Forest Ecology and Management 256 (2008) 922–928

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Long-term spatial dynamics of *Acer saccharum* during a population explosion in an old-growth remnant forest in Illinois

Yiching Lin [a,*], Carol K. Augspurger [b]

[a] *Faculty of Biomedical Science and Environmental Biology, Kaohsiung Medical University, Kaohsiung 807, Taiwan*
[b] *Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA*

ARTICLE INFO

Article history:
Received 21 February 2008
Received in revised form 16 May 2008
Accepted 22 May 2008

Keywords:
Acer saccharum
Disturbance
Dutch elm disease
Forest dynamics
Historical data
Mortality
Point patterns
Recruitment
Ripley's $L(d)$ function
Spatial pattern

ABSTRACT

Species richness and evenness have greatly declined in oak–hickory forests in the central hardwood region in the U.S.A. in the past 100 years due to the rapid population growth of *Acer saccharum*. This study used a 50-year record of spatial dynamics to examine how demographic processes, particularly recruitment, may have contributed to this increase in an old-growth forest remnant, Brownfield Woods, Urbana, Illinois, U.S.A. The impact of canopy disturbance, including the outbreak of Dutch elm disease, on this increase was also evaluated. Historical maps of trees ($\geq$7.6 cm DBH) from 1951, 1988, and 2001 in a 180 m × 280 m area were used to develop a series of univariate Ripley's $L(d)$ functions to study changes in spatial patterns of three size classes of *A. saccharum* over time. Bivariate Ripley's $L(d)$ functions were also utilized to evaluate spatial associations between recruitment and canopy disturbance. Our results indicated that *A. saccharum* was aggregated at most spatial scales up to 80 m during 1951–2001. Such aggregation arose mainly from small individuals. Furthermore, newly recruited individuals were aggregated at multiple spatial scales, and were significantly associated with canopy disturbance in general, as well as gaps created by *Ulmus* trees killed by Dutch elm disease. The aggregation of the 1951 initial group of small individuals changed via mortality to a random distribution over time. The results indicate that tree deaths caused by disturbances of different scales and types were the main cause of increased recruitment of *A. saccharum* in Brownfield Woods. The occurrence of Dutch elm disease further accelerated its population increase. This study demonstrated a direct spatial link between recruitment of *A. saccharum* and disturbance, and provided a long-term case study of a population explosion.

1. Introduction

Species richness and evenness in oak–hickory forests in various parts of the U.S.A. have declined greatly in the past century (Oak et al., 2004), concurrent with the rapid rise of shade-tolerant species, particularly *Acer saccharum* (Ebinger, 1986; Edgington, 1991; Shotola et al., 1992; Roovers and Shifley, 1997; Rentch et al., 2003) and *Acer rubrum* (Abrams, 1998; McDonald et al., 2003). In the central hardwood region in the U.S.A., *A. saccharum* represented a low proportion of witness trees in early land surveys during the 1800s, but its relative abundance has grown steadily since then (Shotola et al., 1992; Dyer, 2001; Rentch et al., 2003). Its continuing increase has become a serious management problem (Ebinger, 1986).

The most prominent hypothesis for the increase in *A. saccharum* is the shift in disturbance regime after fire suppression following European settlement (Ebinger, 1986; Shotola et al., 1992; Abrams, 1998). Gap formation becomes the dominant type of disturbance in forests after fire suppression (Guyette and Dey, 1997). The increase in *A. saccharum* may be better understood by examining how demographic processes responded to its altered disturbance regime. This examination requires an analysis of spatial patterns because trees are sessile organisms. Their spatial patterns change as a result of the demographic processes of recruitment and mortality. In many tree species, these processes do not occur randomly. For example, recruitment occurs in a heterogeneous pattern in many forests and corresponds to the spatial pattern of gap formation (Ward and Parker, 1989; Moeur, 1997; Dovčiak et al., 2001). Therefore, examination of spatial patterns of *A. saccharum* over time should provide a useful means to examine how critical demographic processes responded to disturbance during its population explosion.

---

* Corresponding author. Tel.: +886 7 312 1101x2696.
E-mail address: yichingtree@gmail.com (Y. Lin).

0378-1127/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2008.05.051

Any population explosion is linked to the amount of recruitment relative to mortality. Recruitment of *A. saccharum* must have outnumbered mortality in the past century. This increase in recruitment may have been facilitated by the changes in disturbance regime in two ways. First, fire suppression may have enhanced the survival of a large number of seedlings of *A. saccharum*. As a fire-intolerant species, *A. saccharum* should not have been able to maintain a sizable seedling bank until fire suppression began (Abrams, 1992; Shotola et al., 1992; Abrams, 1998; Dyer, 2001). Second, studies have shown that understory *A. saccharum* show significant growth in small gaps (Canham, 1985, 1988). Growth in response to disturbance may have enhanced the continuing survival of the cohorts of *A. saccharum* that developed soon after fire suppression. As these initial cohorts reached reproductive maturation, the larger number of reproductive *A. saccharum* may have produced a large quantity of offspring that led eventually to its population explosion. Therefore, in this scenario, fire suppression is viewed as a possible ultimate cause of the rise of *A. saccharum* and the initiator of new demographic dynamics.

