A WEIGHTED TESSELATION MODEL FOR STUDYNG PLANT POPULATION DYNAMICS[1]

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Abstract. I describe a modification of a timber volume estimation algorithm (Fraser 1977) for use in studying interplant interaction and dynamics in plant populations. The Fraser tessellation results when triangles connecting neighbour plants (as defined by the Delaunay triangulation) are partitioned. I compare the Fraser tessellation to the commonly-used Dirichlet tessellation, and describe various weighting options for the Fraser tessellation. I use the weighted model to examine plant performance in artificial populations of *Zinnia elegans*, in which germination time is used as the weighting factor. It was found that spatial positioning of plants (as defined by the Dirichlet and unweighted Fraser tessellations) was itself a poor predictor of plant performance. Inclusion of germination time (weighted Fraser tessellation) improved prediction. I suggest that the weighted Fraser tessellation be used to predict plant performance when local interplant interactions are thought to be important. The weighted model is particularly useful when initial individual size differences are present in the population, and when interplant interactions are between first-order spatial neighbours.

Introduction

The study of interactions in plant populations has increasingly focussed on the role that spatial relations play in determining individual plant performance (Kenkel 1990). This emphasis on local interactions recognizes that a sessile organism's performance is determined by the number, proximity and biomass of its immediate neighbours.

A number of methods for defining 'neighbourhoods' of local interaction in plant populations have been described (Daniels, Burkhart and Clason 1986; Hara 1988; Kenkel 1990). Local competition coefficients require the user to make arbitrary decisions regarding the size of an individual's neighbourhood, as well as how neighbours should be weighted (e.g. Weiner 1984; Silander and Pacala 1985). An alternative approach to describing local spatial relationships is tesselation analysis, which uses a mathematical algorithm to identify neighbours. The Dirichlet tessellation (and its dual, the Delaunay triangulation) has been used in a number of studies to predict plant performance based on neighbour proximity (e.g. Firbank and Watkinson 1987; Kenkel, Hoskins and Hoskins 1989a). In this approach, a study area is subdivided into polygons or tiles, one for each individual. Polygons are defined such that all regions within an individual's polygon are nearer to that individual than to any other in the population (Mead 1966). An important assumption of the model is that all individuals in the population are equally weighted, which for plant populations implies that all individuals germinate simultaneously and/or are

of the same size. In this paper, I describe a modification of the weighted tesselation model first proposed by Fraser (1977), and suggest its use in modelling individual plant performance based on neighbour size and proximity.

This study was undertaken to: (a) describe the Fraser tessellation algorithm as a method for studying plant population dynamics; (b) explore the relationship between the Dirichlet and Fraser tessellation models; and (c) apply the weighted tessellation model to predicting individual plant performance in populations of *Zinnia elegans*.

Dirichlet tessellation - Delaunay triangulation

The most commonly used tessellation in biology is that attributed to Dirichlet (1850), and studied in detail by Voronoi (1908). It is intuitively appealing to many ecologists, as each plant is associated with a polygon which delineates a region that is nearer to that plant than to any other. Polygon edges are the perpendicular bisectors of lines connecting each plant to its neighbours. The line network itself is known as the Delaunay triangulation; here, any three plants form the vertices of a Delaunay triangle if and only if the circumcircle of the three plants does not contain any other plants (Fig. 1). It is therefore reasonable to assume that the area of a triangle with vertex plants A, B, and C defines a region within which resources are shared among the three plants.

Boots (1980) described the Dirichlet tessellation using a polygon growth analogy, which is particularly
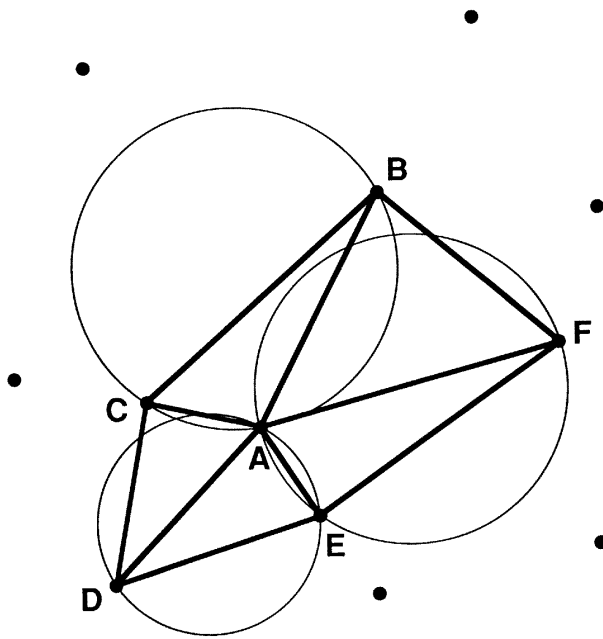
Fig. 1. Delaunay triangulation (solid lines) for the point A. The associated circumcircles are shown for three of the five triangles.

