COENOSES 5 (3): 149-158, 1990

# SPATIAL COMPETITION MODELS FOR PLANT POPULATIONS

N.C. Kenkel, Department of Botany, University of Manitoba, Winnipeg, Manitoba R3T 2N2 Canada

**Keywords**: Ecology, Forestry, Interaction, Neighbour, Nucleation, Pattern, Process, Tessellation, Vegetation

**Abstract.** This review summarizes the major spatial approaches to modelling intraspecific interactions in plants. Spatial models recognize that interactions in plant populations are localized, and therefore use the number, size, and proximity of neighbouring plants to predict an individual's performance. Such models have been used to develop interaction (or competition) indices, to assess the relative importance of spatial patterning on individual plant performance, and to examine mortality patterns and changes in the size distribution of individuals in field, laboratory, and computer-simulated plant populations. The review begins by outlining the competition (or interference) indices developed by foresters and ecologists, and discusses their utility and limitations. Next the 'zone of influence' model, which utilizes overlapping circles in quantifying intraspecific interactions, is reviewed. Specific applications of this model are outlined, examples given, and limitations discussed. This is followed by a detailed outline of spatial tessellation models, which have only recently been applied to examine spatial processes in plant populations. The paper concludes with a discussion of future directions, in which it is argued that tessellation methods should be more widely used in modelling dynamic interactions in plant populations.

## Introduction

There are many approaches to studying intraspecific interactions in plant populations. One is to consider the relationship between mean plant biomass and population density. This approach led to the development of the 3/2 self-thinning rule and related models (Harper 1977) which have recently been critically appraised by Weller (1987) and Zeide (1987). Another approach is to sow plants at various densities and undertake a statistical analysis of the resulting frequency distributions of plant 'size' or biomass (see Hara 1988).

The approaches described above are static, since interest is focused on the final outcome of the intraspecific interactions. Dynamic models, by contrast, examine changes in various population parameters over time. Some of these models are non-spatial in nature; rather than requiring information on the positions of individual plants, a mean 'neighbourhood effect' is assumed. These models, which may be stochastic or deterministic, monitor changes in mortality, mean plant biomass, population skewness, and so forth over time (for a complete discussion, see Hara 1988). Nonspatial dynamic interspecific (community-level) interaction models have also been developed, usually based on consumer-resource interactions (e.g. Grime 1979, Tilman 1988). Spatial interspecific interaction models include island or "patchy environment" simulations (Levin 1986, Pacala 1987), Monte Carlo simulation of local interactions in which a habitat is divided into grid units (Weiner and Conte 1981, Crawley and May 1987, Czárán 1989, Czárán and Bartha 1989), and diffusion models utilizing partial differential equations (Okubo 1980).

Spatial models of intraspecific (population-level) interactions require information about the pattern of individuals plants in a population. With such models one can examine the interaction between individuals and their neighbours, or what is known as 'local competition'. Local interactions between individuals are important, since an individual's fate (fecundity, probability of mortality, biomass, etc.) is determined not by the mean population density, but by the number, size, and proximity of its immediate neighbours (Mack and Harper 1977). Since natural selection operates at the level of the individual, such studies may also lead to a greater understanding of evolutionary processes in plants (Silander and Pacala 1985, Kenkel *et al.* 1989b).

This paper outlines spatial models for examining intraspecific interactions in plants. While simulation models are discussed, emphasis is placed on empirical population interaction models. The review begins with an overview of competitive interaction indices, which is followed by a summary of spatial overlap indices and models. Spatial tessellation models are outlined in the third section, and future directions and prospects are briefly discussed.

## Competition (Interference) Indices

The simplest model for describing competitive interference and examining the effect of local density on plant performance is to consider the distance to the nearest neighbour in the population (Pielou 1962). This is intuitively unappealing to most ecologists, however, since it is generally felt that a given plant interacts with a number of neighbours, not just the nearest one. One alternative is to consider instead the mean distance to the *n* nearest neighbours, where the value of *n* is empirically determined. For example, in a study of interaction between four *Polygonum* species, up to 73% of the variation in dry mass of plants was accounted for by the mean distance to the four nearest neighbours (Hickman 1979).

An alternative approach defines the 'neighbourhood' of each plant as a circle of arbitrary radius *r*. Within this circle the number, size, and dispersion pattern of neighbours may be used to develop various interference indices. An index developed by Mack and Harper (1977), for example, incorporates the size, number, and angular dispersion of plants within the neighbourhood. They used three different neighbourhood radii and fitted the data using polynomial functions. A somewhat simpler index, suggested by Weiner (1982, 1984), incorporates the distance to and size of neighbours within a given radius. One of his indices is:

$$W = \sum_{i=1}^{n} [k\, S_i\, d_i^{-2}]$$

where *d* is the distance to, and *S* the size of the $i^{th}$ neighbour, *k* is a weighting constant, and *n* the number of individuals (neighbours) within radius *r* of the target plant. Similar indices have been developed for use in forestry by Hegyi (1974), Daniels (1976), and others; these are reviewed by Daniels *et al.* (1986) and Tomé and Burkhart (1989).

There are a number of drawbacks to utilizing such empirically derived indices: (a) the choice of the neighbourhood radius *r* is arbitrary; (b) there is little justification in the choice of which variables to include (or not to include) in the index; and (c) the 'weights' given to the variables in the index are also arbitrarily chosen; for example, in Weiner's index the 'influence' of a neighbour is a function of the inverse of the square of the distance from the target plant. It is therefore perhaps best to avoid using interference indices to quantify the effects of local density on individual plant performance. An alternative approach, advocated by Waller (1981), uses stepwise multiple linear regression to determine which variables are the best predictors of performance. Silander and Pacala (1985) extended this idea further, using an 'exploratory data analysis' strategy to determine an empirically optimal neighbourhood radius. In populations of *Arabidopsis thaliana*, they found that the 'best predictor radius' was 5 cm, and that the number of neighbours and their angular dispersion provided the best fit; neighbour size proved to be far less important. It should be remembered, however, that all such models are predicated on the assumption that plant interactions occur only within a given radius, an assumption for which there is little evidence. Furthermore, even the simplest indices have largely unknown and potentially undesirable statistical properties.

