Local competition in a naturally established jack pine stand

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The spatial pattern of 1375 jack pine individuals (459 live, 257 standing dead, and 659 stumps) in a pure, even-aged, naturally established stand was mapped. Three maps corresponding to different stages of stand development were recognized: live + dead (initial pattern, $n = 1375$), live (following self-thinning, $n = 459$), and live + standing dead (survivors plus most recent mortality, $n = 716$). The Dirichlet-Thiessen tessellations of these maps indicated that the distribution of tile areas (area potentially available) becomes increasingly equitable over time. A significant positive correlation between diameter at breast height of surviving trees and their area potentially available was found for each map; this correlation was highest for the live tessellation. In the live + dead and live + standing dead tessellations, the mean tile area of dead trees was significantly smaller than that of survivors. The spatial pattern of diameter at breast height values of survivors revealed a positive autocorrelation: larger trees tend to have large neighbours and smaller trees have small ones. These results suggest a model of differential mortality in which the smaller individuals in a stand, particularly those surrounded by larger individuals, are most likely to die over a given time interval.

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La distribution dans l'espace de 1375 pins gris (459 vivants, 257 morts dressés et 659 souches) dans un peuplement pur, de même âge, établi naturellement est cartographiée. Trois cartes correspondant aux différents stades de développement du peuplement sont reconnues : vivants et morts (distribution initiale, $n = 1375$), vivants (suite à un éclaircissement autonome, $n = 459$), et vivants et morts dressés (suivants et morts les plus récents, $n = 716$). Les tessellations de Dirichlet-Thiessen de ces cartes indiquent que la distribution des aires potentiellement disponibles devient de plus en plus juste avec le temps. Une corrélation positive significative entre le diamètre à hauteur de poitrine des arbres survivants et leur aires potentiellement disponibles est démontrée pour chaque carte. Cette corrélation est plus élevée pour la tessellation vivante. Dans les tessellations vivantes et mortes et vivantes et mortes dressées, l'aire potentiellement disponible des arbres morts est significativement plus petite que celle des survivants. La distribution dans l'espace des valeurs du diamètre à hauteur de poitrine des survivants révèle une autocorrélation positive : les arbres plus gros tendent à avoir des voisins plus gros, alors que les arbres plus petits en ont des petits. Ces résultats suggèrent un modèle de mortalité différente dans lequel les individus plus petits d'un peuplement, particulièrement ceux entourés par des individus plus gros, disparaîtront dans un intervalle de temps donné.

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Introduction

Studies of plant populations have until recently been largely devoted to the examination of the relationship between stand density and total yield (White 1980). However, greater emphasis is now being given to local competition in which interactions between the individual members of a population are emphasized. Given that the yield of an individual is influenced more by neighbourhood effects than overall stand density and that natural selection operates at this level, studies addressing local competitive effects may contribute further to our understanding of evolutionary processes in plants (Silander and Pacala 1985).

In an even-aged stand, variation in local crowding (a result of nonregular establishment) leads to the development of a hierarchy of plant sizes (Mack and Harper 1977; Mithen *et al.* 1984). However, other factors such as germination time, genotypic variability, and microhabitat differences may also contribute to the development of such a hierarchy (Firbank and Watkinson 1987). Size differences, however they arise, may be attenuated over time through asymmetric competition for light (Weiner and Thomas 1986), resulting in eventual mortality of the smallest (suppressed) individuals (e.g., Ford 1975; Gibson and Good 1986). Given an initially random spatial pattern of plants in a homogeneous environment, differential mortality during self-thinning may also result in the development of a regular spatial pattern over time (Antonovics and Levin 1980; Huston 1986; Lepš and Kindlmann 1987; Kenkel 1988).

Studies addressing the importance of local crowding in plant populations have generally utilized short-lived annuals sown at high density (e.g., Mack and Harper 1977; Watkinson *et al.* 1983; Mithen *et al.* 1984). These investigations have invariably found that local crowding can account for only a small proportion of the size variability observed. This led Firbank and Watkinson (1987) to suggest that differences in emergence time, microhabitat, and genotype may largely override the effects of local crowding, at least in dense stands of short-lived annuals. Others have suggested that this may be true of natural populations as well (e.g., Waller 1981; Cannell *et al.* 1984). However, Matlack and Harper (1986) found that local crowding played an important role in determining individual performance and survival in a natural population of the small perennial herb *Silene dioica*.

