

Dynamic tree aggregation patterns in a species-poor temperate woodland disturbed by fire

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Abstract

Question: How does fire affect the aggregation patterns of trees in a species-poor oak woodland?

Location: East-central Minnesota, USA.

Methods: More than 10 000 trees with DBH > 2 cm (comprising more than 11 000 stems) were monitored in a 16-ha grid on an annual basis from 1995- 2001 in a species-poor temperate woodland. Different portions of the grid experienced different frequencies of controlled burns. Aggregation indices were calculated for individual species and individual size classes within species. A community-wide aggregation index was also calculated for different burn units. Spatial data were managed, and many of the aggregation indices calculated using a GIS ArcInfo™ (ESRI).

Results: Fire initially increased clumping, although repeated fires reduced it, a finding that suggests a corollary to the intermediate-disturbance hypothesis, the corollary stating that intermediate levels of disturbance are expected to maximize community-wide patterns of aggregation. Analyses also showed that all species are aggregated at small scales, that the degree of aggregation of a stem type (species or size) declines with distance from individual stems, that the degree of aggregation of large stems is usually less than that of small stems, and that rare species are more aggregated than common species. Findings from this study are consistent with those from similar studies in other temperate and tropical forests, woodlands, and savannas.

Conclusion: The spatial patterns of trees in this woodland are dynamic, continually changing in response to the relative strengths of the often opposing forces of competition, which tends to reduce clumping, and disturbance, which, at low and intermediate frequencies, tends to increase it.

Keywords: Disturbance; Intermediate-disturbance hypothesis; Oak woodland; Spatial pattern; Temperate forest; Tree aggregation.

Nomenclature: Anon. (1991).

Introduction

Spatial patterns of plants can reflect a multitude of ecological processes including competition, predation, herbivory, dispersal, disturbances, microbial interactions, edaphic factors, and meteorological events (Watt 1947; Janzen 1970; Whittaker & Levin 1977; Thompson 1978; Dale 1999; Packer & Clay 2000; Potts 2003; Woods 2004). Previous studies of small-scale (0-100 m) spatial patterns of trees have helped to identify the relative importance of these processes in structuring tree-dominated communities (Christensen 1977; Skarpe 1991; Moeur 1993; Kubota et al. 2004; Valencia et al. 2004). In some cases, the spatial patterns were consistent with a competition-driven model (Kenkel 1988; Moeur 1993), while in other instances, the spatial patterns were believed to reflect primarily disturbance history, e.g., fire (Rebertus et al. 1989; Skarpe 1991; Woods 2004), edaphic factors (Couteron & Kokou 1997), or weather patterns, e.g. droughts (Couteron & Kokou 1997).

Most studies of spatial patterns of trees in forests and savannas typically have relied on data obtained from a single census or on censuses taken several years apart (an exception being Rathbun & Cressie 1994). Thus, most conclusions regarding the effect of disturbances on spatial patterns of trees have been based on extrapolation and inference rather than empirical data collected immediately prior to and after a disturbance. To actually test some of the conclusions and hypotheses derived from these studies, longitudinal studies of mapped forest plots experiencing disturbance are needed.

In the study reported here, the spatial patterns of trees in a temperate woodland were monitored and recorded annually for six years. During this time, different areas of the woodland experienced disturbances (controlled burns) at different frequencies. The objective of the study was to document the way in which fire affects the spatial patterns of trees in this woodland community, to describe the community-wide diversity effects of fire, and to compare the tree aggregation patterns in this species-poor temperate forest with those found in species-rich tropical forests.

Material and Methods

This study was conducted at Cedar Creek Natural History Area (CCNHA), a protected scientific research area in east-central Minnesota, USA (45°25' N, 93°10' W). Situated on the Anoka Sandplain, a glacial outwash area with coarse-textured soil low in nitrogen, CCNHA is located in the transition zone between the central grasslands and the mixed deciduous forest of eastern North America. Prior to European settlement, oak savannas and woodlands were the dominant upland vegetation types at CCNHA (Wovcha et al. 1995).