relevant to the study of plant population dynamics. Given a set of points (plants) on the plane, the Dirichlet tessellation results when a polygon grows from each point under the following constraints:

1. Points appear simultaneously on the plane, and remain fixed in position.
2. All points are equally weighted.
3. Tile growth rates are the same for all individuals. It is also assumed that growth is linear, and that polygons grow at the same rate in all directions.
4. Growth of a polygon ceases once adjacent polygon edges contact.

For plant populations, these growth rules can be translated as follows:

1. Plants germinate simultaneously, and remain at the same position at which they germinate (this implies that the stem and root systems grow perpendicularly to the plane; no bending is permitted).
2. Seedling size is the same for all individuals.
3. Plant growth rates are the same (and linear), and each plant grows equally in all directions. This implies genetic uniformity and equal resource supply rates.
4. Growth in a given direction ceases whenever another plant is contacted. This implies that the leaf and root systems of plants do not overlap.

These growth assumptions indicate that Dirichlet

tessellation analysis should be restricted to even-aged populations growing on uniform substrates. The method has been used to assess individual performance in artificial plant populations sown at high density (Liddle, Budd and Hutchings 1982; Mithen, Harper and Weiner 1984; Firbank and Watkinson 1987), and in naturally occuring stands (Matlack and Harper 1986; Kenkel, Hoskins and Hoskins 1989a). In these studies Dirichlet polygon areas accounted for only a relatively small proportion of total variation in individual performance (e.g. biomass, probability of survival). This led Firbank and Watkinson (1987) to suggest that factors such as differences in germination time, microhabitat variability, and genotypic diversity may override the effects of local crowding in even-aged plant populations.

The major limiting assumption of Dirichlet tessellation analysis is that individuals are equally weighted. This means that only the population's spatial configuration is considered in defining polygon areas. A less restrictive tessellation would allow for the incorporation of initial individual size differences (i.e. differential weights) in defining polygon areas. This would allow, for example, the examination of future tree growth using both the spatial configuration of the population and current tree sizes (e.g. trunk diameters) as predictors. In the following section I outline three weighted tessellation models, and discuss their utility and limitations (see also Kenkel 1990).

Some weighted tessellation models

Johnson and Mehl (1939) described growth of surface films on metals using a model in which points appear (nucleate) at a constant rate, rather than simultaneously as assumed by the Dirichlet model. All other growth rules as outlined above remain in effect. Their model resulted in a curved-boundary tessellation, in which earlier nucleating points on average occupy larger areas than those appearing later. Boots (1980, 1987) explored the relationship between the Dirichlet and Johnson-Mehl tessellations, and Frost and Thompson (1987) extended the algorithm to different nucleation conditions. The Johnson-Mehl model may prove useful in modelling uneven-aged plant populations (Cormack 1979). The algorithm is mathematically complex, however, and the areas occupied by each plant are difficult to determine. The model may be most profitably applied to theoretical models of interaction in sessile organisms (see Armstrong 1974).

Moore, Budelsky and Schlesinger (1973) suggested a simpler weighted tessellation model for use in forestry, in which weights were proportional to tree diameter. Like the Dirichlet tessellation, polygon boundaries are perpendicular to the lines connecting neighbours, but the perpendicular passes through a weighted distance rather than the bisector. A number of modifications to
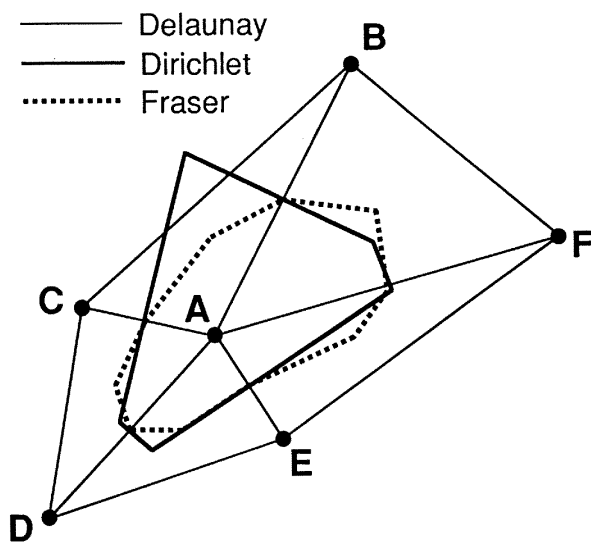
Fig. 2. Delaunay triangulation, Dirichlet tessellation, and unweighted Fraser tessellation for the point A.