Although the above scenario has been suggested by many authors (e.g. Edgington, 1991; Roovers and Shifley, 1997), the direct association between the increase in *A. saccharum* and disturbance has rarely been demonstrated, because most studies that documented the increase in *A. saccharum* were not spatially explicit. Not knowing whether this association has relevance to the increase of *A. saccharum* also has prevented an evaluation of the impact of an infrequent disturbance event, viz. Dutch elm disease, on the ongoing increase in *A. saccharum*. An outbreak of this disease occurred in 1950–1960 in the Midwestern states of the U.S.A. It killed almost all *Ulmus* spp. and greatly increased the frequency of small gap formation (Neely et al., 1960; Neely, 1967). For example, Dutch elm disease increased annual mortality rates of canopy trees 6-fold during 1955–1959 in an old-growth forest in Illinois (Lin, 2003). With this large number of gaps created by dead *Ulmus* spp. in a short period of time, the outbreak of Dutch elm disease may have accelerated the ongoing population increase in *A. saccharum*. Spatial associations between *A. saccharum* and canopy disturbance in the central hardwood region have been demonstrated in only one forest fragment in Indiana (Ward and Parker, 1989). In this forest, the recruitment of *A. saccharum* was aggregated in space and mostly associated with small canopy disturbance (Ward and Parker, 1989).

Over time, the spatial association between recruitment and disturbance may be weakened by mortality. Negative density-dependent mortality of *A. saccharum* has been demonstrated in an old-growth forest in Illinois (Lin and Augspurger, 2006). Such mortality may diminish aggregations of recruitment as individuals age. This transition in spatial pattern has been shown in various types of forests. Studies indicate that newly recruited individuals are aggregated in space (Moeur, 1993; Rathbun and Cressie, 1994; Dale, 1999), but the surviving large individuals have random or uniform distributions as a result of density-dependent mortality, known as "self-thinning" (Kenkel, 1988). A transition in spatial patterns in relation to recruitment and mortality has not been studied in *A. saccharum*.

In this study, we investigated the changes in spatial patterns of *A. saccharum* during a part of its population explosion from 1951 to 2001 in Brownfield Woods, an old-growth, oak–hickory forest remnant in central Illinois, U.S.A. Species richness and evenness have greatly declined during this period corresponding to the population explosion of *A. saccharum* (Lin and Augspurger, 2006). The objective was to examine patterns of recruitment and mortality in *A. saccharum* during its population explosion in relation to spatial dynamics. The hypothesis was that the recent increase in *A. saccharum* was facilitated by small- to medium-size disturbances. The facilitated recruitment was influential enough to compensate the effects of mortality. We predicted that the population of *A. saccharum* as a whole is aggregated in space. Such aggregation arose from a combination of the following spatial patterns associated with recruitment and mortality. First, recruitment of *A. saccharum* is aggregated in space and reflects the location of canopy gaps. Second, recruitment of *A. saccharum* is spatially associated with dead trees killed by Dutch elm disease. Third, larger individuals of *A. saccharum* have a lower level of aggregation as a result of self-thinning. As a result, surviving individuals of *A. saccharum* experience a transition in spatial pattern from aggregation to random or uniform over time.

2. Material and methods

2.1. Study sites

This study was conducted in Brownfield Woods, a 24 ha old-growth forest remnant of a large presettlement forest known as "The Big Grove" in Champaign County (40°09′N, 88°10′W), Illinois, U.S.A. Brownfield Woods, located about 5 km northeast of Urbana, is categorized as a mesic upland forest. Its fragmentation occurred in the late 19th century. Its current size and shape were established by 1918.

The dominant canopy species of Brownfield Woods is *A. saccharum* Marsh. (Mohlenbrock, 1986; Edgington, 1991). Other common species are *Aesculus glabra* Willd. (Ohio buckeye), *Quercus rubra* L. (red oak), *Fraxinus americana* L. (white ash), *Celtis occidentalis* L. (hackberry), and *Ulmus rubra* Muhl. (slippery elm).

Brownfield Woods has experienced mostly small- to medium-scale disturbances (Leffler, 1991). Small-scale disturbances caused by individual treefalls were the dominant disturbance type, but the forest experienced several medium-sized disturbances, including windstorms, Dutch elm disease, and various anthropogenic disturbances (Leffler, 1991). Selective logging, grazing, a wagon road, and public use as a picnic and hiking area occurred prior to 1939 (Leffler, 1991).

2.2. Field sampling

Historical tree maps made in Brownfield Woods in 1951 and 1988 were available (Cortright, 1952; Leffler, 1991). All trees with diameter at breast height (DBH) $\geq$ 7.6 cm had been mapped in one 5.04 ha quadrat (180 m × 280 m) in the NE corner of the fragment.

We revisited the same quadrat in 2000–2001 (hereafter 2001) and mapped all individuals. Their species identity and DBH were recorded. New recruits ($\geq$7.6 cm DBH) and dead trees since 1988 were noted. The 1951 trees were classified into three size classes: small (7.6–19.9 cm), medium (19.9–39.1 cm), and large ($>$39.1 cm) trees. These three size classes were delimited by applying the algorithm developed by Ferson et al. (1994). The size classes were chosen when the sum of two types of negatively correlated errors, "distribution error" and "sampling error", was minimal (Vandermeer, 1978; Moloney, 1986; Ferson et al., 1994). "Distribution error" increases when individuals are lumped into bigger size classes, while "sampling error" occurs when too many size classes are used.

