

Dirichlet tessellation of bark beetle spatial attack points

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Summary

1. Algorithms for Dirichlet tessellation of spatial points are developed and implemented on personal computer. Up to 3000 tessellations of points in an area of any rectangular dimensions can be scaled appropriately and viewed on computer screen or output to laser printer.

2. The program also calculates Dirichlet cell areas and their coefficient of variation (*CV*) as well as the average nearest neighbour distance between points.

3. Simulations revealed the polynomial relationship between the *CV* and the minimum spacing between points. The relationship is used to predict the percentage of maximum spacing that is exhibited by a population. This value times the maximum spacing distance possible between objects in an area (hexagonal arrangement) yields the minimum allowed distance (*MAD*) that is characteristic of individuals of some territorial or 'inhibitive' species.

4. The program and relationship were used to analyse the spatial attack patterns of the bark beetles, *Dendroctonus brevicornis* LeConte, *Tomicus piniperda* (L.), and *Pityogenes chalcographus* (L.) and determine their *MADs*. All three species exhibited spacing between attack sites, in agreement with known behavioural mechanisms that are proposed for avoiding intraspecific competition for food resources.

Key-words: Voronoi polygons, Scolytidae, Coleoptera, intraspecific competition, algorithms.

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Introduction

The distribution and abundance of organisms can be represented by spatial points in a plane. A Dirichlet tessellation surrounds a point as a planar polygon in which all regions are closer to the point than to any other points. This tessellation was proposed in 1850 by Dirichlet (Upton & Fingleton 1985) and a formal mathematical definition is given by Green & Sibson (1978). The latter authors state that 'the Dirichlet tessellation is one of the most fundamental and useful constructs determined by an irregular lattice.' The Dirichlet tessellation cell, also known as Voronoi or Thiessen polygons, has been reinvented several times and is useful to research in many scientific fields (Rogers 1964; Mead 1971; Rhynsburger 1973; Upton & Fingleton 1985; David 1988; Galitsky 1990).

Dirichlet tessellations can be thought of as representing the areas of territorial animals, allelochemic-producing plants, or the packing of cells in a tissue. For example, two adjacent points, representing competitive animals of equal strength, bisect the planar area between them as well as with any other nearby animals. In general, competitors that are

farther away from an organism will be less likely to interfere spatially unless there are no other organisms in between that can contest the areas. Thus, the areas of Dirichlet tessellations should coincide generally with the areas of the territorial or competitive ranges of the organisms (Tanemura & Hasegawa 1980; Kenkel, Hoskins & Hoskins 1989a,b).

The first computer algorithm for drawing Dirichlet cells was offered by Green & Sibson (1978). These authors developed a program in ANSI FORTRAN for use on mainframe computers that has been subsequently utilized in spatial statistics textbooks (Ripley 1981; Diggle 1983; Upton & Fingleton 1985). Another algorithm has been described in Russian and programmed in FORTRAN IV (Galitsky 1990). Dirichlet (Voronoi) cells have been delineated by algorithms that use Delaunay triangles and circumscribing circles on a HITAC M-180 computer (Tanemura & Hasegawa 1980) or elimination of intersecting circles according to a set of rules (Honda 1978). Unfortunately the above algorithms are described in only general terms, or in the program code, so they are generally difficult to use. Recently, the commercial statistical software, SYSTAT 5.0

(Wilkinson 1990), has offered graphical plotting of Voronoi polygons. Wilkinson (1990) says the algorithms of Green & Sibson (1978) were not used, but no references or algorithms are presented. Since none of the previous methods nor SYSTAT calculate areas and variance of Dirichlet cells, my objectives were both to develop algorithms for drawing tessellations with personal computers and to calculate cell areas. These general procedures could then be used specifically to analyse the spatial distributions of bark beetle 'attacks' on their host trees. Statistical regression using the coefficient of variation of cell areas revealed a new method for analysing spatial point distributions. In addition, these analyses offer a second way of determining species-specific spacing distances, termed the minimum allowed distance (*MAD*) as proposed earlier (Byers 1984).

Methods

A computer program, coded in BASIC, implementing Dirichlet tessellation algorithms was developed for personal computer that allows x - and y -coordinates of spatial data in any units to be entered into a file for later retrieval. The data files are compatible with another program for drawing contour maps of point densities (Byers 1992). Alternatively, one can generate x, y coordinates at random, with or without a degree of minimum spacing. For a given rectangular area (*AREA*) containing N points, the maximum distance possible to space apart points is given by $1.0746/\sqrt{N/AREA}$, which means the points are in a perfect hexagonal arrangement (Clark & Evans 1954). Thus, an input value of no more than about 70% of the maximum distance should be attempted since the computer otherwise may not find locations for all the points due to constraints from the initial selections. The algorithms for spacing points have been described earlier (Fig. 1 in Byers 1984).

