	Mod	15	9	3	2	3	0	0	1	0	0	1	0	17	14	3
<i>Prunus serotina</i>	Mod	10	4	0	11	10	1	9	17	3	4	2	0	34	33	4
<i>Gymnocladus dioica</i>	Int	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Juglans nigra</i>	Int	0	0	4	0	0	3	0	3	3	0	1	9	0	4	19
<i>Liriodendron tulipifera</i>	Int	0	0	0	0	0	0	1	1	4	0	0	0	1	1	4
<i>Euonymus alatus</i>	Shr	3	1	0	0	0	0	0	0	0	0	0	0	3	1	0
<i>Euonymus atropurpurea</i>	Shr	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
<i>Lonicera maackii</i>	Shr	0	0	0	1	0	0	2	9	0	2	4	0	5	13	0
<i>Sambucus canadensis</i>	Shr	0	0	0	0	0	0	0	0	0	4	0	0	4	0	0
Total individuals		37	23	26	41	33	20	22	40	21	29	31	26	129	127	93
Average DBH ^b (cm)		3.9	8.3	11.8	3.4	5.2	14.5	4.9	7.2	14.5	2.3	5.7	14.7	3.6	6.5	13.8

^aThe species are broadly ordered with regard to the level of shade tolerance (Burns and Honkala 1990). Tol = tolerant; Mod = moderate; Int = intolerant; Shr = shrub; DBH = diameter at breast heights.

^bDiameter at breast height as of 1977.

^cY1: Woody individuals present in 1977 but died before 1986.

^dY2: Woody individuals present in both 1977 and 1986 but died before 2012.

^eY3: Woody individuals present in 1977, 1986, and 2012.

at the south-central lowland with the poorly drained Newark silt loam mentioned earlier. Plot 2 was put at the upper portion of the lowland or around the interface between the Newark and Maury soil series. Plots 3 and 4 were subsequently located away from Plot 2, toward the higher zones of the woodland.

In each plot, we recorded and mapped all woody individuals with diameter at breast height (DBH) of at least 10 cm. The DBH was measured to the closest whole number of centimeters. In the midpoint of each plot, we also established a subplot of 20 m × 20 m. In these subplots, we recorded the presence of all woody individuals with DBH greater than 0.5 cm. These individuals included both shrub and tree species. Vines were also recorded but excluded from data for this article because the nature of their clonal reproduction could obscure the results of the spatial analyses to be performed (see Peterson and Squiers 1995). We identified each plant to the species level and measured its spatial location (i.e., x and y coordinates) with a precision of 0.1 m. The same type of field survey was performed in 1986 and 2012.

We carefully matched the three resulting maps of woody plants to identify which individuals had died before 1986 (Y1), died before 2012 (Y2), or survived until 2012 (Y3). Multiple stems of a particular species at a single spot were treated in two ways: (1) for displaying the overall species composition of each plot, their DBH values were summed up into the basal areas; (2) for spatial analysis, only the stem having the greatest DBH was considered. Species nomenclature followed Gleason and Cronquist (1991). The whole-plot data (25 m × 25 m) were used to compute the overall species composition in 1977, 1986, and 2012, whereas only the subplot data (20 m × 20 m) were used to perform spatial point pattern analysis.

Spatial Point Pattern Analysis

We evaluated patterns in the spatial distribution of woody individuals, employing both first-order and second-order analyses. The first-order approach was rather simple and concerned with the density or local “crowdedness” of woody plants: For each stem (DBH ≥ 0.5 cm) within each plot, we drew a 2-m radius circle and counted the number of other stems located within that circle. Selecting the size of this neighborhood was inspired by the previous finding that individual stems generally compete with their immediate neighbors (e.g., Kenkel, Hendrie, and Bella 1997).

Ripley’s K -function was used as a second-order test of univariate and bivariate spatial patterns in woody plants distribution (Ripley 1981; Diggle 1983; Upton and Fingleton 1985). It is a technique used to describe the tendency of points to be distributed in aggregated, random, or uniform patterns at different scales (or distance) on a two-dimensional plane (e.g., Kim, Cairns, and Bartholdy 2009). This method considers the spatial location of all individual plants within a certain

distance t , not just nearest neighbors. For a spatially random distribution, $K(t) = \pi t^2$.

The unbiased univariate estimator of the K -function is defined as

$$\hat{K}(t) = \frac{|A|}{n^2} \sum_{i \neq j} \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij}), \quad (1)$$

where A is the area of a plot, n is the total number of woody plants in the plot, i is plant i (focal), j is plant j (neighbor), w_{ij} is included both to correct edge effect and to indicate the proportion of the circumference of a circle with its center at the focal plant i and radius u_{ij} that lies within the plot, u_{ij} is the distance between plants i and j , and I_t denotes the counter variable (if $u_{ij} < t$, then $I_t = 1$, else $I_t = 0$). We performed this univariate analysis separately for Y1, Y2, and Y3 individuals, focusing on their spatial distribution in 1977.

In the case of bivariate analysis, the unbiased estimator is

$$\hat{K}_{12}(t) = \frac{|A|}{n_1 n_2} \sum_{i \neq j}^{n_1} \sum_{i \neq j}^{n_2} w_{ij}^{-1} I_t(u_{ij}), \quad (2)$$

where n_1 and n_2 are the total number of woody individuals in certain categories of 1 and 2, respectively (e.g., small vs. large trees or Y1 vs. Y3 trees). The other terms are of the same interpretation as Equation 1. We performed the bivariate analysis to examine whether Y1 individuals were significantly clustering around Y3 plants as of 1977.