During 1988-1990, the GLADES (Grid for Landscape Analysis and Demographic Study) project was initiated at Cedar Creek with the establishment of a 16 ha grid (with 10 m × 10 m cells) in a portion of Cedar Creek's oak woodland/savanna habitat. The grid was set up in a north-south configuration using surveying technology and 1.5 m iron rebars to mark the grid nodes. A burn program was instituted in study site in 1987, and the study grid (16 ha) contains three different burn units (BU). BU 1 (6.17 ha) was burned six times from 1987 to 2001 (1987, 1988, 1990, 1992, 1996, 1997); BU 2 (6.03 ha) was burned three times during this time period (1992, 1997, 2000); BU 3 (3.25 ha) was burned once (2000). Two corners of the grid (0.55 ha) have not been burned. The study plot area was not burned for at least 25 years prior to 1987. As a result of this fire suppression, shrubs (e.g. *Corylus americana* and *Rhus glabra*) had become established in many parts of the grid. The elevation (above sea level) in the study grid ranges from 278-284 m, with the lower end corresponding to the approximate level of the water table at the site. Historical aerial photos of the site (extending back to 1938) show that approximately one ha of BU 2 was cultivated until the mid-1950s and that farm vehicles regularly traversed through burn units 1 and 2. BU 3 showed fewer signs of human disturbance.

A Cartesian coordinate system was used to map trees in the grid. Each cell is identified by the x-y coordinates in the southwest corner of the cell. In 1995, numbered aluminium tags were nailed into trees 10 cm DBH (diameter at breast height, 1.3 m) and larger and the DBH of each tree recorded. In addition, the cell in which the tree was located was recorded, as well as the stem's xy location within the cell. If a tree possessed multiple stems, the tag was attached only to the largest stem. However, DBH was measured and recorded for all stems of multiple-stemmed trees. If a stem divided into two stems below 1.3 m, it was treated as two stems, while any stem that divided above 1.3 m was treated as a single stem. Condit et al. (1998) dealt with multiple-stemmed trees in tropical plots in the same way. In 1996, tags were nailed into trees 5-10 cm DBH in size and

attached with wire to stems 2-5 cm DBH. Each stem, including all stems of multiple-stemmed trees, was visited annually and its status (live or dead) recorded. Stem DBH was remeasured in 2000 for trees first tagged in 1995, and in 2001 for trees first tagged in 1996. A small number of additional stems were tagged each year, mainly small stems whose DBH had exceeded 2 cm because of new radial growth. The number of annual new recruits was very small since fires killed most small stems. The ten species of trees recorded growing in the study grid (along with their stem counts) are:

<i>Quercus macrocarpa</i> (5674 stems)	<i>Q. ellipsoidalis</i> (4189)
<i>Populus tremuloides</i> (671)	<i>Prunus serotina</i> (410)
<i>Acer rubrum</i> (61)	<i>Fraxinus pennsylvanica</i> (21)
<i>Betula papyrifera</i> (11)	<i>Ulmus americana</i> (6)
<i>Acer negundo</i> (4)	<i>Crataegus</i> sp. (3)

In total, more than 11 000 stems, representing more than 10 000 individual trees, were monitored annually between 1995 and 2001.

The aggregation of a particular stem type (e.g. species or size class) was calculated using a method developed by Condit et al. (2000). First, for a given stem type, i , (e.g. species and/or size), the number of stems of the same type (N_i) were counted within a specific 5-m annulus or distance range, $a-b$, (e.g. 0-5, 5-10, 10-15 m) for each stem; next, the area (A) of the annulus within the boundaries of the study area was calculated for each stem (A_i); then, the density (D) of neighbouring stems of the same type within the specified annulus or distance range (D_{a-b}) was calculated as $\Sigma N_i / \Sigma A_i$; finally, the relative neighbour density, or Aggregation Index (AI), for a particular stem type was calculated as D_{a-b}/D_p , where D_p = the density of the stem type in the entire study plot or portion of the study plot being analysed. This method yields an AI value for specified distance ranges from individual stems in which a value of 1.0 indicates that the stems are distributed randomly at that distance, a value > 1.0 indicates clumping, and a value < 1.0 indicates some degree of regular spacing. AI was calculated for the following distance ranges in this study: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 50-55 and 95-100 m.

The aggregation index calculated in this way is similar to the pair-correlation function (Penttinen et al. 1992) and the well-known Ripley's K -statistic. The primary difference between the aggregation index calculated in this article (following Condit et al. 2000) with the K -statistic is that the latter is a cumulative function, taking into account all conspecifics within a specific distance from the focal tree. One drawback of the K -statistic is that it confounds effects from small and large distances. The aggregation index describes aggregation at specific distance classes, thereby providing a more detailed spatial characterization of aggregation patterns.