Once the x, y coordinates of the points are entered, an inner border area should be chosen in order to avoid tessellating points on the periphery. Points near the edges of the area are not surrounded by other points so the tessellation outline would be altered by the boundary of the area. It was found empirically that for randomly distributed points the use of a border width of at least 1.5 times the distance expected for the fourth nearest neighbour ($1.0937/\sqrt{N/AREA}$, Thompson 1956) gave good results. The distance used, however, is arbitrary and can be adjusted.

Dirichlet tessellation algorithms

The program draws tessellations about each point within the inner border area, although all points including those in the peripheral area are considered. Real coordinates and dimensions are scaled on the

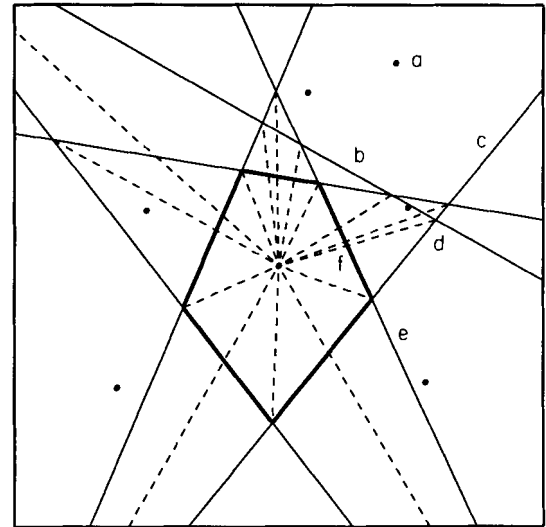


Fig. 1. Dirichlet tessellation (irregular pentagon) composed of perpendicular bisectors (solid lines) between centre point and six surrounding points. Dashed lines connect the centre point with the 15 intersection coordinates of the bisector lines. Bisector line *b* between the centre and point *a* is included in the calculation but in this case was not necessary for the drawing of the Dirichlet cell (see text for more details).

monitor screen as well as on laser printers. The algorithms are described in six steps.

1. The first step is to find the nearest neighbours which might affect the Dirichlet cell outline. Coordinates of all points (N) are scanned to count the number of points contained within a 'box' centred about the point in question. The size of the initial box is smaller than that expected to hold p neighbours (equal to $N-1$ or 35 points, whichever is smaller) if they were distributed at random ($0.2(\sqrt{[(AREA/N)P]}/2)$). However, if less than p points (hereafter 35 points) fall within the box, then the box is successively enlarged by 10% until the required points are obtained. The actual distances from the 'centre' (x_c, y_c) point to its neighbours (x_n, y_n) in the box are then computed, $d_n = \sqrt{(x_c - x_n)^2 + (y_c - y_n)^2}$, and the 35 lowest distances are sorted with an exchange sort algorithm.

2. The next step is to calculate the equations of the lines that are perpendicular bisectors between the centre point and each of its 35 neighbours (as well as the four boundary lines). The 35 resulting equations have the form $a_n x + b_n y + c_n = 0$, where $a_n = 2x_c - 2x_n$, $b_n = 2y_c - 2y_n$, and $c_n = x_n x_n - x_c x_c + y_n y_n - y_c y_c$. In Fig. 1, a simplified case is shown where a centre point is surrounded by six neighbours with six perpendicular bisector lines (solid lines).

3. The above 35 equations plus the four boundary equations are then compared to each other non-redundantly to obtain a total of $\sum_{j=1}^{n-1} j$, or 741 possible intersection coordinates. The x_j, y_j coordinates

of the intersection of two such equations, $a_1x_1 + b_1y_1 + c_1 = 0$ and $a_2x_2 + b_2y_2 + c_2 = 0$, are $x_j = (-c_1b_2 + c_2b_1)/(a_1b_2 - a_2b_1)$ and $y_j = (-a_1c_2 + a_2c_1)/(a_1b_2 - a_2b_1)$.

4. The program then calculates the equations of the 741 lines between the centre point (x_c, y_c) and each of the intersection coordinates (x_j, y_j) , where $a_j = y_j - y_c$, $b_j = -(x_j - x_c)$, and $c_j = -y_c b_j - x_c a_j$. In Fig. 1 these lines are represented by the 15 dashed lines

(lines to the boundary intersections are not shown).

5. The perpendicular bisector lines, found in (2) above, are compared to each of the dashed lines (Fig. 1) found in (4) above, to see if any intersections occur (x, y) ; method as in part 3 above) but only in the segment from the centre point to and including the intersection point of the two respective bisectors (x_j, y_j) ; from part 3). Thus, if the x -coordinate is greater or smaller than both x_c and x_j or the y -coordinate is greater or smaller than both y_c and y_j then no intersection can occur. If the number of intersections is more than two (both intersecting bisector lines intersect with a dashed line) then the intersection point found in (3) cannot be one of the legitimate vertices of the Dirichlet cell. This can be seen in one case in Fig. 1 where the bisector line b , between point a and the centre, intersects the bisector line c at d (a dashed line connects d to the centre) but bisector line e intersects the dashed segment at f , thus invalidating the intersection coordinates at d as a vertex of the Dirichlet cell.