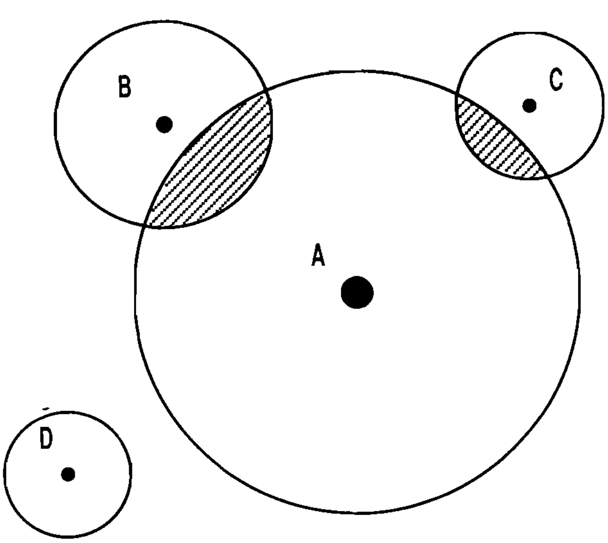

**Fig. 1. An example of the 'zone of influence' model of spatial interaction in plants. Circles whose radius is proportional to plant 'size' (solid dots) define the zones. Regions of overlap are shaded. In asymmetric interaction, shaded regions are 'occupied' by individual *A*. If interaction is symmetric, resources in the shaded regions are shared. In this example individual *D* is not interacting with individuals *A*, *B*, and *C*.**

## Spatial Overlap Indices and Models

In these models of plant interaction, a 'zone of influence' consisting of a circle of radius *r* is centred around each plant in a population (Zinke 1962, Antonovics and Levin 1980, Gates 1982). The radius is empirically defined; in forestry, for example, the zone radius is often determined from predictions of open-grown crown radius as a function of trunk diameter at breast height (DBH). The circles of neighbouring trees overlap to the greater of lesser extent, the amount of overlap determining the degree of 'competitive stress' experienced (Fig. 1). A number of such indices have been developed by foresters (e.g. Bella 1971, Arney 1973, Ek and Monserud 1974), some of which are reviewed by Daniels *et al.* (1986) and Tomé and Burkhart (1989).

Ecologists have generally used 'zones of influence' in simulation modelling of plant populations over time, typically to determine the dynamics of size distributions (Hara 1988). With such models, two types of interaction are possible. If competitive interactions are symmetric, the areas of overlap (shaded regions, Fig. 1) are regions in which resources are 'shared'; smaller individuals reduce the growth of larger ones as much as larger individuals reduce the growth of small ones. Competition for water and nutrients is likely to be of this type. In asymmetric competition, a larger plant 'occupies' the area of overlap to the exclusion of the smaller one; this is probably true of competition for light, in which larger plants shade smaller ones.

These simulation models have yielded some interesting results. Gates (1982) produced bimodal distributions of plant biomass when competition was asymmetric, in agreement with results obtained using experimental populations of *Tagetes patula* (Ford 1975). Ford and Diggle (1981) obtained similar results from a model using plant heights and overlapping cones to quantify individual competitive interactions. Pacala and Silander (1985) modelled population dynamics in annual plant populations. Their neighbourhood analyses examined dynamics at the level of the individual, incorporating species fecundity, survivorship, and dispersal as predictor variables. The 'ecological field theory' model (Wu *et al.* 1985) extends the 'zone of influence' concept by considering the dynamic nature of plant-environment interactions. Like other models of its type, the intensity of interaction is a function of the degree to which circular fields overlap. The 'strength' of these ecological fields, however, varies in time (or 'pulses') depending on prevailing environmental conditions. Thus, in this model "the intensity and dynamics of the ecological fields about individuals, together with the resource response characteristics of the influenced plants, determine spatial interactions within plant communities." (Walker *et al.* 1989).

Spatial methods have also been used to model temporal changes in the spatial pattern of populations with self-thinning. The model of Lepš and Kindlmann (1987) found that spatial regularity increased over time, a result which the authors attributed to competitive interactions between neighbours. By contrast, the aspatial model of Kent and Dress (1979) suggested that an initial random pattern remains random with self-thinning. However, empirical studies have demonstrated an increase in spatial regularity over time (Laessle 1965, Kenkel 1988), supporting the idea that neighbour effects must be considered in determining mortality patterns in plant populations.

## Spatial Tessellation Models

### *The Dirichlet Tessellation*

A tessellation is a 'tiling' of a set of points (e.g. plant positions) in a plane. Of the many algorithms, that proposed by Dirichlet (1850) is the most familiar and perhaps the most appealing to ecologists. The tiles or 'domains' of the Dirichlet tessellation are also known as Voronoi or Thiessen polygons, Wigner-Sietz cells, the Meijering cell model, or the S-mosaic, reflecting the independent discovery of this model in various branches of science (Boots and Murdoch 1983). The Dirichlet tessellation subdivides the plane such that each point has a polygonal area associated with it. This area defines a region nearer to the point than to any other point in the plane. In practice the tessellation is obtained by first calculating the Delaunay triangulation, which determines the polygon neighbours of all points in the plane. Next, perpendicular bisectors are drawn between the Delaunay neighbours to define the polygon edges (Fig. 2). Using a 'growth' analogy, the Dirichlet tessellation model assumes the following (after Boots 1980):