As was found in tropical plots, the *AI* values of nearby annuli in this study were highly correlated, and thus in some comparisons we followed Condit et al.'s (2000) method of using *AI* at the smallest distance (5 m in this case) as a simple measure of a species' degree of aggregation. The low tree diversity in the woodland meant there were large number of stems of the most common species, and this enabled us to examine aggregation patterns for different size classes of these species. The relationship between stem size and Aggregation Index was examined for *Quercus macrocarpa*, *Q. ellipsoidalis*, and *Prunus serotina* (the three species with sufficient numbers of stems in at least three different size classes) using 1996 data for stems growing in BU 3, which in 1996 had not yet experienced any burns. Aggregation indices at the 5-m distance were examined for five size classes for the two oak species: DBH = 2-5 cm, 5-10 cm, 10-20 cm, 20-30 cm and > 30 cm, and for the lower three size classes for *P. serotina*.

Fire's effect on the species diversity of the woodland community was assessed by examining changes in the dominance-diversity distributions of the species (Hubbell 2001). In order to assess how disturbances may affect tree aggregation patterns, we compared community-wide patterns of aggregation before and after fires in the study plot using a Community Aggregation Index (*CAI*), which we defined as the weighted average (weighted by stem abundance) of the individual *AI* values (at the 5 m distance) of the specific stem groups being investigated: $\sum \sum (n_{ij} AI_{ij}) / N$ (n_{ij} = number of stems of the *i*th size class of the *j*th species, AI_{ij} = aggregation index of the *i*th size class of the *j*th species, $N = \sum n_{ij}$). Given the frequency and years of occurrence of burns in the respective burn units, we were able to compare *CAI* values before and after the first burn in BU 3, before and after the 6th burn in BU 1, and before and after the 2nd and 3rd burns in BU 2.

In some of our analyses, trees were assigned either a fire-sensitive or fire-resistant status. Oaks are regarded as fire-resistant species (Abrams 1992) and, at this site, oak stems ≥ 5 cm DBH survived fire at a rate of 88%. Thus, oak stems ≥ 5 cm DBH were considered fire-resistant stems. The other eight species, along with oak stems < 5 cm DBH, survived fire at a rate of only 26% and are considered fire-sensitive stems in this study.

Many analyses were restricted to BU 3. Since BU 3 had not yet been burned for at least 33 years when trees were tagged in 1995 and 1996, this burn unit was able to provide density and aggregation data prior to the first controlled burn. Pre-burn tree data were not available for BUs 1 and 2, which had experienced one or more controlled burns prior to 1995.

Confidence intervals (95%) for *AI* values of stems of individual species and size classes and fire-resistant

and fire-sensitive stems were estimated by calculating the 95% *CI* (based on a *t*-statistic) for the mean of 15 random samples each consisting of one-half of the stems of the target group (sampled without replacement) and dividing this number by $2^{1/2}$ (Condit et al. 2000).

Tree data were managed using ArcInfo™ (ESRI), and ArcInfo was used to calculate N_i , A_i , and D_p . Errors presented in figures are 95% confidence intervals, and means with non-overlapping confidence intervals are considered to be significantly different from one another. If error bars are not present, the confidence intervals were too small to be visible.

Results

The dominance-diversity distributions for the respective burn units were geometric in nature as expected for low diversity forests (Hubbell 2001), and fire usually increased the slope of the dominance-diversity curves (Fig. 1). All the species were aggregated at small scales (5 m) and the degree of aggregation declined with distance from the stems (Fig. 2).

Small size classes showed a higher degree of aggregation than larger size classes for *Q. macrocarpa* and *P. serotina* (Fig. 3). The absence of the inverse relationship between stem size and aggregation index for *Q. ellipsoidalis* stems > 5 cm DBH is because larger individuals of this species commonly produce multiple stems. In BU 3, 18% of the stems of this species were part of multiple-stemmed trees, and of these stems only 3% were in the smallest size class. Thus, the aggregation indices of the larger *Q. ellipsoidalis* size classes at the 0-5 m distance range were increased because of the abundance of multiple-stemmed trees. The effect of multiple stems would be absent at other distance ranges and the inverse relationship between stem size and aggregation index becomes evident at the 5-10 m size range (Fig. 3).

The degree of aggregation of a species was strongly inversely correlated with its abundance (Fig. 4), which is consistent with the finding in the tropical sites that rare species are more clumped than common species (Condit et al. 2000).