6. The final step takes the coordinates of the true vertices of the Dirichlet cell and sorts them in ascending order by angular direction from the centre point. This must be done since it is not yet known what the correct order of drawing is between vertices. The general method for obtaining polar coordinates uses $\cos \alpha = x/r$ and the appropriate quadrant (Batschelet 1979, p. 121).

Coefficient of variation of Dirichlet cell areas

The Dirichlet cell area (A) is calculated by means of summing the areas of the triangles constructed from the centre point and the vertices (x_i, y_i) :

$$A = \sum_{i=1}^k |0.5[x_c(y_i - y_{i+1}) + x_i(y_{i+1} - y_c) + x_{i+1}(y_c - y_i)]|$$

where k = number of vertices - 1.

The mean and standard deviation (SD), $\sqrt{(N \sum A_n^2 - (\sum A_n)^2)/(N(N-1))}$, of the cell areas are used to calculate the coefficient of variation, $CV = SD/\text{mean} \times 100$. Computer simulations were carried out to determine the relationship between the CV and the degree of uniformity in spacing apart of points. A square area of 447.21 units on a side had 250 points placed within it to obtain a density of 0.00125 per unit area. Points in areas were in-

creasingly spaced apart at distances from 0 (random) to 70% of the maximum possible spacing (30.39 units) in increments of 10%. A total of 32 point sets, each of 250 points, at each of the spacing constraints were simulated. The algorithms for spacing have been reported earlier (Byers 1984) and comprise an inhibition model where points are sequentially placed at random unless they are closer to an established point than the minimum allowed distance (MAD). The inner border width used for the points was 2.5 times the expected fourth nearest neighbour distance (random distribution), 77.36 units.

The CV of the cell areas will be distorted if tessellations are attempted on points near the edges of the area. Thus, a border area must be chosen that is a compromise between reducing the 'edge effects' and having sufficient points remaining for statistical analysis. As mentioned above, it was found that a distance of 1.5 times the expected fourth nearest neighbour distance gave adequate results. The border can be somewhat larger if more points are available (>100). The effect of changing the border width on the CV and the estimated percentage of the maximum point spacing was investigated by using increasingly larger widths during tessellations of natural bark beetle attack patterns (described below).

Analysis of bark beetle attack patterns

The patterns of attack entrances of the bark beetles *Dendroctonus brevicornis* LeConte on ponderosa pine, *Pinus ponderosa* Doug. ex. Laws., *Pityogenes chalcographus* (L.) on Norway spruce, *Picea abies* (L.) Karst., and *Tomicus piniperda* (L.) on Scots pine, *Pinus sylvestris* L., were recorded from bark samples in the field. This was done by overlaying a plastic sheet on each of the bark areas and marking the plastic with ink. The marks were then measured for x and y coordinates. An average nearest neighbour distance analysis was done on the attack distributions (Clark & Evans 1954; Thompson 1956) with a previously described computer program (Byers 1984). A minimum allowed distance analysis (MAD) using six simulation runs of 300 points at each of eight spacing steps also was performed on each of the attack densities (Byers 1984). A simulated placement of 179 attacks at random was done by the computer program for comparison with the natural attacks of *P. chalcographus* above. Dirichlet tessellations were then done on the point patterns to evaluate the program as well as the attack distributions.

Results

Coefficient of variation of Dirichlet cell areas

Simulated placements of 250 points at a density of 0.00125 points per unit area revealed the relationship

(Fig. 2) between the minimum distance of separation between points and the coefficient of Dirichlet cell area variation (CV). The minimum separation distance between otherwise randomly placed points was increased in increments of 10% of the maximum hexagonal spacing distance possible at this density (i.e. 30–39 units, Clark & Evans 1954). It was found that the CV of cell areas was about 55.6% regardless of the density or number of points when simulating random point distributions (test up to 3000 points). At the maximum point spacing possible it is intuitive that the CV of the areas would be zero since all the cells are perfect hexagons of identical size. This 'point' cannot be found by simulation, although the theoretical value was used with the simulated points to find the best-fitting cubic equation (Fig. 2).

Several indexes of dispersion have been proposed to describe the degree of uniformity or aggregation among spatial points representing organisms (Clark & Evans 1954; Pielou 1959; Morisita 1965; Lloyd 1967; Goodall & West 1979). One of the most widely used is the R index of Clark & Evans (1954) which is the ratio of the observed nearest neighbour distance to the expected nearest neighbour distance when points are distributed randomly. A value greater than 1 indicates that points are more uniformly spaced than at random. It is significant that this ratio is independent of density. In Fig. 2, the CV of Dirichlet cells is also independent of density. Thus, one could tessellate a spatial point pattern and determine the CV and then use the cubic regression equation (Fig. 2) to obtain a value for the percentage of the maximum spacing that organisms exhibit. Solving algebraically for X in polynomial equations is not possible but must be done by 'binary successive approximation' until a value is found that gives the known Y (CV). This method has been incorporated into the program. For an algebraic solution, the best