A number of empirically derived local competition coefficients have been developed to predict the future growth of individual plants, based on neighbour size and proximity (Daniels *et al.* 1986; Hara 1988). In most of these, arbitrary decisions

are made as to what constitutes a neighbour (Mack and Harper 1977) and the weights given to neighbour size and proximity (Weiner 1984). Note that such coefficients should only be used to predict future growth, since variable interdependence arises when an individual's competition index is related to its current size (Weiner 1984; Fairbank and Watkinson 1987).

Local crowding in even-aged stands can be investigated by defining an individual's "area potentially available" (APA; Brown 1965). This involves computation of the Dirichlet-Thiessen tessellation (Upton and Fingleton 1985, p. 96) or S-mosaic (Pielou 1977, p. 185), which subdivides or "tiles" a study area such that any given region is assigned to the nearest individual in the population (Mead 1966). Each individual therefore occupies a tile (or polygon) that defines its APA (or "area of available resources," Firbank and Watkinson 1987), which can in turn be used as a predictor of plant performance. Whether the APA corresponds to the "ecologically effective distance" of Antonovics and Levin (1980) is open to question, though recent evidence appears to suggest that local competition in forest trees is in fact largely restricted to interactions with tile edge neighbours (Cannell et al. 1984; Hara 1985; Kenkel 1988).

Most studies of local competition in trees have been based on even-aged, regularly spaced plantations (e.g., West and Borough 1983; Cannell et al. 1984; Daniels et al. 1986). Because local crowding is invariant in such stands, the development of a size hierarchy is presumably attributable to micro-habitat and genotypic variability. While these and other studies (e.g., Weiner 1984) have related the future growth of an individual to its current competitive status, few have addressed the role of initial spatial arrangement in determining the fate of individuals in naturally established forest stands.

A previous study (Kenkel 1988) demonstrated that spatial pattern in a jack pine stand changes over time: an established random pattern of trees becomes a highly regular one as self-thinning occurs. The objective of the present study is to determine whether local crowding (as defined by the spatial arrangement of trees) plays a role in determining survival probability and individual performance in the same stand.

Materials and methods

Species and study area

Jack pine (*Pinus banksiana* Lamb.) is a pioneer species of sandy soils and rock outcrops throughout much of the North American boreal forest. It produces serotinous cones that normally only release seed following a devastating crown fire. The species is therefore most commonly found in fire-prone areas, where it forms extensive, even-aged pure stands (Yarranton and Yarranton 1975). It is highly shade-intolerant and relatively short-lived, with greatest growth occurring in the first 50 years (Fowells 1965).

In July 1986, a 50 × 50 m study area was located at random within an extensive, even-aged (65 ± 1 year, n = 58) pure stand of jack pine. The site is on a uniform, flat, sandy podzolic substrate near Elk Lake, Ontario (47°50′N, 80°27′W). The stand, which established following a severe fire in the 1920s (Donnelly and Harrington 1978), contains trees averaging approximately 15 cm in diameter and 16 m in height. The understory is characterized by low ericaceous shrubs (principally *Kalmia angustifolia* L. and *Vaccinium myrtylloides* Michx.) and the moss *Pleurozium schreberi* (Brid.) Mitt. (vegetation type VII, Kenkel 1986). Variability in substrate conditions was determined from a grid of 25 soil samples taken from within the study area. All were classified as fine sand, and were uniformly acidic and nutrient poor. No spatial trends in substrate variability were indicated (see Kenkel 1988 for details).

Tree mapping

The 50 × 50 m study area was demarcated and subsequently gridded into twenty-five 10 × 10 m contiguous squares using a surveyor's transit. The coordinate position of each living, standing dead (snag), and dead (stump) individual was recorded within each square using a modification of the method suggested by Rohlf and Archie (1978) (see Kenkel 1988 for details). A total of 1375 individuals (corresponding to a stand density of 5500 trees/ha) were mapped, of which 659 were dead (stumps), 257 were standing dead, and 459 were alive. Diameter at breast height (DBH) was recorded for the live and standing dead trees.