2.3. Data analysis

A series of Ripley's univariate $L(d)$ functions were used to determine whether trees of *A. saccharum* were aggregated, or uniformly or randomly distributed. Ripley's $L(d)$ functions were defined as:

$$\hat{L}(d) = \sqrt{\frac{\hat{K}(d)}{\pi^{-d}}}$$

where $\hat{K}(d)$ is Ripley's K function and d is distance between trees (Besag, 1977). Ripley's K functions were defined as:

$$\hat{K}(d) = \frac{A}{N^2}\sum_{i}^{n}\sum_{j,i\neq j}^{n}\frac{I(d_{ij})}{W_{ij}}$$

where I (d_{ij}) is the summation of the number of other points, j, found within distance, d_{ij}, for the point i; A is the area of the plot; and N is the number of trees within the plot (Ripley, 1976; Ripley, 1981). W_{ij} is a circular edge-correction (Ripley, 1976; Ripley, 1981), defined as the inverse of the proportion of a circle of radius, d_{ij}, placed over each point within the total study area.

Monte Carlo simulations based upon a homogenous Poisson process were used to create confidence intervals of random

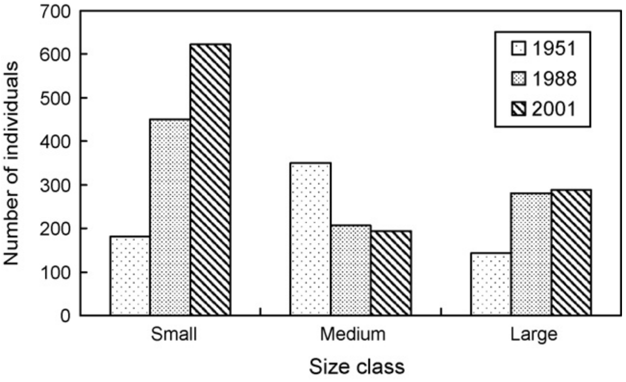

Fig. 1. Number of individuals of *A. saccharum* in three different size classes in 1951, 1988, and 2001 in Brownfield Woods.

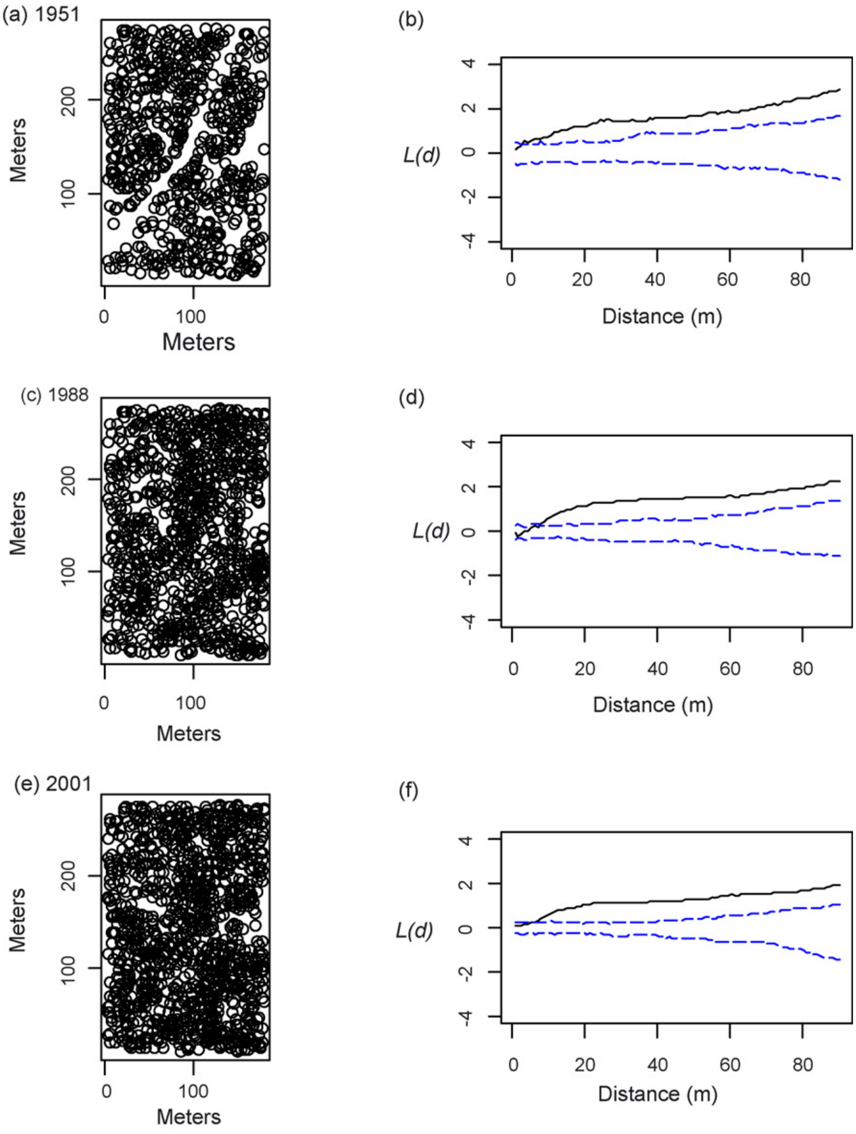

Fig. 2. Stem maps of *A. saccharum* in 1951 (a), 1988 (c), and 2001 (e) in Brownfield Woods. Their spatial patterns were evaluated via univariate Ripley's $L(d)$ (b, d, f), a transformed form of Ripley's $K(d)$. Each circle in the stem maps represents a tree (a, c, e). The observed $L(d)$ values are expressed as solid lines; the dashed lines indicate the upper and lower limits of the 95% confidence intervals of $L(d)$ values generated by Monte Carlo simulations.