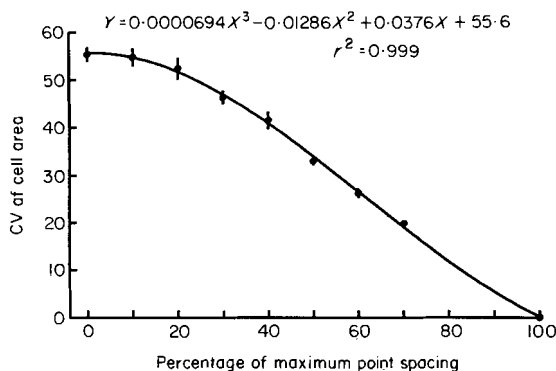


Fig. 2. Relationship between the coefficient of variation (CV) of Dirichlet cell areas and the minimum spacing between points in any area expressed as the percentage of the maximum possible point spacing if the points were hexagonally arranged. The vertical lines represent 95% confidence limits ($n = 32$ simulations of 250 points each per spacing increment; about 100 tessellations per simulation were analysed).

quadratic regression is $Y = aX^2 + bX + c$ where $a = -0.002386$, $b = -0.354$, and $c = 57.9$; and $X = (-b - \sqrt{b^2 - 4a(c - Y)})/2a$.

Earlier I proposed a method called the minimum allowed distance (MAD) which purports to find the preferred or instinctive minimum distance that individuals will space themselves apart from others (Byers 1984). Beyond this species-specific distance individuals are free to colonize sites at random. The method relies on construction of a quadratic regression curve from computer simulations of increasing minimum allowed distances of separation and the resulting average nearest neighbour distances obtained at a density corresponding to natural spatial data. The observed nearest neighbour distance for the natural data is then used to solve the quadratic equation to obtain the MAD for the species. This distance is independent of density since it is based on a behavioural distance that is relatively constant regardless of density.

It now is apparent that one may also find the MAD , assuming one exists, from the CV of the Dirichlet areas. Cells with a lower CV than expected indicate that the points are more uniformly spaced, and from the relationship in Fig. 2 one may find the percentage of the maximum point spacing at a particular density. This percentage multiplied by the maximum point spacing distance is equal to the MAD . The results of the two methods will be compared subsequently for several examples of the bark beetle attacks.

Analysis of bark beetle attack patterns

The CV of the Dirichlet cells becomes incorrectly large when the border within which tessellations are drawn is made too narrow. However, an increase in the width of the border after a certain amount does not appreciably effect the magnitude of the CV and the estimate of the percentage of maximum spacing (Fig. 3). The estimate of the percentage of maximum spacing was relatively constant (Fig. 3) for different sized areas (and numbers of Dirichlet cells) for the attacks of *Pityogenes chalcographus* and *Tomicus piniperda* as well as the random point distribution, but not for the attacks of *Dendroctonus brevicomis* (data from Figs 4–6). This indicates that the samples of the former two species and the random pattern are consistent at all scales while the data for *D. brevicomis* is more variable.

The pattern of attacks of *D. brevicomis* can be seen in Fig. 4. The average Dirichlet cell area was $33.9 \pm 5.4 \text{ cm}^2$ ($\pm 95\%$ confidence limits, CL). The coefficient of variation in the cell area was 48% (41.5–57.1%, 95% confidence interval, CI) which yields a spacing value of 28.1% (0–39.3%, 95% CI), of the maximum possible spacing as estimated from cubic regression (Fig. 2). The estimated MAD using the Dirichlet CV method is then

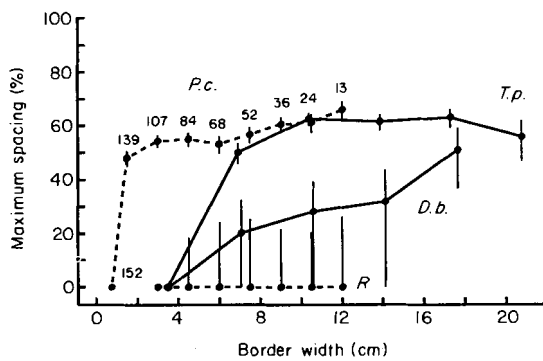
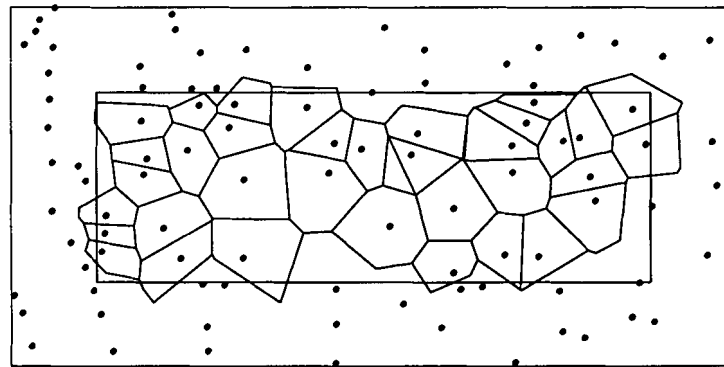


Fig. 3. Effect of border width on the estimated percentage of maximum spacing value (obtained from the cubic regression in Fig. 2) for the attack patterns of the bark beetles *Pityogenes chalcographus* (*P.c.*), *Tomicus piniperda* (*T.p.*), and *Dendroctonus brevicomis* (*D.b.*) and for a simulated pattern of randomly placed points (*R*). Vertical lines represent 95% confidence limits. The numbers along the dashed line are the number of attacks that were both tessellated and within the area inside the border.