In both univariate and bivariate approaches, we calculated the K -function at 0.5-m intervals to capture any possible microscale biological interactions among plants and to ensure sufficient neighboring pairs (Gray and He 2009). The estimation was performed up to 10 m distance (i.e., $t_{\max} = 10$ m), which corresponded to half the length of the shortest subplot side. An edge effect occurred when a circle with radius t was not wholly situated within the plot. We used a toroidal correction to account for such an effect, assuming that bordering stands around the plot have a similar distribution of plants to that plot (Haase 1995).

To enhance interpretation, the K -function is often linearized to and reported in the form of L -function (after Besag 1977):

$$\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{\pi}} - t, \quad (3)$$

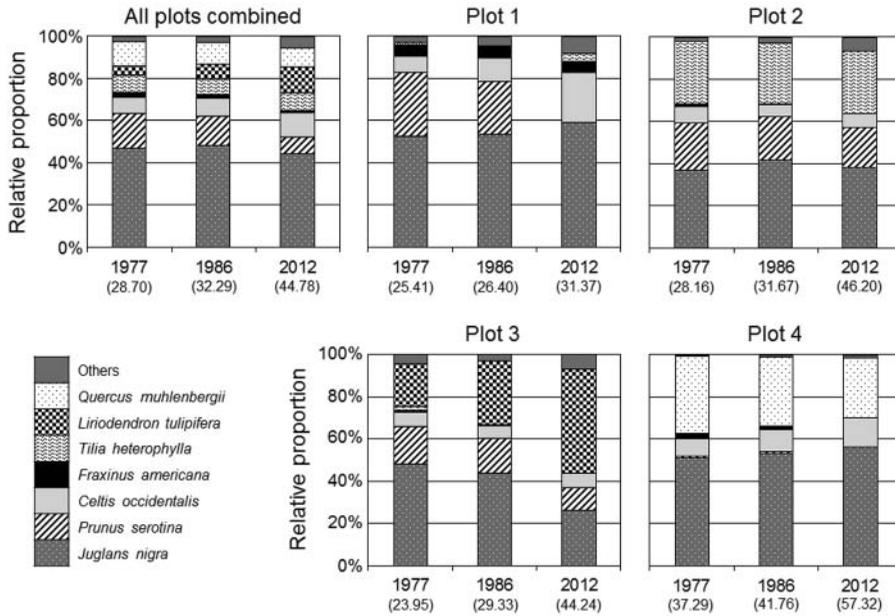
which scales the test statistic so that the expectation becomes zero for all values of t under complete spatial randomness. With this transformation, positive values of $L(t)$ would indicate spatial aggregation, whereas negative values would suggest spatial uniformity.

The departures from a random distribution were evaluated by performing Monte Carlo tests of randomized data sets (Manly 1991), which produced a simulation

envelope at a 95 percent confidence level. In the randomization procedure for the univariate analysis, we altered distances between individual plants by multiplying their

locations by a random number within the range of the corresponding plot size to generate new, randomized coordinates. For the bivariate approach, we maintained

(A) Dynamics of species composition



(B) Spatial distribution of woody individuals in 1977

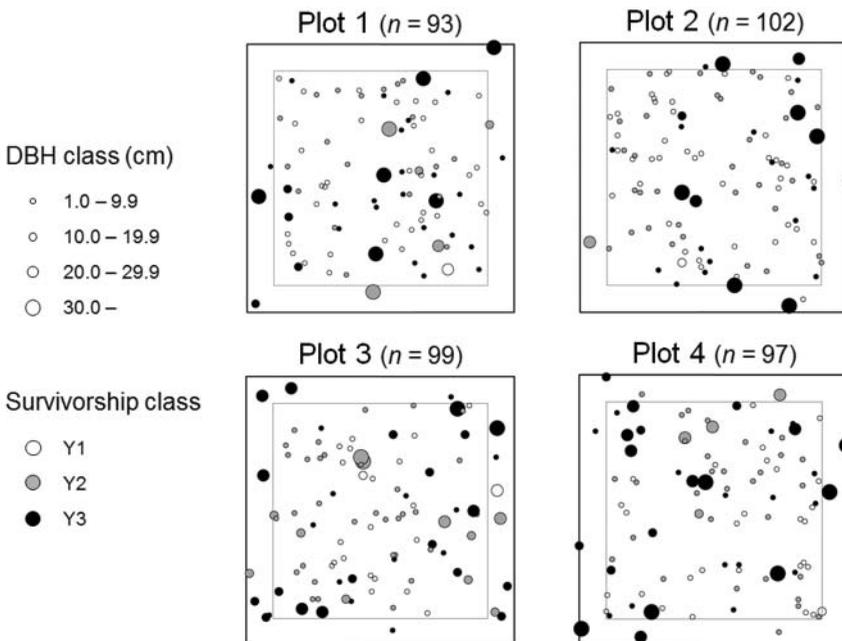


Figure 1 (A) Changes in species composition over time observed in the four plots established at the University of Kentucky Arboretum. Values in the parentheses represent total basal area ($m^2 ha^{-1}$). (B) The spatial distribution of woody individuals as of 1977. The plot size is 25 m \times 25 m. In the middle of each plot, we also put a subplot of 20 m \times 20 m. DBH = diameter at breast height; Y1 = woody individuals present in 1977 but died before 1986; Y2 = woody individuals present in both 1977 and 1986 but died before 2012; Y3 = woody individuals present in 1977, 1986, and 2012.

the spatial position of all plants, but their labels (e.g., small, large, Y1 or Y3) were randomly shuffled. These spatial analytic procedures were all performed using SPPA 2.0 (Haase 2002).

