

A long-term study of *Pinus banksiana* population dynamics

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Abstract. The long-term population dynamics of a pure, naturally-established stand of *Pinus banksiana* (jack pine) in south-eastern Manitoba, Canada is described. The study was initiated at stand age 15, when all 468 trees in a plot were mapped and their trunk diameter at breast height (DBH) measured. The plot was remeasured eight times – every five years (six years in one case) – and mortality and DBH changes recorded. Total mortality over the 41-yr study period was ca. 84 %. Mortality was initially very low, increased once the stand entered the self-thinning stage from ages 25 - 46, and declined at ages 46 - 56. Mortality was restricted to the smallest size classes throughout. The stand reached the self-thinning line at ca. age 30. The self-thinning slope was significantly less steep than the theoretically expected value of -0.5 .

The distribution of DBH values was initially symmetric, showed increasing positive skewness during the period of highest mortality, and became symmetric again at later stages. Size (DBH) inequality was highest just prior to the onset of density-dependent mortality, and subsequently declined. Tree DBH values were positively autocorrelated both initially and at later stages of stand development, but were spatially independent during the period of highest density-dependent mortality. The stand initially had a strongly clumped pattern at all spatial scales. Patterns of mortality were non-random during stand development, however, resulting in increased spatial regularity over time. Mortality was initially restricted to high density patches of the stand, but occurred throughout the plot once the self-thinning line was reached. Mortality during the self-thinning stage deviated from random expectation at local spatial scales (1 - 2 m radius), suggesting that individuals were competing with their immediate neighbours. It is argued that an integrated approach, incorporating both population size and spatial structures, is essential in improving our understanding of long-term plant population dynamics.

Keywords: Autocorrelation; Boreal forest; Competition; Density-dependent mortality; Self-thinning; Size asymmetry; Size inequality; Spatial pattern.

Abbreviations: CE = Clark-Evans nearest neighbour statistic; CV = coefficient of variation; DBH = diameter at breast height.

Nomenclature: Scoggan (1978) for vascular plants; Anderson et al. (1990) for mosses.

Introduction

Intraspecific competition occurs when the supply of resources falls below the combined requirements of individuals in a population (Cannell et al. 1984). In plant populations, resources are shared disproportionately, with larger plants obtaining a greater fraction. Competition is therefore a spatial process, since an individual's performance is dependent on the size of and proximity to its neighbours (Ford & Diggle 1981).

Even-aged, monospecific plant populations have spatial, size and genetic structures. A complete understanding of the dynamics and interactions of these structures (Benjamin & Hardwick 1986; Hara 1988). However, most plant population studies have only examined changes in size structures (Hara 1988; Weiner 1990) or spatial structure (Czárán & Bartha 1992), while the dynamic interaction between size and spatial structures has received very little attention.

The results obtained from even-aged herbaceous plant populations grown over a single season have been used to develop dynamic plant population models. However, it is questionable whether such models are applicable to trees and other long-lived species (West & Borough 1983). Unfortunately, few studies of the long-term dynamics of monospecific forest stands exist, presumably because trees are so long-lived (Peet & Christensen 1987). Furthermore, much of the information on long-term population dynamics of trees is derived from forest plantations (e.g. West & Borough 1983; Cannell et al. 1984; Hara 1985). Since plantation trees are evenly-spaced and are established at comparatively low densities, the results of such studies are relevant only to managed forest stands. Another approach involves reconstructing forest stand dynamics using data from 'replicate' stands of various ages. This approach is often used to produce stand yield-tables, which have been used to derive self-thinning trajectories for forest stands (Weller 1987; Lonsdale 1990). A major drawback of this approach is that temporal trends are confounded by natural stand-to-stand variation. Not surprisingly, many

authors have commented on the need for long-term, repeated measure studies of natural thinning forest stands (e.g. Carleton & Wannamaker 1987; Zeide 1987; Knox et al. 1989; Lonsdale 1990). Very few such studies exist, however (Weiner 1995).

A number of generalizations have been made regarding the dynamics of size and spatial structures in monospecific forest stands. Examination of the relationship between forest stand density and total yield reveals an overall adherence to the '-1.5 self-thinning rule', though recent investigations have questioned the generality of the self-thinning slope coefficient (Lonsdale 1990). Despite this, foresters have used self-thinning theory to develop stand density management models (Drew & Flewelling 1979; Long 1985; Archibald & Bowling 1995).

Size differences within plant populations arise early and are accentuated over time (Benjamin & Hardwick 1986), and this has consequences on the size and spatial structures of populations. Over a given time interval, mortality probability is greatest for trees in the smallest size classes (West & Borough 1983; Hara 1985; Peet & Christensen 1987). Since individual size is expected to be correlated with neighbour size and proximity, mortality patterns should result in increasing spatial regularity over time as high density phases are differentially thinned (Kenkel 1988).

Generalizations have also been made regarding the size structures of tree populations. In dense stands, the distribution of tree sizes is affected by both stand growth and differential mortality. Size distributions tend to become increasingly positively skewed (L-shaped) up to the time of self-thinning, a result that has been attributed to asymmetric competition for light (Weiner & Thomas 1986). With self-thinning, the size distribution becomes progressively less skewed since mortality is concentrated in the smallest size classes (Mohler et al. 1978; Hara 1985). Size inequality is also expected to increase prior to self-thinning, but to decrease during the self-thinning stage as smaller individuals die (Weiner & Thomas 1986; Knox et al. 1989).

Peet & Christensen (1980) have pointed out that once an even-aged forest is established 'forest succession becomes a thinning process'. This type of succession has been almost ignored in past ecological research despite its importance in disturbance-driven ecosystems (Sprugel 1984). Stand thinning is critical to our understanding of boreal forest temporal dynamics, for two reasons: (1) one or only a few species dominates regrowth in most boreal forest stands; (2) much of the boreal ecosystem is characterized by frequent, broad-scale, catastrophic fires, usually well within the mean lifespan of pioneer trees (Hirsch 1991). Extensive, self-perpetuating pure stands of 'pioneer' species therefore dominate

much of the boreal forest, implying that forest dynamic models involving species replacements are of limited utility.

Studies focussing on the interaction between the spatial and size structures of plant populations are lacking. Since the development of a size hierarchy in populations is affected by spatial considerations (e.g. the size and proximity of neighbours, Kenkel 1988), an approach integrating population spatial and size structures is critical to developing a more complete understanding of plant population dynamics. In this study, we examine the long-term size and spatial dynamics of a naturally established, pure stand of *Pinus banksiana* (jack pine) in southeastern Manitoba, Canada. Because it forms extensive stands that undergo substantial self-thinning, *P. banksiana* is an ideal species for examining population-driven stand dynamics. The stand was monitored between ages 15 and 56, which incorporates the period prior to, during, and following extensive individual mortality. Our objective is to examine the dynamic interaction that occurs between size and spatial structures during self-thinning of a natural forest stand. We approach this objective by examining five related issues in stand development: (1) self-thinning; (2) changes in size distribution; (3) size-specific mortality; (4) changes in spatial pattern and pattern scaling; and (5) spatial autocorrelation.

