5-1982

Plant Spacing: A Size Sensitive Model With Implications for Competition

Robert L. Bayn Jr.
Utah State University

PLANT SPACING:

A SIZE SENSITIVE MODEL

WITH IMPLICATIONS FOR COMPETITION

by

Robert Leon Bayn, Jr.

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology Ecology

Approved:

Major Professor	Committee Member
Committee Member	Committee Member
Committee Member	Dean of Graduate School

UTAH STATE UNIVERSITY
Logan, Utah

1982

ACKNOWLEDGMENTS

I wish to thank my major professor, James A. MacMahon, for his support and guidance during this study and for bringing me back to the central questions when I would go off on a tangent. Thanks are also due my committee members, I. G. Palmblad, M. M. Caldwell, N. E. West, and M. P. Windham. Special thanks go to Dr. West for originally bringing the paper of Vincent *et al.* (1976) to my attention and for use of his desert shrub and lodgepole pine map data, and to Dr. Windham for refurbishing my too-rusty recollections of geometry.

For ideas, discussions, and other assistances I would thank Jim Richards, Pat Johnson, and Val Grant. Support for an abundance of computer services was provided by the College of Science via Don Sisson and by the Computer Center via Martell Gee. Val Grant of Bio-Resources, Inc., generously provided convenient access to remote computer terminal facilities.

Finally, financial, editorial, and emotional support was provided by Kathy Bayn. This work is dedicated to her and to our son, Billy, in the sure and certain hope that life can return to normal.

Robert L. Bayn, Jr.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

ABSTRACT

Plant Spacing:

A Size Sensitive Model

with Implications for Competition

by

Robert Leon Bayn, Jr., Doctor of Philosophy
Utah State University, 1982

Major Professor: Dr. James A. MacMahon
Department: Biology

An algorithm is presented which partitions space among mapped plants according to their relative sizes and positions using one of eight rules for locating boundaries between individuals. The performance of those rules is examined using several natural and artificial data sets with diverse measures of individual size. The relative performance of the rules was the same for all natural data sets examined. The best rule, as measured by a high correlation between individual size and assigned space, placed the boundary at a distance between neighbors proportional to the relative sizes of neighbors as long as a maximum distance (also a function of size) was not exceeded. It is inferred that the algorithm identifies contact neighbors and quantifies the extent of their contact. A field experiment is proposed to test this inference.

(85 pages)

INTRODUCTION

For several decades workers have been concerned with characterizing the spatial arrangement of plants in an attempt to explain or identify phenomena ranging from competition and segregation (Pielou 1961) to population dynamics (Morisita 1954) and productivity (Mead 1967). Various schools of research emphasis in this field have been summarized by Pielou (1977) and Harper (1977).

Among field ecologists, the main thrust of quantitative development in the study of spatial pattern has grown around two strategies which attempt to partition pattern by the trichotomy of 'aggregated/random/regular.' In one approach, random quadrats or hierarchically nested quadrats (Grieg Smith 1952) are selected and the number of individuals in each quadrat is counted. The alternative approach involves selecting random plants (Clark & Evans 1954) or random points (Pielou 1959) and measuring the distance to the nearest neighboring plant. Pielou (1977) summarizes the extent to which various point and quadrat methods are sensitive to two components of pattern: intensity and grain. Intensity is a measure of the variability in local density with high intensity indicating high variability. Grain describes the amount of space required to encompass the full range of local densities with coarse-grained indicating a large space.

Some attention has been paid, in recent years, to comparisons of the various dispersion indices applied to the same field data (Barbour *et al.* 1977), to artificially generated population maps with known dispersion characteristics (Goodall & West 1979), or to synthetic populations designed to confuse an index (Pielou 1977). Such investigations have created some doubt about the usefulness of various indices, especially since many have no described means for establishing confidence limits or some other measure of significance.

Studies of pattern, as it describes an individual's placement and success with respect to its neighbors, are largely confined to agricultural and greenhouse examples. Some references to requirements for space appear in the ecological literature, especially with regard to arid land vegetation.

The effect of intraspecific competition, as measured by yield of individual mangold plants (*Beta vulgaris*), was inversely related to the cube of distance to its neighbors, as determined by Goodall (1960), with varying density trials and a regular planting arrangement. Mead (1966) demonstrated that productivity of individual carrot plants was a function of the space available to the individual as well as the eccentricity of the individual's location within that space. In a separate work, Mead (1967) observed that many studies related yield to density (or average space per plant), but the relationship was not often examined on a plant-by-plant basis.