Using the coordinate positions of the 1375 trees, three data sets representing different stages of stand development were recognized. The entire data set (live + dead, n = 1375), termed for convenience the "initial" pattern, represents the spatial pattern of individuals prior to the onset of density-dependent mortality. The live + standing dead (n = 716) represents the pattern of survivors plus those individuals that died most recently. Finally, the spatial pattern of survivors (live, n = 459) represents the current (July 1986) map of living trees (i.e., following death of approximately two-thirds of the "initial" population). The spatial pattern of these coordinate data sets was determined using the modified Clark-Evans (CE) statistic (Sinclair 1985; Kenkel 1988). The initial (live + dead) pattern is random (CE = 1.567, P = 0.117), whereas both the live + standing dead (CE = 3.767, P < 0.001) and live (CE = 5.560, P < 0.001) maps show a highly significant regular pattern.

Data analysis

Dirichlet-Thiessen tessellation

The Dirichlet-Thiessen tessellation (Upton and Fingleton 1985, p. 96) was computed for each of the three coordinate data sets (live + dead, live + standing dead, and live). Edge effect problems were avoided by excluding all tiles that could potentially be influenced by individuals lying outside the mapped area (Kenkel et al. 1989). By this criterion, the number of tiles utilized were as follows: live + dead, n = 1182; live + standing dead, n = 578; and live, n = 347. The area of each tile defined an individual's APA. These computations were performed using an interactive graphics program developed by the authors.
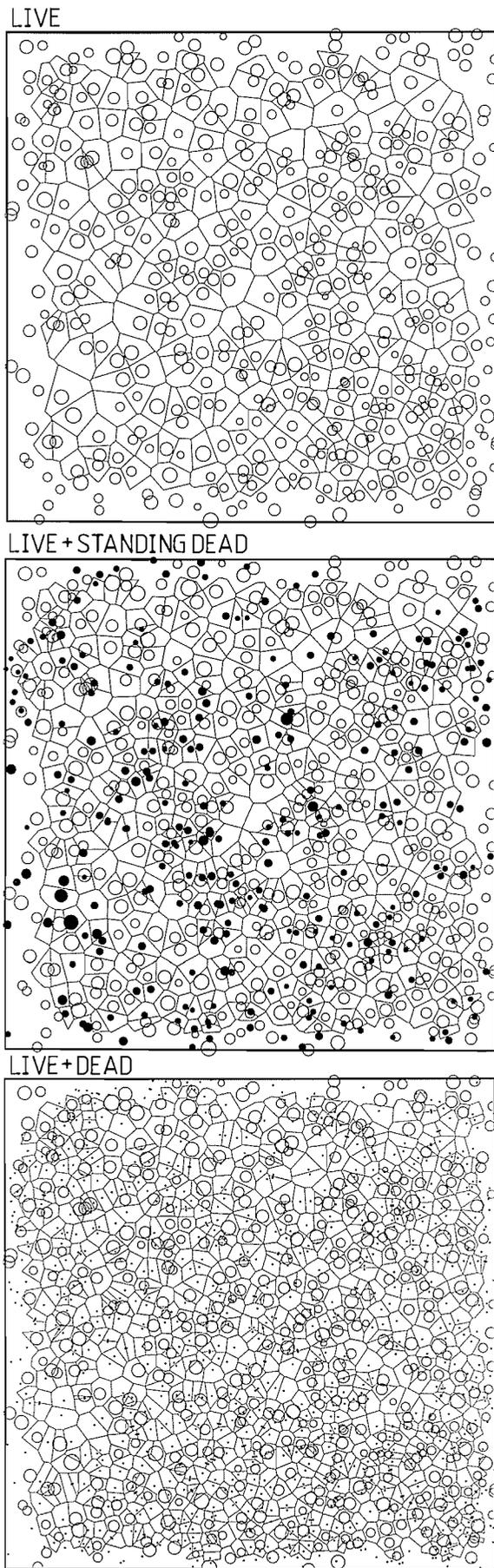
The distribution of tile areas, with its variability (coefficient of variation) and inequality (Gini coefficient; Weiner and Solbrig 1984), was determined for each of the three data sets. In addition, the product moment correlation was calculated between the current size (DBH) of surviving trees (n = 459) and their tile area (APA), again for each of the three data sets. For the live + dead and live + standing dead tessellations, the proportion of individuals surviving as a function of APA was calculated, and differences in the mean tile area between surviving and dead trees were determined using the Student's t-test.