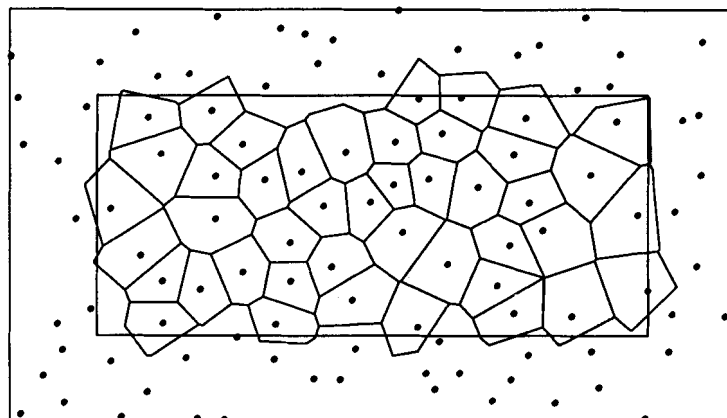
$0.281 \times (1.0746/\sqrt{97/(90 \times 45)}) = 1.95$ cm (0–2.73 cm, 95% CI). The observed average nearest neighbour distance was 3.63 ± 0.39 cm (95% CL) and the expected corresponding distance if points were random is 3.23 ± 0.34 which gives $R = 1.12$, indicating a significant degree of spacing ($P = 0.02$, Clark & Evans 1954). The alternative analysis using the nearest neighbour distances and simulation of spaced points (Byers 1984) gave a $MAD = 1.67$ cm (0.38–2.56 cm, 95% CI). The two methods give slightly different estimates of the MAD possibly because the spatial distribution of attacks was not consistent at different border widths (Fig. 3).

The average Dirichlet cell area for *Tomicus piniperda* (Fig. 5) was 33.4 ± 2.4 cm² with a $CV = 24.5\%$ (22.8–26.4%, CI) and a maximum spacing percentage of 62.8 (60.3–64.9%, CI). The MAD was thus estimated to be 4.27 cm (4.10–4.42, CI). The average nearest neighbour distance was 4.62 ± 0.19 cm (CL), the expected distance was 3.16 ± 0.31 , giving $R = 1.46$, indicating significant spacing ($P < 0.001$).



DB-N90.C00
Total points = 97
Border = 10.60062
In. border = 35 pts
 $X = 90$
 $Y = 45$
Mean tile area = 33.89395
 $\pm 95\% \text{ CL} = 5.39465$
SD = 16.28325
CV = 48.04176
NN = 3.630283 SD = 1.581293
%UMX = 39.27345
%MX = 28.10059
%LMX = 0
MAD = 2.0

Fig. 4. Dirichlet cell tessellations of 35 attacks of *Dendroctonus brevicomis* inside a border width of 1.5 times the expected fourth nearest neighbour distance in an area of 90×45 cm ($n = 97$). The average cell area is 33.9 cm² ± 5.4 (95% confidence limits) and the coefficient of variation (CV) is 48%. The percentage of maximum spacing was 28.1 (0–39.3, 95% confidence interval, Fig. 2).



TP-N90.C00
Total points = 108
Border = 10.38175
In. border = 44 pts
 $X = 86.5$
 $Y = 50$
Mean tile area = 33.35677
 $\pm 95\% \text{ CL} = 2.410397$
SD = 8.157532
CV = 24.4554
NN = 4.679659 SD = 0.7660629
%UMX = 64.9498
%MX = 62.76913
%LMX = 60.25162
MAD = 4.3

Fig. 5. Dirichlet cell tessellations of 44 attacks of *Tomicus piniperda* inside a border width of 1.5 times the expected fourth nearest neighbour distance in an area of 86.5×50 cm ($n = 108$). The average cell area is 33.4 cm² ± 2.4 (95% confidence limits) and the coefficient of variation (CV) is 24.5%. The percentage of maximum spacing was 62.8 (60.3–64.9, 95% confidence interval, Fig. 2).

The nearest neighbour simulation analysis estimated the *MAD* to be 3.71 cm (3.4–4.0 cm, CI).

Dirichlet tessellations of *Pityogenes chalcographus* attacks (Fig. 6a) produced cells with an average area of $6.87 \pm 0.44 \text{ cm}^2$ and a *CV* = 30.28% (28.4–32.4%, CI) yielding a maximum spacing percentage of 55% (52.2–57.5%, CI). The *MAD* was thus calculated to be 1.62 cm (1.54–1.7, CI). The average nearest neighbour distance was $1.99 \pm 0.1 \text{ cm}$ (CL), the expected distance was 1.37 ± 0.11 , giving $R = 1.45$, indicating significant spacing ($P < 0.001$). The nearest neighbour simulation analysis estimated the *MAD* to be 1.58 cm (1.42–1.75 cm, CI). The estimates of the two methods are very close. In comparison, the random distribution at the same

point density (Fig. 6b) gave a *CV* = 58.8% which, as expected, was not different from random distributions (Fig. 2 at 0). The average nearest neighbour distance was 1.47 cm (greater than the expected distance) and gave $R = 1.07$, but this was not statistically significant from $R = 1$ for a random pattern ($P = 0.08$).