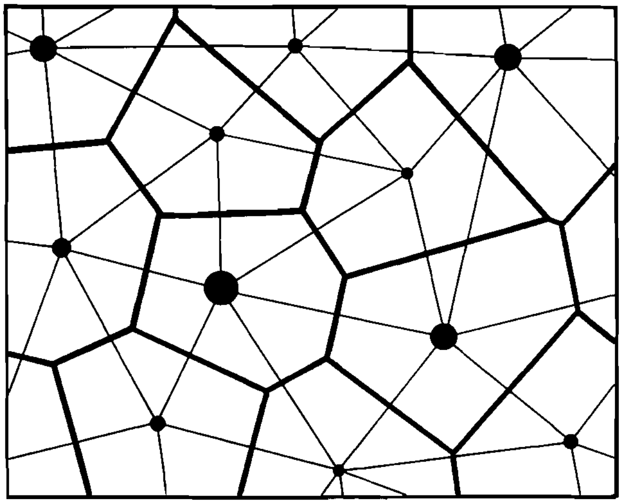

**Fig. 2. The Delaunay triangulation (fine lines) and Dirichlet tessellation tiles (solid lines) for a subset of points from a larger population.**

a. all individuals appear simultaneously, and remain fixed in position.

b. all individuals are equally 'weighted'.

c. tiles 'grow' at the same rate in all directions.

d. the growth rates of tiles are linear, and the same for all individuals.

e. tile growth ceases when neighbours (polygon edges) contact.

These appear to be restrictive assumptions: for a plant population, they imply simultaneous germination, a homogeneous substrate, and lack of genotypic variability. The utility of the Dirichlet tessellation, however, lies in its ability to model pattern: for example, a significant relationship between tile area and plant biomass indicates that spatial pattern plays a role in determining plant performance (Cormack 1979).

The Dirichlet tessellation has a long history of use in various fields of study, including biology, archeology, metallurgy, geography, physics, mathematics, and statistics. In biology it has been used to model cell packing (Honda 1978, Saito 1982), crop-weed interactions (Fischer and Miles 1973), and the development of animal territories (Hasegawa and Tanemura 1976). It was first described in the biological literature by Brown (1965), who recommended its use in estimating timber resources. Mead (1966) independently suggested using this tiling to study interactions in mapped plant populations. Brown described a Dirichlet polygon as the "area potentially available" (APA) to a plant, since the polygon defines a region closer to the target plant than to any other plant. Green and Sibson (1978) used a territorial analogy, while Firbank and Watkinson (1987) described the polygon as an "area of available resources".

The Dirichlet tessellation offers an objective definition of the 'zone of influence' of a plant, though whether this definition is biologically realistic remains to be demonstrated. Silander and Pacala (1985) dismissed the use of Dirichlet polygons to define neighbourhoods, since "only neighbours of adjacent polygons are considered". However, Mead (1971) found the definition of neighbours implied by the Dirichlet tessellation to be "intuitively appealing", since "all plants excluded from the set of neighbours are in the 'shadow' of a neighbour". Mead developed a series of interaction indices similar to those discussed above, but using the Dirichlet-Delaunay definition of neighbours. The variables used in the indices were distance to and size of each neighbour, and the angle subtended by a side of the polygon corresponding to a given neighbour (thus 'weighting' each neighbour according to the length of the shared edge).

There is some evidence to suggest that plant interactions are mainly between neighbours sharing a tile edge. Cannell *et al.* (1984) planted *Picea sitchensis* and *Pinus contorta* in hexagonal lattices and computed various intraspecific interaction indices to predict individual plant performance. They found that predictions obtained by considering the sizes of the six 'first-order' neighbours were not improved upon by considering the twelve 'second-order' neighbours as well. In stands of *Picea sachalinensis*, Hara (1985) found that the optimal number of neighbours required to predict performance decreased over time, but was almost constant at a value of six for much of the time. Kenkel (1988) examined temporal changes in the spatial pattern of a *Pinus banksiana* stand. Using a second-order statistical procedure in which increasing 'zones of influence' are defined, it was found that the pattern of surviving trees was regular at a local scale (up to a radius of about 3.5 m, corresponding to a mean of six neighbours). Interestingly, six is also the mean number of neighbours of a Dirichlet tessellation (Upton and Fingleton 1985, p. 97). These empirical results offer indirect evidence that a given plant may compete mainly with its tile edge neighbours, at least in even-aged monocultures (c.f. Mithen *et al.* 1984, Matlack and Harper 1986).

A number of studies have related individual plant performance to various Dirichlet polygon parameters (e.g. tile area, number of neighbours, etc.; see Mead 1966). In such investigations, edge effect problems must be taken into account (Kenkel *et al.* 1989a). Studies relating tile area to final dry biomass include Liddle *et al.* (1982), Mithen *et al.* (1984), Matlack and Harper (1986), and Firbank and Watkinson (1987). Most authors have found that polygon area can only account for a relati-