Spatial autocorrelation

The spatial relationship of size (DBH) for the surviving trees (live, n = 459) was tested using Moran's I statistic (Moran 1948; Upton and Fingleton 1985, p. 170). For this purpose, joins were defined between individuals sharing a common boundary, as defined by the Dirichlet-Thiessen tessellation (cf. Reed and Burkhart 1985); edge effects were again considered. The calculated value of I is referred to the standard normal distribution. A negative value indicates that large trees are surrounded by smaller neighbours, and vice versa. If large trees are surrounded by large neighbours and smaller trees by small ones, spatial autocorrelation is positive (Cliff and Ord 1981, p. 42).

Results

The coordinate maps for each of the three data sets, together with their associated Dirichlet-Thiessen tessellations, are shown in Fig. 1. In Fig. 2, the distributions of tile areas (APA) for each of these three tessellations are shown. The coefficient of variation (CV) and Gini coefficient of inequality (G) values indicate that greatest variability and inequality are found for

LIVE

LIVE + STANDING DEAD

LIVE + DEAD

FIG. 1. Spatial pattern maps and associated Dirichlet-Thiessen tessellations for the three data sets. Tiles potentially influenced by individuals outside the mapped study area are not shown. Open circles denote surviving trees, solid circles (or dots) represent dead individuals. Circle size is proportional to tree diameter at breast height.

the initial (live + dead) pattern and that these values are least for the live pattern. Thus differential mortality in the stand over time results in a reduction in the variability and inequality of tile areas.

The influence of the APA on the size of surviving individuals was examined by correlating tile area with DBH of the surviving trees for each of the three data sets. For the live + dead tessellation, this resulted in a correlation $r = 0.215$ ($n = 401$, $P < 0.001$). For the live + standing dead tessellation, the correlation increases to $r = 0.277$ ($n = 370$, $P < 0.001$). The correlation is greatest for the live tessellation ($r = 0.324$, $n = 347$, $P < 0.001$). These correlations indicate that larger surviving trees tend to be associated with larger tiles (higher APA values). Furthermore, the degree of correlation increases with stand thinning, being greatest for the live tessellation.

The proportion of individuals surviving as a function of tile area (APA) is shown in Fig. 3. For the live + dead tessellation, the results indicate that the probability of survival increases with increasing tile area: while over half of the trees initially occupying tiles greater than 3.0 m^2 in area have survived, only about one quarter of those occupying the smallest tile areas (less than 1.0 m^2) remained alive in July 1986. Similar results were obtained for the live + standing dead tessellation, indicating that this trend also holds true for recent mortality. For both data sets, the mean tile area of the dead trees was significantly smaller than that of the living trees. For the live + dead tessellation, mean tile area for the living trees was $\bar{X}_L = 1.993$ m^2 ($n = 401$), whereas that for dead trees was $\bar{X}_D = 1.659$ m^2 ($n = 781$): Student's $t = 6.287$ ($P < 0.001$). For the live + standing dead tessellation, $\bar{X}_L = 3.564$ m^2 ($n = 370$) and $\bar{X}_D = 2.990$ m^2 ($n = 208$): Student's $t = 4.481$ ($P < 0.001$).

The size class (DBH) distribution of the 459 surviving individuals is shown in Fig. 4. The distribution is only slightly positively skewed, which is expected in stands having undergone substantial self-thinning (Hara 1985). Spatial relations in size (DBH) among the surviving trees indicated a positive spatial autocorrelation (Moran's $I = 0.062$, $n = 347$, $P = 0.017$). This indicates that the neighbours of large trees also tend to be large, whereas smaller trees tend to have small neighbours.

Discussion

Previous studies of local competition in forest trees have demonstrated that neighbour size is an important determinant of an individual's future growth (e.g., Cannell et al. 1984; Daniels et al. 1986). Because these studies dealt with evenly spaced plantation trees, the initial development of size differences must have been attributable to genotypic and habitat heterogeneity; subsequently, differences were presumably attenuated as a result of resource competition. The present study indicates that the spatial pattern of trees also plays a role in determining an individual's fate in forest stands. That individuals with small APA values are more likely to die has been previously demonstrated in populations of short-lived annuals (Watkinson et al. 1983; Matlack and Harper 1986).