Fig. 3. Partioning of an acute angle triangle, using the Dirichlet and unweighted Fraser tessellation algorithms.

this basic model have been described (see Zuuring, Tesch and Faurot 1984, Tomé and Burkhart 1989). Unfortunately, the resulting tessellation is not space-exhaustive, so that there remain regions which are not assigned to any individual.

Fraser (1977) described another weighted tessellation model for use as a field method in timber volume estimation. I am unaware of the model having been used to examine plant interactions. The algorithm itself is straightforward: a triangulation is defined, with each triangle being subdivided into three regions in proportion to the weights associated with the vertex plants. A given plant's polygon area is simply the sum of the areas of its associated triangles (Fig. 2). In the following section, I describe this tessellation in more detail and argue for its use in studying plant population interactions. Since Fraser (1977) first suggested the idea of defining polygons through triangle division, I have adopted the name "Fraser tessellation" for the model.

The Fraser tesselation

Unweighted tessellation

Fraser (1977) used the 'least-diagonal-neighbour' (LDN) triangulation to determine polygon areas, as the vertices of such triangles are easily located in the field. In practice, the LDN and Delaunay triangulations are closely related (Upton and Fingleton 1985, p. 140). Throughout this paper I use the Delaunay triangulation to determine Fraser polygon areas, for two reasons. First, doing so allows direct comparisons of the Fraser and Dirichlet tessellations to be made. Secondly, the Delaunay triangulation is widely available in program packages.
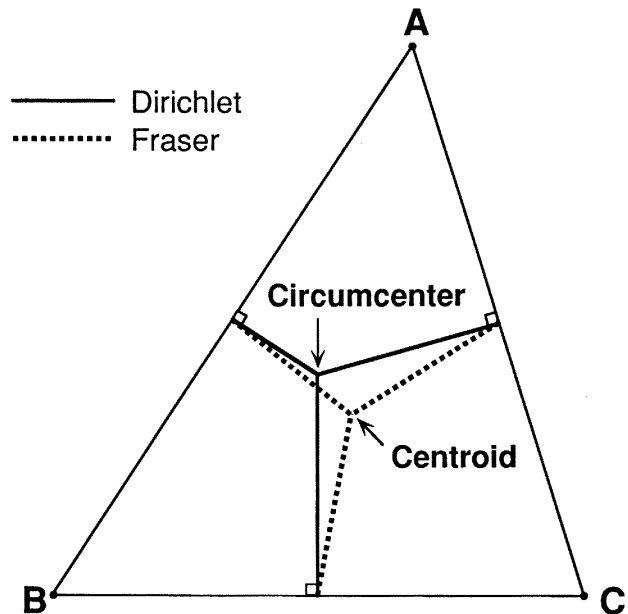
An unweighted Fraser tessellation results when all triangles are divided into three equal areas. It should be noted that Dirichlet and unweighted Fraser tessellation polygon areas are not the same (except in the trivial case of the entire triangulation consisting of equilateral triangles). This is because Dirichlet polygon edges meet at a triangle's circumcenter, while those of an unweighted Fraser polygon meet at the triangle's centroid (Fig. 3). Note also that Fraser polygons have twice as many edges as Dirichlet polygons (Fig. 2). One would nonetheless expect Dirichlet and unweighted Fraser polygon areas to be similar for a given point configuration, as both are based on the same triangulation. I explored this by generating ten unit square sets of 500 random points. Polygon area was determined for each point (after accounting for edge effects using the method of Kenkel, Hoskins and Hoskins 1989b), and the product-moment correlation between Dirichlet and Fraser polygon areas was computed. R-squared values ranged from 0.845 to 0.922. An example of the relationship between unweighted Fraser and Dirichlet polygon areas is shown in Fig. 4, while the distributions of polygon areas are presented in Fig. 5.