Material and Methods

Species characteristics

Pinus banksiana is a boreal conifer indigenous to North America. The species is widely distributed in Canada, from the Maritime provinces in the east to Alberta and the Northwest Territories in the west. In the United States, jack pine is restricted to the northern portions of Minnesota, Wisconsin, Michigan and Maine. The species is most abundant in a region extending through the central portions of Saskatchewan, Manitoba, and Ontario (Halliday & Brown 1943). It occurs on excessively drained, nutrient-poor, somewhat acidic substrates, and is most frequently found on soils of the podzolic order, from coarse to fine sands and gravels.

P. banksiana is a relatively short-lived tree, 80 - 100 yr, of medium size, growing to 15 - 25 m in height and 20 - 30 cm in diameter on typical sites. The species grows quite rapidly in youth, and under good growing conditions can reach a height of 1.5 m by ages 4 - 6 yr and 6 m by 18 yr. Merchantable stands (mean stem diameter > 13 cm) are often obtained by age 35 (Cayford et al. 1967). At typical stocking densities, total aboveground biomass increases to age 50, then levels

off. *P. banksiana* is one of the most shade-intolerant of northern trees, confirming its status as a pioneer, early succession species (Fowells 1965).

The species produces serotinous cones that normally do not shed their seeds until the occurrence of a catastrophic crown fire. Seeds are released immediately following a fire and germinate on newly-exposed inorganic substrates. Stands often establish at very high densities, and undergo substantial self-thinning by ages 20 - 30 (Chrosiewicz 1971; Yarranton & Yarranton 1975). The mortality rate of jack pine is among the highest of all northern tree species (Buchman et al. 1983), and the vast majority of trees in a stand die before the next catastrophic fire (Bella & DeFranceschi 1974).

Study area and data collection

The study site is one of 14 one-tenth-acre (20.12 × 20.12 m = 0.0405 ha) plots established to examine the long-term effects of thinning in jack pine (Cayford et al. 1967). In 1952, plots were established in a 15-yr-old pure jack pine stand in the Sandilands Forest Reserve, Manitoba (49° 35' N, 96° 15' W). The stand established naturally following a catastrophic forest fire. 12 of the plots underwent various manipulations (different types of artificial thinning), while two served as 'fully stocked' untreated controls. This study presents the results from one of the control plots. In this plot, each living tree was permanently marked with a numbered aluminum tag, its spatial coordinates determined, and its diameter at breast height (DBH) measured. The DBH of each living tree was remeasured at stand ages 20, 25, 30, 35, 41, 46, 51 and 56. At age 15, the plot had 468 trees (11 564/ha), which is considered a 'moderate' density for natural jack pine stands (Chrosiewicz 1971).

The study region is boreal forest, and is characterized by extensive, poorly-drained lowlands dominated by *Picea mariana* (black spruce) and *Larix laricina* (tamarack), interrupted by uplands of glacio-fluvial deposits and beach remnants. Well-drained upland sites are dominated by *Populus tremuloides* (trembling aspen) and *Picea glauca* (white spruce), while pure stands of *P. banksiana* occur on excessively-drained sandy uplands (Mueller-Dombois 1964; Bella 1968). Climate is sub-humid continental, with short warm summers and long, cold winters. Mean annual temperature is ca. 2 °C (mean for January -19.6 °C, for July 18 °C). Mean annual precipitation is ca. 530 mm, with 355 mm falling as rain during the growing season (May - September).

The substrate of the study plot is a moist grey-wooded soil, sandy to gravelly in texture. The dominant understory species are *Pleurozium schreberi* and *Polytrichum juniperinum*; shrub cover is sparse. In 1994, five randomly-located soil cores were analyzed for

available macronutrients and pH (Norwest Laboratories, Winnipeg). The results indicated nutrient-poor, acidic conditions, with mean values for pH = 5.62; nitrogen < 1 ppm; phosphate = 15 ppm; potassium 40.6 ppm.

Data analysis

Life table and mortality analysis

A life table analysis was performed by computing annual mortality rates (Sheil et al. 1995) for the eight age intervals (stand ages 15 - 56). In addition, a mortality curve was obtained by fitting the Richards function to the mortality data (Buford & Hafley 1985).

Self-thinning curve

A log-log stand density vs. total aboveground biomass trajectory was fitted to examine self-thinning in the stand. Many studies have used mean biomass when determining the self-thinning slope, but for statistical reasons total biomass should be used instead (Weller 1987). Most studies of self-thinning in forest stands have used tree bole volume or biomass (rather than total above-ground biomass) in fitting the self-thinning line. Sprugel (1984) suggests that this can lead to biased results, since smaller trees have disproportionately less biomass allocated to the bole. In this study, we estimated total individual biomass from measured tree DBH values using Hegyi's (1972) DBH-biomass equation, which is based on a sample of 77 trees (three age classes: 11 - 20, 21 - 30, 56 - 65 yr) from 12 naturally-established jack pine stands in northwestern Ontario. Hegyi (1972) determined total above-ground dry biomass of each tree, and related total biomass (kg) to DBH (cm) using log-log regression analysis:

$$\log_{10} \text{biomass} = -1.0368 + 2.4206 \log_{10} \text{DBH} \quad (1)$$

$$R^2 = 0.986, n = 77.$$

Although several other jack pine biomass equations are available, we used Hegyi's since environmental conditions in north-western Ontario and south-eastern Manitoba are similar. For completeness we also computed total biomass using Ker's (1980) DBH-biomass equation for natural stands in Nova Scotia, and two equations ('Isabella' and 'Pembine') for planted stands in the upper Great Lakes states (Zavitkovski et al. 1981). Other published equations were unsuitable as they required tree height measurements.

Following Mohler et al. (1978), we determined the slope of the principal component rather than that of a linear regression line. Confidence limits (95 %) for the principal component slope were determined following Creasy (1956). A persistent problem in fitting

a self-thinning line to empirical results is the inclusion of data points not on the thinning line, as this inflates (makes steeper) the slope estimate (Osawa & Sugita 1989; Lonsdale 1990). In recognition of this problem, we computed separate principal component slopes using the last 6, 7 and 8 stand ages.

Size distributions

Histograms of size (DBH) distributions were computed for each of the nine measurement years, and trees dying in the subsequent measurement year were highlighted. Skewness was used to quantify size distribution asymmetry, and the coefficient of variation (CV) to quantify size inequality (Weiner & Thomas 1986). To examine the relationship between tree size and mortality, DBH values at each measurement year were plotted after first grouping trees into eight 'age-at-death' classes (dead at stand age 20, 25, 30, 35, 41, 46, 51, and still alive at stand age 56).