Phillips & MacMahon (1981) noted a relationship between plant size and distance to nearest neighbor for *Larrea* in the Mojave Desert. Pielou (1960) produced a synthetic model of tree distributions which involved assigning space of varying radii around points (trees) that were randomly located in unoccupied space. Her model required a tree to be centered in its assigned circle of space with no overlapping of circles. Eventually the only trees that could be added to the population were 'small' trees that were assigned locations in the small parcels of remaining space. She showed that the dispersion of the points could be controlled by selecting an appropriate range of radii and final density. Then, examining a *Pinus ponderosa* stand, she demonstrated a strong correlation between sum of trunk radii and distance between nearest neighbors and proposed the dispersion pattern resulted 'in part at least' from competition between individuals.

Yeaton and coworkers have compared Pielou's model to a variety of field studies of plant size to available space. In the Mojave Desert, Yeaton & Cody (1976) examined the relationships between nearest neighbor distance, plant size, and neighbor species combinations to infer competition. They concluded that a good correlation between size and distance was a consequence of competition for resources in space and noted that the correlation was different for interspecific and intraspecific neighbor pairs. Subsequently, Yeaton, Travis & Gilinsky (1977) performed a similar study in the Arizona uplands. A significant size-distance relationship was found and vertical stratification of the root systems of the species studied was implicated in the differences between interspecific and intraspecific pairs. In a New England study comparing individual space and mortality of *Pinus strobus*, Yeaton (1978) applied Pielou's tree model to explain the high mortality of understory members of the population. He determined that understory trees were constrained by an upper size limit that was a function of the distance to the nearest canopy tree. If a young tree reached its critical size, it was doomed unless its canopy neighbor was removed.

Ross (1968) developed a model relating time of seedling emergence to capture of space and so ability to grow. Through time, his model showed the preempted space of individuals growing as circles until adjacent circles came into contact. Then the larger circle would surround the smaller one, which would then have to stop growing as the larger continued to expand in other directions. However, his model-generated maps of space preemption over time indicate that the model is more conceptual than quantitative.

In a study comparing plant size, spacing, and transpiration rates in the desert grass, *Hilaria rigida*, Nobel (1981) found a high correlation between nearest neighbor distance and the sum of the number of culms in the reference plant and its neighbor as a measure of size. He also excavated root systems and found that the area of ground invaded by the root system of a clump was accurately predictable from the number of culms in the clump.

Two codominant shrubs (*Larrea* and *Ambrosia*) in the Mojave Desert were examined experimentally by Fonteyn & Mahall (1981) to determine pattern and interference as measured by a change in water status of selected individuals after neighbors were removed. They found a weak, positive correlation (r^2=0.33) between nearest neighbor distance and the sum of neighbor pair canopy volumes. They also demonstrated a high correlation (r^2=0.88) between canopy volume and canopy biomass as interchangeable measures of plant size.

Vincent *et al.* (1976) brought together some concepts of pattern from other disciplines, notably geography, and attacked the plot and point methods that had been occupying quantitative ecologists. They suggested that 'current methods for detecting random patterns are not, in fact, measuring pattern at all' and observed that 'it is important to distinguish pattern from shape and dispersion' (Vincent *et al.* 1976, p. 374). They then proceeded to develop an analysis which used three frequency distributions to assess the departure of a population map from one generated by a Poisson process.

Their technique involved partitioning map space containing the population of individuals into a 'Dirichlet tessellation' of cells called 'Thiessen polygons' which surround each individual such that all points in a cell are closer to the individual in that cell than to any other individual (Fig. 1). Neighbors are defined as individuals sharing polygon boundaries. A 'Simplicial graph' is constructed as a network connecting all neighbors (Fig. 1). The three distributions are number of neighbors, neighbor distance, and angle size of nodes.

The technique had several new features: (a) it used the entire map of a population rather than sampling it; (b) it assigned space to individuals and defined a finite number of neighbors of each individual; (c) it did not order the neighbors of an individual; and (d) it compared the frequency distributions with the expected distributions for the Poisson case.