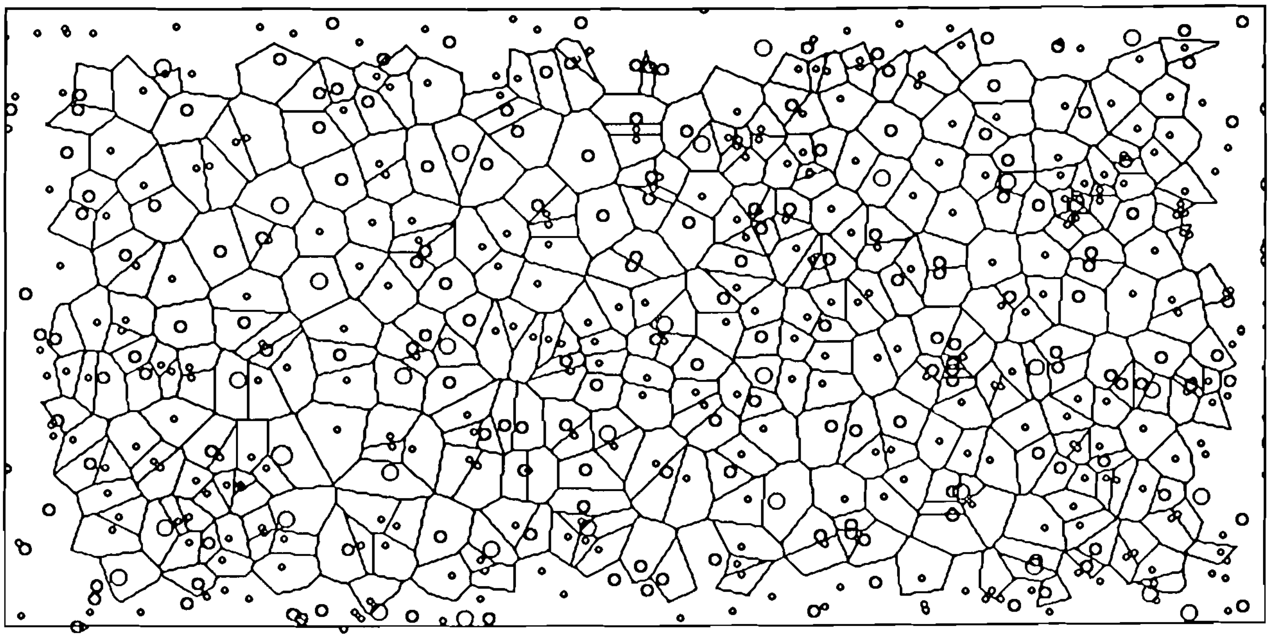

**Fig. 3. Spatial coordinate map and Dirichlet tessellation of 562 ramets of a clone of the ostrich fern *Matteuccia struthiopteris*. Circle diameter is proportional to the number of fronds produced by each ramet rootstock. The area mapped is 6 × 12 m in size. Ramets along the study area edge were excluded from consideration, using the algorithm proposed by Kenkel *et al.* (1989a).**

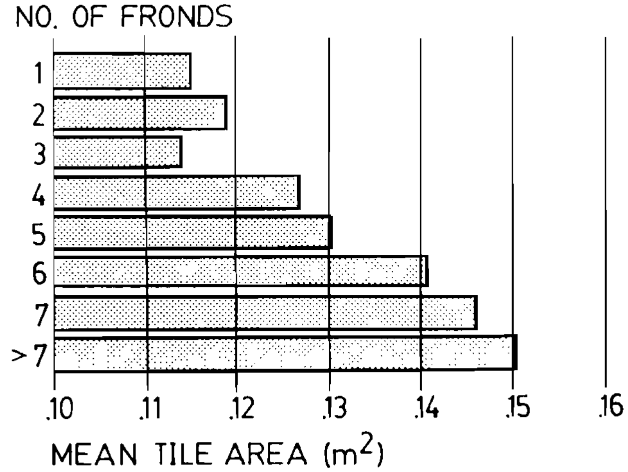

**Fig. 4. The relationship between frond number and mean tile area ($m^2$) for an ostrich fern clone. Results are based on the 420 tessellation tiles shown in Fig. 3.**

vely small proportion of variation in final yield, leading Firbank and Watkinson (1987) to suggest that factors such as differences in emergence time, microhabitat, and genotype may be more important than local crowding. Other studies have related polygon area to probability of mortality. Watkinson *et al.* (1983) found initial polygon area to be a good predictor of survival probability in artificial populations of *Helianthus annuus*. Owens and Norton (1989), in a study of natural populations of *Artemesia tridentata*, found that greatest survival occurred in plants occupying the largest polygons. Finally, a study of mortality patterns in a naturally established *Pinus banksiana* stand found that less than 25% of trees occupying the smallest areas survived, while over half of those occupying the largest tiles were alive after 65 years (Kenkel *et al.* 1989b).

To further illustrate the utility of the Dirichlet tessellation, a mapped pattern of the clonal fern *Matteuccia struthiopteris* is shown in Fig. 3. This clone formed the understory of a portion of open, mature *Quercus macrocarpa* gallery forest near Delta, Manitoba, Canada. Ramets are erect rootstocks with a projecting crown of one or more fronds, and are connected by stout, persistent runners. The spatial coordinates of each rootstock, and the number of fronds produced, were recorded. A positive relationship between frond number and tile area was found, suggesting that neighbour relations play a role in determining the number of fronds produced (Fig. 4). Since the ramets are interconnected, this result presumably reflects competition for light.

There are a number of other applications of tessellation analysis to plant biology. The edges of the Dirichlet tessellation ('neighbours' as defined by the Delaunay triangulation) give an objective definition of 'joins' in spatial autocorrelation analysis (Reed and Burkhart 1985, Kenkel *et al.* 1989b). The method can also be used as an alternative to the 'zone of influence' method of modelling spatial interactions in plants (e.g. Miller and Weiner 1989). Sibson (1980) and Boots (1987a) discuss other applications, including point-pattern analysis (Hutchings and Discombe 1986), the modelling of ter-