A comparison of the aggregation patterns of the fire-sensitive stems before and after the first and only fire in BU 3 showed that *AI* was significantly higher among the surviving stems (Fig. 5). Conversely, in the case of the fire-resistant stems, *AI* was significantly higher among those stems that were killed by the fire (Fig. 5). This means that most fire-sensitive stems were killed by the fire, as would be expected, but that some survived in scattered cool spots, resulting in clumps of surviving stems. At the same time, although most fire-resistant stems were able to survive the fire, those few that

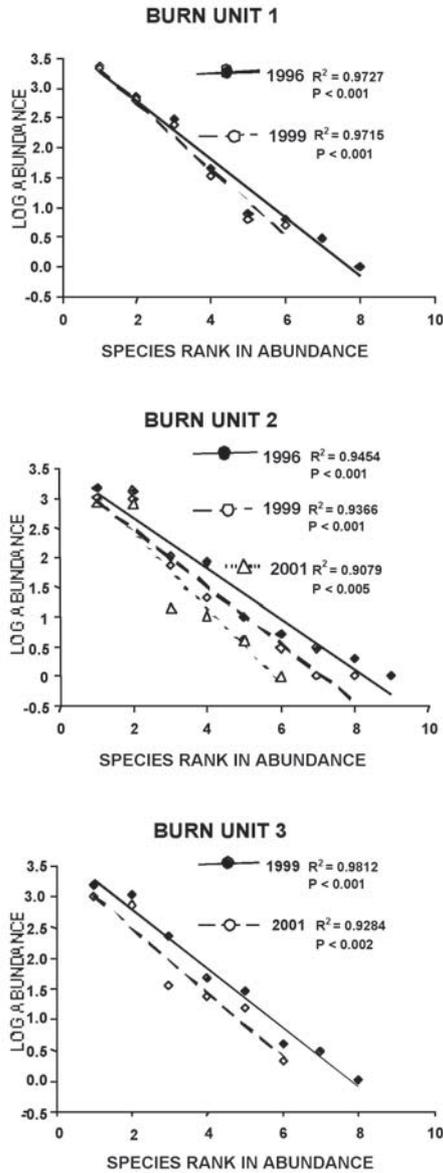


Fig. 1. Dominance-diversity distributions for the respective burn units before (solid lines) and after fires (dashed and dotted lines). The respective slopes differed in burn unit 1 ($t = 2.79$; $p = 0.02$), approached significance in burn unit 2 ($t = 2.07$; $p = 0.065$, 1996 vs 2001 curves), but did not differ in burn unit 3 ($t = 0.77$; $p > 0.20$).

happened to be in particularly hot spots, where the fire's intensity was much greater than average, were killed, resulting in clumps of dead fire-resistant stems.

Community-wide aggregation patterns (CAI) were affected by fire. CAI increased following the 1st burn in BU 3 (3rd column of BU 3, Fig. 6) and following the 2nd burn in BU 2 (2nd column of BU 2, Fig. 6) and decreased following the 3rd burn in BU 2 (3rd column of BU 2, Fig. 6) and following the 6th burn in BU 1 (2nd column of BU 1, Fig. 6).

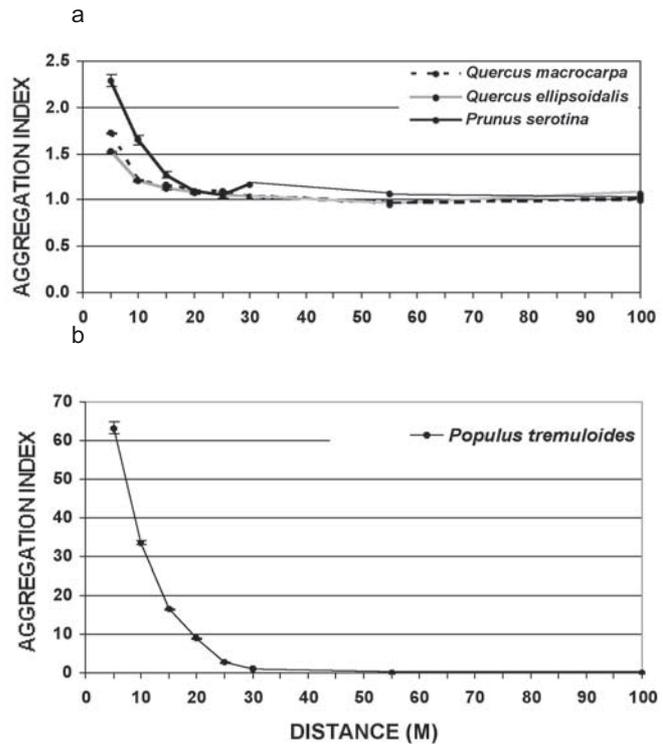


Fig. 2. Aggregation Indices shown for four species as a function of distance from individual stems in burn unit 3 before it was burned.

