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PATTERN OF SELF-THINNING IN JACK PINE: TESTING THE RANDOM MORTALITY HYPOTHESIS[1]

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Abstract. Spatial statistics were used to examine the pattern of self-thinning in a 0.25-ha even-aged (65 yr old), pure stand of jack pine in the boreal forest near Elk Lake, Ontario, Canada. The positions of 459 living and 916 dead trees were recorded, and refined nearest neighbor analysis [$\widehat{G(w)}$] and second-order spatial statistics [$\widehat{L(t)}$] were used to examine distributional deviations from both the Poisson expectation and the hypothesis of random mortality. The results indicate that the initial (live + dead, $n = 1375$) distribution was locally random. By contrast, the distribution of live trees was locally highly regular, while the dead trees were significantly more clumped than random mortality would dictate. It is suggested that the development of a strong regular pattern in the survivors is attributable to differential mortality involving two distinct competitive phases: an early scramble phase involving two-sided competition for soil resources, and a later contest phase involving one-sided competition for light. Analysis of $\widehat{L(t)}$ for the live trees indicated a mean "area of influence" for each individual of an $\approx$3.5 m radius, suggesting that trees may compete directly only with their immediate neighbors.

Key words: boreal; density dependence; forest; intraspecific competition; jack pine; pattern; random mortality; self-thinning; spatial statistics.

INTRODUCTION

Density-dependent intraspecific competition occurs when one or more resources required by a population fall below a critical level (Ford and Diggle 1981). Experimental plant populations grown at moderate densities tend to show a "plastic response," which typically involves an overall decrease in the mean growth rate and reproductive output of individuals. Mortality ensues at higher densities, with populations generally adhering to the "1.5th power law of self-thinning" (Yoda et al. 1963; but see Weller 1987). Such experiments reveal the overall effect of changing density in plant populations but fail to address the role of competition at the level of the individual. As Mack and Harper (1977) point out, an individual plant is influenced not by population density per se, but rather by the proximity, size, and activity of its immediate neighbors.

Although generally accepted as an important driving force in natural populations, the role of density-dependent competition remains poorly documented and has proven difficult to demonstrate unequivocally (Fowler 1986, Long and Dean 1986). Perturbation studies (addition and removal experiments), which may offer the most convincing demonstrations of competition in natural populations (Ebert and McMaster 1981), are amenable only to some life forms and habitat types (e.g., grasses, forbs, widely spaced desert shrubs, and annuals). Whether the results of such studies are applicable to other life forms and habitats is open to question (West and Borough 1983).

When competition is examined at the level of the individual, the "effective density" experienced by an individual is dependent on the location of its immediate neighbors. We expect that plant size and "available area" of an individual will be positively correlated, and that a shift toward a more regular spatial pattern will occur over time as mortality occurs (Antonovics and Levin 1980). Most studies relating plant size and/or reproductive output to the location of neighbors have generally been performed on natural or sown populations of annuals, and have invariably shown a rather low correlation between plant performance and neighbor proximity. Investigators have attributed this low correlation to differences in emergence time (Mack and Harper 1977, Watkinson et al. 1983, Fowler 1984, Matlack and Harper 1986, Weiner and Thomas 1986, Firbank and Watkinson 1987) and other confounding factors. The definition and description of the "competitive zone" of an individual is also open to question. Pielou (1962) considered only nearest neighbors in a study of competition in ponderosa pine. More often, a circle of arbitrary radius is centered on each plant, and only individuals falling within its bounds are deemed competitors (Mack and Harper 1977, Waller 1981, Weiner 1982, 1984, Fowler 1984, Pacala and Silander 1985). Dirichlet/Thiessen polygons have also been used to delineate "available area" (Mead 1966, Mithen et al. 1984, Matlack and Harper 1986). Fowler (1984) has pointed out that the competitive influence of neighbors reflects highly complex cross-correlations between the individuals making up a population. It therefore seems unlikely that simple neighborhood models can adequately define the complex interactions

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between rooted plants, particularly when differences in germination time and spatial environmental heterogeneity are present.