Local crowding in the study area is a stochastic phenome-
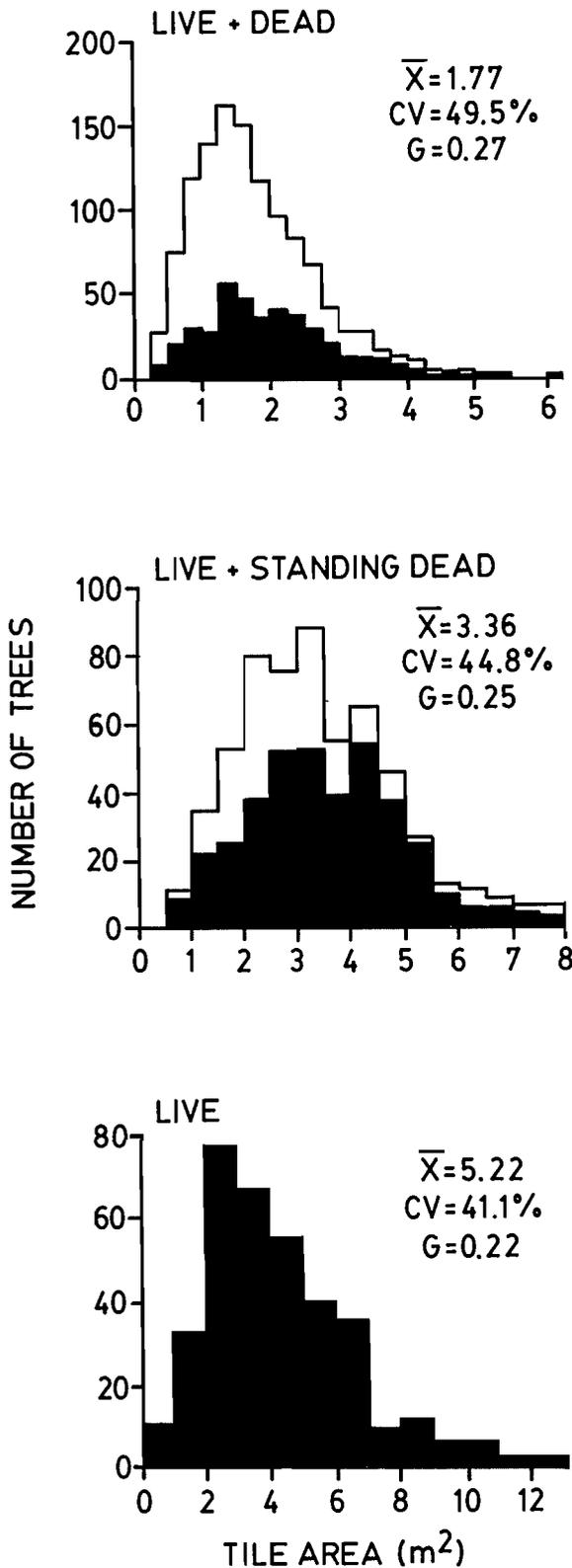
FIG. 2. Histograms of tile areas for each of the three tessellations shown in Fig. 1. The black areas denote surviving trees. $\overline{X}$, mean tile area; CV, coefficient of variation; G, Gini coefficient of inequality.
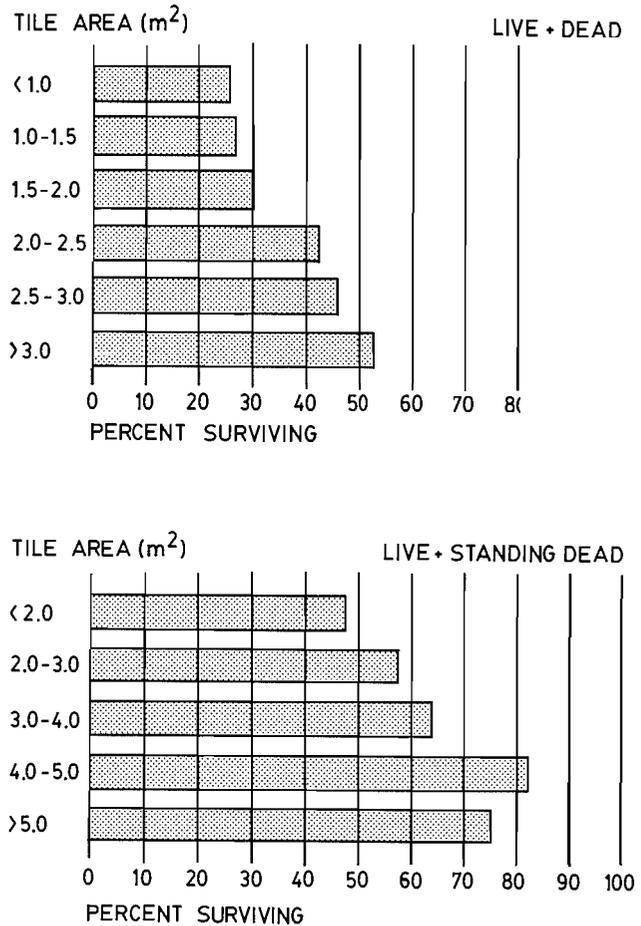