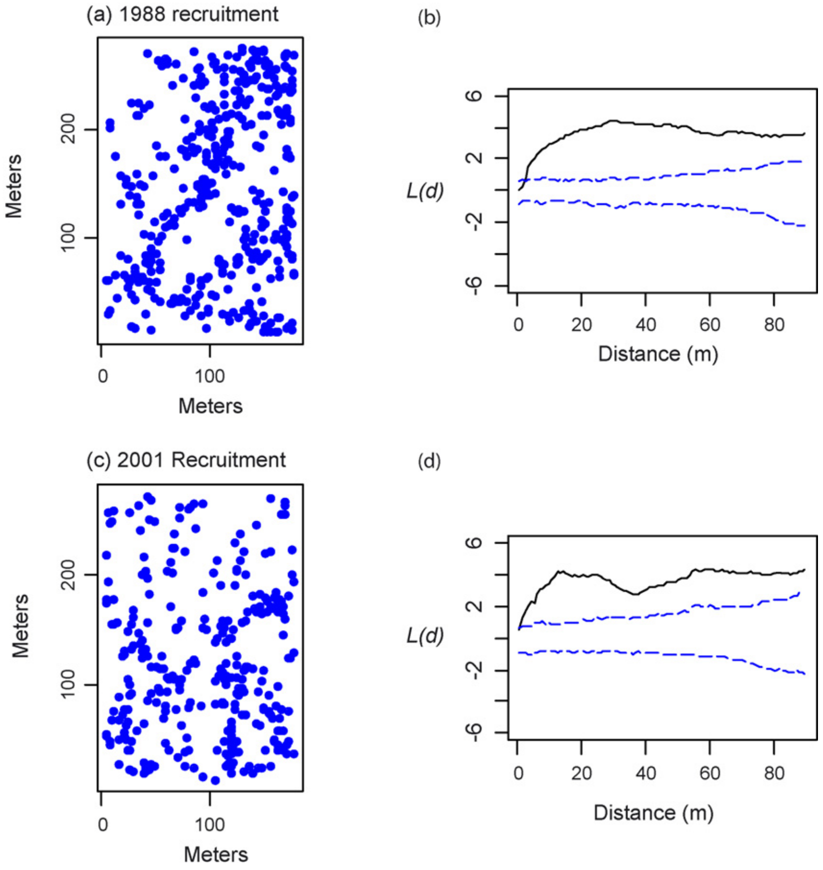

Fig. 3. Locations of newly recruited individuals of *A. saccharum* in 1988 (a) and 2001 (c) in Brownfield Woods. Their spatial patterns were estimated by univariate Ripley $L(d)$ (b and d). The observed $L(d)$ values are expressed as solid lines; the dashed lines represent the 95% confidence intervals of $L(d)$ simulated by Monte Carlo simulations.

distributions (Besag and Diggle, 1977; Ripley, 1976, 1981). Trees were aggregated when $\hat{L}(d)$ was larger than the upper limit of the confidence interval. Trees were uniformly distributed when $\hat{L}(d)$ was smaller than the lower limit of the confidence interval. Otherwise, trees were randomly distributed.

Bivariate Ripley's *L* functions were used to evaluate the spatial associations between newly recruited *A. saccharum* and two types of canopy disturbances: canopy gaps in general and gaps created by Dutch elm disease. Canopy gaps were represented by dead canopy trees; trees of *Ulmus* spp. that died from Dutch elm disease in the 1950s were specified. If $\hat{L}(d)$ of the bivariate function was located within the range of the confidence interval, a random association between recruitment and disturbances was shown. If $\hat{L}(d)$ of the bivariate function was greater than the upper limit of the confidence interval, a positive association between these two groups was shown. Statistical analyses were performed by "Spatial" (Venables and Ripley, 2002) and "Splancs" packages (Rowlingson and Diggle, 1993) in the R environment version 2.4.1 (R Development Core Team, 2006).

3. Results

3.1. Spatial patterns of A. saccharum

The population of *A. saccharum* increased 1.7-fold within the plot during 1951–2001. This increase, however, was uneven among size classes. The greatest increase occurred in the small-size class (Fig. 1). The population of *A. saccharum* was aggregated in 1951, 1988, and 2001 at all spatial scales, except for the scale smaller than 5 m (Fig. 2). The level of aggregation increased with distance at all three censuses (Fig. 2b, d, and f). Notably, a linear-shaped area from the northeast to southwest corner of the plot was evident in the1951 map, but not in subsequent maps (Fig. 2a, c, and e). This area overlapped the tract of an abandoned wagon road, and was dominated by *Ulmus* spp. in 1951 (Leffler, 1991).

3.2. Spatial patterns of newly recruited individuals of A. saccharum

Newly recruited individuals, defined as individuals that were recorded in the small-size class for the first time, were aggregated in both 1988 and 2001 at almost all distances (Fig. 3). By 1988, newly recruited individuals had filled the linear-shaped area (Fig. 3a), where no *A. saccharum* had been located in 1951 (Fig. 2a).