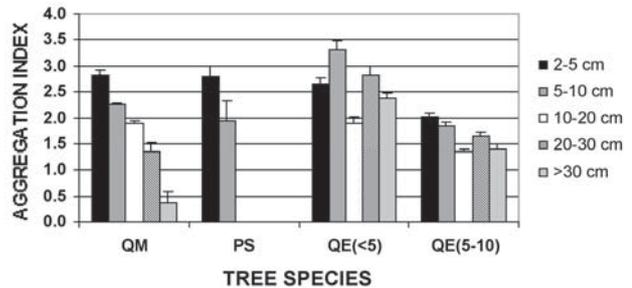


Fig. 3. Aggregation Index values AI at the 5 m distance for different size classes (DBH) of three species in Burn Unit 3 before it was burned. QM = *Quercus macrocarpa*; QE = *Q. ellipsoidalis*; PS = *Prunus serotina*. AI values at the 5-10 m distance are also shown for *Q. ellipsoidalis*. The third size class (10-20 cm) did exist for *P. serotina*, but AI for these stems was 0, and thus does not show up in the figure.

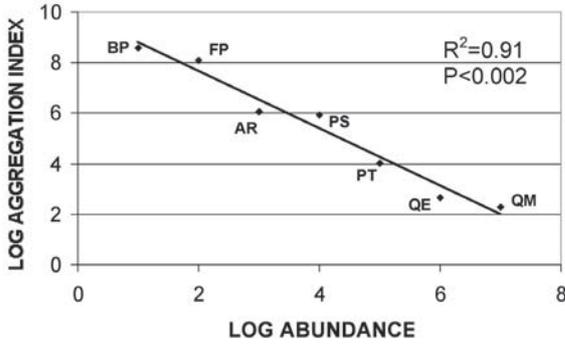


Fig. 4. Natural log of the Aggregation Index values *AI* (5 m distance) for all species with at least eight stems in Burn Unit 3 before it was burned shown as a function of log abundance. QM = *Quercus macrocarpa*; QE = *Q. ellipsoidalis*; PT = *Populus tremuloides*; PS = *Prunus serotina*; AR = *Acer rubrum*; FP = *Fraxinus pennsylvanica*; BP = *Betula papyrifera*.

Discussion

Although it was not possible to establish the role of competition directly in this study, the decline in aggregation with stem size observed in BU 3 in the absence of fire for at least 33 years is consistent with the common understanding that tree aggregation declines as a stand ages because of intraspecific competition (thinning) (Kenkel 1988; Rebertus et al. 1989; Moerur 1993). This is consistent with the notion that clumping should decline during succession in the absence of disturbance (Greig-Smith 1964; Christensen 1977). Water and nitrogen have been shown to be limiting soil resources at Cedar Creek (Davis et al. 1999; Tilman 1987), and adjacent stems in the study woodland likely compete with one another for these soil resources as well. The four most abundant species (*Q. macrocarpa*, *Q. ellipsoidalis*, *P. tremuloides*, and *P. serotina*) are to varying degrees shade intolerant, and thus adjacent stems likely also compete with one another for light.

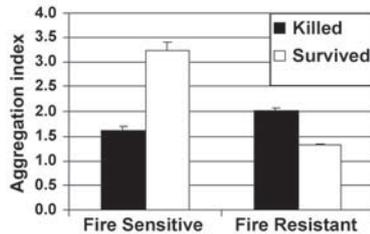


Fig. 5. Aggregation Index values *AI* for stems in Burn Unit 3 prior to the first burn in this unit. Separate values were calculated for stems that were killed or survived the first burn based on whether the stems were designated as fire-sensitive or fire-resistant (based on species and size of stem). (See text for criteria regarding fire-sensitivity and fire-resistance.)