In examining the spatial pattern of sessile organisms for evidence of competition, it must be recognized that expected patterns resulting from intraspecific interactions may be masked by environmental heterogeneity (Antonovics and Levin 1980). Other potentially confounding factors include the uneven age distribution of a population (Phillips and MacMahon 1981), restricted seed dispersal (Fowler 1986), and random input via germination (Matlack and Harper 1986). Thus, while a regular pattern normally offers strong empirical evidence of competition (Pielou 1962, Greig-Smith 1964, Antonovics and Levin 1980), failure to detect such a pattern cannot be used as evidence that competition is unimportant (Fowler 1986). However, in clonal populations even the detection of a regular pattern may be misleading. Ebert and McMaster (1981; also, Cox 1987) used simulation modeling to demonstrate that random patterns may be perceived as being regular if two or more individuals occuring in close proximity are counted as one. They claim that most if not all examples of regular patterns in desert shrubs may be attributable to this sampling artifact. While it would be rash to dismiss as artifactual all demonstrations of regular pattern in desert shrubs (King and Woodell 1984, 1987), such studies should be regarded with some skepticism.

Apart from studies of desert shrubs, few published accounts of regular patterning in plants are available. Cooper (1961) used nearest neighbor analysis to examine spatial patterning in ponderosa pine stands. Although his study has often been cited as an example of the development of regular patterns in forest trees, in fact only 2 of the 14 populations he studied showed significant regularity. Pielou (1962), working with the same species, suggested that the occurrence of a localized regular pattern within small high density phases may be obscured when an entire population is tested for pattern. Laessle (1965) used both living and dead individuals of sand pine to compare the distribution of the original population (live + dead) with that of the survivors. In some sites a shift from randomness toward regularity was seen. However, the author failed to test whether these differences were significant; that is, could such distributional shifts have arisen through random mortality?

I conclude that few studies have convincingly demonstrated the generally accepted idea that intraspecific competition in plants leads to spatial regularity. While the presence of a regular pattern is likely indicative of competition, more convincing evidence may be obtained through careful mapping of the fates of individuals over time (Mack and Harper 1977, Matlack and Harper 1986). With such information one can infer a competitive effect if the pattern of survivors is more regular than would be predicted given that mortality is a random event (the random mortality hypothesis of Sterner et al. 1986). Ideally, the species and site should be chosen so as to minimize confounding factors that might otherwise mask the pattern of self-thinning. One should therefore choose a long-lived, nonclonal species that forms even-aged, pure stands, and whose seeds are randomly dispersed at high initial density over a relatively homogeneous substrate. Spatial pattern studies should also take advantage of the newer, more powerful statistical methods for analyzing mapped point patterns (Ripley 1981, Diggle 1983, Upton and Fingleton 1985, Sterner et al. 1986).

This study investigates the pattern of self-thinning in a pure, even-aged stand of jack pine (*Pinus banksiana* Lamb.) on a uniform sandy substrate near Elk Lake, Ontario, Canada. The mapped spatial distributions of living and dead individuals are used to test the random mortality hypothesis, which states that the distribution of surviving (living) trees does not differ significantly from what would be expected given that mortality is a random event. Refined nearest neighbor analysis and second-order spatial statistics are used to examine spatial and mortality patterns within the study area.

Materials and Methods

*Jack Pine (*Pinus banksiana *Lamb.)*

Jack pine is a pioneer tree species of sandy podzolic soils and rocky sites throughout the North American boreal forest. It is a relatively short-lived, medium-sized tree, growing to 15–20 m in height and 20–30 cm in diameter. Growth is greatest in the first 50 yr, but virtually ceases after ≈80 yr (Fowells 1965). The ecology of jack pine makes it ideal for the study of intraspecific competition. The species is well adapted to pyric ecosystems, producing serotinous cones that open immediately following a crown fire. The large number of seeds so released germinate in the same year, establishing extensive, even-aged, pure stands on sandy upland substrates (Yarranton and Yarranton 1975).