The algorithm of Vincent *et al.* (1976) uses the same geometry that was presented by Matern (1960) and used by Pielou (1977) for the purpose of describing vegetation mosaic pattern. Neither set of workers gives any indication of the other's use of the same geometric model.

Thiessen polygons were termed 'domains of danger' by Hamilton (1971). He presented a geometric model intended to explain the evolution of gregarious behavior by selection of individuals that move to minimize their domain of danger when a predator is sensed or suspected.

Liddle, Budd & Hutchings (1982) generated a Dirichlet tessellation for an experimental *Festuca rubra* cohort. They examined the correlation between number of tillers and polygon area repeatedly over

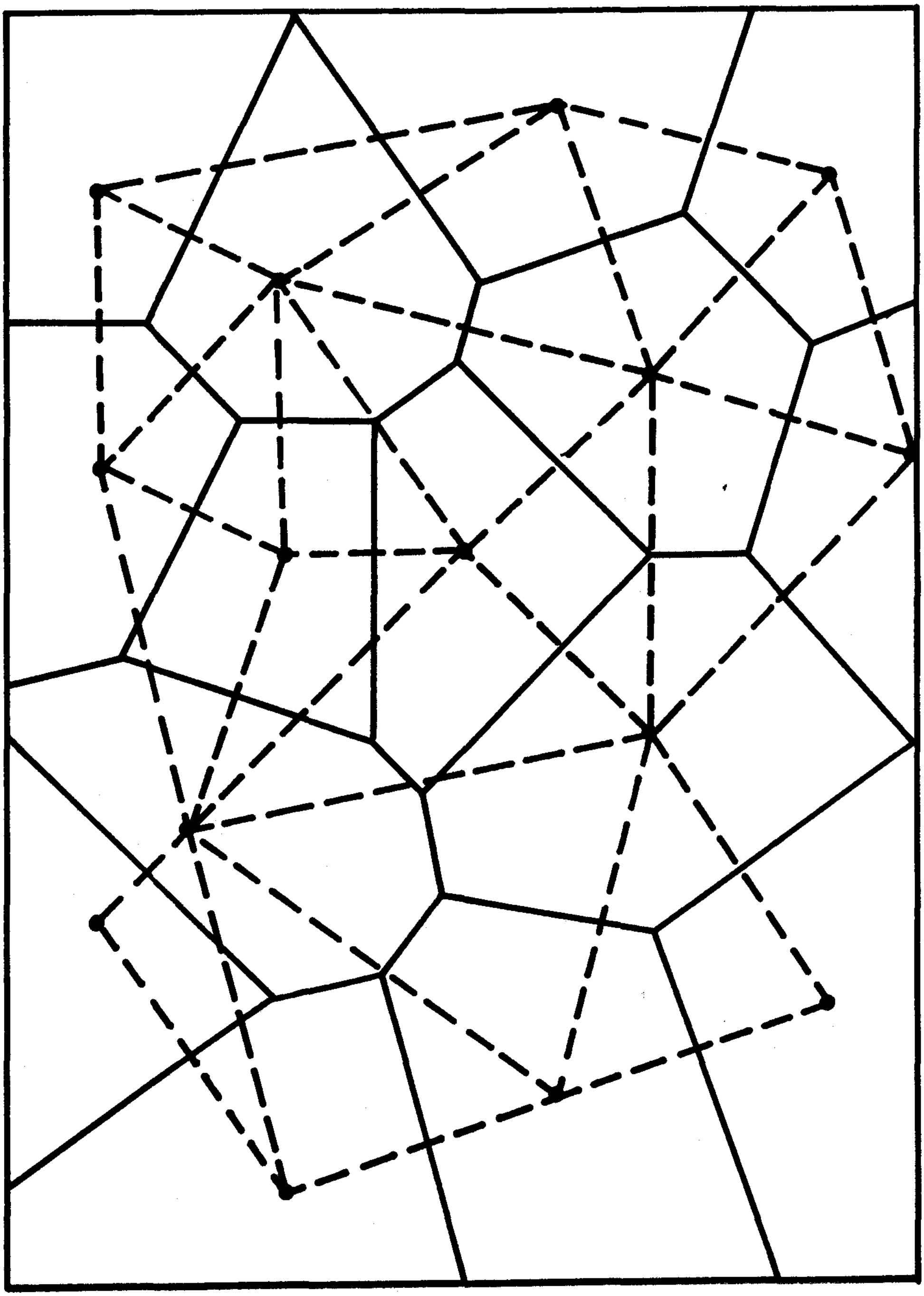

Fig. 1. A 'Dirichlet tesselation' (solid lines) of cells surrounding several individuals such that all points in a cell are closer to the individual in the same cell than to any other individual and the resulting 'Simplicial graph' (dashed lines) connecting all the individuals that share a common boundary in the tesselation.