Weighted Tessellation

Fraser (1977) suggested a number of possible triangle weightings, but all were in the context of timber volume estimation. In studying interactions in plant populations, weights will normally be a function of the relative sizes of individuals. In predicting the future performance of individual trees, for example, weights might correspond to present trunk diameters. Suppose that the three individuals forming the vertices of
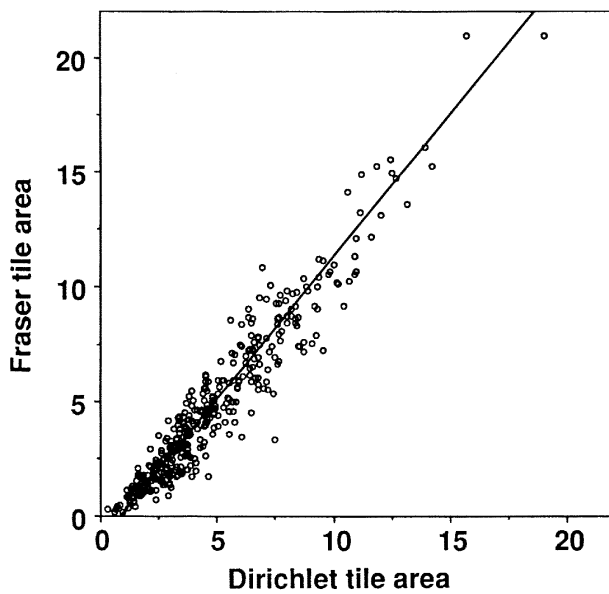
Fig. 4. Relationship between unweighted Fraser and Dirichlet tile areas ($R^2 = 91.4\%$) for a random point pattern of 500 points. Based on $n = 371$ points (after consideration of edge effects). Fitted line is the principal component.

triangle of area A have trunk diameters of a, b and c respectively. These are scaled to unit total, giving weights of w_a, w_b and w_c. The triangle is then divided into the three areas Aw_a, Aw_b and Aw_c respectively (Fig. 6). This weighting approach is appropriate if only polygon areas are required (Upton and Fingleton 1985). A more complex weighting function results if a graphical representation of the resulting tessellation is required (Fraser 1977). However, a tessellation graphic is normally not required in studies of plant interactions, as interest is focussed on the relationship between plant performance and polygon area. Thus the simple weighting approach described above is usually adequate.

Other weighting functions are of course possible. One could for example weight according to the angles subtended by the triangle vertices (the lesser the angle, the smaller the weight). Another possibility would be to use the size of the Dirichlet tessellation polygons as weights. This would result in a tessellation determined by second-order neighbours, since Fraser polygon areas would depend on the proximity of Delaunay neighbours as well as the proximity of the neighbour's neighbours. There are in fact many possible weighting functions, with the choice depending on the suitability of a particular weighting definition to the investigation's objectives.

The weighted Fraser tessellation - an example

Introduction

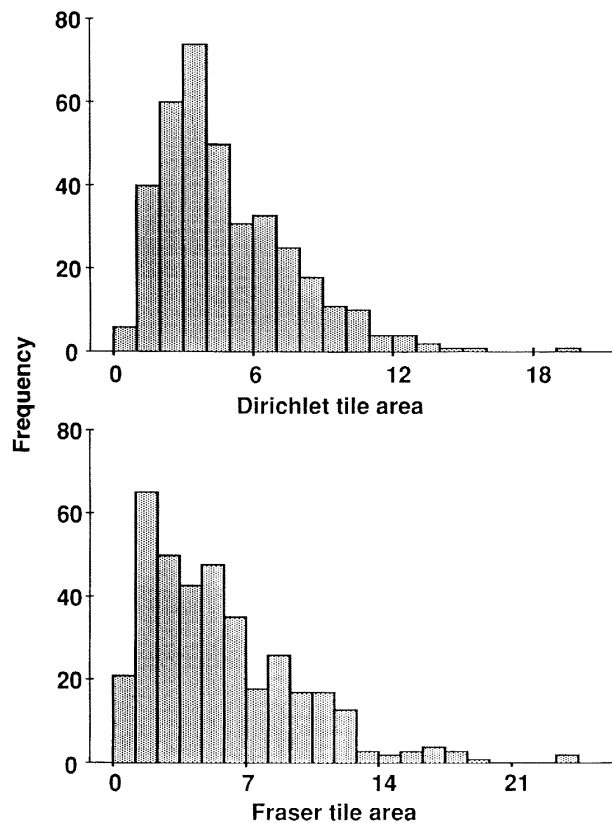Many factors determine an individual's performance

Fig. 5. Distributions of Dirichlet and unweighted Fraser tile areas. Data as in Fig. 4.