Study area

A 50 × 50 m (0.25-ha) study area was located at random within a pure stand of jack pine on a flat, sandy plain near Elk Lake, Ontario (47°50′ N, 80°27′ W). The stand is part of a forest reserve and has therefore been protected from logging, selective cutting, and other disturbances. It contains jack pine trees averaging ≈15 cm in diameter and 16 m in height. The strongly podzolized sandy soil supports an understory dominated by low ericaceous shrubs and mosses. The study area occurs within vegetation type VII (*Pinus banksiana-Pleurozium schreberi-Kalmia angustifolia-Vaccinium myrtylloides*) described by Kenkel (1986), which is characteristic of flat, sandy, well-drained upland plains of low nutrient status. A map of the Elk Lake region, together with details of its vegetation, topography, substrates, and climate can be found in Kenkel (1986).

The stand established following a severe fire in the early 1920s (Donnelly and Harrington 1978). Ring counts obtained by coring 58 trees within the study area indicated that the stand was even-aged (65 ± 1 yr); this is typical of jack pine stands on sandy soils (Fowells 1965, Yarranton and Yarranton 1975). To test for substrate homogeneity, the study area was gridded into 25 10 × 10 m squares and a soil sample taken from the center of each square at a mean depth of 10 cm below the organic horizon. Samples were air dried for later analysis by the Manitoba Provincial Soil Testing Laboratory. All samples fell within the soil texture class "fine sand," lacked carbonate, and had conductivities of 0.1 mS/cm. The values for pH, nitrogen, phosphorus, and potassium (Table 1) also suggest substrate homogeneity, and indicate that acidic, nutrient-poor conditions prevailed. Pattern analysis using join-count statistics (Upton and Fingleton 1985:158) indicated no spatial trends in pH and nutrient levels within the study area.

Data collection

The mapping of trees was undertaken in July 1986. The 50 × 50 m study area was carefully delineated and subsequently gridded into 25 10 × 10 m contiguous squares using a surveyor's transit. Within each square, the positions of all living trees, standing dead trees, and stumps were recorded. It is likely that very few dead trees were missed, since they are well preserved in jack pine stands (Yarranton and Yarranton 1975). However, it is likely that saplings that had died during the early years of stand establishment had decayed beyond detectability. Thus the map of live + dead trees represents not the initial distribution (at the time of stand establishment), but rather that following early sapling mortality. However, since early mortality is attributable to density-independent factors, the map of live + dead trees represents the distribution of individuals prior to the onset of density-dependent mortality (Yarranton and Yarranton 1975). I therefore refer to the map of live + dead trees as the "initial" distribution.

Positions were recorded using a modification of a method outlined by Rohlf and Archie (1978). The distances (d) of an individual to the four corners of the 10 × 10 m square were measured. The (x, y) coordinates of an individual i with respect to a corner point j are $x_i = d_{ij} \cos \theta$ and $y_i = d_{ij} \sin \theta$, where $\theta = \cos^{-1}[(d_{ij}^2 + d_{jk}^2 - d_{ik}^2)/(2d_{ij}d_{jk})]$, and j and k are adjacent corner points. Coordinates were calculated with respect to each of the four pairs of adjacent corner points, and a mean was calculated to obtain the final coordinate position within the 10 × 10 m region. All coordinates were later expressed relative to the southeastern corner of the study area. A total of 1375 individuals (density = 5500 trees/ha) were mapped, of which 459 (≈one-third) were living.

TABLE 1. Means and standard deviations (n = 25) for soil nutrient (mg/kg) and pH values within the study area.

	Mean	Standard deviation
pH	5.17	−0.16, +0.27*
Nitrate-nitrogen†	0.35	±0.14
Available phosphorus†	2.84	±0.93
Available potassium‡	22.60	±4.90

* Inequality of positive and negative standard deviation values reflects the skewed distribution of pH.
† Sodium bicarbonate extractable.
‡ Ammonium acetate exchangeable.

Statistical methods

The following methods were used to analyze spatial patterns within the study area. The first three univariate methods were used to examine pattern in each of three data sets: live (n = 459), dead (n = 916), and live + dead (n = 1375). The fourth method is bivariate and was used to analyze spatial interrelationships between living and dead individuals.