Spatial autocorrelation

For each of the nine age intervals, spatial autocorrelation of size (DBH) was tested using Moran's *I*-statistic (Upton & Fingleton 1985: 170). In these tests, joins (neighbours) were defined as trees sharing a common boundary as defined by the Voronoi-Delaunay tessellation (Reed & Burkhart 1985; Kenkel et al. 1989a). A negative value of the test statistic indicates that large trees tend to have small neighbours, and vice versa. Positive autocorrelation means that larger trees are surrounded by larger neighbours, and smaller trees by smaller neighbours. Statistical significance of Moran's *I* is assessed by referring to the standard normal distribution.

Spatial pattern analysis

Local (nearest-neighbour) spatial pattern analysis was undertaken using a form of the Clark-Evans (CE) statistic modified to account for edge effects (Donnelly 1978; Sinclair 1985). The calculated CE is referred to the standard normal distribution to test for departures from spatial randomness (negative values indicate clumping, while positive values indicate regularity). Separate analyses were undertaken for each of the nine measured stand ages to summarize temporal changes in stand spatial pattern.

Second-order spatial analysis (Ripley 1977; Haase 1995) was developed to allow examination of the relationship between spatial pattern and scale. In this approach, a circle of radius t is centered on each individual, and the number of neighbours within the circle is counted. By varying the circle radius t , spatial pattern can be examined at various spatial scales. For a completely random pattern, the expected number of neighbours within a distance t of a randomly chosen

individual is $\lambda K(t)$, where $K(t) = \pi t^2$ (2)

and λ is the stand density. The observed number of neighbours within distance t of a randomly selected individual is a biased estimate unless an edge correction is implemented. Ripley (1977) suggested a toroidal edge correction:

$$\widehat{K}(t) = n^{-2} A \sum k(x,y) \quad (3)$$

where n is the number of individuals within a plot of area A , and $k(x,y)$ is a weighting function (specified for each ordered pair of individuals x,y) that is inversely proportional to the circumference of a circle, centered on individual x and passing through individual y , that lies within the bounds of the study area. Summation is over all ordered x,y pairs less than t apart. A more straightforward interpretation is obtained by plotting $\widehat{L}(t)$ against t , where:

$$\widehat{L}(t) = t - \sqrt{\widehat{K}(t)/\pi} \quad (4)$$

The function $\widehat{L}(t)$ has zero expectation when the point pattern is random at scale t . The degree to which $\widehat{L}(t)$ deviates from zero offers insight into the empirical point pattern at spatial scale t . For each stand age, we computed the $\widehat{L}(t)$ vs. t plot for all spatial scales $0 < t \leq 6$ m.

Statistical significance of the $\widehat{L}(t)$ vs. t plot can be determined using randomization or Monte Carlo methods (Manly 1991). The Monte Carlo approach is appropriate when testing for departures from spatial randomness (Kenkel 1988). In this study, however, we used a randomization procedure to test for departures from random mortality at each of 8 age intervals (ages 15-20, 20-25, 25-30, 30-35, 35-41, 41-46, 46-51 and 51-56). As an example, consider the interval from age 20 ($n = 457$) to 25 ($n = 388$). Random mortality confidence limits for the spatial pattern at age 25 were determined as follows: (1) randomly select and remove $457 - 388 = 69$ individuals from the age 20 data (this represents random mortality of 69 individuals in the age interval 20-25); (2) determine the $\widehat{L}(t)$ vs. t plot for this 'random mortality'

data set; (3) repeat the first two steps 100 times; (4) use the maximum and minimum values of these 100 simulations to define a 'random mortality' confidence envelope (Kenkel 1988) for stand age 25. Using the same approach, we also tested the hypothesis of random mortality over the entire 41 years of the study, by comparing the spatial pattern at age 56 to that expected given random mortality of the age 15 spatial pattern.

The degree of 'local crowding' experienced by each tree was determined as the area of its corresponding Voronoi-Delaunay polygon (Okabe et al. 1992). Polygon (tile) areas were determined by computing the Voronoi-Delaunay tessellation, which subdivides or 'tiles' the study plot such that any given region is assigned to the nearest individual in the population (Mead 1966). Each tree therefore occupies a polygon that defines its 'area of available resources' (Firbank & Watkinson 1987). Polygons are computed based on neighbour proximity, and do not consider neighbour size. Voronoi-Delaunay tessellations were computed for seven of the stand ages (20-46), after accounting for edge effects (Kenkel et al. 1989b). Polygon areas were determined for each tree, and trees were classified as either alive or dead by the next measurement period. Mean polygon areas were then compared using a *t*-test, to determine whether dying trees were experiencing greater local crowding (i.e. had smaller polygon areas) than surviving trees.

Results

Life table and mortality analysis

Mortality rate for the 15 - 20 age period is low, indicating that the stand has not yet reached the density-dependent mortality stage (Table 1). Mortality increases after age 20, with the highest mean mortality rate occurring between ages 30 - 35. Mortality rates decline after age 35, and by age period 51 - 56 mortality is quite low. Ca. 84 % of the trees died over the 41 yr of the study, with the majority (ca. 72 %) dying between stand ages 25 - 46. The mortality curve (Fig. 1) shows a clear sigmoidal trend (fit by the Richards function), with an inflection point at age 28.

Self-thinning curve

Between the ages 15 - 20, the appreciable increase in total biomass combined with very low mortality indicate that the stand has not yet reached the self-thinning line (Fig. 2). Between stand ages 20 - 30, mortality increases and a 'leveling-off' of total stand biomass is apparent. The slope of the principal component fitted to stand ages 30 - 56 is -0.162 ($n = 6$, $R^2 = 0.88$, 95 % limits: -0.079 , -0.245). This principal component is shown in Fig. 2, together with a line of expected slope -0.5 (the theoretically predicted value under the self-thinning rule; Weller 1987). Principal component slopes were computed for four total biomass equations for *P. banksiana* (using $n = 6, 7$ and 8 data points), as summarized in Table 2. Hegyi's equation produced the steepest

Table 1. Summary of mortality trends in the study plot.

Age interval (yr)	Number of trees	Number of trees dying	Annual mortality rate
15-20	468 ¹	11	0.0047
20-25	457	69	0.0322
25-30	388	90	0.0514
30-35	298	101	0.0794
35-41	197	55	0.0531
41-46	142	37	0.0586
46-51	105	21	0.0436
51-56	84	8	0.0198

¹Number of living trees at start of age interval.

slopes, and slope values were steeper when more data points were included. In all cases, however, the 95% confidence limits did not include the theoretically predicted value of -0.5 .