3.3. Spatial associations between newly recruited individuals and disturbance

Newly recruited individuals were spatially associated with dead canopy trees in general and specifically with dead *Ulmus* spp. The bivariate Ripley's $L(d)$ indicated that newly recruited individuals were significantly associated with dead canopy trees in both 1988 and 2001, but at different scales (Fig. 4a and b). In 1988, the newly recruited individuals were significantly associated with dead canopy trees within 10 m, while the association occurred only at 20 m in 2001 (Fig. 4). Finally, newly recruited individuals in 1988 were spatially associated with dead *Ulmus* spp. within 20 m (Fig. 5).

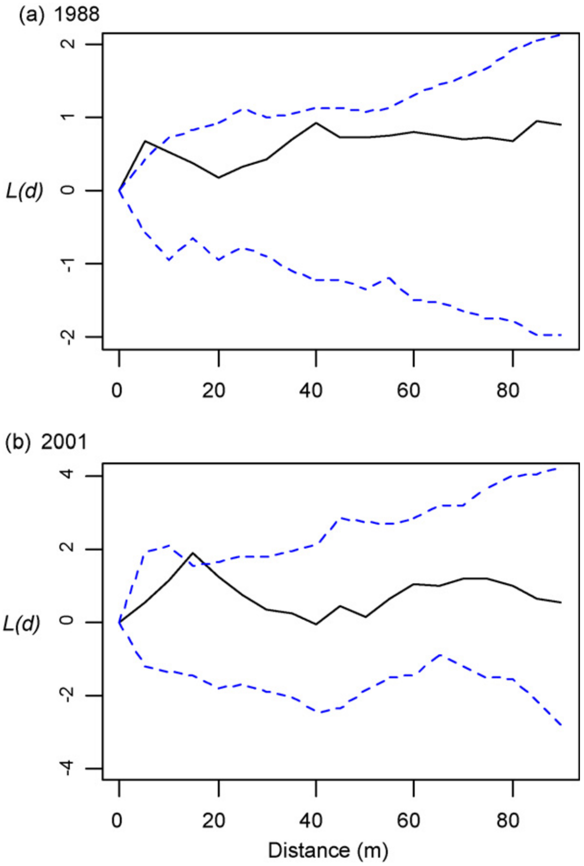

Fig. 4. Bivariate Ripley's $L(d)$ was used to indicate spatial associations between newly recruited individuals of *A. saccharum* in 1988 (a) and 2001 (b) with canopy trees dying between 1951 and 1988 (a) and 1988 and 2001 (b). The observed $L(d)$ values are expressed as solid lines; the dashed lines represent the 95% confidence intervals of $L(d)$ simulated by Monte Carlo simulations.

3.4. Size-specific spatial patterns of *A. saccharum*

Spatial patterns of *A. saccharum* differed among size classes at all three censuses. Small individuals were aggregated at all spatial scales except for the scale smaller than 5 m (Fig. 6a, d, and g). Values of Ripley's $L(d)$ for small individuals increased with distance (Fig. 6 a, d, and g). Medium-sized individuals were aggregated in 1951 (Fig. 6b), but became randomly distributed at most spatial scales by 1988 and 2001 (Fig. 6e and h). Finally, large individuals were randomly distributed in 1951 and 2001, but were aggregated at spatial scales larger than 40 m in 1988 (Fig. 6c, f, and i).

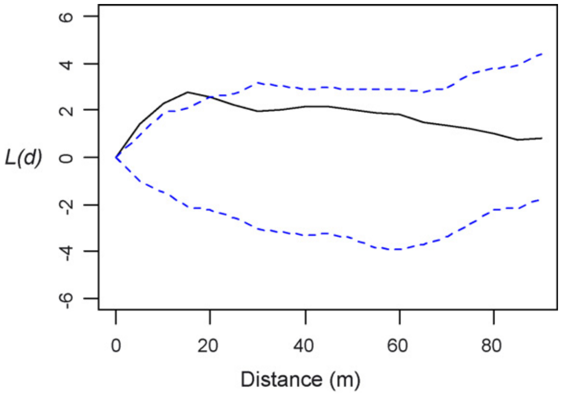

Fig. 5. Bivariate Ripley's $L(d)$ was used to indicate the spatial associations between newly recruited individuals of *A. saccharum* and *Ulmus* spp. that died from Dutch elm disease during 1951–1988 in Brownfield Woods. The observed $L(d)$ values are expressed as solid lines; the dashed lines represent the 95% confidence intervals of $L(d)$ simulated by Monte Carlo simulations.

3.5. Changes in spatial patterns from 1951 to 2001

Individuals in the small-size class in 1951 that survived to 1988 and 2001 experienced the greatest change in their spatial pattern over time (Fig. 7). Initially in 1951, small individuals were aggregated at most spatial scales (Fig. 7a). Such aggregation gradually disappeared over time (Fig. 7b), and ended in a random distribution by 2001 (Fig. 7c). The spatial patterns of medium and large individuals in 1951 did not show substantial changes over time. The medium individuals in 1951 remained aggregated over time (Fig. 7d, e, and f), while the large individuals were randomly distributed from 1951 to 2001 (Fig. 7g, h, and i).

4. Discussion

Our results indicate that *A. saccharum* was aggregated at most spatial scales in Brownfield Woods during 1951–2001. The aggregation of small individuals was the main cause of this aggregation. Furthermore, newly recruited individuals were aggregated at multiple spatial scales, and were spatially associated with dead canopy trees in general and *Ulmus* spp. that died from Dutch elm disease. However, the aggregated distribution of individuals in the small-size class in 1951 became randomly distributed by 2001.