Modified Clark-Evans statistic (Donnelly 1978).—The summary statistic outlined by Clark and Evans (1954) assumes a lack of interdependence and, more important, that edge effects are not present (Sinclair 1985); Donnelly's variant accounts for edge effects. The calculated value of this statistic (CE) is referred to the standard normal distribution, with spatial randomness rejected in favor of clumping or regularity for values in the upper and lower tails respectively.

Refined nearest neighbor analysis (Roder 1975, Diggle 1979).—If n individuals are randomly distributed within a region of area A, the expected cumulative distribution function for nearest neighbor distances w is given by

$$G(w) = 1 - \exp(-\rho\pi w^2),$$

where $\rho = n/A$. This is compared with the empirical cumulative distribution function $\widehat{G(w)}$. The calculation of $\widehat{G(w)}$ is complicated by edge effect corrections; see Upton and Fingleton (1985:80) for details. A plot of $\widehat{G(w)} - G(w)$ against w describes a process indicating the extent to which the observed distribution departs from the Poisson expectation across the entire spectrum of nearest neighbor distances w. Since the complete distribution function is examined, a more detailed analysis is obtained than that offered by the modified Clark-Evans statistic. Significance is evaluated using Monte Carlo techniques (Diggle 1983). This involves generating m random configurations of n plants within a region of area A, and comparing the observed cumulative distribution with those obtained from the m random alternatives.

Combined count-distance analysis (Ripley 1976, 1977).—Because this method utilizes all plant-to-plant distances, it can offer greater insight regarding the nature of spatial pattern than methods restricted to examining only nearest neighbor distances. The function $\rho K(t)$ is defined as the expected number of individuals

within a distance t of a randomly chosen individual in a population; here, $K(t) = \pi t^2$. The empirical function $\rho\widehat{K(t)}$ is the observed number of individuals within distance t of a randomly chosen individual. Its calculation is complicated by the requirement to allow for edge effects. The appropriate estimate is

$$\rho\widehat{K(t)} = \sum\sum k(x_r, y_s)/n,$$

where $k(x_r, y_s)$ is defined as the inverse of the proportion of the circumference of a circle, passing through individual y and centered on individual x, which lies within the study area, and the summation is over all interplant distances $<t$. It is a second-order statistic since the variation rather than the mean of distances is of interest (Getis and Franklin 1987). The function $\widehat{L(t)} = t - [\widehat{K(t)}/\pi]^{1/2}$ has expectation zero given randomness; the square root stabilizes the variance (see Besag in the discussion of Ripley 1977). A plot of $\widehat{L(t)}$ against t reveals spatial pattern at various values of the neighborhood distance t. Positive values of $\widehat{L(t)}$ indicate regularity, while negative ones signify clumping. Monte Carlo simulation is required to assess the significance of departures in $\widehat{L(t)}$ from zero.

Bivariate combined count-distance analysis (Ripley 1977).—The univariate second-order statistic $K(t)$ can readily be generalized to analyze a bivariate point process. The function $\rho_1 K_{12}(t)$, where $\rho_1 = n_1/A$, is defined as the expected number of individuals of type 1 within a distance t of a randomly chosen individual of type 2. When the two types are spatially independent, $K_{12}(t) = \pi t^2$. The empirical function is calculated as

$$\widehat{K_{12}(t)} = [n_2\tilde{K}_{12}(t) + n_1\tilde{K}_{21}(t)]/(n_1 + n_2),$$

where $\rho_1\tilde{K}_{12}(t) = \Sigma\Sigma\, k(x_r, y_s)/n_2$ and $\rho_2\tilde{K}_{21}(t) = \Sigma\Sigma\, k(y_s, x_r)/n_1$. The value $k(x_r, y_s)$ is defined as in the univariate version of the statistic. The function $\widehat{L_{12}(t)} = t - [\widehat{K_{12}(t)}/\pi]^{1/2}$ has zero expectation given spatial independence. A plot of $\widehat{L_{12}(t)}$ against t permits examination of the spatial dependence of types 1 and 2 at various neighborhood distances t. Positive values of $\widehat{L_{12}(t)}$ indicate repulsion between types, whereas negative values indicate attraction. Statistical independence of the distribution of types indicates a lack of interaction. Monte Carlo confidence envelopes must be generated to assess the significance of departures of $\widehat{L_{12}(t)}$ from zero.