Size (DBH) distributions

Distributional asymmetry (skewness) is very low at age 15 (Table 3), but increases (positive skewness, L-shaped curve) over the period of greatest mortality (ages 25 - 46). Skewness declines again between ages 46 - 51, and by age 56 the size distribution displays little evidence of asymmetry. Size inequality, as measured by the coefficient of variation (CV), shows a somewhat different trend. CV is initially high (age 15) and continues to increase prior to the onset of high stand mortality

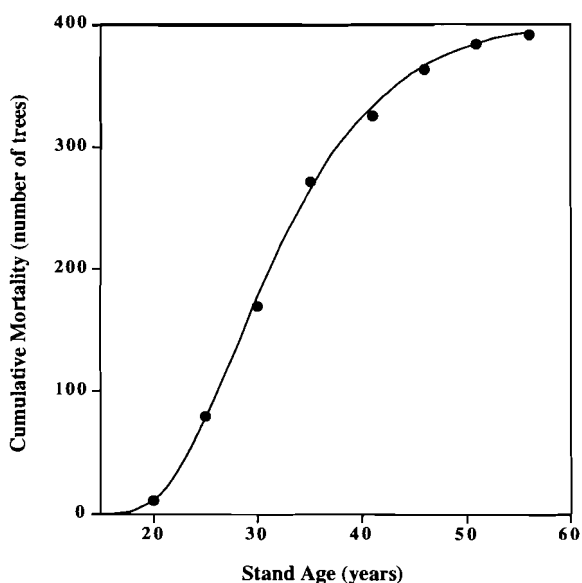


Fig. 1. Cumulative mortality in a *Pinus banksiana* stand, fitted to the Richards function.

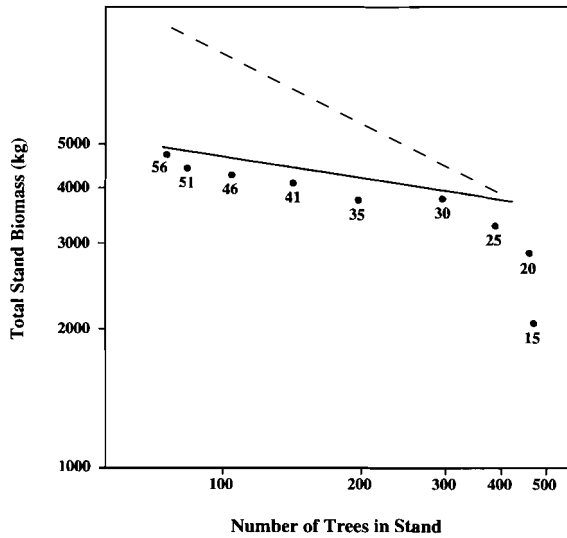


Fig. 2. Self-thinning relationship for a 0.04 ha *Pinus banksiana* stand. The solid line is the principal component of the six leftmost points, ages 30 - 56 (slope = -0.162, $R^2 = 0.88$). The dashed line has slope -0.5, the theoretically expected value.

(ages 20 - 25). Size inequality declines with the onset of appreciable stand mortality (age 30 - 46), and levels off at a lower value by ages 46 - 56. Mortality is restricted to the smallest trees throughout the study period (Fig. 3). A plot of mean size (DBH) at each measurement year for each of eight 'age at death' classes is presented in Fig. 4. These results indicate that the size hierarchy achieved by stand age 15 is a good predictor of subsequent trends in stand mortality. The smallest trees are the first to die, whereas the largest trees at age 15 have a much higher likelihood of surviving the self-thinning stage. These results also demonstrate that trees show very little increase in size (DBH) in the 5 - 10 yr prior to their death.

Table 2. Comparison of self-thinning slopes (principal component) using four published biomass equations and three age intervals. R^2 values are in brackets.

Age interval (yr)	Hegy	Ker	Zavitkovski et al.(1981)	
	(1972)	(1980)	'Isabella'	'Pembine'
30-56 (n = 6)	-0.162 (0.880)	-0.119 (0.818)	-0.100 (0.752)	-0.078 (0.664)
25-56 (n = 7)	-0.181 (0.922)	-0.142 (0.886)	-0.119 (0.849)	-0.100 (0.800)
20-56 (n = 8)	-0.218 (0.905)	-0.175 (0.871)	-0.150 (0.838)	-0.127 (0.800)

Table 3. Summary of population size structure characteristics in the study plot.

Age (yr)	Mean DBH (cm)	Asymmetry ¹ (skewness)	Inequality ¹ (CV)
15	4.65	0.054	30.53
20	5.36	0.197	34.24
25	6.07	0.238	33.40
30	7.19	0.397	31.86
35	8.64	0.409	27.43
41	10.34	0.365	25.23
46	12.06	0.461	21.03
51	13.41	0.172	20.93
56	14.34	0.075	20.99

¹of size (DBH) distributions.

Spatial autocorrelation

Prior to heavy mortality (ages 15 - 20), spatial autocorrelation of tree sizes is positive (Table 4). A decline in positive autocorrelation occurs between stand ages 25 - 41, as mortality rates increase. Spatial autocorrelation increases again at later stages of stand development (ages 46 - 56), although statistical significance is not achieved.

Spatial pattern analysis

Nearest neighbour pattern analysis (modified Clark-Evans statistic, Table 4) indicates a highly clumped spatial pattern at age 15. This persists up to age 30, but by age 35 the spatial pattern does not significantly deviate from random. An overall trend toward increasing spatial regularity occurs between stand ages 35 - 56.

Comparisons of Voronoi-Delaunay polygon areas between living and dying trees in each of six time intervals (ages 20 through 51) are summarized in Table 5.

Table 4. Summary of nearest-neighbour spatial pattern (Clark-Evans CE-statistic) and spatial autocorrelation (Moran's I-statistic) of DBH values in the study plot.

Age (years)	Clark-Evans (CE)		Moran	
	(CE)	P^1	I	P^2
15	-4.912	< 0.001	0.135	<0.001
20	-5.165	< 0.001	0.114	<0.001
25	-3.828	< 0.001	0.036	0.097
30	-2.714	0.003	0.010	0.348
35	0.785	0.216	0.005	0.404
41	0.751	0.226	-0.004	0.472
46	1.693	0.045	0.054	0.132
51	1.259	0.104	0.060	0.131
56	1.523	0.064	0.040	0.212

¹Probability of obtaining a value > ICEI.

²Probability of obtaining a value > I.