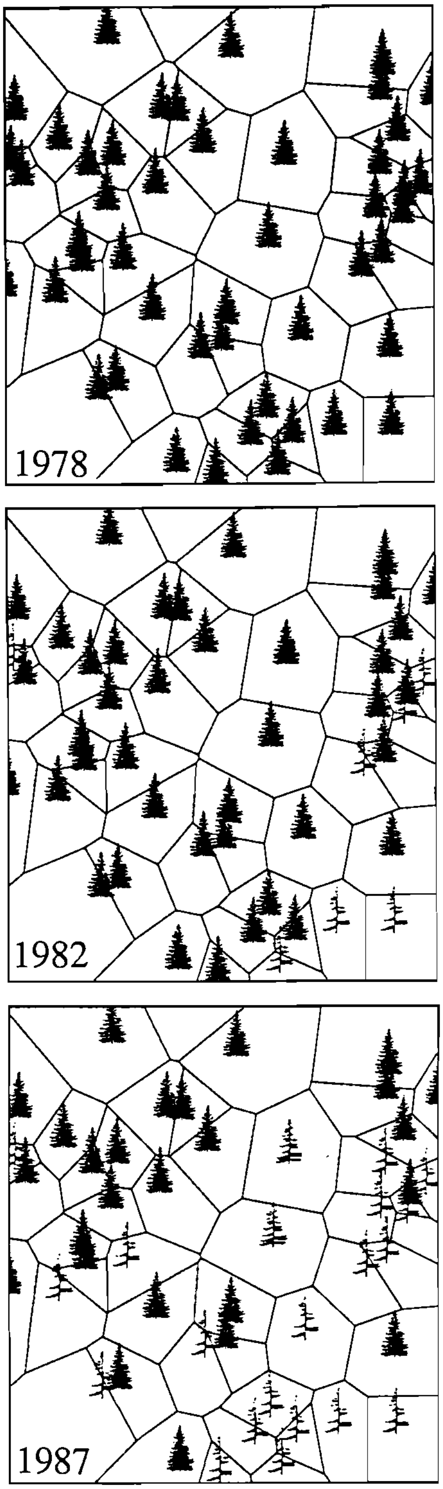

**Fig. 5. The spread of dwarf mistletoe infection in a jack pine stand in south-eastern Manitoba, Canada. Uninfected trees are 'bushy'. Increase levels of infection are represented by more 'spindly' icons.**

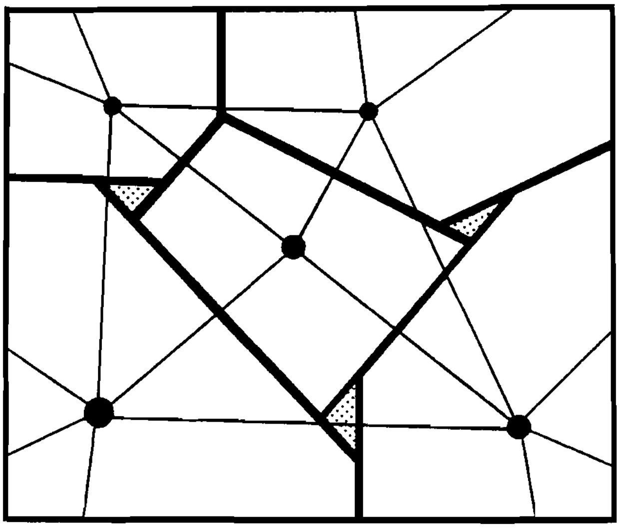

**Fig. 6. Delaunay triangulation (fine lines) and the weighted Moore tessellation (solid lines). Circle diameters, which are proprotional to plant size, are used as weights. Unoccupied regions are stippled.**

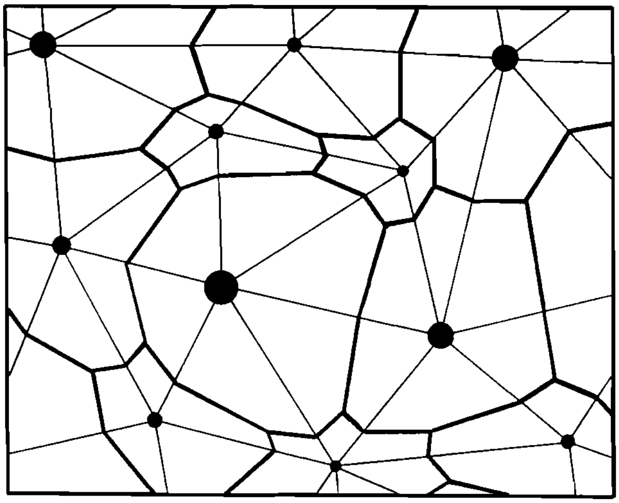

**Fig. 7. Delaunay triangulation (fine lines) and the weighted Fraser tessellation (solid lines) for the point pattern shown in Fig. 2. Weights are proportional to circle diameter.**

ritories, multivariate data analysis, and predicting the spread of an infection (Mollison 1977). An example of the latter is the progress of dwarf mistletoe infection in a stand of *Pinus banksiana* (Fig. 5). It can be seen that the infection generally spreads between trees sharing a common polygon edge. Examples of applications in geography can be found in Getis and Boots (1978) and Dudycha (1987).

### *Straight-boundary weighted tessellations*

The Dirichlet tessellation assumes equal weighting of individuals, since the 'boundary' between any two points is a perpendicular bisector. When individual plants in a population vary in 'size', however, interest may focus on methods to weight the polygons to account for size differences. Moore *et al.* (1973) developed a 'competition index' for use in forestry based on a weighted polygon model. Their model has the following properties: (a) like Dirichlet tiles, weighted polygons are mutually exclusive, and (b) the weighting is proportional to the relative size of neighbouring trees. The weighting model used is:

$$d_i' = d_i\ [w_o^2/(w_o^2 + w_i^2)]$$

where $d_i'$ is the weighted distance from the target individual to the $i^{th}$ neighbour, $d_i$ is the distance to the ith neighbour, $w_o$ is the size of the target individual, and $w_i$ is the size of the $i^{th}$ neighbour. A given polygon border is perpendicular to the line joining two individuals, but passing through the weighted distance $d_i'$ instead of the bisector. The resulting tessellation has the undesirable property of not being space-exhaustive: there remain areas which are not assigned to any individual (Fig. 6). Polygon overlap is avoided by having lines nearest the target individual take precedence over those further away. Modifications of this model were suggested by Pelz (1978), Zuuring *et al.* (1984), Nance *et al.* (1987) and Tomé and Burkhart (1989).