Discussion

The Dirichlet cell was first proposed in 1850 but has been rediscovered several times and given names such as Voronoi polygons, 1909, Thiessen polygons, 1911, Wigner-Seitz cells, 1933, the cell model, 1953, and the S-mosaic, 1977 (Upton & Fingleton 1985).

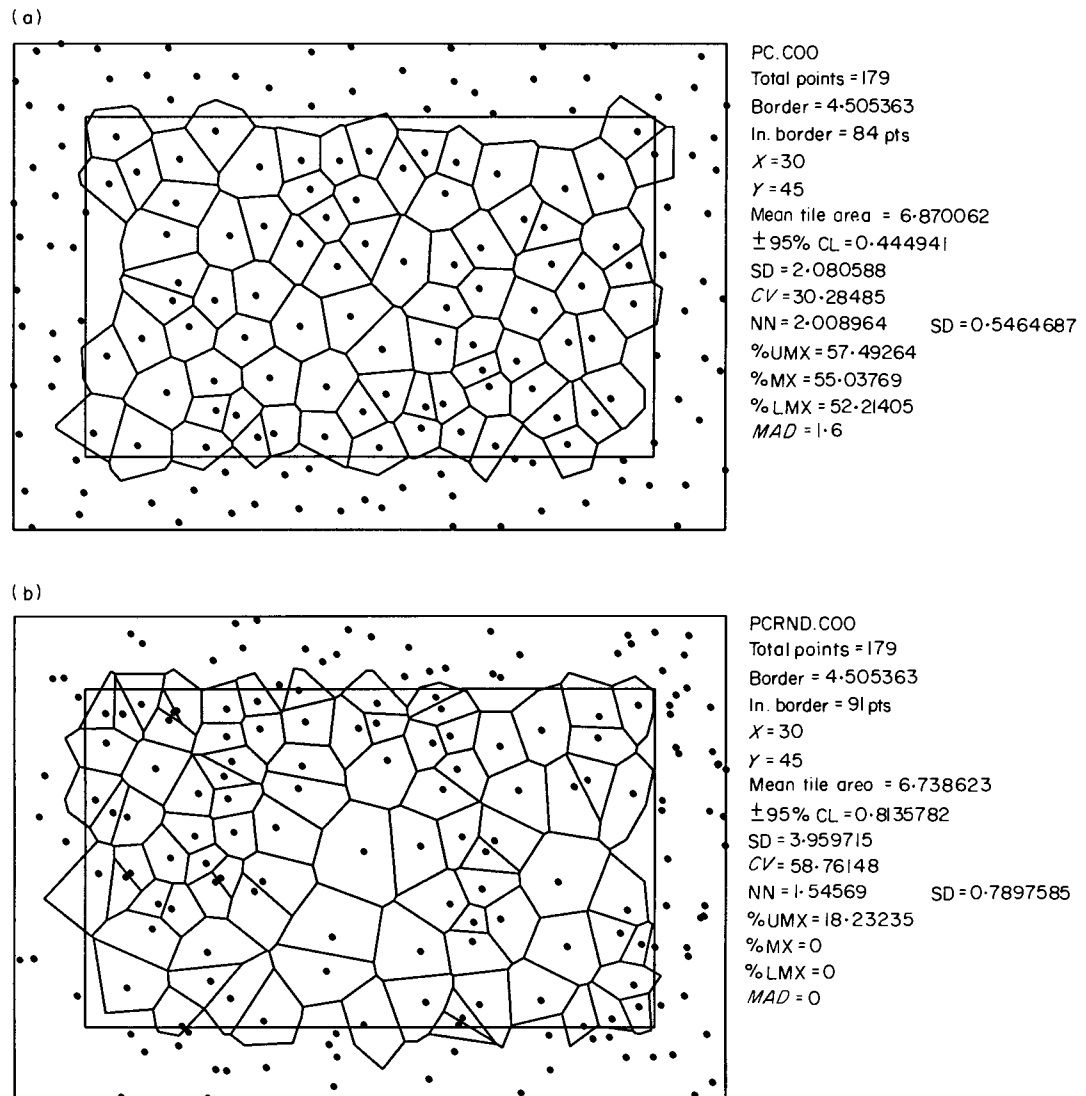


Fig. 6. Dirichlet cell tessellations of 84 attacks of *Pityogenes chalcographus* inside a border width of 1.5 times the expected fourth nearest neighbour distance in an area of $30 \times 45 \text{ cm}$ ($n = 179$). The average cell area is $6.87 \text{ cm}^2 \pm 0.44$ (95% confidence limits) and the coefficient of variation (*CV*) is 30.3%. The percentage of maximum spacing was 55 (52.2–57.5, 95% confidence interval, Fig. 2). (b) Dirichlet cell tessellations of 91 points placed at random inside a border width of 1.5 times the expected fourth nearest neighbour distance in an area of $30 \times 45 \text{ cm}$ ($n = 179$). The average cell area is $6.74 \text{ cm}^2 \pm 0.81$ (95% confidence limits) and the coefficient of variation (*CV*) is 58.8%. The percentage of maximum spacing was 0 (0–18.2, 95% confidence interval, Fig. 2).