in even-aged plant monocultures. These include the degree of local crowding, small differences in germination time, genetic diversity, microhabitat variability, differences in seed size, effects of pathogens, and the occurrence of developmental abnormalities. It is therefore not surprising that the Dirichlet tessellation model, which only considers local crowding, has been found to be a relatively poor predictor of individual plant performance (Firbank and
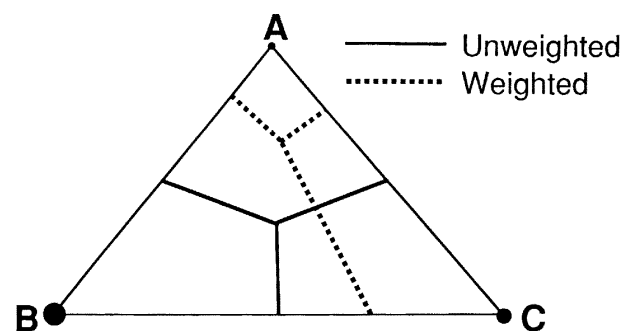

Fig. 6. Unweighted and weighted Fraser tessellation partitioning of the triangle ABC. Weights are proportional to the circle diameters of points A, B and C.

Watkinson 1987).

The weighted Fraser tessellation model also considers local crowding. In addition, however, one or more of the factors mentioned above can be incorporated through suitable definition of a weighting function. Thus the weighted model should improve on predictions of individual performance. I tested this using artificial populations of *Zinnia elegans*, in which relative germination time was used as the weighting function.

Materials and methods

Two 71×71 cm wooden flats, each 12 cm in depth and lined with black polyethylene sheeting, were placed in a single controlled environment chamber with 16L:8D light (ca. 400 $\mu E/m^2/sec$) and 22°C:15°C temperature cycles. Flats were filled with a standard greenhouse sterilized soil mixture. The top of each flat was fitted with a 71×71 cm plexiglass sheet; within the central 55×55 cm area of each sheet were drilled 500 randomly located holes. Toothpicks were pushed through these holes into the soil surface. The plexiglass was then removed, and a single seed of *Zinnia elegans* 'Whirligig' (T and T Seeds, Winnipeg MB, Canada) was planted adjacent to each toothpick (only seeds of biomass 6 to 8 mg were used in the experiment). The 8 cm perimeter edge was sown at the same density. As each seed within the 55×55 cm area germinated, its germination time (to the nearest 8 hours) and spatial coordinates were recorded. Seed germination occurred over a two week period.

Above ground biomass was harvested 4 weeks after seeds were sown (i.e. prior to the onset of flowering). Below ground biomass was not considered since it was impossible to separate individual root systems. Plant material was dried at 85°C and massed to ±0.01 g. A total of 342 seeds (68.4%) germinated in flat 1, and 284 (56.8%) in flat 2.

Data analysis

The Delaunay triangulation was computed for each flat (see Kenkel, Hoskins and Hoskins 1989a for details) and used to produce three tessellations: the Dirichlet, the unweighted Fraser, and the weighted Fraser. I used germination time as the weighting factor; the first plants to germinate were given a weight of 1, the last a weight of 0.01, with the others linearly scaled within this range. For all three tessellations, edge effects (within the 55×55 central area) were accounted for by using the algorithm described in Kenkel, Hoskins and Hoskins (1989b). After accounting for edge effects, there were 256 tiled plants in flat 1 and 197 in flat 2.

The product-moment correlation coefficient between final plant biomass and polygon area was computed for each of the three tessellations. For comparative purposes, the correlation between germination time and

final plant biomass (i.e. ignoring the spatial configuration of plants) was also computed.

Results

For both data sets, the correlations between Dirichlet and unweighted Fraser polygon areas and final plant biomass were low (Table 1). For the weighted Fraser tessellation (i.e. incorporation of germination time into the model), correlations were statistically significant though the predictive power was low ($R^2 = 7.7\%$ for flat 1, $R^2 = 7.1\%$ for flat 2). The correlations between germination time and final plant biomass were high ($R^2 = 36.2\%$ for flat 1, and $R^2 = 27.4\%$ for flat 2).

Table 1. Correlation between polygon area and above-ground biomass for two *Zinnia elegans* populations.