FIG. 3. The percentage of individuals surviving as a function of tile area for the live + standing dead and live + dead tessellations.

non, since neighbour proximity is determined by chance effects related to seed dispersal and initial establishment. Because survivorship is determined in part by the degree of local crowding experienced by an individual, spatial relations may play a role in determining an individual's probability of contributing seed to the next generation. Specifically, a genetically "inferior" individual, should it become established where local crowding is low, may survive until a devastating fire and therefore contribute seed. Conversely, an individual that establishes in an area of high local crowding may die before a fire event, irrespective of its genetic fitness. In this way, chance may serve to maintain high genetic diversity in a population. It is interesting to note that jack pine displays a high degree of intrapopulation genetic variability (Rudolph and Yeatman 1982), though the exact cause of this high diversity remains unknown.

The result indicating that the positive correlation between individual size (DBH) and tile area (APA) increases as self-thinning occurs is most readily explained in terms of a positive feedback mechanism. Mortality of a given individual increases the APA (and therefore the availability of resources) of its surviving tile edge neighbours: the larger the increase in a survivor's APA, the greater will be its increase in available resources. Such an individual will therefore grow larger and compete more effectively with its neighbours for these resources. This may in turn lead to mortality of one or more of its immediate neighbours, thus further increasing its APA. This is analogous to the development of a hierarchy in plant
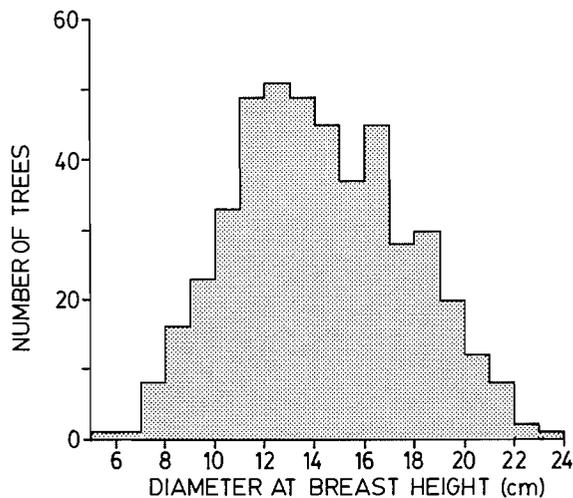
FIG. 4. Distribution of tree diameter at breast height of the surviving individuals ($n = 459$).

size resulting from asymmetric competition for light (Ford 1975; Weiner and Thomas 1986).

The distribution of tile areas was shown to become more equitable and less variable as self-thinning occurs; this is also indicative of a trend toward a more regular pattern of survivors (Hutchings and Discombe 1986). Indeed, a previous study (Kenkel 1988) indicated a shift from a random to a highly regular spatial pattern over time, consistent with theoretical expectations (Antonovics and Levin 1980; Huston 1986). However, such results contradict those obtained by Kent and Dress (1979). Their stochastic model for even-aged stands predicted that a random pattern of individuals at establishment will remain random as self-thinning occurs. Note, however, that their model did not incorporate neighbour effects. Its failure to correctly predict the changes in spatial pattern observed in this study indicates that neighbour effects should be included when modelling mortality patterns in pure, even-aged forest stands (Lepš and Kindlmann 1987).