For a theoretical Poisson forest, the expected number of sides of the Dirichlet cell is 6, the expected area is $1/d$, and the expected perimeter length is $4/\sqrt{d}$, where d is the density of 'trees' (Meijering 1953). Matérn (1979) calculates the expected length of border areas between Dirichlet cell mosaics of two species, if the distributions of the species are random.

Applications of the Dirichlet cell in plant ecology and forestry have been discussed with regard to interplant competition and prediction of growth for individual trees (Brown 1965; Mead 1971; Cormack 1979; Kenkel, Hoskins & Hoskins 1989a, b; Welden, Slauson & Ward 1990). Dirichlet polygons describe territories of pectoral sandpipers, *Calidris melanotos*, male mouthbreeder fish, *Tilapia mossambica*, and nest areas of Royal terns, *Sterna m. maxima* (Grant 1968; Barlow 1974; Buckley & Buckley 1977). The cellular patterns of coenobial green algae, *Pediastrum boryanum*, as well as cultured epithelial cells of chicks (retinal and lung), rat (intestine) and mudpuppy (gallbladder) show Dirichlet packing (Honda 1978).

Boots & Murdoch (1983) used Monte Carlo procedures (programmed in FORTRAN IV) to investigate the properties of Dirichlet tessellation of random points. Their program, however, is not generally useful to ecologists since 'there is no input to the program'. It is not known if the algorithms used in the present study are as efficient as those of Green & Sibson (1978), Honda (1978) or Tanemura & Hasegawa (1980). However, the use of a math-coprocessor allows drawing of 500 cells within a few minutes by personal computer (computation time is similar to that for SYSTAT). The computation cost of the algorithm of Green & Sibson (1978) increases roughly as $n^{1.5}$ (Diggle 1983), while the computational time for the algorithm presented here increases as $n^{1.36}$ (geometric regression, $n = 7$).

Dirichlet polygons can represent the competitive interactions of a colony of bark beetles packed onto the bark surface. Most temperate bark beetles (Coleoptera: Scolytidae), including *Dendroctonus brevicomis*, *Tomicus piniperda*, and *Pityogenes chalcographus* attack the outer bark and bore into the thin layer of phloem/cambium covering the woody xylem tissue of trees. The beetles construct a two-dimensional system of tunnels or galleries within the layer where they feed and reproduce. The thickness of the layers is similar to that of a beetle so competition is expected to be severe for this limited food resource. In fact, reports of intra-specific competition in several species in the genera *Ips*, *Dendroctonus*, *Scolytus* and *Tomicus* have shown that brood output per female decreases at higher attack densities (Miller & Keen 1960; McMullen & Atkins 1961; Eidmann & Nuorteva 1968; Ogibin 1973; Beaver 1974; Mayyasi *et al.* 1976; Wagner *et al.* 1981; Light, Birch & Paine 1983; Anderbrant, Schlyter & Birgersson 1985).

Bark beetles can minimize potential competition by avoiding areas releasing pheromone components that indicate higher densities of established individuals (Byers *et al.* 1988; Byers 1989). Another mechanism that may require little time and energy expenditure to gain large advantages in reproductive success is to avoid boring too closely to established attack holes and their galleries. Several bark beetle species, including *Tomicus piniperda*, are known to space their attacks (Nilssen 1978; Byers 1984) and this is evident also for *Dendroctonus brevicomis* and *Pityogenes chalcographus* (Figs 3, 4 & 6a).

Dendroctonus brevicomis is the most important pest bark beetle of forests in California (Miller & Keen 1960). The female initiates the attack and bores a sinusoidal tunnel under the bark in the phloem layer. She produces a pheromone component, *exo-brevicomin*, which attracts primarily males (Silverstein *et al.* 1968; Byers 1989). The male arrives and joins a female in her gallery and he releases a second attractive pheromone component, frontalin, which is synergistic with *exo-brevicomin* (Kinzer *et al.* 1969; Wood *et al.* 1976). This causes beetles to aggregate en masse and overcome the tree's resistance, resulting in its death and successful reproduction by the beetle. Over-crowding would result if not for several mechanisms, only partly understood, to avoid severe competition (Byers 1989).

Both sexes produce *trans-verbenol* which at close range inhibits the female sex from entering holes releasing attractive pheromone components (Byers 1983). Verbenone is produced by males and this compound as well as *trans-verbenol* inhibits both sexes from flying to sources releasing attractive pheromone (Bedard *et al.* 1980; Byers *et al.* 1984). Still another compound, ipsdienol, is produced in small amounts by males and inhibits both sexes (Byers *et al.* 1984). Thus, these compounds may function together to limit the overall attack density as well as close-range spacing.