Population 1 (n=256)	r	P-value
Dirichlet	0.004	>0.45
Fraser (Unweighted)	0.035	>0.25
Fraser (Weighted)	0.277	<0.001

Population 2 (n=197)	r	P-value
Dirichlet	0.132	0.032
Fraser (Unweighted)	0.077	0.141
Fraser (Weighted)	0.267	<0.001

Discussion

The results indicate that local crowding (as defined by the Dirichlet and unweighted Fraser tessellations) is by itself a poor predictor of individual performance in *Zinnia elegans* monocultures. A number of factors could explain the low predictive power of unweighted tessellation models. It is clear, for example, that germination time is important, as its incorporation in the weighted model led to a statistically significant relationship between polygon area and plant biomass. However, most of the variation in plant performance remained unaccounted for even after incorporation of germination time, indicating that other factors were also important. These might have included microhabitat and genetic variability, both of which could mask the effect of local crowding as a predictor of plant performance.

Another possible explanation for the poor correlation between polygon area and plant performance is that spatial tessellation models are inappropriate for the analysis of *Zinnia elegans* populations. Evidence for this comes from the high positive correlations between germination time and final biomass ($R^2 = 36.2\%$ for flat 1, and $R^2 = 27.4\%$ for flat 2), which suggest that inclusion of spatial information actually degrades predictive ability. Examination of the flats prior to biomass harvest indicated two possible reasons for this.

First, shoots of *Z. elegans* bent to take advantage of openings in the canopy (recall that tessellation models assume that the stem system grows perpendicularly to the plane). Secondly, mature plants showed considerable canopy overlap, with leaves encroaching on first, second and higher-order polygon neighbours (tessellation models assume no spatial overlap). Violation of these two assumptions could explain the poor performance of the tessellation models.

To conclude, weighted tessellations permit incorporation of additional information about individuals in the population, and so result in models with improved predictive power. However, the *Zinnia elegans* populations violated two important assumptions of the Dirichlet-Delaunay definition of neighbourhoods, suggesting that caution should be exercised when applying tessellation models. In the following section I discuss the conditions under which tessellation models should prove most useful in predicting individual plant performance.

General discussion

Unweighted tessellation models are of limited utility in predicting plant performance since they assume that all individuals in a population are equally weighted. Weighted tessellations models, because they permit differential weighting of individuals, are more robust. Of the available weighted tessellations, I feel that the model proposed by Fraser (1977) offers the most promising approach to analyzing plant population dynamics. It has none of the disadvantages of the tessellations proposed by Johnson and Mehl (1939) and Moore, Budelsky and Schlesinger (1973), and has the advantage of being derived from the well-known Delaunay triangulation.

Weights can be defined in various ways depending on the objectives of the study and the nature of the population investigated. Examples include using germination time to predict final biomass, and using trunk diameter to predict the future growth or fate of forest trees. Interspecific interactions could also be modelled, by giving each species in a community a different "competitive weight".

The weighted Fraser tessellation can be used to model plant population and community dynamics whenever local crowding is thought to be important. However, it should be recognized that tessellation analysis is not always appropriate, as indicated by the results of the *Zinnia elegans* experiment. There are two situations in which the Delaunay definition of neighbourhoods would be inappropriate. The first is when population density is low. In this case plant interactions are minimal, so that models incorporating local crowding are not required. The second occurs at high population density. Here there is strong interplant interaction since individuals will encroach upon their first, second and higher-order polygon neighbours. Standard tessellation approaches are inappropriate in such cases, since they assume that interactions occur only between neighbours sharing a polygon edge. It follows that spatial models based on the Delaunay triangulation definition of neighbours are most appropriate when only first-order interactions are important. This is most likely to occur at the relatively low to intermediate plant densities often encountered in the field (see Kenkel, Hoskins and Hoskins 1989a for an example).

REFERENCES

ARMSTONG, R.A. 1974. Dynamics of expanding inhibitory fields. Science 183: 444-445.

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

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

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. Intl. Coop. Publ. House, Fairland, MD. pp. 151-212.

DANIELS, R.F, BURKHART, H.E. and T.R. CLASON. 1986. A comparison of competition measures for predicting growth of loblolly pine tress. 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.

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

FRASER, A.R. 1977. Triangle based probability polygons for forest sampling. For. Sci. 33: 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.

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

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

KENKEL, N.C. 1990. Spatial competition models for plant populations. Coenoses 5: 149-158.

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

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

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

MATLACK, G.R. and J.L. HARPER. 1986. Spatial distribution and

the performance of individual plants in a natural population of Silene dioica. Oecologia (Berlin) 70: 121-127.

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

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

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

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

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.

VORONOI, G. 1908. Nouvelles applications des paramètres continus à la thérie des formes quadratiques. J. für die reine und angewandte Mathematik 134: 198-287:

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

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