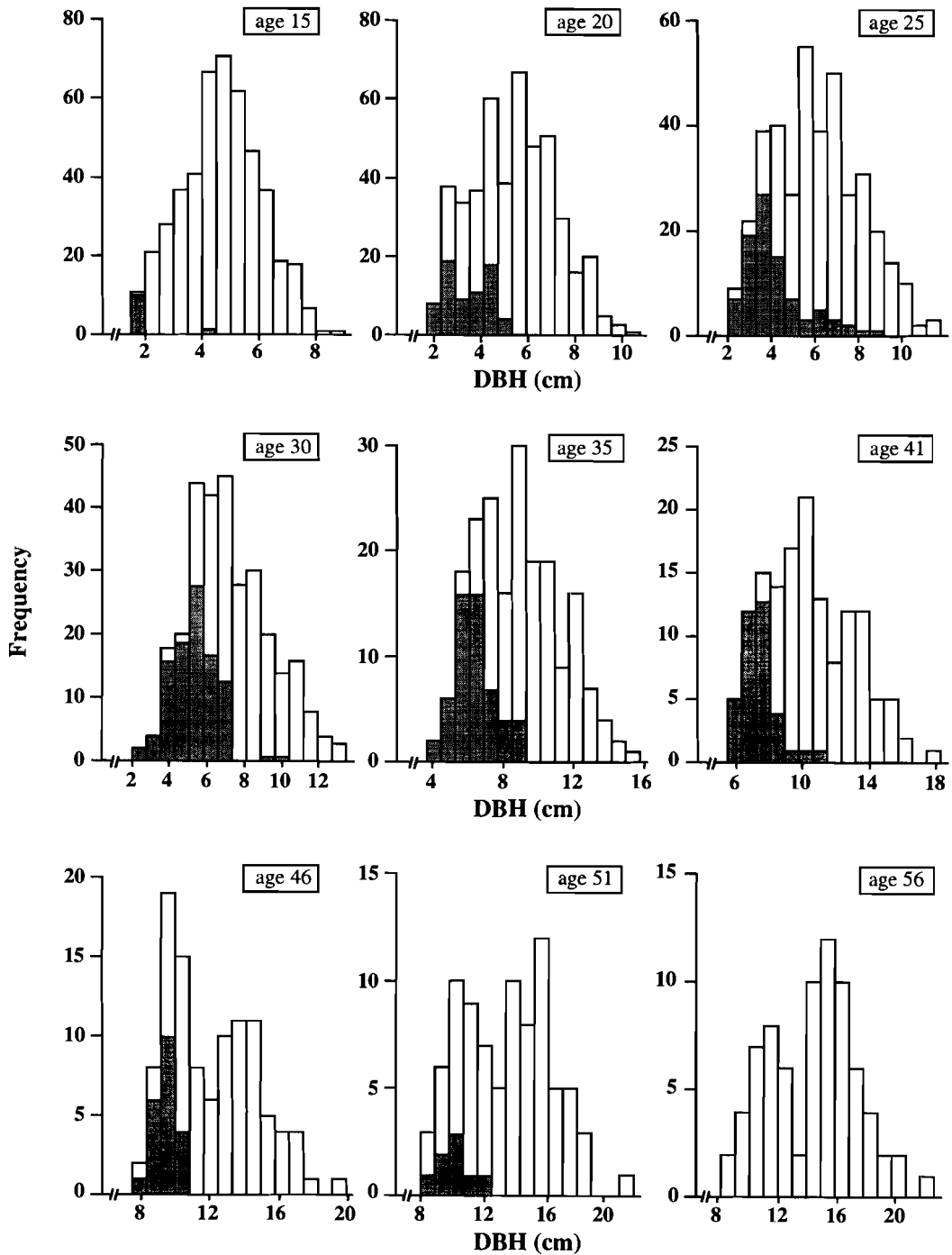


Fig. 3. Frequency histograms of size (DBH) for each of nine stand ages. Shaded areas are trees dying in the subsequent age class. For clarity, each histogram is represented by 15 classes. Note that the scaling of classes differ between histograms.

Between stand ages 20 - 30, dying trees experienced on average greater degrees of local crowding (occupied smaller polygons) than surviving trees, indicating that mortality is restricted to high density patches in the stand. This is generally not the case during the period of

highest stand mortality (ages 30 - 46), however. With the exception of the 35 - 41 age period, degree of local crowding (tile area) is unrelated to the probability of mortality. For the ages 46 - 51 period, dying trees again experienced greater local crowding than surviving trees.

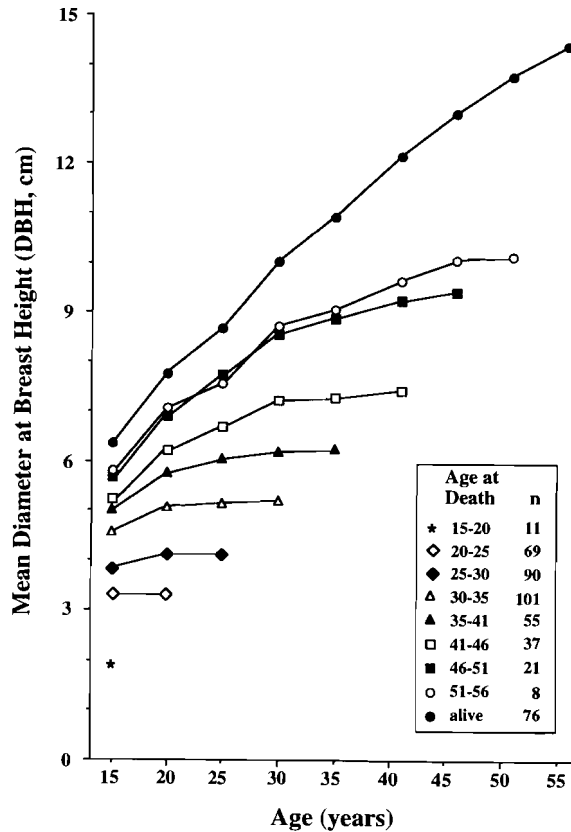


Fig. 4. Mean DBH as a function of stand age, for each of the eight 'age at death' classes.

Second-order spatial pattern and 'random mortality' test results are presented in Fig. 5. Only 11 trees died between stand ages 15 - 20, and the mortality pattern does not deviate from random expectation. Between ages 20 - 25, mortality deviates significantly from random expectation at all spatial scales, since mortality is restricted to high density patches of the stand. A similar trend appears between ages 25 - 30; deviations from random mortality are significant at higher spatial scales (3 - 6 m), again reflecting greater mortality in higher density patches of the stand. The spatial pattern of mortality changes with the onset of strong self-thinning (stand ages 30 - 46), with significant deviations from random mortality occurring only at local spatial scales (generally between 1 - 2 m). Between ages 20 - 46 a consistent trend toward greater spatial regularity emerges. Mortality rates fall by ages 51 - 56, and the mortality pattern is random.

We also tested the hypothesis that the spatial pattern at age 56 could have arisen through random mortality in the 15 yr-old stand. The results (Fig. 6) indicate that, over all local spatial scales (0 - 4.5 m), the observed spatial pattern at age 56 deviates significantly from what would be expected given random mortality.

Table 5. Summary of mean Voronoi tile areas at various ages in the study plot. Sample sizes are in brackets.

Age (years)	Mean Voronoi Tile Area (m ²)		P ¹
	Live	Dead	
20	0.862 (292)	0.5472 (62)	<0.001
25	1.215 (209)	0.843 (76)	0.017
30	1.357 (138)	1.243 (67)	0.311
35	2.045 (94)	1.434 (33)	0.002
41	2.642 (62)	2.381 (23)	0.977
46	3.649 (47)	2.496 (11)	0.011

¹Probability of no mean difference between live and dead tile areas.