Random confidence envelope.—Monte Carlo confidence envelopes were generated using high-quality congruential random number generators (Arnason 1977). Confidence envelopes for the $\widehat{G(w)}$ and $\widehat{L(t)}$ functions were generated as follows: (1) generate a set of n random coordinates; (2) calculate the appropriate function based on this random coordinate set; (3) repeat steps 1 and 2 a total of $m = 99$ times; (4) use the maximum and minimum values of the m random simulations to define a confidence envelope (Diggle 1983); (5) compare the empirical function with the confidence envelope. Portions of the empirical function falling outside the confidence envelope are deemed significant.

Random mortality hypothesis.—The hypothesis of random mortality was tested as follows: (1) select at random (using sampling without replacement) 459 of the total 1375 individuals (coordinates); (2) calculate $\widehat{G(w)}$ and $\widehat{L(t)}$ for the partitioned data sets, where the $n_1 = 459$ are live trees, and the remaining $n_2 = 1375 - 459 = 916$ are dead; (3) repeat this $m = 99$ times; (4) generate a confidence envelope as outlined previously; (5) if the empirical function lies outside these limits, significant deviation from the hypothesis of random mortality is indicated.

Results

Modified Clark-Evans statistic

The resultant statistics indicate that the live + dead ("initial") distribution was random ($CE = 1.567$, $P = .117$), with a mean spacing of 0.554 m. By contrast, the distribution of live trees was highly regular ($CE = 5.560$, $P < .001$; mean spacing = 1.107 m). The distribution of dead trees tended toward a clumped distribution ($CE = -1.898$, $P = .058$), with a mean spacing of 0.633 m.

Refined nearest neighbor analysis

Results for the live + dead distribution suggest no significant departure from randomness over the entire range of the cumulative distribution function (Fig. 1). For the distribution of dead trees, there is a trend toward clumping when compared with the Poisson expectation, though significance is rarely achieved over the range of the cumulative distribution function. By contrast, the random mortality model indicates significant clumping in the range 0.25–1.25 m, suggesting greater clumping of dead trees than random mortality would predict. Results for the distribution of live trees indicate highly significant regularity in the range 0.25–1.75 m for departures from both the Poisson expectation and that predicted given that mortality is a random event.

Combined count-distance analysis

For each of the three data sets, a plot of $\widehat{L(t)}$ over a 20-m range (together with the simulation envelopes) was produced (Fig. 2). Results for the live + dead distribution indicate no deviation from the Poisson expectation to a distance of 3 m, but that significant clumping occurs beyond this point. This suggests that randomness at the local (nearest neighbor) scale gives way to clumping at higher scales. For the distribution of dead trees, the results indicate significant deviations from the Poisson expectation in the direction of clumping in the range 0.4–0.8 m, and again between 3 and 18 m. However, the confidence envelope defined by the random mortality model indicates that the dead trees were significantly clumped only up to a distance