The above spatial patterns and dynamics provide support for the hypothesis that the recruitment of *A. saccharum* in Brownfield Woods was facilitated by the disturbance regime in Brownfield Woods during 1951–2001. The association between recruitment and disturbance was reflected in the continuing aggregation of recruitment. This aggregation was strong enough to compensate for the weakening effects of mortality on the spatial pattern and resulted in overall aggregation of *A. saccharum* in Brownfield Woods. The occurrence of mortality was expected to weaken the level of aggregation because the aggregation of surviving individuals gradually disappeared over time.

The spatial dynamics of *A. saccharum* in Brownfield Woods from 1951 to 2001 were similar to those of other tree species in other forests (Kenkel, 1988; Dovčiak et al., 2001; McDonald et al., 2003). Aggregation of *A. saccharum* in an old-growth forest in Indiana (Aldrich et al., 2003) differed from this study. In that forest, the highest level of aggregation was at the scale of 20–40 m, while the level of aggregation increased with distance up to 80 m in this study.

The heterogeneous recruitment of *A. saccharum* at multiple spatial scales in Brownfield Woods arose from the combined effects of different scales and types of disturbances. Brownfield Woods experienced small- and medium-sized disturbances during the past 150 years, including gap formation, windstorms, a wagon road, and an outbreak of Dutch elm disease. First, the aggregated seed rain of *A. saccharum* (Lin, personal observation) set the stage for the initial aggregation of new recruits. Single treefall gaps then contributed to the aggregation of *A. saccharum* at a spatial scale around 12 m, the estimated mean crown diameter of canopy trees in Brownfield Woods (Lin, 2003). Second, windstorms occurred in Brownfield Woods periodically and caused single and multiple treefall gaps (Lin et al., 2004). These windstorms further contributed to the aggregation of *A. saccharum* at a spatial scale up to 50 m. Third, recruitment of *A. saccharum* was enhanced by Dutch elm disease. The bivariate Ripley's $L(d)$ analysis indicated that newly recruited individuals of *A. saccharum* were spatially associated with dead *Ulmus* spp. in 1988. A considerable

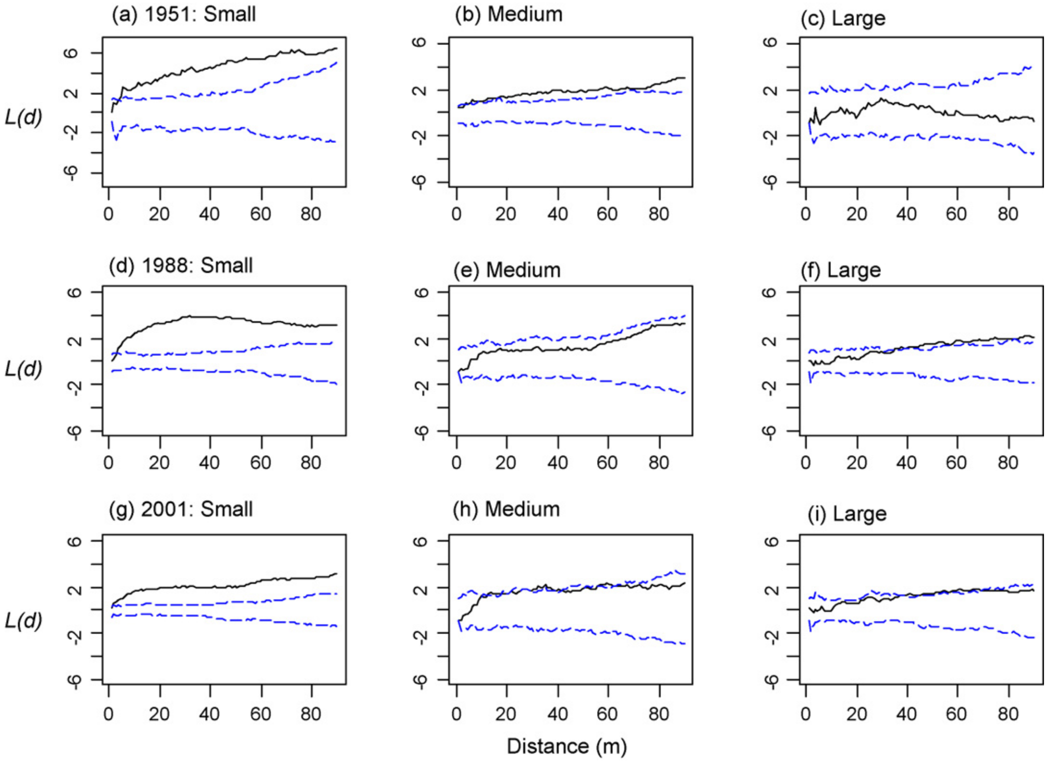

Fig. 6. Univariate Ripley's $L(d)$ was used to evaluate size-specific spatial patterns of *A. saccharum* in 1951 (a–c), 1988 (d–f), and 2001 (g–i) in Brownfield Woods. The $L(d)$ values are expressed as solid lines; the dashed lines represent the upper and lower limits of the 95% confidence intervals of $L(d)$ generated by Monte Carlo simulations. Minimum cut-off points for size classes were 7.6, 19.9, and 39.1 cm for the small-, medium-, and large-size classes, respectively.