An alternative, more mathematically tractable weighted tessellation was suggested by Fraser (1977). His model involves partitioning the areas of Delaunay triangles (the closely related 'least-diagonal-neighbour' triangulation can also be used; see Upton and Fingleton 1985, p. 140). Specifically, each triangle is divided into three areas in proportion to the 'weights' of the plants at the vertices. Fraser developed this method to estimate total wood volume, and therefore suggested that weights be defined as the fraction of a tree's basal area lying within a given triangle. The weights for the three vertex plants *a*, *b*, and *c* are scaled ($w_a + w_b + w_c = 1$), and the area *A* of the triangle divided into three regions with areas $A\ w_a$, $A\ w_b$, and $A\ w_c$ respectively. Computation of the corresponding tessellation is more complicated and is not outlined here: an example is given in Fig. 7. Although this method was developed to estimate forest parameters such as timber volume, it may be useful in studying intraspecific interactions as well. Note that even if all weights are equal, the Dirichlet and Fraser tessellations are not the same: the sides of the Dirichlet tessellation intersect at the triangle's circumcentre, while those of the Fraser tessellation intersect at the centroid (Upton and Fingleton 1985).

### *Curved-boundary tessellations*

Johnson and Mehl (1939) developed a model in which points 'appear' on the plane at a constant rate (rather

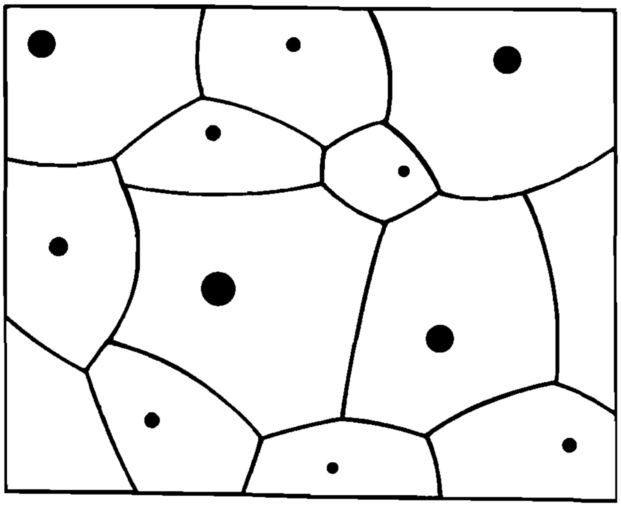

Fig. 8. Johnson-Mehl curved-boundary tessellation of the point pattern shown in Fig. 2. Weights are proportional to circle diameter.

than simultaneously as in the Dirichlet tessellation), with the provision that any points falling inside the polygon of another point are immediately deleted. All other assumptions of the Dirichlet tessellation remain in effect. The result is a tessellation with curved boundaries, in which points appearing earlier occupy, on average, a greater proportion of the total area (Fig. 8). This model could be used, for example, to model neighbour effects on plant performance when differences in germination time are present (Cormack 1979).

Boots (1980, 1987b) described a number of other curved-boundary tessellations for use in geography. His 'minimum threshold model' was shown to be a close spatial relative of the Johnson-Mehl model, and produced an identical tessellation. He also explored the relationship between Dirichlet and Johnson-Mehl tessellations. Frost and Thompson (1987) examined this relationship in more detail using various 'nucleation conditions'. Site saturation (all points or 'nuclei' appearing simultaneously) produced the Dirichlet tessellation, while continuous nucleation resulted in the Johnson-Mehl model. Tessellations between these two extremes were produced when the nucleation rate decreased exponentially with time.

Curved-boundary tessellations have not been used in ecology, though they have considerable potential. For example, such models could be used to predict individual plant performance when initial differences in plant size are present. The continuous nucleation tessellation may offer a more realistic approach to modelling plant populations than the 'zone of influence' approach.

## Future Directions

This review has shown that there are a number of empirical and simulation approaches to modelling spatial interactions in plant populations. Underlying all these approaches is the idea that the performance of an individual plant is affected not by overall population density but instead by a plant's 'effective density', which is a function of the size, proximity and dispersion of its immediate neighbours. While ecologists agree that competitive interactions in sessile organisms are localized, there is little agreement as to what constitutes a 'neighbour' and how neighbourhood effects should be quantified. If progress is to be made in understanding intraspecific interactions in plant populations, however, a unified approach to the problem of determining a plant's 'competitive zone' or 'ecologically effective distance' will be required (Antonovics and Levin 1980). This is a formidable challenge, particularly since a sound theoretical basis for developing interaction models in plants is lacking.

The three major approaches to defining 'neighbourhoods' in interaction indices were previously outlined. The first and simplest approach is to consider the nearest neighbour, or alternatively the *n* nearest neighbours. The problem here is the choice of *n*. Consider, for example, a value of $n=3$ and the four nearest neighbour distances $d_1=0.5$, $d_2=0.6$, $d_3=1.0$ and $d_4=1.1$. Is it sensible or realistic to include the third individual as a neighbour, but not the fourth one? Clearly this approach is at best a crude approximation of the definition of a neighbourhood. A second approach involves centering a circle of specified radius about a plant, and defining as neighbours all individuals falling within this region. This approach also has its problems. Determination of the circle radius, while often empirically based, is nonetheless somewhat arbitrary. Furthermore, the inclusion-exclusion problem remains. For example, given a zone of influence radius $r=1.5$, is it sensible to exclude from consideration an individual which is 1.51 units away while at the same time including one which is 1.49 units from the target plant? The problem with the 'nearest neighbours' and 'circle radius' approaches is that they imply an aspatial definition of a plant's neighbourhood: number and dispersion of neighbours are only considered *after* the neighbourhood is defined. This gives rise to a troubling paradox: while the overall model is spatial (since individual performance is modelled as a function of the number, size, and dispersion of neighbours), the determination of which individuals are neighbours is itself aspatial. Only the third approach offers a truly spatial definition of a plant's 'neighbourhood'. Here neighbours are defined as those individuals sharing a Dirichlet tile edge with the target plant (or equivalently the first-order Delaunay triangulation joins). This spatial definition of neighbourhoods can easily be modified to consider second and higher order neighbours as well, and Boots (1987b) outlines an algorithm for the calculation of order-*k* Dirichlet tessellations. I would argue that spatial models of intraspecific interactions should utilize a spatial definition of a plant's neighbourhood. 'Nearest neighbours' and 'circle radius' definitions are therefore probably best avoided in favour of the Dirichlet tessellation definition of neighbourhoods.