Results

Species Composition

The four plots in the Arboretum exhibited somewhat different trends of dynamics in species composition from 1977 to 2012, as indicated by the relative proportion of woody species based on their basal area (Figure 1A). In Plot 1, located in the lowland, there were slight increases in the relative proportion of *Juglans nigra* and *Celtis occidentalis* (common hackberry) over time, but the individuals of *Prunus serotina* (black cherry) were all dead by 2012. In contrast, in Plot 2, the proportion of these three species has been more or less constant. Plot 3 was characterized by an increase in the proportion of *Liriodendron tulipifera* and a decrease in the proportion of *J. nigra*. In Plot 4, in 2012, three tree species were dominant in terms of their basal area: *J. nigra*, *Quercus muhlenbergii* (chinkapin oak), and *C. occidentalis*. See Figure A1 in the Appendix for a detailed description of the DBH distribution of each species in each year of the forest survey.

In 1977, there was no clear sign of anisotropy with regard to the spatial distribution of woody individuals in the four plots (Figure 1B). In other words, we did not find any directionality in their distribution or particular hot spots showing a concentration of stems.

Effects of Tree Size

At first glance, the average DBH values acquired from each category—Y1, Y2, and Y3—seemed to show

Table 2 Classification of the Y3 plants (i.e., long-term survivors; present in 1977, 1986, and 2012) at the University of Kentucky Arboretum, based on their diameter at breast height as of 1977

	Number of stems	Proportion (%)
Total Y3 ^a	93	100.0
Trees with DBH < 9.5 ^b cm	54	58.1
Trees with DBH < 6.5 ^c cm	31	33.3
Trees with DBH < 3.6 ^d cm	12	12.9
All <i>Celtis occidentalis</i> of Y3	44	100.0
Trees with DBH < 9.5 cm	37	84.1
Trees with DBH < 6.5 cm	20	45.5
Trees with DBH < 3.6 cm	7	15.9

Note: Y3 = present in 1977, 1986, and 2012; DBH = diameter at breast height; Y2 = present in both 1977 and 1986 but died before 2012; Y1 = present in 1977 but died before 1986.

^aNone of the recorded shrub individuals belonged to Y3.

^b9.5 cm: The level based on which trees are divided into small and large individuals.

^c6.5 cm: The overall average DBH of Y2 individuals as of 1977 (see the bottom right of Table 1).

^d3.6 cm: The overall average DBH of Y1 individuals as of 1977 (see the bottom right of Table 1).

clearly the importance of size to the long-term survivorship of woody individuals. When all plots were combined (see the far right of Table 1), the individuals of Y1 were generally considered saplings with an overall average DBH of only 3.6 cm as of 1977, whereas Y3's average was already greater than 10 cm. Y2 plants showed an intermediate average of 6.5 cm.

A detailed analysis, however, revealed that the size effect cannot be fully recognized in such a simplistic manner based on averaging. In many cases, even those individuals that had been considered small (i.e., DBH < 9.5 cm; mostly subcanopy plants) in 1977 survived until 2012 ($n = 54$), whereas several larger individuals underwent early mortality either before 1986 or 2012 (Figure 2). As indicated in Table 2, more than half of Y3 individuals (fifty-four of ninety-three) had a DBH smaller than 9.5 cm in 1977. The DBH of one third of

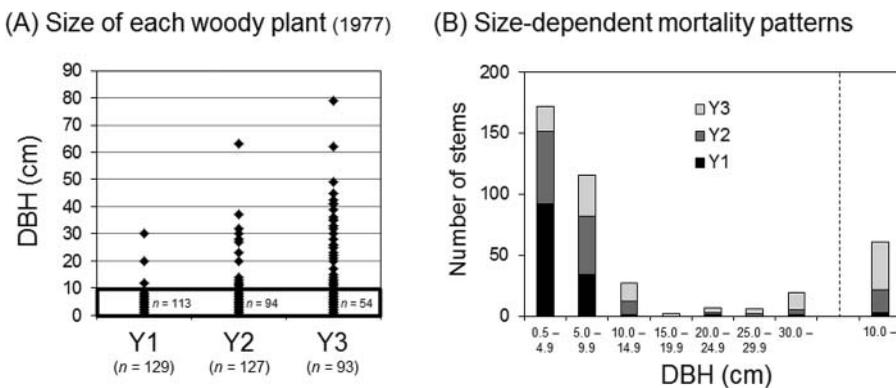


Figure 2 (A) Woody individuals in the Y1, Y2, and Y3 categories plotted against their diameter at breast height in 1977. The individuals within the rectangular box at the bottom (i.e., DBH < 10 cm) were used to produce Figure 3. (B) Patterns in the long-term survivorship of Y1, Y2, and Y3 individuals across different DBH classes. The last bar at the right of the vertical dotted line combined all stems with DBH \geq 10 cm. Y1 = woody individuals present in 1977 but died before 1986; Y2 = woody individuals present in both 1977 and 1986 but died before 2012; Y3 = woody individuals present in 1977, 1986, and 2012; DBH = diameter at breast height.

Table 3 Classification of all stems in the four plots with DBH greater than 10 cm at the University of Kentucky Arboretum, based on their long-term survivorship

	Number of stems	Proportion (%)
Total	61	100.0
Trees of Y1 ^a	3	4.9
Trees of Y2 ^b	19	31.1
Trees of Y3 ^c	39	63.9

Note: DBH = diameter at breast height as of 1977.

^aY1: Woody individuals present in 1977 but died before 1986.

^bY2: Woody individuals present in both 1977 and 1986 but died before 2012.

^cY3: Woody individuals present in 1977, 1986, and 2012.

Y3 plants (thirty-one of ninety-three) was < 6.5 cm, the overall average of Y2 plants. Most notably, twelve stems with DBH smaller than 3.6 cm (Y1's average as of 1977) survived until 2012. The size distribution of the forty-four individuals of *Celtis occidentalis* that belong to Y3 (see the bottom half of Table 2) best illustrated among species the long-term survival of many small individuals. Another analysis showed that, among the sixty-one individuals having DBH of at least 10 cm in 1977, three died before 1986 and only thirty-nine trees (i.e., ca. 64 percent) were still alive in 2012 (Table 3).