²Mean tile area (at age 20) for trees dying in the 20-25 age interval.

Dynamic interaction of size and spatial structures

We present here a brief summary of stand dynamics, and the interaction between population size and spatial structures. For simplicity, we have divided the 41-year study period into four stages of stand development:

Stage I. Density-independent (ages 15-20)

The combination of very low stand mortality and high biomass accumulation indicates that the stand has not reached the self-thinning stage. The spatial pattern is highly clumped at all scales, indicating the presence of alternating high and low density patches within the stand. The size (DBH) distribution is symmetrical, and size inequality is highest at age 20. Positive spatial autocorrelation of tree sizes is indicated, with smaller trees occupying the higher density patches within the stand.

Stage II. Approach to the self-thinning line (ages 20-30)

Stand mortality increases as the self-thinning line is approached. While the spatial pattern remains clumped, the concentration of mortality within high density patches reduces clumping at all spatial scales. Differential mortality of smaller trees results in the development of a positively skewed size distribution, and reduces size inequality. Positive spatial autocorrelation of tree sizes is no longer statistically significant, the result of differential mortality of clumps of small trees in the high density patches of the stand. The tessellation results indicate that relative proximity of neighbours is the primary determinant of mortality pattern at this stage.

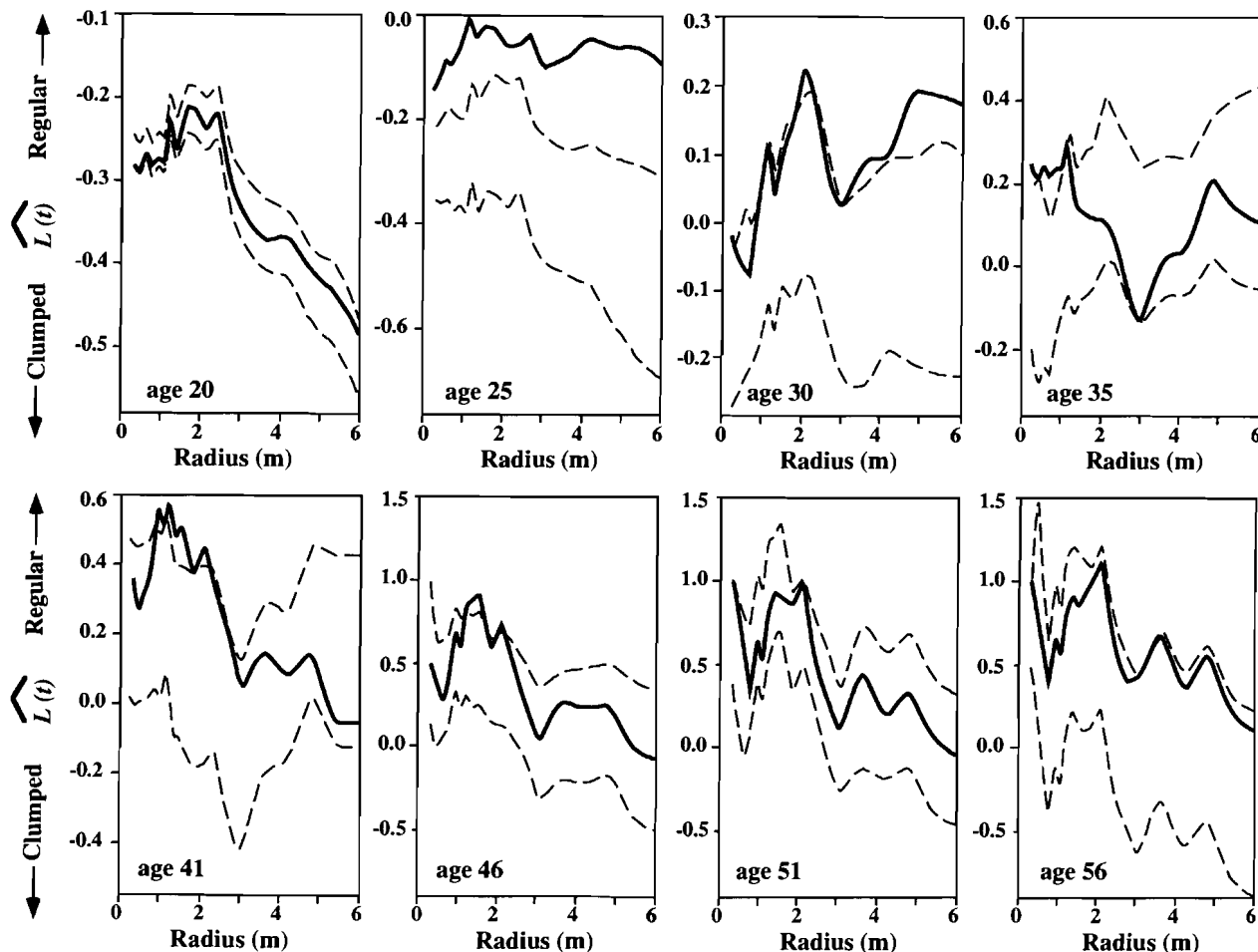


Fig. 5. Second-order spatial analysis, relating intensity of spatial pattern $\widehat{L}(t)$ and scale. The thick line is the observed pattern. Dashed lines delimit the ca. 95 % confidence interval (100 random simulations) given random mortality since the previous age class.

Stage III. High density-dependent mortality (age 30 - 46)

Stand mortality is highest at this stage, peaking between ages 30-35. A strong shift in the pattern of mortality is seen, from a concentration of mortality in high density phases (Stage II) to an even distribution of mortality across the stand. This results in increased spatial regularity, particularly at local (near-neighbour) spatial scales. The tessellation results indicate that mortality is largely independent of neighbour proximity at this stage, suggesting that neighbour size is the primary determinant of mortality. Mortality continues to be restricted to the smaller size classes, resulting in further increases in size asymmetry and decreases in size inequality. The lack of spatial autocorrelation in tree sizes at this stage may be attributable to high mortality rates.

Stage IV. Low density-dependent mortality (age 46 - 56)

Mortality rates decline considerably during this stage, and the locally regular spatial pattern established by age 46 is maintained. Asymmetry in the distribution of tree sizes declines, and by age 56 the distribution is only slightly positively skewed. Size inequality remains more or less constant (CV = 21%). Positive spatial autocorrelation of tree sizes emerges at this stage, though statistical significance is not achieved. This may be explained by the fact that, following considerable stand mortality (Stage III), the only small trees remaining in the stand are those surrounded by other smaller-than-average trees.