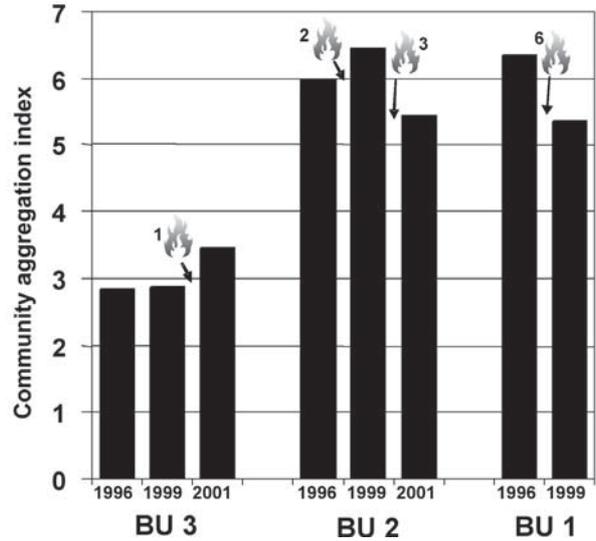


Fig. 6. Community Aggregation Index values *CAI* calculated before and following burns in the three burn units. The fires occurred during the spring of the year shown following the flame symbol, and the number next to a flame indicates which burn (first, second, etc) that burn represented for that burn unit. Aggregation data collected during the year of a fire were collected during the summer, i.e., after the fire. Thus, the fire shown in Burn Unit 1 occurred in spring 1999 and was the sixth burn in this burn unit since 1987. The fire in Burn Unit 3 occurred in spring 2001 and was the first burn in this burn unit. Two fires are shown in Burn Unit 2, one occurring in spring 1999, the second burn in this burn unit, and one occurring in spring 2001, the third burn in the burn unit. (See text for details on how *CAI* is calculated.)

Disturbances have been shown to affect spatial patterns of trees (Sprugel 1976; Miura et al. 2001; Woods 2004), and disturbance by fire has been found to increase the degree of clumping (Rebertus et al. 1989; Skarpe 1991), as was found in this study. The increase in aggregation that occurred in fire-sensitive species following an initial fire was because most stems of these species were killed, except those that survived in scattered safe sites (cool spots). Depending on the type and quantity of fuel present in the immediate area, surface fire temperatures in the study site have been recorded higher than 400 °C and as low as less than 60 °C in the same fire in locations less than 40 m apart (Davis unpubl.). Rebertus et al. (1989) and Skarpe (1991) likewise emphasized the role played by scattered cool spots in contributing to the increase in the degree of clumping of fire-sensitive stems.

The results from this study show how disturbances can create or reinforce some of the patterns of tree aggregation described in this and other studies, e.g. (1) that rare species are more aggregated than common species; and (2) that small stems are more aggregated

than large stems. For example, a drastic reduction in live stem abundance of fire-sensitive stems, combined with an increase in stem aggregation in the few surviving fire-sensitive stems (as shown in this study) would yield a strong inverse correlation between stem abundance of a species and the extent of its aggregation, in which the rare and highly aggregated species would be disturbance-sensitive species surviving in a few safe spots. If small stems are more disturbance-sensitive than large stems (also the case in this study), then, since aggregation increases for disturbance-sensitive stems following initial or periodic disturbances, disturbances could also partly explain the increased level of aggregation exhibited by small stems. In some ways, this finding is analogous to that of Moer (1993), who found that competitively inferior species were more clumped than competitively superior species. In both cases, the sensitive species (competition-sensitive in Moer's study, fire-sensitive in our study) likely persist mainly in 'cool spots' (competition cool spots and real cool spots, respectively).

One would expect the impact of fire on tree aggregation patterns to be similar to that of other forest disturbances that would be likely to affect individual stems differently, such as drought and wind storms. For example, owing to differences in stem size, species, and microhabitat, some stems would be expected to be more drought or wind resistant than others. Thus, unless the drought or wind disturbance was uniformly intense throughout the forest site, some disturbance-sensitive stems would be expected to survive in clumps in scattered safe sites. In the case of drought, Potts (2003) found that the patchy survival of trees during drought in an East Malaysian rainforest was largely the result of spatial variation in topography, specifically slope. Coueron & Kokou (1997) found that drought reinforced clumping of trees in a West African savanna and emphasized the importance of patchiness in edaphic factors in contributing to this finding.