Effects of Shade Tolerance

Overall, the degree of shade tolerance has not been a critical determinant of the survivorship of all woody plants at the Arboretum (Table 1). For example, *Aesculus glabra* (Ohio buckeye) and *Celtis occidentalis* are generally regarded as shade tolerant, but their individuals were more or less evenly distributed across the three categories of Y1, Y2, and Y3, rather than mainly belonging to Y3. *Fraxinus americana* (American ash) and *Prunus serotina* are known as having broadly

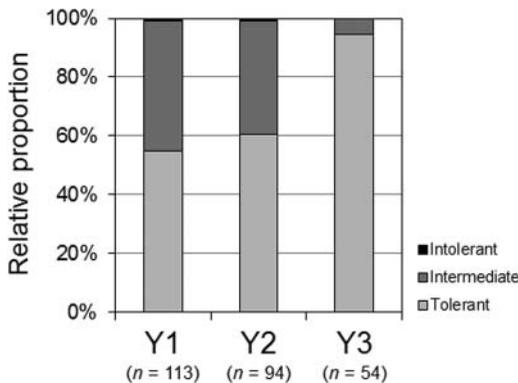


Figure 3 Classification of small woody individuals (DBH < 10 cm in 1977) based on the level of shade tolerance. DBH = diameter at breast height in 1977; Y1 = woody individuals present in 1977, but died before 1986; Y2 = woody individuals present in both 1977 and 1986, but died before 2012; Y3 = woody individuals present in 1977, 1986, and 2012).

Table 4 Analysis of neighbors for each individual woody plant at the University of Kentucky Arboretum

	Average neighboring stem number				
	Plot 1	Plot 2	Plot 3	Plot 4	All plots combined ^a
Y1	2.5	3.0	2.9	2.2	2.7
Y2	2.0	2.2	2.7	1.9	2.2
Y3	2.0	2.1	2.0	1.9	2.0

Note: Centering each stem, we drew a circle with radius of 2 m. The woody plants located inside that circle as of 1977 were considered neighbors. Y1 = present in 1977 but died before 1986; Y2 = present in both 1977 and 1986 but died before 2012; Y3 = present in 1977, 1986, and 2012.

^aThe mean difference was statistically significant (analysis of variance performed; $F = 5.665$, $p = 0.004$).

intermediate tolerance to light limitation, but most of their stems showed early mortality, and only a few were alive in 2012. *Juglans nigra* presented the most dramatic contrast to our original expectation: It is a light-demanding species, but most of its individuals belonged to Y3 and none to Y1.

When we restricted our analysis to only the small stems with DBH < 9.5 cm as of 1977 in each category of Y1 ($n = 113$), Y2 ($n = 94$), and Y3 ($n = 54$; see the rectangular box at the bottom of Figure 2A), however, the importance of shade tolerance seemed apparent (Figure 3): The proportion of shade-tolerant species in the Y1 and Y2 classes was similar (54.9 percent vs. 60.6 percent), but the percentage dramatically increased in the Y3 category (94.4 percent).

Effects of Spatial Pattern

The first-order approach revealed that, in general, the average number of neighboring stems was greatest, intermediate, and smallest in the Y1, Y2, and Y3 categories, respectively (Table 4). When all plots were combined, such an among-class difference was statistically significant ($F = 5.665$, $p = 0.004$).

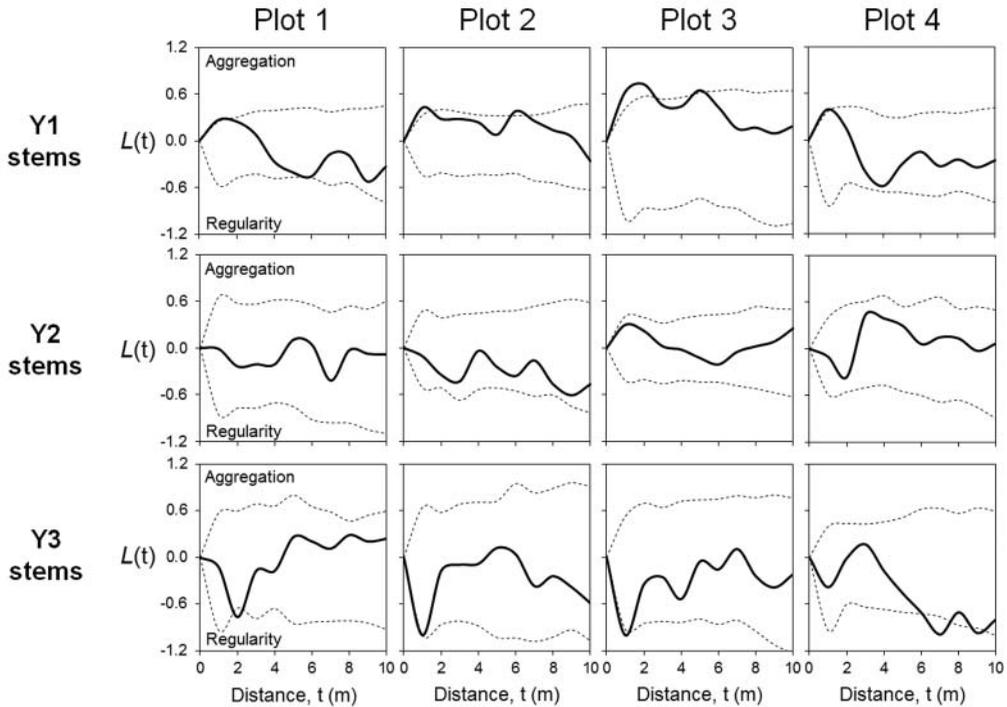
The second-order spatial point pattern analysis (Ripley's K -function) produced a clear trend of univariate point patterns in 1977 (Figure 4A): Y1 individuals exhibited spatial aggregation at a local scale of 1 m, whereas the long-term survivors (i.e., Y3 stems) were regularly dispersed. In the four plots surveyed, these patterns of clumping among the Y1 plants and spatial uniformity among the Y3 plants were always statistically significant. The spatial pattern of Y2 plants was in between these two; the stems were randomly distributed. The second-order bivariate approach demonstrated that, in 1977, Y1 plants were significantly aggregated around Y3 plants at varying distances with the exception of Plot 4 (Figure 4B).