A number of studies have indicated that the distribution of plant sizes, which is normal at the initial establishment stage, becomes increasingly positively skewed over time (e.g., Obeid et al. 1967). In some situations, the distribution may take on a bimodal appearance (Ford 1975; Huston and DeAngelis 1987). A highly skewed distribution, which is characteristic of populations prior to the onset of self-thinning, is generally attributed to asymmetric competition for light (Weiner and Thomas 1986). The distribution of plant sizes changes dramatically with the onset of self-thinning, however, since mortality is concentrated in the smallest size classes (Hara 1985). This results in the size distribution becoming progressively less skewed over time. The size (DBH) class distribution of Pinus banksiana observed in the present study (Fig. 4) is consistent with previous empirical results obtained for the conifers Abies balsamea (Mohler et al. 1978) and Picea sachalinensis (Hara 1985) following substantial self-thinning.

The observed positive spatial autocorrelation of tree size (DBH) is most readily explained by assuming that mortality is attributable to asymmetric competition for light. At early stages of stand development, density-independent factors such as habitat heterogeneity will often result in a positive autocorrelation of sizes. Once the trees become large enough that local competition for light becomes important, larger individuals

will begin to shade their smaller neighbours, slowing their growth and resulting in a suppressed subcanopy (West and Borough 1983). At this stage, a negative autocorrelation is expected, since large trees will tend to be surrounded by smaller, suppressed individuals (Ford and Diggle 1981). With the onset of mortality, these smaller trees will be selectively removed from the canopy. This will result in a positive autocorrelation of tree sizes, since only those small trees surrounded by other small trees will survive the self-thinning stage. Reed and Burkhart (1985) used a similar argument to explain the positive autocorrelation of tree size in populations of Pinus taeda.

In conclusion, this study has demonstrated the importance of initial spatial pattern on the growth and mortality of individuals in a pure, even-aged population of jack pine. A random pattern of individuals at early stages of stand development implies differences in the degree of crowding each experiences. This leads to differential growth rates within the stand that are attenuated over time as a result of asymmetric competition for light. Self-thinning results in a regular pattern of survivors and greater equitability in the distribution of the area potentially available to each. Thus the mortality pattern in even-aged plant populations is determined in part by the degree of local crowding each individual experiences. Future studies should focus on determining the importance of this stochastic factor relative to microhabitat and genetic variability, which have in the past received greater attention.

Acknowledgements

ANTONOVICS, J., and LEVIN, D. A. 1980. The ecological and genetic consequences of density-dependent regulation in plants. Annu. Rev. Ecol. Syst. 11: 411–452.

BROWN, G. S. 1965. Point density in stems per acre. N.Z. For. Res. Notes, 38: 1–11.

CANNELL, M. G. R., ROTHERY, P., and FORD, E. D. 1984. Competition within stands of Picea sitchenis and Pinus contorta. Ann. Bot. (London), 53: 349–362.

CLIFF, A. D., and ORD, J. K. 1981. Spatial processess: models and applications. Pion, London.

DANIELS, R. F., BURKHART, H. E., and CLASON, T. R. 1986. A comparison of competition measures for predicting growth of lobolly pine trees. Can. J. For. Res. 16: 1230–1237.

DONNELLY, R., and HARRINGTON, J. P. 1978. Forest fire history maps of Ontario. Can. For. Serv. Dep. Environ. Misc. Rep. FF-Y-6.

FIRBANK, L. G., and WATKINSON, A. R. 1987. On the analysis of competition at the level of the individual plant. Oecologia, 71: 308–317.

FORD, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. J. Ecol. 63: 311–333.

FORD, E. D., and DIGGLE, P. J. 1981. Competition for light in a plant monoculture modelled as a spatial stochastic process. Ann. Bot. (London), 48: 481–500.

FOWELLS, H. A. 1965. (Compiler). Silvics of forest trees of the United States. U.S. Dep. Agric., Agric. Handb. 271.

GIBSON, D. J., and GOOD, R. E. 1986. Population structure and thinning in natural stands of Atlantic white cedar (Chamaecyparis thyoides [L] BSP.). Oecologia, 69: 348–353.

HARA, T. 1985. A model for mortality in a self-thinning plant population. Ann. Bot. (London), **55**: 667–674.

—— 1988. Dynamics of size structure in plant populations. Trends Ecol. Evol. **3**: 129–133.

HUSTON, M. 1986. Size bimodality in plant populations: an alternative hypothesis. Ecology, **67**: 265–269.