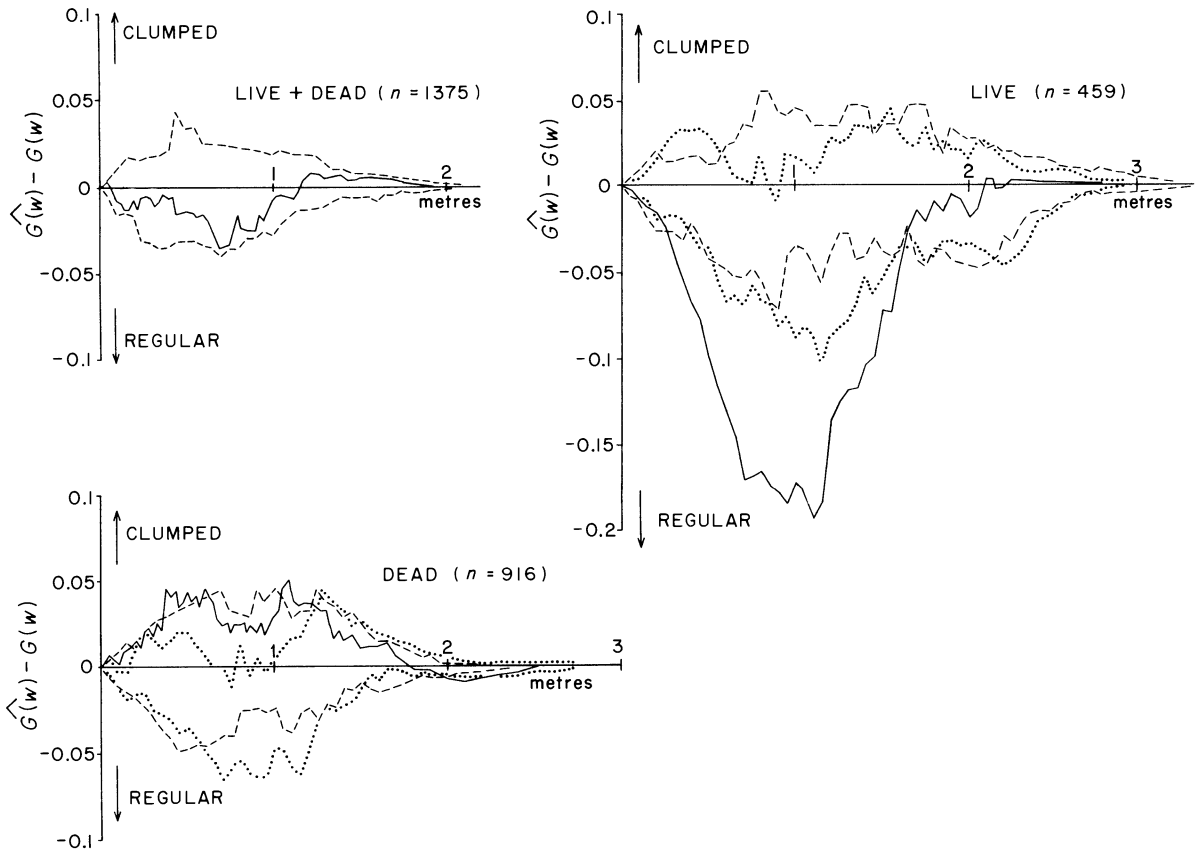

FIG. 1. Cumulative distribution function of nearest neighbor distances $\{[\hat{G}(w) - G(w)]$ vs. $w\}$ for the three data sets. —— = observed distribution; – – – = confidence envelope for Poisson expectation; ····· = confidence envelope for random mortality.

of ≈3.5 m. For the live trees, the results indicate a highly significant departure from the Poisson expectation toward regularity up to ≈3.5 m, and significant clumping beyond ≈10 m. By contrast, the confidence envelope generated by the random mortality model indicates a highly significant trend toward regularity up to 4.5 m. At greater distances, the observed $\hat{L}(t)$ does not differ significantly from that predicted given that mortality is a random event, suggesting that intraspecific interactions occur at a local scale.

Bivariate combined count-distance analysis

The bivariate interaction between live and dead trees (Fig. 3) indicates significant departures from Poisson expectation toward repulsion to ≈2.5 m, and significant attraction at distances >3 m. However, the confidence envelope obtained from the random mortality model indicates that the interaction between live and dead trees does not deviate significantly from that expected given random mortality over the entire 20-m range.

DISCUSSION

This study clearly indicates rejection of the random mortality hypothesis in favor of a model of differential mortality in jack pine. From an initial random distribution a strong local regular pattern of surviving trees developed, a result which is most reasonably ascribed to intraspecific competition (Ford 1975, Antonovics and Levin 1980). Indeed, potentially confounding factors such as environmental heterogeneity and pathogen attack would, if anything, render a distribution less rather than more regular (Chalupsky and Leps 1985, Fowler 1986).