Although disturbance by fire can explain many of the aggregation patterns of species in this oak woodland, the high degree of aggregation in *Populus tremuloides* is due primarily to topographic and edaphic factors. Stems of this species were found almost exclusively in four wetland depressions throughout the study plot. The fact that vegetative reproduction through suckering is common in *P. tremuloides* also contributes to the high levels of aggregation for this species at short distances. Topographic location has been found to account for some of the tree aggregation patterns in tropical forests as well (Valencia et al. 2004).

Although an initial disturbance, or occasional disturbances, seems to increase the degree of clumping in trees, repeated and frequent disturbances, or a single

catastrophic disturbance, would be expected to drastically reduce the number of disturbance-sensitive stems, possibly eliminating some disturbance-sensitive species completely. Thus, one might expect community-wide patterns of aggregation to increase following moderate or occasional disturbances but to decrease following frequent and/or intense disturbances when disturbance sensitive stems could be eliminated completely, or at least reduced to such a minimal extent that their contribution to community-wide clumping patterns would be minimal. This pattern was documented by Rebertus et al. (1989), who found that repeated fires left only a few scattered clumps of fire sensitive species. We found the same pattern in this study. For example, although the Community Aggregation Index (CAI) increased after the second fire in BU 2 because of the increased aggregation of several of the fire-sensitive groups, the third fire eliminated some of these fire-sensitive species completely (*Fraxinus pennsylvanica*, *Acer negundo*, *Crataegus* spec.) and considerably reduced the number of fire-sensitive stems and hence the contribution to CAI of some of the other fire-sensitive groups (e.g., live stems of *Populus tremuloides* declined from 71 stems before the 3rd fire to 14 stems following the fire). The result of this subsequent mortality of fire-sensitive stems was a decline in the CAI (Fig. 6).

Note that it is the pattern illustrated in Fig. 6 that is important, i.e., an initial increase in tree aggregation after the reintroduction of fire followed by a subsequent decline in tree aggregation after successive fires. The fact that the community aggregation index in BU 1 is higher after six burns than that in BU 3 after a single burn is not informative since there is no reason to assume that the level of tree aggregation prior to burning was the same in both burn units. It is possible the overall higher aggregation indices found in BUs 1 and 2 are because they experienced increased disturbance from the activities of local farmers prior to 1960.

Fig. 7 illustrates a hypothetical relationship between disturbance frequency/intensity and community-wide aggregation patterns suggested by the findings of this and other studies. This hypothesis could be considered a corollary to the intermediate-disturbance hypothesis (Connell 1978), the corollary stating that intermediate levels of disturbance are expected to maximize community-wide patterns of aggregation. Rebertus et al. (1989) made a similar observation, suggesting a kind of 'intermediate-disturbance rule' in which 'pattern diversity' is maximized at intermediate frequencies of disturbances.

The increase in the slope of the dominance-diversity curves with subsequent fires suggests a decline in species richness, which in fact was documented, as described above. This would seem to be contrary to the original intermediate-disturbance hypothesis (Connell 1978)

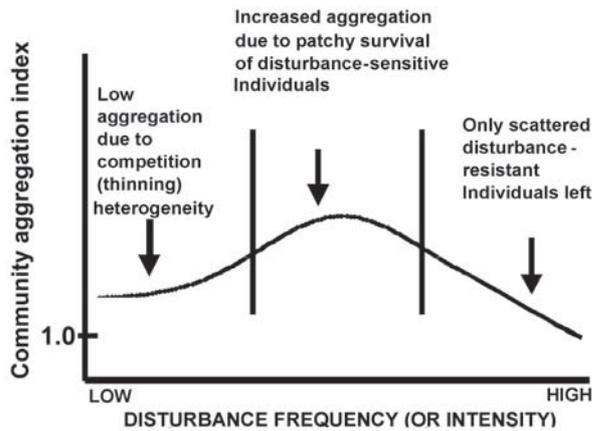


Fig. 7. Graphical representation of a model predicting how community-wide patterns of aggregation in a forest are hypothesized to vary as a function of the frequency or intensity of disturbances.

which holds that species diversity is expected to be higher in environments experiencing disturbances at intermediate frequencies. This apparent paradox is likely due to the time frame of the current study. Although fire can produce an immediate change in the community-wide aggregation pattern (since many stems are killed during the fire) and an immediate reduction in species diversity (as documented above), colonization and establishment of new species often occurs over a much longer period of time, e.g. many years. Although disturbance may temporarily reduce the species diversity of a forest or woodland, it may also create sizeable mortality patches of trees, as was documented in this study. Couteron and Kokou (1997) also documented distinct patches of dead trees following disturbance by drought. Tree mortality in these patches should free up previously monopolized resources. Pulses of available resources are believed to increase the invasibility of a habitat (Davis et al. 2000) and thus would be expected to facilitate subsequent colonization and establishment of additional tree species into the forest, provided disturbances are not so frequent, or intense, as to exclude all but the most disturbance-resistant species.