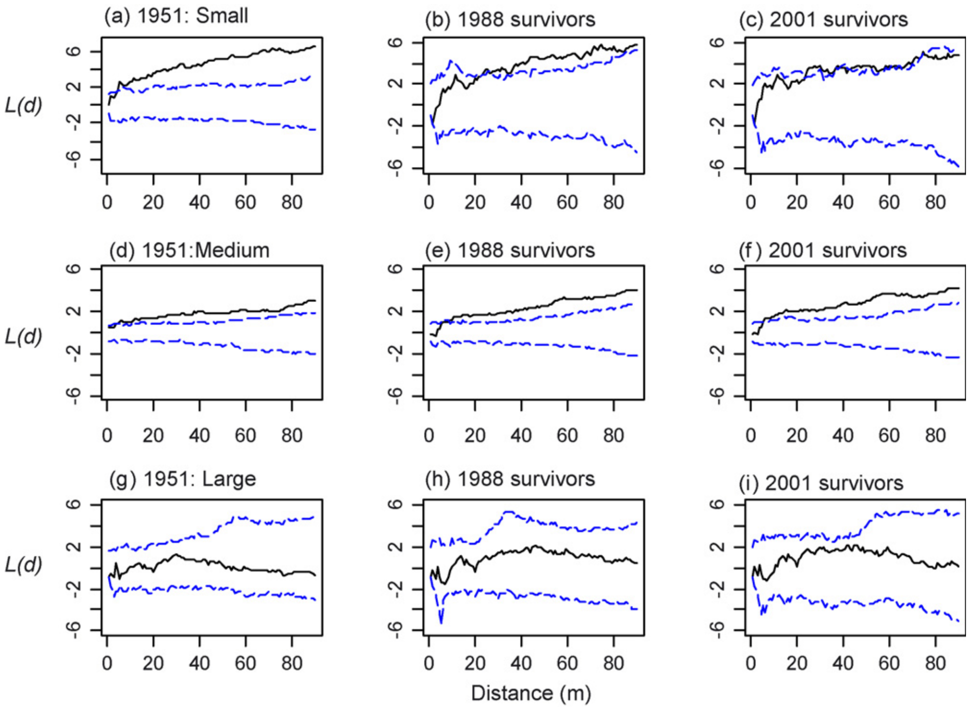

Fig. 7. Univariate Ripley's $L(d)$ of the surviving individuals of the initial group of *A. saccharum* in Brownfield Woods in 1951 (a, d, g), 1988 (b, e, h), and 2001 (c, f, i). The observed $L(d)$ values are expressed as solid lines; the dashed lines represent the 95% confidence intervals of $L(d)$ simulated by Monte Carlo simulations. The classification of size classes was based upon the initial size of trees in 1951. A portion of the trees grew into a larger size class in later years. Minimum cut-off points for size classes were 7.6, 19.9, and 39.1 cm for the small-, medium-, and large-size classes, respectively.

proportion of this recruitment occurred along the abandoned wagon road. This road is still visible in aerial photos today with a canopy height slightly lower than the surrounding areas (S. Buck, personal communication). Prior to 1951, the road was dominated by *Ulmus* spp. with almost no *A. saccharum* (Leffler, 1991). Dutch elm disease killed most *Ulmus* spp. along the wagon road (Lin, 2003). Our data indicated many newly recruited individuals of *A. saccharum* in 1988 occurred along the road (Fig. 2a and c). This filling by *A. saccharum* contributed to its aggregation at the larger spatial scales (up to 80 m). An alternative explanation for the increase in *A. saccharum* on the wagon road was that differences in the soil on the wagon road were sufficient to account for the increase in *A. saccharum* on the wagon road. Dead *Ulmus* spp. from the Dutch disease has no relationship to the establishment of *A. saccharum*. The authors, however, did not think it was the main cause, because the soils along the wagon road were compact and relatively poor in drainage. Such soils were considered to be less favorable for *A. saccharum* (Abrams, 1998). Therefore, we attributed the increase in *A. saccharum* on the wagon road to the increase in canopy gaps associated with Dutch elm disease.

Overall, the spatial dynamics of *A. saccharum* in Brownfield Woods during 1951–2001 indicate that its demographic processes were driven mainly by recruitment in disturbances. This disturbance-facilitated increase in *A. saccharum* has been demonstrated in other oak–hickory (Ebinger, 1986; Dyer, 2001) and beech–maple forests (De Steven et al., 1991; Poulson and Platt, 1996).

5. Conclusions

We conclude that spatial patterns of *A. saccharum* in Brownfield Woods from 1951 to 2001 arose mainly by spatially heterogeneous recruitment due to disturbances at multiple scales. Such disturbance-facilitated recruitment was likely the main proximate driver of the rapid population growth of *A. saccharum* during this period. A medium-sized disturbance event, Dutch elm disease, further accelerated the ongoing increase of *A. saccharum* in Brownfield Woods during this period.

Acknowledgements

We thank S. Buck for locating the historical maps, Dr. D. Johnson and S. Leffler for generously allowing the use of their 1988 map, Dr. B.T. Guan for statistical advice, Dr. P. Attiwill and two anonymous reviewers for their constructive comments. Also, we thank A. Vestal, D.F. Cortright, and C. Young who undertook the 1939 and 1951 censuses in Brownfield Woods. This research was supported by grants to Y.L. from the University of Illinois Graduate College, School of Life Sciences, and the Illinois Academy of Science, and a Smith Memorial Grant from the Illinois Natural History Survey.