several months after establishment of the experiment. That correlation improved with time as small polygons, defined by nearby neighbors, limited growth earlier than did larger polygons.

Few applications of the Vincent *et al.* (1976) method have appeared in the literature since 1976. A study of male frog calling stations around the periphery of a pond presents a one-dimensional modification using only the neighbor distance frequency distribution (MacNally 1979). Diggle (1979), reviewing techniques for parameter estimation for spatial point patterns, acknowledges the Vincent *et al.* (1979) method as unused but 'the general approach has possibilities' (Diggle 1979, p. 94).

Ripley (1981) reviews applications of Thiessen polygons for detection of non-randomness in stem maps of forest stands in Norway and Sweden as well as nesting sites of golden eagles and peregrine falcons, and magnetite crystals imbedded in the face of a rock, all with data borrowed from sources that had applied other analyses.

Growing space models for competition were presented in two categories by Cormack (1979). One class of models represented individuals by circles. The intensity of competitive interactions with neighbors was indicated by the amount of overlap of neighboring circles. The other class of models included Dirichlet tesselations. Cormack mentions both the applicability and shortcomings of such models for the study of competition:

> '...in an area of uniform environment the polygons represent the resource available to the individual if it is restricted by contact inhibition with immediate neighbors and if the individuals have equal competitive strength. ...it is unlikely that the area of a polygon will be the sole determinant of the strength of its occupant. Some part of the polygon will be less accessible to the occupant than others...' (Cormack 1979, p. 172)

He then considers the departure of the polygon from a compact shape and the departure of the individual from the geometric center of the polygon as covariates with polygon area upon which 'plant strength' might depend.

Cormack concludes that the tessellation's inability to accommodate variations in the 'strength' of individuals could be overcome by forming a boundary, not by a bisector between individuals, but by '...some other proportion according to the relative strengths of the individuals' (Cormack 1979, p. 174). Unfortunately, it appears that he constrains himself to requiring that the boundaries continue to be composed of straight line segments with the loss of some nice properties of the Dirichlet tessellation (i.e., triple point intersections, exclusive assignment of space, contiguity of an individual's cell, etc.). He then introduces the time dimension and envisions a model of intersections of growing cones of different heights or different angles.

A size-sensitive modification of the Dirichlet tessellation would bring a two-dimensional application to the neighbor distance/size relationship originally proposed by Pielou (1960). Such a model would permit assessment of the simultaneous effects of all neighbors rather than simple pairwise comparisons.

If structure and functioning of communities arise out of characters and interactions of individuals (MacMahon *et al.* 1981), then it is appropriate to examine the relationship between an individual's size and the combined effect of all of its neighbors' sizes and relative locations. Assigning area to a plant by placing boundaries between neighbors according to relative size would result in an area which represents a weighted integration of the size and location of all effective neighbors. The proposed technique allows for an assortment of different rules for locating the boundaries as well as a variety of possible measures of plant size.

The objectives of this study were to:

(a) Develop an algorithm for generation of a Dirichlet-like tessellation with boundaries located as a function of relative individual sizes.

(b) Examine, for several artificial and real data sets, the properties of a variety of biologically defensible boundary rules as well as various measures of plant size.

(c) Determine the usefulness of an extension of Pielou's (1960) distance versus size relationship for nearest neighbors to an area versus size^2 relationship based on boundaries with all neighbors.

(d) Examine the effects of eccentricity and shape of assigned space on the size of individuals (Mead 1966).

(e) Compare the frequency distributions generated by the method of Vincent *et al.* (1976) with those generated by a size sensitive model.

Traditional dispersion analysis has relied upon mathematical properties of point distributions, not distributions of finite sized objects. While this has often been acknowledged by workers using such techniques, they have chosen to minimize considerations of size in order to take advantage of the available mathematical theory.