Discussion

Factors Influencing Demographic Processes

We cannot claim that extrinsic factors, such as weather events, pathogens, and herbivory, have had negligible

(A) Univariate spatial point pattern analysis



(B) Bivariate spatial point pattern analysis

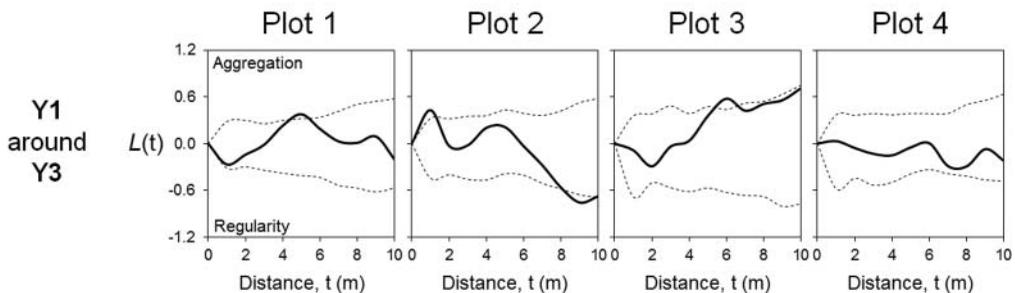


Figure 4 (A) Results of the univariate spatial point pattern analysis for the distribution of Y1, Y2, and Y3 individuals in 1977. (B) Results of the bivariate pattern analysis between Y1 and Y3 plants in 1977. In all graphs, dotted lines indicate simulated envelopes at the 0.05 significance level, and the solid line represents estimated Ripley's L -function. Y1 = woody individuals present in 1977 but died before 1986; Y2 = woody individuals present in both 1977 and 1986 but died before 2012; Y3 = woody individuals present in 1977, 1986, and 2012.

effects on the mortality of woody plants during this study period. The area has been fenced from larger herbivores for several decades, however. There have been no epidemics of pathogens during this period, other than Dutch elm disease, which killed a few large trees in other parts of the Arboretum. The obvious effects of storms (with wind or ice) have been the acceleration of damage to large walnuts and cherries.

Many biogeographers have emphasized the importance of tree size, shade tolerance, and competition as critical factors in the mortality of woody plants. Although each of these three factors has been

intensively investigated in the past, few empirical attempts have been made to evaluate their simultaneous and relative importance in a single study (e.g., Wright et al. 2010). Our results support the initial hypothesis we developed for Y1, Y2, and Y3 individuals: In 1977, the Y1 plants that died before 1986 were generally small in size, light-demanding, and crowded at a fine spatial scale, whereas the long-term survivors to 2012 (Y3) exhibited the opposite characteristics, namely, already large, shade tolerant, and regularly dispersed (uncrowded) over space. The traits of Y2 stems were in between those of Y1 and Y3. Therefore,

we posit that tree size, shade tolerance, and competition (indicated by spatial pattern) are all important factors that contribute to the fundamental demographic processes of the forest community at the University of Kentucky Arboretum over multiple decades.

Although all three factors are important in controlling forest dynamics in our woodland, each factor has limited explanatory power and does not have pervasive importance over the other factors. For example, when all stems were considered, the shade tolerance of a species could not fully account for the overall pattern of long-term survivorship of that species (Table 1). This accords with the previous evidence that species within the same shade tolerance level do not necessarily show the same or consistent patterns of survival and mortality (Bloor and Grubb 2003; Comita et al. 2009; Ma et al. 2014). Moreover, our results indicate that being small did not directly lead to the mortality of plants within a short time period and that being large did not always guarantee long-term survival (Figure 2; Tables 2 and 3). The importance of tree size to long-term survivorship has been discussed by several authors (e.g., Uriarte et al. 2004; King, Davies, and Nur Sapardi 2006; Das et al. 2008; Ma et al. 2014), but these authors also recognized that size itself cannot be the sole factor and that spatial components (e.g., conspecific density or crowding effects of neighboring plants) should receive as much attention.

The three factors complement the limitations of one another: When a factor could not fully explain the mortality and survival of an individual or a group of individuals, the other factors helped to explain possible underlying mechanisms. For example, the long-term survival until 2012 of many individuals that had actually been small in 1977 (i.e., DBH < 9.5 cm) is understandable because these individuals were predominantly shade tolerant (see the column of Y3 in Figure 3), and they did not undergo intensive competition as indicated by their spatial “uncrowdedness” and regularity (Figure 4A, Table 4). Also, most individuals of *Juglans nigra*, which is a light-demanding species, did survive until 2012, and this can be attributed to their large size; that is, a DBH already greater than 20 cm in 1977 (data not shown). These discussions imply that the factors of size, shade tolerance, and competition are intertwined in a complex way, thereby exerting an overall influence on the mortality patterns of individual woody plants at the Arboretum. This idea itself is not novel, but it has seldom been supported by empirical investigations (Ma et al. 2014). Such a paucity of convincing past research reflects the difficulty of combining field surveys multiple times across multiple plots over multiple decades to acquire fully mapped forest data.

Spatial Pattern and Competition

The significant aggregation of individuals that did not survive to 1986 (Y1), either among themselves or around survivors to 2012 (Y3), accords with the previous literature.