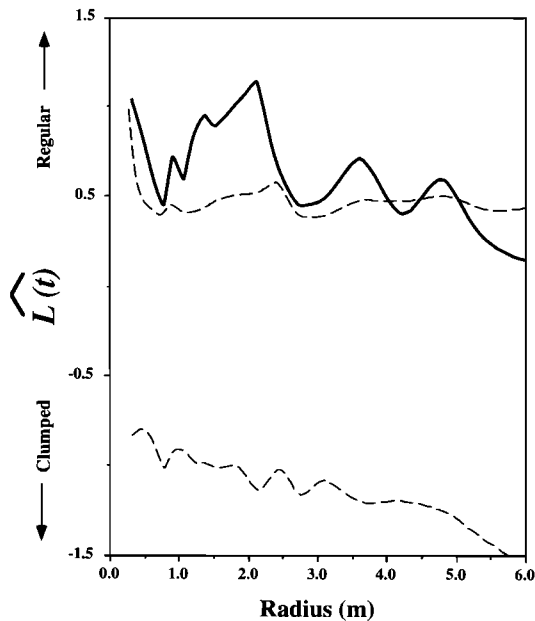


Fig. 6. Second-order spatial analysis of the stand at age 56 (thick line). The dashed lines delimit the ca. 95 % confidence interval given random mortality, based on the spatial pattern at age 15.

Discussion

It is generally assumed that resource competition leads to the development of size hierarchies in plant populations, and that 'local' competition for limiting resources determines mortality patterns in forest stands (Kenkel et al. 1989a). Mechanistically, asymmetric competition for light is thought to predominate once individuals are large enough to shade one another (Hara 1985; West et al. 1989; Weiner 1990). It may be pointless to the search for a single limiting factor, however, since competition is an integrated function of total resource availability (Cannell & Grace 1993). Trees weakened by density-dependent resource competition are also more susceptible to pathogens (Burdon et al. 1994), defoliators, and other 'density-independent' events (Franklin et al. 1987; Vacek & Lepš 1996). Mortality trends are thus determined by a complex, synergistic interaction between population size and spatial structures, as emphasized in the sequel.

Mortality trends

We found that ca. 84 % of the trees died over 41 years, with stand mortality peaking between ages 30 - 35. Our results agree with the observation that the period of competitive mortality occurs earlier, and for a shorter period of time, in tree species that grow and mature rapidly (Franklin et al. 1987; Peet & Christensen

1987). The *P. banksiana* mortality curve is sigmoidal and shows good fit to the Richards function. Other examples of sigmoidal mortality trends in natural stands include jack pine in northern Ontario (Yarranton & Yarranton 1975), black spruce in north-eastern Ontario (Carleton & Wannamaker 1987), chaparral shrub in California (Schlesinger & Gill 1978), and fir forests in the Adirondacks and Japan (Sprugel 1984). By contrast, Peet & Christensen (1980) found an almost linear mortality curve for loblolly pine in North Carolina.

Our results indicate that, over the entire 41 years, mortality is restricted to the smallest individuals in the stand. Lee (1971) obtained similar results for lodgepole pine, a species closely related to jack pine. A number of studies in both planted and natural forest stands have shown that mortality is generally restricted to the smallest size classes (e.g. West & Borough 1983; Hara 1985; Peet & Christensen 1987; Nilsson & Albrektson 1994; Nagashima et al. 1995). In Japanese birch stands, Kikuzawa (1993) found that the size hierarchy established early on was maintained over the course of stand development (see also Watkinson et al. 1983; Nilsson & Albrektson 1994). Our results indicate that the size hierarchy established by age 15 (prior to self-thinning) is a good predictor of long-term survivorship trends (Fig. 4), implying that early-established size differences are accentuated during stand development (Benjamin & Hardwick 1986).

Self-thinning

While early studies found that most tree species adhere closely to a self-thinning line of slope -0.5 , the generality of the self-thinning slope has recently been questioned (Weller 1987; Zeide 1985, 1987; Osawa & Sugita 1989; Lonsdale 1990). Most analyses based on stand yield table data have found self-thinning slopes steeper than -0.5 . However, using forest yield data for such purposes is highly problematic. Lonsdale (1990) notes that much yield table data are based on low-density forest plantations, and generally report only stem or merchantable timber (a subset of the stand) rather than total biomass. Furthermore, using tree bole mass (or volume) to fit a self-thinning line is problematic unless it can be demonstrated that the bole is a constant fraction of total biomass (Sprugel 1984). This is generally not the case: in jack pine, for example, 11 - 20 yr old trees have ca. 48 % of total biomass contained in the bole, but this increases to > 80 % after age 30 (Hegyí 1972). Bole mass (or volume) therefore disproportionately underestimates the total biomass of younger trees, resulting in an inflated (more negative) estimate of the self-thinning slope.

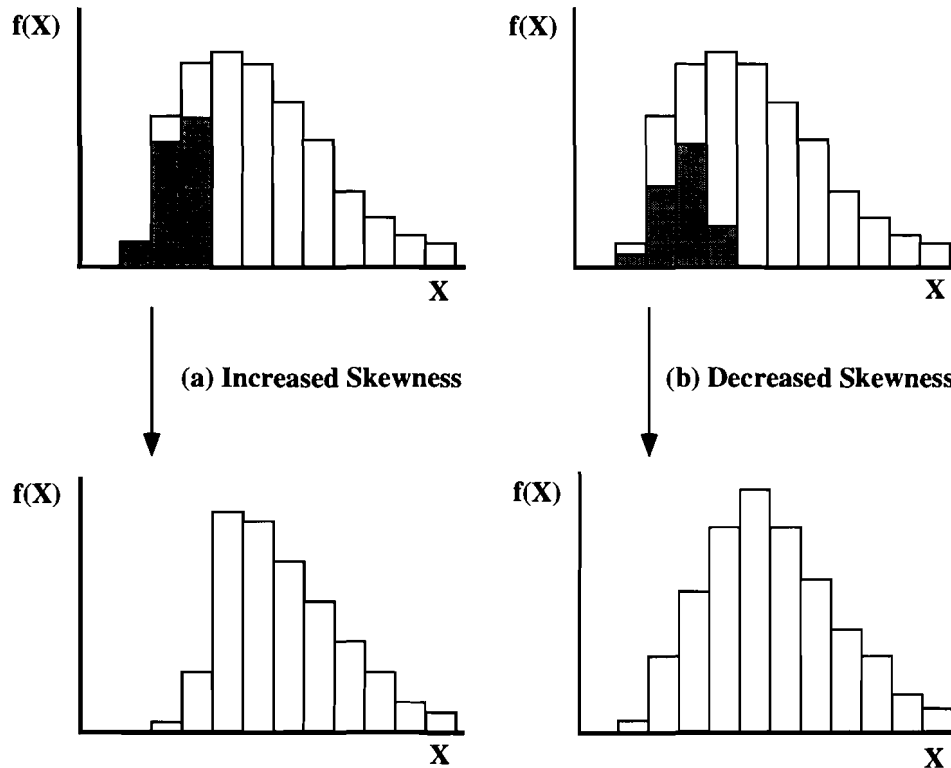


Fig. 7. Illustration of possible changes in distributional asymmetry (skewness) of survivors under two mortality scenarios. Shaded areas represent tree dying. In case (a), asymmetry (positive skewness) is increased; in case (b) it is decreased.