This work, based as it is on an emphasis on considerations of relative individual size, attempted to modify a geometric model for dispersion in such a way that its usefulness for dispersion analysis might be lost but its ability to quantify interacting neighbor relationships would be improved.

METHODS

This study examined eight different rules for partitioning space according to relative size and distance between nearby individuals. An algorithm was developed to apply any one of the rules to a data list of coordinates and sizes and to summarize and analyze the resulting tessellation. That algorithm was implemented as the FORTRAN77 program SPACE.FOR on the Utah State University VAX 11/780. A program listing appears in Appendix A.

The program is organized into four modules that sequentially perform separate operations required for the analysis. First, the data set, previously sorted by x coordinate, is scanned and various attributes (ranges of coordinates and sizes) and initial estimates of parameters (e.g., size to distance conversion, maximum distance to search) are provided (Fig. 2, Module A). The desired assignment rule and parameters are then selected.

Determination of the appropriate measure of size is accomplished separately from the initial analysis. It is often constrained by what can be cost-effectively measured. Dimensional analysis studies suggest that many different metrics (height, cover, d.b.h., leaf area, biomass, etc.) could be used, possibly with the aid of a transformation (power, root, logarithmic, etc.) to produce a good linear metric. The program does allow a constant multiplicative transformation relating size and distance. All other transformations must be performed separately.

For each small increment of area (cell) on the map, the program calculates a score for all 'nearby' individuals using the distance from

MODULE A

1. Provide data sorted by x-coord and format for X, Y, SIZE.
2. Datafile is scanned to report ranges of coords and sizes and to suggest values for increment size and multiplier.
3. Select a Rule, boundaries and maximum distance to search.

MODULE B

1. For each cell in the gridded map area, scores for nearby individuals are calculated. The individual with the high score is assigned the cell unless no score is above zero.
2. Cell coordinates, assigned I.D.#, high score and distance are stored for module C and for graphical presentation.
3. Record a neighbor contact whenever two adjacent cells are assigned to two different individuals.

MODULE C

1. The assignments are summarized by individual and stored:
   a. total number of cells assigned (area)
   b. sum of scores from each assigned cell.
   c. maximum distance to a neighbor boundary.
   d. geometric center of assigned space.
   e. eccentricity (individual to geometric center).
   f. ID number of each neighbor.
   g. boundary individuals are flagged.
2. Regression of area and score on size squared.

MODULE D

1. Frequency distributions of number of neighbors and classes of distances and angles are calculated using non-boundary individuals.
2. The observed distributions are compared with the random distributions using a Kolmogorov-Smirnov goodness of fit test.

Fig. 2. Flow diagram of the algorithm for space assignments, summary, and analysis.

the cell to the individual, the size of the individual, and the selected assignment rule (Fig. 2, Module B). The cell, initially unassigned with a score of zero, is assigned to the individual with the highest score. The identification number of the winner is stored with the winning score, distance, and coordinates of the cell for later summarization and analysis.

The eight rules all decrease monotonically with distance for a given size and, almost surely, result in assignment of a single contiguous space to each individual. Some of the rules approach zero asymptotically with increased distance and so guarantee that all map space will be assigned. Other rules cross zero and may leave some space unassigned, allowing individuals to share a portion of their boundaries with unassigned space rather than a neighbor. The rules are presented in Table 1 with some of their characteristics. Fig. 3 depicts the form of the eight rules for three relative sizes of individual and Fig. 4 shows the score surfaces resulting from application of each of the eight rules to the same map of a few individuals.

Table 1. Rules for calculating an individual's score at an increment of space as a function of the size of the individual and the distance to the increment of space. (Dmax is the maximum distance of influence of the largest size under Rule 7).