Another mechanism that has been postulated to regulate density of attack is acoustic stridulation. Compared to males, females stridulate very weakly and it has been reported that females increased their chirping rate when other stridulating females were boring holes in the vicinity (Rudinsky & Michael 1973). However, male chirps can be heard from the onset of colonization, and for several days, from even a metre or more away by the human ear (Byers *et al.* 1984). Vibrations from the male stridulation could possibly be felt by walking females which would then decide to leave the area. Alternatively, males within holes with females may stridulate to warn walking males not to attempt entry into their tunnels. The function of stridulation is poorly understood.

Nilssen (1978) used nearest neighbour analysis to show that the pattern of attacks of *Tomicus piniperda*

was more uniform than a random pattern. Presumably the spacing of attacks is to avoid competition between larvae as has been shown in simulation models (DeJong & Saarenmaa 1985). The *MAD* of 3.7–4.3 cm indicates that *T. piniperda* spaces further apart than either *D. brevicomis* (1.7–2 cm) above or the European spruce bark beetle, *Ips typographus* (2.5 cm, Byers 1984).

T. piniperda, although a pest of Scots pine in Europe, does not produce an aggregation pheromone, as do most bark beetles that aggregate on trees, but instead is attracted to host volatiles. A combination of the monoterpenes α -pinene, 3-carene, and terpinolene emanating from wound oleoresin of storm-damaged trees serves in a mechanism for recognition of the host as well as its susceptibility to attack (Byers *et al.* 1985). Both sexes contain a small amount of verbenone in their hindguts (Lanne *et al.* 1987) which is probably released with the faecal pellets as are pheromone components in other bark beetle species (Byers 1989). Verbenone, at a range of a few mm to cm, could inhibit beetles from boring nearby. Beetle infested logs of Scots pine increasingly released verbenone with time while a control log released a constant and very low amount (Byers, Lanne & Löfqvist 1989). Release of verbenone at rates comparable to several infested logs significantly reduced the attraction of flying beetles to host monoterpenes. This indicates that verbenone may function in spacing of attacks as well as a cue that the host is now unsuitable for colonization (Byers, Lanne & Löfqvist 1989). Males of *T. piniperda* also stridulate audibly so this could be part of a mechanism for spacing. Stridulation appears to play a role in mate recognition, and undoubtedly in male–male fighting (Byers 1991).

In contrast to *D. brevicomis* and *T. piniperda* where the female attacks, the male of *Pityogenes chalcographus* chooses the attack site on Norway spruce and thus is responsible for avoiding competition. The males produce two pheromone components (*E, Z*)-(2, 4)-methyl decadienoate and chalcogran, which are attractive to both sexes (Francke *et al.* 1977; Byers *et al.* 1988). Several host monoterpenes, including 3-carene, α - and β -pinene, stimulate entering of artificial holes when the pheromone components are present, indicating that the monoterpenes play a role in host recognition (Byers *et al.* 1988). There are no known olfactory inhibitors which might regulate spacing. However, higher release rates of the attractive pheromone components cause the males, but not apparently the females, to be less attracted (Byers *et al.* 1988). This mechanism may inhibit males from boring too closely to established attacks. Neither sex seems to be able to stridulate. Therefore, a suitable explanation for spacing in this species is lacking.

Bark structure also has been postulated as enforcing spacing in bark beetles (Safranyik & Vithayasai

1971). Ponderosa pine has rather deep furrows running longitudinally that branch in diagonal directions. It was observed that 79 of 97 attacks of *D. brevicomis* were in crevices, visible as the longitudinal 'dotted-lines' in Fig. 4. The deep crevices in ponderosa pine allow a more rapid and efficient entry into the phloem, this combined with competition probably has provided the selection pressure for evolution of the sinusoidal gallery making. The boring of a gallery parallel to the wood grain, as in many other bark beetles, would be disadvantageous for *D. brevicomis* since it would soon encounter attacks of neighbours. However, a sinusoidal gallery would avoid nearby neighbours immediately above and below in the crevice.

At the base of Scots pine trees the furrows are more numerous and attacks of *T. piniperda* are associated with crevices (all 67 attacks in an area of 64 × 56 cm), but higher up the trunk the attacks occur more often under bark flakes (as in Fig. 5). It appears that the density of suitable sites for attack on the bark is higher than the observed attack density. Also, if the number of bark flakes is limiting then one would expect clumping of attacks, which does not appear to occur (Fig. 5). However, in the case of *P. chalcographus* (Fig. 6a) the bark of Norway spruce was like that of a fine-grained 'sandy' surface so bark irregularities seem unlikely to have caused the spacing between attacks.

The Dirichlet tessellation program and calculation of the *MAD* of spacing will allow many other plant and animal species to be analysed. The program is available from the author; please send a formatted disk and mailer for IBM-compatible personal computers.

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