Spatial interrelationships of the living and dead individuals suggest possible competitive mechanisms that may give rise to a regular pattern of survivors. The significant local clumping of dead trees over that expected given random mortality indicates that the development of regularity may be attributable to differential mortality within higher density patches of the initial distribution. However, the bivariate analysis shows no significant trend toward repulsion, suggesting that clumped mortality cannot entirely explain the development of regularity.

Given these results, I suggest that the spatial pattern of mature jack pine stands results from two distinct competitive phases: (1) an early scramble phase, in which two-sided competition for soil nutrients and water results in resource depletion. This depletion would

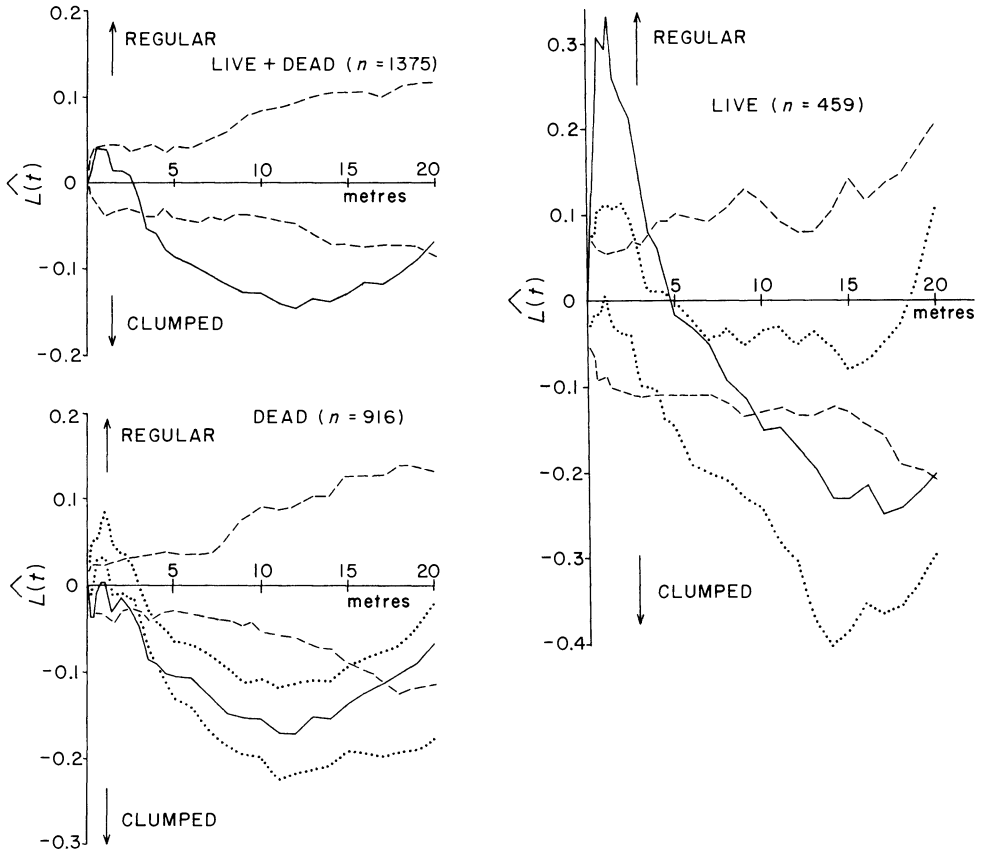

FIG. 2. Combined count-distance analyses [$\widehat{L(t)}$ vs. t] for the three data sets. Line types as in Fig. 1.

be most pronounced in higher density phases, leading to clumps of suppressed young trees, which are eventually shaded out by their larger neighbors; (2) at later stages of stand development, a contest phase involving one-sided competition for light becomes the major competitive interaction. This results in the development of a canopy consisting of both dominant and suppressed trees, and eventual mortality of the smaller trees. While local clumping of dead individuals would lead to repulsion in the bivariate analysis (the clumps of dead trees alternating with live ones), one-sided competition implies attraction (the "loser" in the contest being near its rival). It seems likely that the lack of significant attraction or repulsion in the bivariate analysis is attributable to the cancelling of these two competitive phases.