References

Abrams, M.D., 1992. Fire and development of oak forests. BioScience 42, 346–353.
Abrams, M.D., 1998. The red maple paradox. BioScience 48, 355–364.
Aldrich, P.R., Parker, G.R., Ward, J.S., Michler, C.H., 2003. Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession. Forest Ecol. Manage. 180, 475–491.
Besag, J.E., 1977. Comment on modeling spatial patterns by B.D. Ripley. J. R. Stat. Soc. B 39, 193–195.
Besag, J., Diggle, P.J., 1977. Simple Monte Carlo tests for spatial pattern. Appl. Stat. 26, 327–333.
Canham, C.D., 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bull. Torrey Bot. Club 112, 134–145.
Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786–795.
Cortright, D.F., 1952. Twelve years of growth and mortality in Brownfield Woods. Master's thesis. University of Illinois, Urbana.
Dale, M.R.T., 1999. Spatial Pattern Analysis in Plant Ecology. Cambridge University Press, Cambridge.
De Steven, D., Kline, J., Matthiae, P.E., 1991. Long-term changes in a Wisconsin (USA) *Fagus Acer* forest in relation to glaze storm disturbance. J. Veg. Sci. 2, 201–208.
R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Dovčiak, M., Frelich, L.E., Reich, P.B., 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. J. Ecol. 89, 280–291.
Dyer, J.M., 2001. Using witness trees to assess forest change in southeastern Ohio. Can. J. Forest Res. 31, 1708–1718.
Ebinger, J., 1986. Sugar maple (*Acer saccharum*), a management problem in Illinois (USA) forests? Trans. Illinois Acad. Sci. 79, 25–30.
Edgington, J.M., 1991. Brownfield Woods, Illinois: present composition and changes in community structure. Trans. Illinois Acad. Sci. 84, 95–112.
Ferson, S., Millstein, J.A., Silva, P., 1994. CatSize: two programs for determining category sizes. Software technical report. Applied Biomathematics, Setauket, New York.
Guyette, R.P., Dey, D.C., 1997. Fire and logging history at Huckleberry Hollow, Shannon County, Missouri. Forestry Research Report 1, 1-14. The Missouri Department of Conservation, Jefferson City.
Kenkel, N.C., 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69, 1017–1024.
Leffler, S.M., 1991. Changes in the spatial autocorrelation of trees in Brownfield Woods from 1951 to 1988. Master's thesis. University of Illinois, Urbana.
Lin, Y., 2003. The impact of neighborhood-based processes on demography and a decline in species diversity in a temperate deciduous forest. Ph.D. dissertation. University of Illinois, Urbana.
Lin, Y., Augspurger, C.K., 2006. A long-term study of neighbour-regulated demography during a decline in forest species diversity. J. Veg. Sci. 17, 93–102.
Lin, Y., Hulting, M.L., Augspurger, C.K., 2004. Causes of spatial patterns of dead trees in forest fragments in Illinois. Plant Ecol. 170, 15–27.
McDonald, R.I., Peet, R.K., Urban, D.L., 2003. Spatial pattern of oak regeneration limitation in a complex forest environment. J. Veg. Sci. 14, 441–450.
Moeur, M., 1993. Characterizing spatial patterns of trees using stem-mapped data. Forest Sci. 39, 756–775.
Moeur, M., 1997. Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla–Thuja plicata* forests. Forest Ecol. Manage. 94, 175–186.
Mohlenbrock, R.H., 1986. Guide to the Vascular Flora of Illinois. Southern Illinois University Press, Carbondale.
Moloney, K.A., 1986. A generalized algorithm for determining category size. Oecologia 69, 176–180.
Neely, D., 1967. Dutch elm disease in Illinois cities. Plant Dis. Rep. 51, 511–513.
Neely, D., Carter, J.C., Campana, R.J., 1960. The status of Dutch elm disease in Illinois. Plant Dis. Rep. 44, 163–166.
Oak, S.W., Steinman, J.R., Starkey, D.A., Yockey, E.K., 2004. Assessing oak decline incidence and distribution in the southern U.S. using forest inventory and analysis data. In: Spetich, M.A. (Ed.), Proceedings of Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, N.C.
Poulson, T.L., Platt, W.J., 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. Ecology 77, 1234–1253.
Rathbun, S.L., Cressie, N., 1994. A space-time survival point process for a longleaf pine forest in southern Georgia. J. Am. Stat. Assoc. 89, 1164–1174.
Rentch, J.S., Fajvan, M.A., Hicks Jr., R.R., 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. Forest Ecol. Manage. 184, 285–297.
Ripley, B.D., 1976. The second-order analysis of stationary point processes. J. Appl. Prob. 13, 255–266.
Ripley, B.D., 1981. Spatial Statistics. John Wiley & Sons, New York.
Roovers, L.M., Shifley, S.R., 1997. Composition and dynamics of Spitler Woods, an old-growth remnant forest in Illinois (USA). Nat. Areas J. 17, 219–232.
Rowlingson, B., Diggle, P., 1993. Splancs: spatial point pattern analysis code in S-Plus. Comput. Geosci. 19, 627–655.
Shotola, S.J., Weaver, G.T., Robertson, P.A., Ashby, W.C., 1992. Sugar maple invasion of an old-growth oak–hickory forest in southwestern Illinois. Am. Midl. Nat. 127, 125–138.
Vandermeer, J., 1978. Choosing category size in a stage projection matrix. Oecologia 32, 79–84.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer, New York.
Ward, J.S., Parker, G.R., 1989. Spatial dispersion of woody regeneration in an old-growth forest. Ecology 70, 1279–1285.