We found that the self-thinning line for jack pine is significantly less steep than the theoretical value of -0.5 . Analyses based on actual forest stand data, rather than yield tables, have often found slopes less steep than -0.5 (e.g. Mohler et al. 1978; Schlesinger & Gill 1978; West & Borough 1983; Sprugel 1984; Verwijst 1989; Kikuzawa 1993). The present study offers further support to Sprugel's (1984) contention that woody plants generally have self-thinning slopes less steep than -0.5 .

Size inequality and asymmetry

In this study, size (DBH) inequality peaked at age 20 (prior to the onset of self-thinning), and then declined during the stage of strong density-dependent mortality (ages 20 - 46) to a stable value between ages 46 - 56. Knox et al. (1989) obtained similar results for stands of loblolly pine (see also Weiner & Thomas 1986). A decrease in size inequality during self-thinning has generally been attributed to higher mortality in the smaller age classes.

The dynamics of size distribution asymmetry in even-aged stands is complex. Mohler et al. (1978) proposed that size distributions become increasingly positively skewed (L-shaped) prior to the onset of self-

thinning, but that skewness decreases during self-thinning since mortality is restricted to smaller size classes. Many studies have confirmed this trend (e.g. Ford 1975; Mohler et al. 1978; Schlesinger & Gill 1978; Hara 1985). However, Knox et al. (1989) found that size distributions of natural *Pinus taeda* stands were generally symmetric prior to self-thinning, and became increasingly positively skewed during self-thinning (see also Peet & Christensen 1987). The observation that natural stands of *P. taeda* (Knox et al. 1989) and *P. banksiana* (present study) have symmetric size distributions prior to self-thinning contrasts strongly with the hypothesis (Mohler et al. 1978) of maximum skewness at this stage. In this study, a combination of substrate uniformity, simultaneous (post-fire) germination, and low genetic variability may account for the observed symmetric size distribution prior to self-thinning (see also Weiner & Thomas 1986).

In this study, a symmetric size (DBH) distribution prior to the onset of self-thinning became increasingly positively skewed during the period of greatest density-dependent mortality (stand ages 30 - 46). Positive skewness declined between ages 46 - 56, and by age 56 the size distribution was again symmetric. Previous investigators have stated that differential mortality of

the smallest individuals (left-truncation of the distribution) results in: (1) increased symmetry, if the initial distribution is positively skewed (e.g. Mohler et al. 1978); (2) greater positive skewness, if the initial distribution is symmetric (e.g. Knox et al. 1989). However, our results indicate that the situation is more complex. We propose that it is the size distribution of dying individuals that determines change in the distribution of survivors. Consider a positively skewed initial distribution (Fig. 7). Two cases are illustrated: (a) very high mortality in the smallest size classes, which increases positive skewness of survivors; (b) less severe mortality in the smallest size classes, which decreases positive skewness. In our study, case (a) predominates during the high mortality phase of self-thinning (e.g. ages 41 - 46, Fig. 3), whereas case (b) occurs later, during the low mortality phase (e.g. age 46 - 51, Fig. 3). In practice, the situation is complicated somewhat by differences in the growth rates of surviving individuals (Westoby 1982).

Spatial pattern

Although few studies have investigated long-term changes in the spatial pattern of forest stands, it has been suggested that differential mortality promotes the development of increased spatial regularity over time (e.g. Antonovics & Levin 1980; Huston 1986). This suggestion is based on studies demonstrating that older stands of a given species tend to show greater spatial regularity than do younger stands (e.g. Cooper 1961; Laessle 1965). A more convincing argument can be made if it can be demonstrated that stand mortality patterns deviate from random expectation (e.g. Kenkel 1988; Kenkel et al. 1989a). Alternatively, changes in spatial pattern can be followed in a single stand. Both approaches have been used in this study. Nearest neighbour analysis indicated that a systematic change in spatial pattern occurs over time, from a clumped pattern at early stages of stand development (ages 15 - 30), to a random pattern at intermediate stages (ages 30 - 41), and a tendency toward spatial regularity at later stages (ages 41 - 56). Second-order spatial analysis gives a more complete picture of stand spatial pattern dynamics. Deviations from random mortality occurred between ages 20 - 46, but the spatial scale of these deviations varied. Between ages 20 - 30, deviations from random mortality occurred at higher spatial scales, reflecting differential mortality in higher density phases of the stand. Once the stand reached the self-thinning line (ages 30 - 46), however, deviations from random mortality occurred only at local spatial scales, suggesting that trees compete directly only with their immediate neighbours (cf. Kenkel 1988). These results can be explained by taking a dynamic view of the self-thinning process. When

spatial pattern is initially clumped, high-density stand patches will reach the self-thinning stage earlier than will low-density patches. Density-dependent mortality first occurs in these high-density patches ('local' self-thinning). As the stand develops, more and more regions begin to undergo self-thinning, until eventually the entire stand reaches the self-thinning stage ('global' self-thinning).

Spatial autocorrelation

In an early study of spatial autocorrelation in forest stands, Cooper (1961) found a negative correlation between nearest neighbour size 'as would be expected' (see also Ford & Diggle 1981). For forest plantations, (Reed & Burkhart 1985; see also Liu & Burkhart 1994) hypothesized that spatial autocorrelation of tree size changes over time: (1) in young stands, variation in microsite conditions results in positive autocorrelation; (2) as the stand develops (but prior to self-thinning), spatial autocorrelation becomes negative as individuals 'lose their place' in the stand; (3) stand mortality results in the removal of smaller individuals, resulting in the development of positive autocorrelation. In a 65-year-old jack pine stand, Kenkel et al. (1989a) found that tree diameters showed significant positive autocorrelation. In explaining this result, they hypothesized that only small trees that are surrounded by other small trees will have survived the self-thinning stage. In the present study, tree sizes showed positive autocorrelation prior to the onset of self-thinning. The stand spatial pattern is clumped at this stage, and smaller trees are concentrated together in high density stand patches. These smaller trees are the first to die, reducing autocorrelation. Spatial autocorrelation does not deviate from random expectation during the period of greatest density-dependent mortality (ages 25 - 40), presumably because the highly dynamic nature of near-neighbour relationships precludes the development of strong size-spatial relationships. The tendency for positive autocorrelation to develop at later stages of stand development (ages 46 - 56) supports the hypothesis that older stands display positive size autocorrelation (Kenkel et al. 1989a).

In conclusion, our results illustrate how a pluralistic approach integrating population size and spatial structures can offer new insights into the long-term dynamics of plant populations. In particular, we have demonstrated the strong interdependence between population size and spatial structures. Since changes in stand spatial pattern, mortality trends, spatial autocorrelation and size distribution are irrevocably linked, their simultaneous analysis results in a much more complete view of stand dynamics than would be obtained from a series of independent analyses.

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