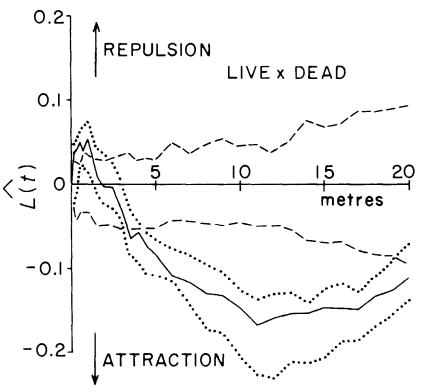

FIG. 3. Bivariate combined count-distance analysis [$\widehat{L(t)}$ vs. t]. Line types as in Fig. 1.

Weiner and Thomas (1986) have also advocated a two-phase competition model in plants that involves early interference through resource depletion followed by competition for light. Competition for light is one-sided, with the result that smaller, suppressed individuals are selectively removed from the canopy over time (Cooper 1961, Lee 1971, Gibson and Good 1986). In plantations of *Pinus radiata,* West and Borough (1983) found that there developed a group of small trees showing little or no growth. They attributed this to competition for light, since this species forms root grafts and therefore presumably shares belowground resources. Weiner (1984), working with a natural stand of the same species, found local variation in stand density to be of considerable importance in determining the growth of individual trees. This, together with Ford and Diggle's (1981) contention that one-sided competition for light leads to the development of a regular pattern of survivors, is substantiated by the present

study. Since jack pine forms root grafts (Graham and Bormann 1966) and is highly shade intolerant (Fowells 1965), competition for light is presumably of overriding importance in older stands.

The nearest neighbor techniques used in this study indicated that the live + dead distribution was locally random. Pacala and Silander (1985) have suggested that an initial random pattern is expected when the distance of seed dispersal is over an area greater than that occupied by the parent plant, and when the environment is homogeneous. Significant clumping at distances >3 m [as indicated by $\widehat{L(t)}$] is likely attributable to alternating high- and low-density phases within the initial distribution (Pielou 1962, 1977).

All the statistical methods used have shown a highly significant locally regular pattern for the live trees, in terms of deviation from both Poisson expectation and the random mortality model. Both $\widehat{G(w)}$ and $\widehat{L(t)}$ indicate that regularity is strongest at a distance of 1.1 m, which corresponds closely to the mean spacing (nearest neighbor distance) between living trees. The combined count-distance analysis $\widehat{L(t)}$ for the live trees also indicates the "area of influence" of individuals. Such an area is defined in terms of the interplant distance beyond which the effects of density are absent; this corresponds to the "ecologically effective distance" of Antonovics and Levin (1980). Portions of the graph of $\widehat{L(t)}$ lying outside the confidence envelope that was derived from the random mortality hypothesis indicate regions where intraspecific interactions differentially modify the spatial distribution of trees. The results (Fig. 2) indicate that the upper limit for the circle radius is $\approx$4.5 m, with greatest deviation in the 0.5–3.5 m range. Beyond this distance, the distribution does not deviate significantly from the random mortality expectation, indicating that intraspecific interactions operate at a local level (Harper 1977). For a radius of 3.5 m, each living tree is competing with an average of six neighbors. Interestingly, $n = 6$ is the expected number of sides of a Dirichlet/Thiessen tile (Upton and Fingleton 1985:97), suggesting that a given tree may be competing directly only with its tile edge neighbors (Mithen et al. 1984, Matlack and Harper 1986).

In conclusion, the present study illustrates how distributional data can be used to demonstrate the pattern of self-thinning in a natural forest stand. The data corroborate the hypotheses that self-thinning in natural plant populations leads to the development of a regular spatial pattern of survivors, and that competitive interactions in plants occur on a local scale. Further studies on the distribution of jack pine and other tree species should be undertaken to verify the results presented here.

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