For example, Aakala et al. (2007) documented a clustered distribution of dead individuals of *Picea mariana* in boreal old-growth forests of northeastern Quebec. Also, the aggregation detected at a local scale of 1 m in our article (Figure 4A) corresponds to the result of Kenkel, Hendrie, and Bella (1997), supporting their argument that “individuals were competing with their immediate neighbors” (241). In our bivariate approach, Plots 1, 2, and 3 exhibited a significant clustering of Y1 around Y3, but a random association between them was found in Plot 4 (Figure 4B). These patterns are also consistent with results of Gray and He (2009), who found that dead trees were either aggregated or randomly distributed around live trees. Thus, the random mortality hypothesis is not supported in this article (see also Sterner, Ribic, and Schatz 1986; Kenkel 1988; Goreaud and Pélissier 2003; Ma et al. 2014).

Reconsidering Size-Based Classification Approach

Our approach of classifying all woody individuals into the categories of Y1, Y2, and Y3 greatly helped to understand the demographic processes of different plots, each having distinct plant species composition. In contrast, much of the previous research has relied on a single snapshot pattern of plants’ spatial distribution. Accordingly, one typical strategy in the past was to divide woody individuals into different size classes defined by DBH (or height), assuming that these classes would effectively represent distinct stages in the life history of trees, their ages, and abilities to compete.

In our preliminary analyses, we tried a size-based classification of all recorded stems, but we could not clearly interpret the resulting patterns (see Appendix, Figures A2 and A3). We designated individuals with DBH smaller and greater than 10 cm as small and large, respectively. Univariate spatial analyses then revealed that both small and large stems were distributed in a generally random manner. Moreover, in bivariate analyses, the distribution of the small around the large was found to be primarily random.

Indeed, the small versus large approach has produced varying—often, even equivocal—results in the previous research. In mixed deciduous–coniferous forests of Poland and the Czech Republic, Szwagrzyk and Czerwczak (1993) found predominantly independent spatial associations between different size classes. Also, Frelich et al. (1993) reported from a multispecies stand that most of the pairs of species they considered exhibited a neutral association, in which adults of neither species significantly influenced the understory abundance of the other. Dovčiak, Frelich, and Reich (2001), however, documented significant spatial relationships in a white pine forest of the western Great Lakes region in the United States. They classified white pine individuals into five size classes to produce a total of ten pairs; in nine cases, there were significant positive or negative spatial associations across scales.

We propose that the size-based approach might help an understanding of size-dependent

neighborhood effects in monospecific stands, but it is unlikely to be useful in multispecies forests like our study site. In monospecific stands, different individuals share the same life history traits, if not the same genetic characteristics (Stearns 1992): they show very similar germination timing, size at birth, growth rate, longevity, mortality, trade-off, allelopathy, and effects on soil resources. Thus, individuals within a certain size class are expected to be in the same stage of their life, potentially undergoing direct facilitative or inhibitive interactions with those of the adjacent and distant size classes, as shown in the previously mentioned white pine forest by Dovčiak, Frelich, and Reich (2001; see also Mast and Veblen [1999] for an example of ponderosa pine). In multispecies stands, results of bivariate spatial analysis for between-class associations will most likely prove difficult to interpret (Frelich et al. 1993; Szwagrzyk and Czerwczak 1993). Varying life histories of different species—especially size at birth and growth rate—play as confounding factors, such that plants of the same size might actually be situated at different life stages, thus possessing different competitive abilities. It is increasingly reported that the relationship between tree size and survivorship greatly varies among species (e.g., Stewart 1989; Woods 2000; Brown et al. 2004; Coomes 2006). Moreover, there have been considerable variations among past studies with regard to what exactly is meant by small versus large (or subcanopy vs. canopy trees) and which size level one should choose as a relevant threshold: for example, Sterner, Ribic, and Schatz (1986): 5 or 10 cm DBH; Szwagrzyk (1990): 35 cm DBH; Ward, Parker, and Ferrandino (1996): 25 cm DBH. Sterner, Ribic, and Schatz (1986) even acknowledged that “no assumptions are made that these DBHs are biologically meaningful discontinuities in the life histories of trees” (623). Given these limitations posed by the size-based classification of trees of multiple species, we suggest that more studies, in which trees are classified based on their survivorship (e.g., Y1, Y2, and Y3 as in this study), be reported in biogeographical literature.

Inclusion of Subcanopy Trees in Biogeographical Research and Management

This study illustrates the importance of spatial positioning and multidecadal monitoring of individual woody plants for informed forest management. Such efforts should not be limited to the so-called large trees (e.g., DBH \geq 10 cm); rather, subcanopy plants should receive as much care and attention as their canopy counterparts do. In many forest management plans, until small individuals enter a certain size class (i.e., “ingrowth”), they are not included in regular monitoring or surveys (Ward, Parker, and Ferrandino 1996; Wolf 2005; Cowell, Hoalst-Pullen, and Jackson 2010). It is important, however, to take into account the presence of small plants and their relational positionality (Szwagrzyk

1990; McDonald, Peet, and Urban 2003). It should be noted that, in this work, more than half of the long-term survivors to 2012 (Y3) were small, subcanopy individuals in 1977 (fifty-four of ninety-three; see Table 2). In a long-term survey of forest dynamics in southwestern Denmark, Wolf (2005) could not find any indication that tree mortality was driven by competition, and she acknowledged that this was likely because only trees larger than 10 cm DBH were recorded and analyzed over five decades of management effort. Other biogeographers had previously addressed the importance of including small subcanopy plants to obtain full insight into competitive interactions and the resulting mortality (e.g., Duncan 1991; Ward, Parker, and Ferrandino 1996; Shackleton 2002). ■