Theoretical models of population dynamics have generally used a 'zone of influence' approach to quantify individual interactions. Interaction is defined in terms of the extent of area (or volume) overlap of neighbouring zones. This is a truly spatial approach, since the amount of overlap is a function of the size and proximity of neighbouring individuals. A major drawback, however, is that there is no unequivocal way to specify what the radius of a 'zone of influence' circle should be. An empirical approach to this problem is generally taken (e.g. in forestry models circle radius is equal to the crown diameter of open-grown trees for a given trunk diameter), but a number of problems nonetheless remain. For example, is it reasonable to use information about open-grown trees to model individuals in closed forest stands? Is the 'zone of influence' of a root system larger, or smaller, than the crown diameter? Is a circle (or cone) a realistic model for a plant? It should also be appreciated that any change in the circle radius-plant size relationship will result in different levels of spatial interaction, since the amount of overlap and the number of individuals overlapping will change. As a result, small differences in the circle radius values could conceivably alter the results of the simulation. 'Zone of influence' models must therefore be used with some caution, and ideally alternative approaches which circumvent the problem of defining an interaction zone should be sought. Weighted tessellations, which have been used to model forest populations, are one possible alternative. A potentially more realistic approach would involve modifying the Johnson-Mehl growth tessellation model: a dynamic approach could be taken in which superior competitors 'invade' the spatial territories of less competitive ones. In such a model, tile area would reflect the 'growth potential' of an individual rather than a true spatial 'territory'.

Sibson (1980) called the Dirichlet tessellation "... one of the most basic and useful invariants associated with a point pattern in the plane". It is my belief that tessellation analysis offers the most promising approach to modelling spatial processes in plant populations.

**Acknowledgements.** I thank Charles Burchill and Roger Garrod for help in mapping the ferns, Alex McIlraith for commenting on an earlier version of the manuscript, and Drs. Mark Dale and Tim Meyer for providing me with some useful references. The Dirichlet tessellation was produced using a computer program developed by Drs. J.A. and W.D. Hoskins and the author. This research was supported by Natural Sciences and Engineering Research Council of Canada grant A3140. Contribution number 212 from the University of Manitoba Field Station (Delta Marsh).

## REFERENCES

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

ARNEY, J.D. 1974. An individual tree model for stand simulation in Douglas-fir. In: Fries, J. (ed.), Growth models for tree and stand simulation. pp. 38-46. Royal College of Forestry, Stockholm.

BELLA, I.E. 1971. A new competition model for individual trees. For. Sci. 17: 364-372.

BOOTS, B.N. 1980. Weighting Thiessen polygons. Econ. Geogr. 57: 248-259.

BOOTS, B.N. 1987a. A review of the applications of Voronoi (Thiessen) polygons. In: Dufournaud, C. and Dudycha, D. (eds.), Quantitative analysis in geography. pp. 47-73. Waterloo lectures in geography, Vol. 3. Dept. of Geography, Univ. of Waterloo, Canada.

BOOTS, B.N. 1987b. Modifying Thiessen polygons. Can. Geogr. 31: 160-169.

BOOTS, B.N. and D.J. MURDOCH. 1983. The spatial arrangement of random Voronoi polygons. Computers and Geosciences 9: 351-365.

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

CANNELL, M.G.R., P. ROTHERY and E.D. FORD. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. 53: 349-362.

CORMACK, R.M. 1979. Spatial aspects of competition between individuals. In: Cormack, R.M. and Ord, J.K. (eds.), Spatial and temporal analysis in ecology. pp. 151-212. Intl. Coop. Publ. House, Fairland, Md.

CRAWLEY, M.J. and R.M. MAY. 1987. Population dynamics and plant community structure: competition between annuals and perennials. J. Theor. Biol. 125: 475-489.

CZÁRÁN, T. 1989. Coexistence of competing populations along an environmental gradient: a simulation study. Coenoses 4: 113-120.

CZÁRÁN, T. and S. BARTHA. 1989. The effect of spatial pattern on community dynamics; a comparison of simulated and field data. Vegetatio 83: 229-239.

DANIELS, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci. 22: 454-456.

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

DIRICHLET, G.L. 1850. Uber die Preduction der positiven quadritschen Formen mit drei unbestimmten ganzen Zahlen. J. für die reine und angewandte Mathematik 40: 209-234.

DUDYCHA, D.J. 1987. Contouring based on Delaunay triangulation. In: Dufournaud, C. and Dudycha, D. (eds.), Quantitative analysis in geography. pp. 75-93. Waterloo lectures in geography, Vol. 3. Dept. of Geography, Univ. of Waterloo, Canada.

EK, A.R. and R.A. MONSERUD. 1974. FOREST: a computer model for simulating the growth and reproduction of mixed species forest stands. Univ. Wisconsin School Nat. Res., Report R2635.

FISCHER, R.A. and R.E. MILES. 1973. The role of spatial pattern in the competition between crop plants and weeds. A theoretical analysis. Math. Biosci. 18: 335-350.

FIRBANK, L.G. and A.R. WATKINSON. 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 P.J. DIGGLE. 1981. Competition for light in a plant monoculture modelled as a spatial stochastic process. Ann. Bot. 48: 481-500.

FRASER, A.R. 1977. Triangle based probability polygons for forest sampling. For. Sci. 23: 111-121.

FROST, H.J. and C.V. THOMPSON. 1987. The effect of nucleation conditions on the topology and geometry of two-dimensional grain structures. Acta Metall. 35: 529-540.

GATES, D.J. 1982. Competition and skewness in plantations. J. Theor. Biol. 94: 909-922.

GETIS, A. and B.N. BOOTS. 1978. Models of spatial processes: an approach to the study of point, line, and area patterns. Cambridge U. Press, Cambridge.