In sum, the tree aggregation patterns in this species-poor temperate woodland were found to be similar to those found in other temperate and tropical forests and savannas, including species-rich tropical forests in Central America, South Asia, and Malaysia. The dynamics of the spatial patterns in Cedar Creek's oak-woodland suggest that that these spatial patterns are shaped by the often opposing forces of competition, which tends to reduce clumping, and disturbance, which, at low and intermediate frequencies, tends to increase it.

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References

- Anon. (Great Plains Flora Association) 1991. *The Flora of the Great Plain*. University Press of Kansas, Lawrence, KS, US.
- Abrams, M. 1992. Fire and the development of oak forests. *BioScience* 42: 346-353.
- Christensen, N.L. 1977. Changes in structure, pattern, and diversity associated with climax 3 forest maturation in piedmont, North Carolina. *Am. Midl. Nat.* 97: 176-188.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Hua Seng, L., Itoh, A., LaFrankie, J.V., Losos, E., Manokaran, N., Sukumar, R. & Yamakura, T. 2000. Spatial patterns in the distribution of common and rare tropical tree species: a test from large plots in six different forests. *Science* 288: 1414-1418.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1309.
- Couteron, P. & Kokou, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecol.* 132: 211-227.
- Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge, UK.
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T. & Muermann, C. 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a multiple resource gradient. *Plant Ecol.* 145: 341-350.
- Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88: 528-536.
- Greig-Smith, P. 1964. *Quantitative plant ecology*. 2nd ed. Butterworths, London, UK.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.
- Janzen, D.H. 1970. Herbivores and the number of species in tropical forests. *Am. Nat.* 104: 501-528.
- Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.
- Kubota, Y., Murata, H. & Kikuzawa, K. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. *J. Ecol.* 92: 230-240.
- Miura, M., Manabe, T., Nishimura, N. & Yamamoto, S. 2001. Forest canopy and community dynamics in temperate old-growth evergreen broad-leaved forest, SW Japan: a 7-year and 4-ha plot study. *J. Ecol.* 89: 841-849.
- Moeur, M. 1993. Characterizing spatial patterns of trees using

- stem-mapped data. *For. Sci.* 39: 756-775.
- Packer, A. & Clay, K. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404: 278-281.
- Penttinen, A.K., Stoyan, D. & Henttonen, H.M. 1992. Marked point processes in forest statistics. *For. Sci.* 38: 806-824.
- Potts, M.D. 2003. Drought in a Bornean everwet rain forest. *J. Ecol.* 91: 467-474.
- Rathbun, S.L. & Cressie, N. 1994. A space-time survival point process for a longleaf pine forest in southern Georgia. *J. Am. Stat. Ass.* 89: 1164-1174.
- Rebertus, A. J., Williamson, G. B. & Moser, E. B. 1989. Fire-induced changes in *Quercus laevis* spatial pattern in Florida sandhills. *J. Ecol.* 77: 638-650.
- Skarpe, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* 2: 565-572.
- Sprugel, D.G. 1976. Dynamic structure of wave regenerated *Abies balsamea* forests in northeastern United States. *J. Ecol.* 64: 889-912.
- Thompson, J.N. 1978. Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore. *Ecology* 59: 443-448.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57: 189-214.
- Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J., Hernández, C., Romoleroux, K., Losos, E., Magård, E. & Balslev, H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J. Ecol.* 92: 214-229.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- Whittaker, R.H. & Levin, S.A. 1977. The role of mosaic phenomena in natural communities. *Theor. Pop. Biol.* 12: 117-139.
- Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 92: 464-476.
- Wovcha, D.S., Delaney, B.C. & Nordquist, G.E. 1995. *Minnesota's St. Croix River Valley and Anoka Sandplain: a guide to native habitats*. University of Minnesota Press, MN, US.

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