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Appendix

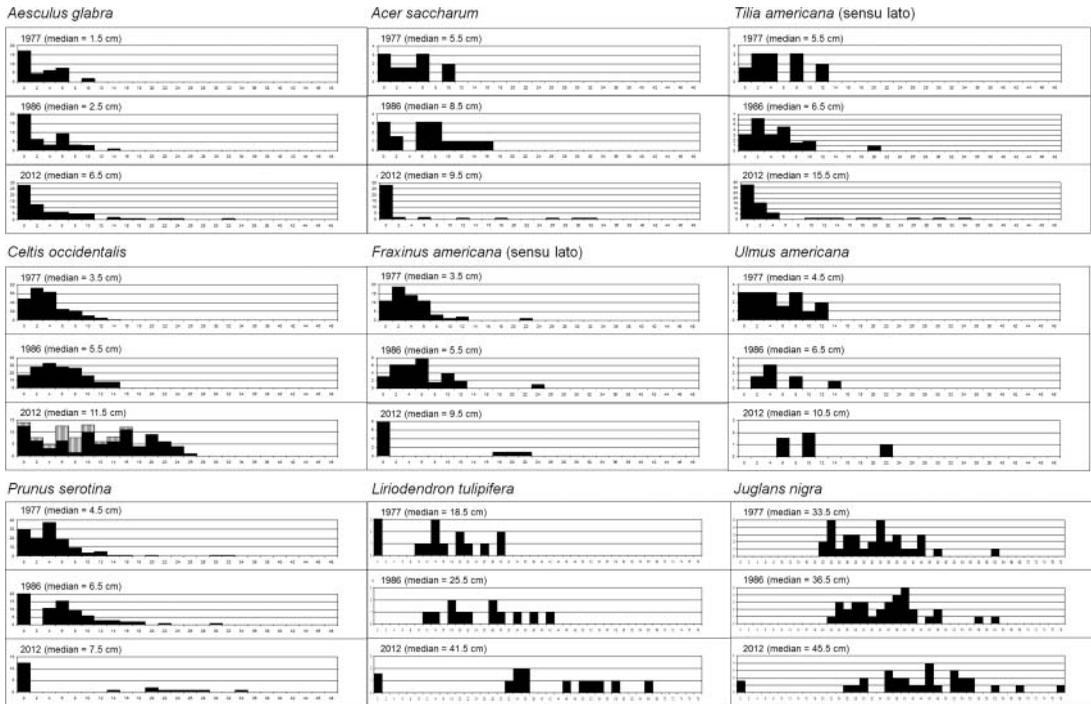
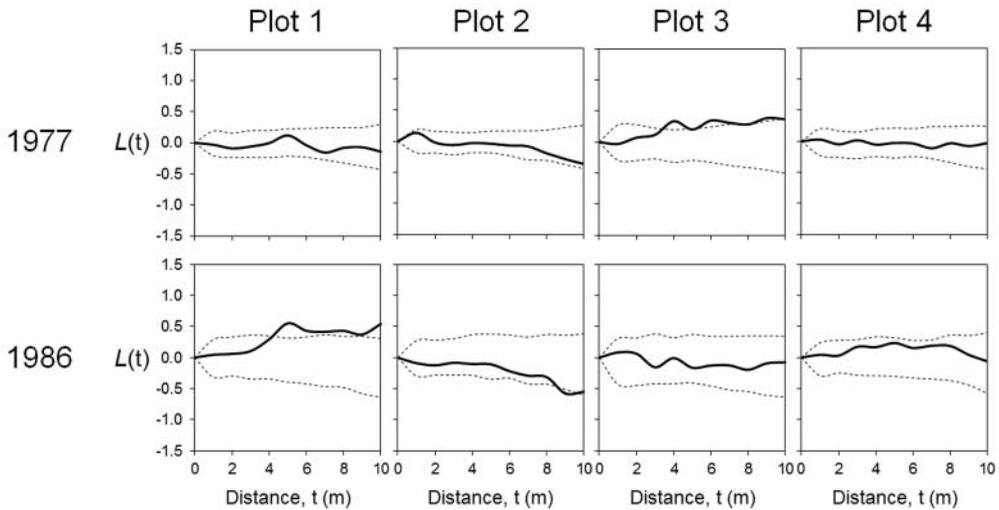


Figure A1 Patterns in size distributions (based on diameter at breast height among individual species with sufficient data are of three types: (1) concentrated in 0–10 cm DBH classes at all dates but with a few stems reaching 30–34 cm DBH by 2012; increasing in overall numbers and basal area. Species are sugar maple (*Acer saccharum*), buckeye (*Aesculus glabra*), and basswood (*Tilia americana*); (2) concentrated in 0–12 cm class during 1977, then several growing into 12–24 cm class by 2012 but decreasing in overall numbers and mostly without increase in basal area. Species are hackberry (*Celtis occidentalis*, which did increase in basal area), white ash (*Fraxinus americana sensu lato*), elm (*Ulmus americana*), and cherry (*Prunus serotina*); and (3) almost absent in 0–10 cm classes, except for a few weak sprouts—not seedlings; decreasing little in overall density and increasing much in basal area. Species are walnut (*Juglans nigra*) and tulip tree (*Liriodendron tulipifera*)—the latter planted in about 1950. These differences between species in their size distributions are generally interpretable in terms of shade tolerance, suggesting three classes here (see Table 1). DBH = diameter at breast height.