GREEN, P.J. and R. SIBSON. 1978. Computing Dirichlet tessellations in the plane. Comp. Journal 21: 168-173.

GRIME, J.P. 1979. Plant strategies and vegetation processes. Wiley, New York.

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

HARA, T. 1988. Dynamics of size structure in plant populations. Trends Ecol. Evol. 3: 129-133.

HARPER, J.L. 1977. Population biology of plants. Academic Press, London.

HASEGAWA, M. and M. TANEMURA. 1976. On the pattern of space division by territories. Ann. Inst. Stat. Math. 28: 509-519.

HEGYI, F. 1974. A simulation model for managing jack-pine stands. In: Fries, J. (ed.), Growth models for tree and stand simulation. pp. 74-90. Royal College of Forestry, Stockholm.

HICKMAN, J.C. 1979. The basic biology of plant numbers. In: Solbrig, O.T., Jain, S.K., Johnson and Raven, P.H. (eds.), Topics in plant population biology. pp. 232-263. Columbia U. Press, New York.

HONDA, H. 1978. Description of cellular patterns by Dirichlet domains: the two-dimensional case. J. Theor. Biol. 72: 523-543.

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

JOHNSON, W.A. and R.F. MEHL. 1939. Reaction kinetics in processes of nucleation and growth. Trans. Amer. Inst. of Mining, Metall., and Petroleum Engineers 135: 416-456.

KENKEL, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69: 1017-1024.

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

KENKEL, N.C., J.A. HOSKINS and W.D. HOSKINS. 1989b. Local competition in a naturally established jack pine stand. Can. J. Bot. 67: 2630-2635.

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

LAESSLE, A.M. 1965. Spacing and competition in natural stands of sand pine. Ecology 46: 65-72.

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

LEVIN, S.A. 1986. Population models and community structure in heterogeneous environments. In: Hallam, T.G. and Levin, S.A. (eds.), Mathematical ecology: an introduction. pp. 295-320. Springer, Berlin.

LIDDLE, M.J., C.J.S. BUDD and M.J. HUTCHINGS. 1982. Population dynamics and neighbourhood effects in establishing swards of *Festuca rubra*. Oikos 38: 52-59.

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

MATLACK, G.R. and J.L. HARPER. 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. 30: 301-309.

MEAD, R. 1971. Models for interplant competition in irregularly distributed populations. In: Patil, G.P., Pielou, E.C. and Waters, W.E. (eds.), Sampling and modeling biological populations and population dynamics. pp. 13-32. Intl. Coop. Publ. House, Burtonsville, Md.

MILLER, T.E. and J. WEINER. 1989. Local density variation may mimic effects of asymmetric competition on plant size variability. Ecology 70: 1188-1191.

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

MOLLISON, D. 1977. Spatial contact models for ecological and epidemic spread. J. Roy. Stat. Soc. Ser. B 39: 283-313.

MOORE, J.A., C.A. BUDELSKY and R.C. SCHLESINGER. 1973. A new index representing individual tree competitive status. Can. J. For. Res. 3: 495-500.

NANCE, W.L., J.E. GRISSOM and W.R. SMITH. 1987. A new competition index based on weighted and constrained area potentially available. In: Forest growth modelling and prediction, Vol. 1. pp. 134-142. U.S.D.A. Forest Service General Tech. Report NC-120.

OKUBO, A. 1980. Diffusion and ecological problems: mathematical models. Springer, Berlin.

OWENS, M.K. and B.E. NORTON. 1989. The impact of 'available area' on *Artemisia tridentata* seedling dynamics. Vegetatio 82: 155-162.

PACALA, S.W. 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. Theor. Pop. Biol. 31: 359-392.

PACALA, S.W. and J.A. SILANDER. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. Am. Nat. 125: 385-411.

PELZ, D.R. 1978. Estimating individual tree growth with tree polygons. In: Fries, J., Burkhart, H. and Max, T. (eds.), Growth models for long-term forcasting of timber yields. pp. 172-178. Virginia Polytech. Inst. and State Univ., School of Foresty and Wildlife Publ. FWS-1-78.

PIELOU, E.C. 1962. The use of plant-to-neighbour distances for the detection of competition. J. Ecol. 50: 357-367.

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

SAITO, N. 1982. Asymptotic regular pattern of epidermal cells in mammalian skin. J. Theor. Biol. 95: 591-599.

SIBSON, R. 1980. The Dirichlet tessellation as an aid in data analysis. Scand. J. Statist. 7: 14-20.

SILANDER, J.A. and S.W. PACALA. 1985. Neighborhood predictors of plant performance. Oecologia 66: 256-263.

TILMAN, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton U. Press, Princeton.

TOMÉ, M. and H.E. BURKHART. 1989. Distance-dependent competition measures for predicting growth of individual trees. For. Sci. 35: 816-831.

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

WALKER, J., P.J.H. SHARPE, L.K. PENRIDGE and H. WU. 1989. Ecological field theory: the concept and field tests. Vegetatio 83: 81-95.

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

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

WEINER, J. 1982. A neighborhood model of annual-plant interference. Ecology 63: 1237-1241.

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

WEINER, J. and P.T. CONTE. 1981. Dispersal and neighborhood effects in an annual plant competition model. Ecol. Modelling 13: 131-147.

WELLER, D.E. 1987. A reevaluation of the -3/2 power rule of self-thinning. Ecol. Monogr. 57: 23-43.

WU, H., P.J.H. SHARPE, J. WALKER and L.K. PENRIDGE. 1985. Ecological field theory (EFT): a spatial analysis of resource interference among plants. Ecol. Modell. 29: 215-243.

ZEIDE, B. 1987. Analysis of the 3/2 power law of self-thinning. For. Sci. 33: 517-537.

ZINKE, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43: 130-133.

ZUURING, H.R., S.D. TESCH and J.L. FAUROT. 1984. Past tree spacing levels estimated by current stand conditions and past radial growth rates. For. Sci. 30: 209-218.

*Manuscript received: March 1990*