HUSTON, M., and DEANGELIS, D. L. 1987. Size bimodality in monospecific populations: a critical review of potential mechanisms. Am. Nat. **129**: 678–707.

HUTCHINGS, M., and DISCOMBE, R. J. 1986. The detection of spatial pattern in plant populations. J. Biogeogr. **13**: 225–236.

KENKEL, N. C. 1986. Structure and dynamics of jack pine stands near Elk Lake, Ontario: a multivariate approach. Can. J. Bot. **64**: 486–497.

—— 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology, **69**: 1017–1024.

KENKEL, N. C., HOSKINS, J. A., and HOSKINS, W. D. 1989. Edge effects in the use of area polygons to study competition. Ecology, **70**: 272–274.

KENT, B. M., and DRESS, P. 1979. On the convergence of forest stand spatial pattern over time: the case of random initial spatial pattern. For. Sci. **25**: 445–451.

LEPŠ, J., and KINDLMANN, P. 1987. Models of the development of spatial pattern of an even-aged plant population over time. Ecol. Modell. **39**: 45–57.

MACK, R. N., and HARPER, J. L. 1977. Interference in dune annuals: spatial pattern and neighbourhood effects. J. Ecol. **65**: 345–363.

MATLACK, G. R., AND HARPER, J. L. 1986. Spatial distribution and the performance of individual plants in a natural population of *Silene dioica*. Oecologia, **70**: 121–127.

MEAD, R. 1966. A relationship between individual plant-spacing and yield. Ann. Bot. (London), **30**: 301–309.

MITHEN, R., HARPER, J. L., and WEINER, J. 1984. Growth and mortality of individual plants as a function of "available area". Oecologia, **62**: 57–60.

MOHLER, C. L., MARKS, P. L., and SPRUGEL, D. G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. **66**: 599–614.

MORAN, P. A. P. 1948. The interpretation of statistical maps. J. R. Stat. Soc., Ser. B, **10**: 243–251.

OBEID, M., MACHIN, D., and HARPER, J. L. 1967. Influence of density on plant to plant variations in fiber flax, *Linum usitatissmum*. Crop Sci. **7**: 471–473.

PIELOU, E. C. 1977. Mathematical ecology. John Wiley & Sons, New York.

REED, D. D., and BURKHART, H. E. 1985. Spatial autocorrelation in individual tree characteristics in loblolly pine stands. For. Sci. **31**: 575–587.

ROHLF, F. J., and ARCHIE, J. W. 1978. Least-squares mapping using interpoint distances. Ecology, **59**: 126–132.

RUDOLPH, T. D., and YEATMAN, C.W. 1982. Genetics of jack pine. U.S. For. Serv. Res. Pap. WO-38.

SILANDER, J. A., AND PACALA, S. W. 1985. Neighborhood predictors of plant performance. Oecologia, **66**: 256–263.

SINCLAIR, D. F. 1985. On tests of spatial randomness using mean nearest neighbor distance. Ecology, **59**: 126–132.

UPTON, G., and FINGLETON, B. 1985. Spatial data analysis by example. Vol. 1. Point pattern and quantitative data. John Wiley & Sons, New York.

WALLER, D. M. 1981. Neighbourhood competition in several violet populations. Oecologia, **51**: 116–122.

WATKINSON, A. R., LONSDALE, W. M., and FIRBANK, L. G. 1983. A neighbourhood approach to self-thinning. Oecologia, **56**: 381–384.

WEINER, J. 1984. Neighbourhood interference amongst *Pinus rigida* individuals. J. Ecol. **72**: 183–195.

WEINER, J., and SOLBRIG, O. T. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia, **61**: 334–336.

WEINER, J., and THOMAS, S. C. 1986. Size variability and competition in plant monocultures. Oikos, **47**: 211–222.

WEST, P. W., and BOROUGH, C. J. 1983. Tree suppression and the self-thinning rule in a monoculture of *Pinus radiata* D. Don. Ann. Bot. (London), **52**: 149–158.

WHITE, J. 1980. Demographic factors in populations of plants. *In* Demography and evolution in plant populations. *Edited by* O. T. Solbrig. Blackwell, Oxford. pp. 21–48.

YARRANTON, M., and YARRANTON, G. A. 1975. Demography of a jack pine stand. Can. J. Bot. **53**: 310–314.