(a) Univariate analysis for small individuals (DBH < 10 cm)



(b) Bivariate analysis between small and large plants

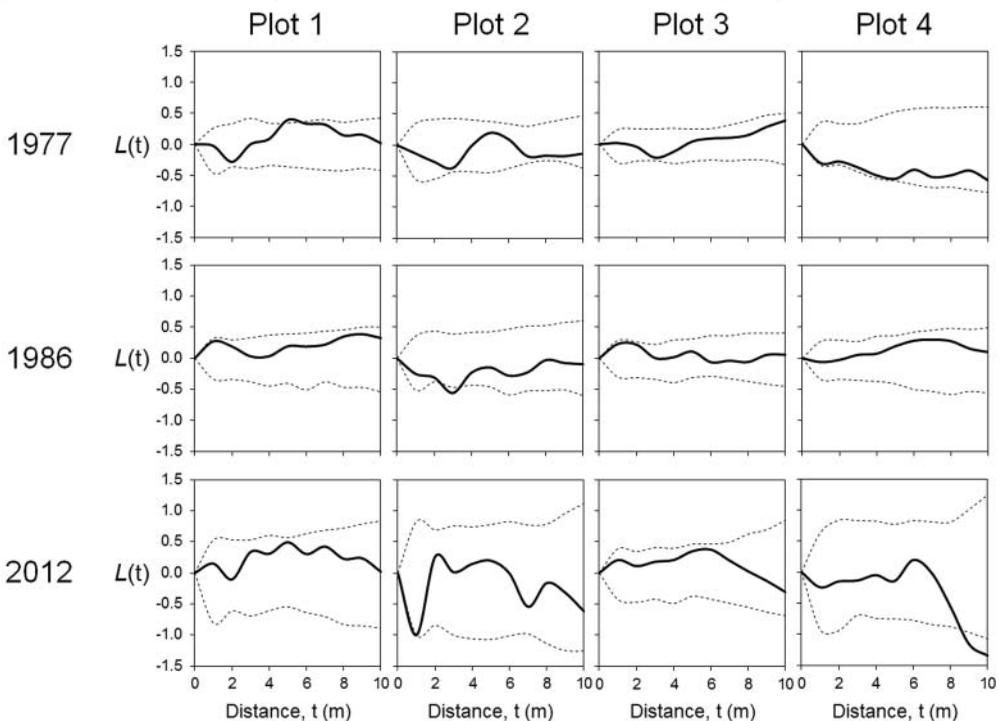


Figure A2 (A) Results of the univariate spatial point pattern analysis for small individuals with diameter at breast height smaller than 10 cm. Analysis for 2012 was not performed due to the small sample size of that year. (B) Results of the bivariate pattern analysis between small and large (DBH ≥ 10 cm) plants. In all graphs, dotted lines indicate simulated envelopes at the 0.05 significance level, and the solid line represents estimated Ripley's L-function. The univariate spatial analyses indicated that only Plot 3 in 1977 and Plot 1 in 1986 exhibited a significant clumping of small plants. In all of the other cases, small stems were distributed in a predominantly random manner across the spatial scales tested. In the twelve cases of the bivariate spatial analyses, only Plot 1 of 1977 suggested a significant (but still very minor) clustering of small individuals around larger ones. DBH = diameter at breast height.

Univariate analysis for large individuals (DBH ≥ 10 cm)

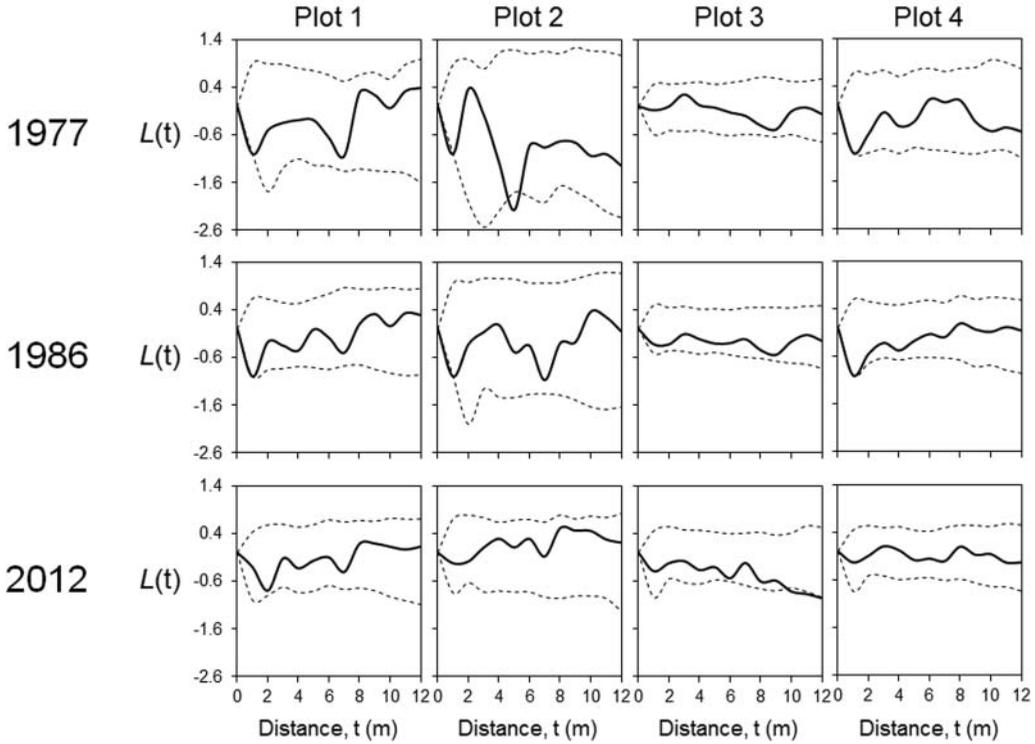


Figure A3 Results of the univariate spatial point pattern analysis for large individuals with diameter at breast height ≥ 10 cm. In all graphs, dotted lines indicate simulated envelopes at the 0.05 significance level, and the solid line represents estimated Ripley's L-function. Among the twelve cases we tested, only Plot 2 of 1977 and Plot 3 of 2012 exhibited a significant (but still very minor) spatial regularity. In the other ten cases, the distribution was predominantly random across scales. DBH = diameter at breast height.