No.	Rule	Boundary Shape at Unequal Sized Neighbors	Unassigned Space Possible?
1.	SCORE=1.0/(DIST+1.0)	straight	No
2.	SCORE=SIZE/(DIST+SIZE)	circle	No
3.	SCORE=(2.0*SIZE/(DIST+SIZE))-1.0	circle	Yes
4.	SCORE=1.0-(DIST/SIZE)	circle	Yes
5.	SCORE=1.0-(DIST/SIZE)**2	circle	Yes
6.	SCORE=SIZE-DIST	parabola	Yes
7.	SCORE=2.0*(1-((DIST+DMAX)/(SIZE+DMAX)))	circle	Yes
8.	SCORE=EXP((-(DIST/SIZE)**2)/2.0)	circle	No

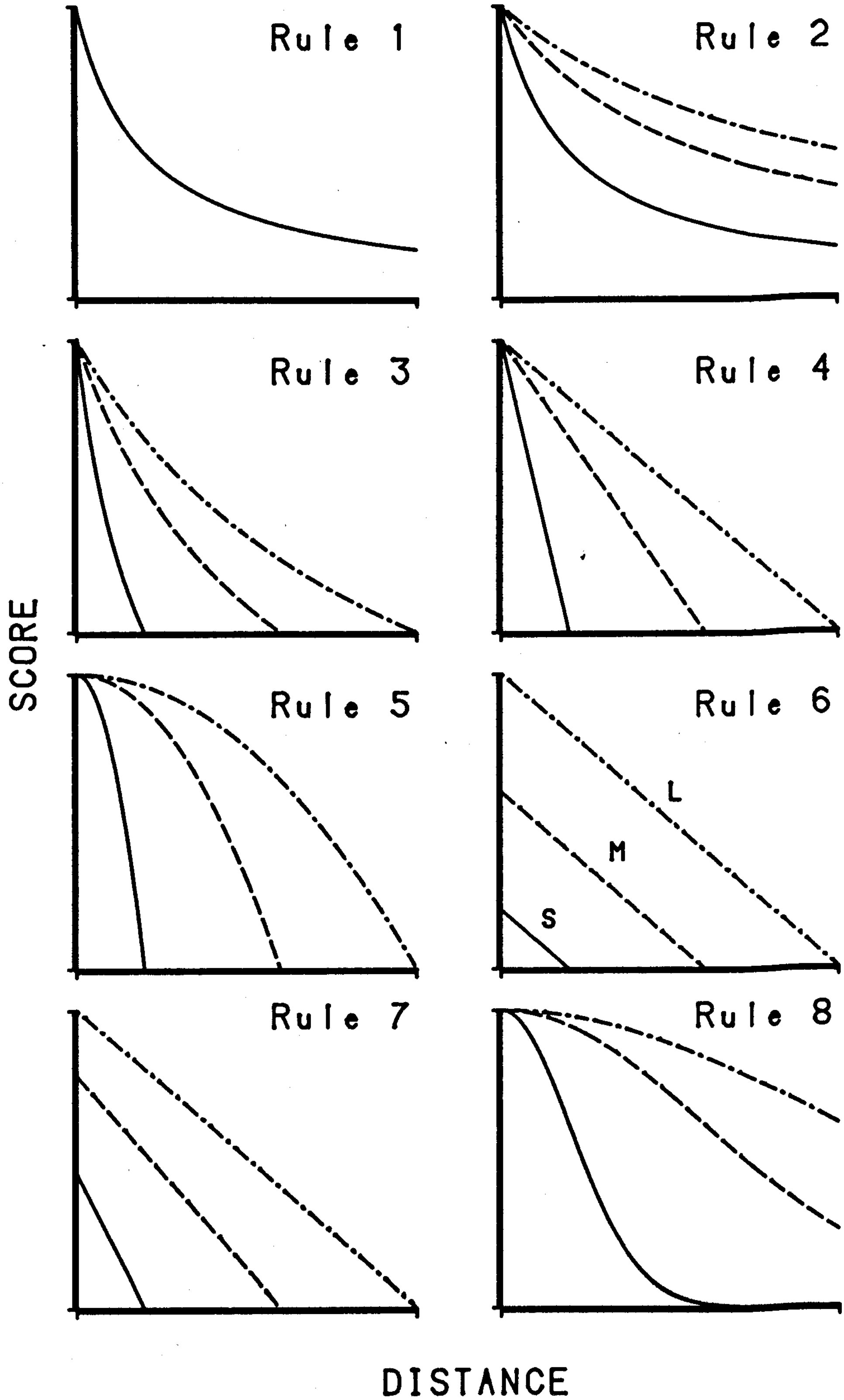

Fig. 3. Three sample curves for the assignment scores for three sizes of individual as a function of distance under each of the eight rules given in Table 1. Note that Rule 1 is size-insensitive.

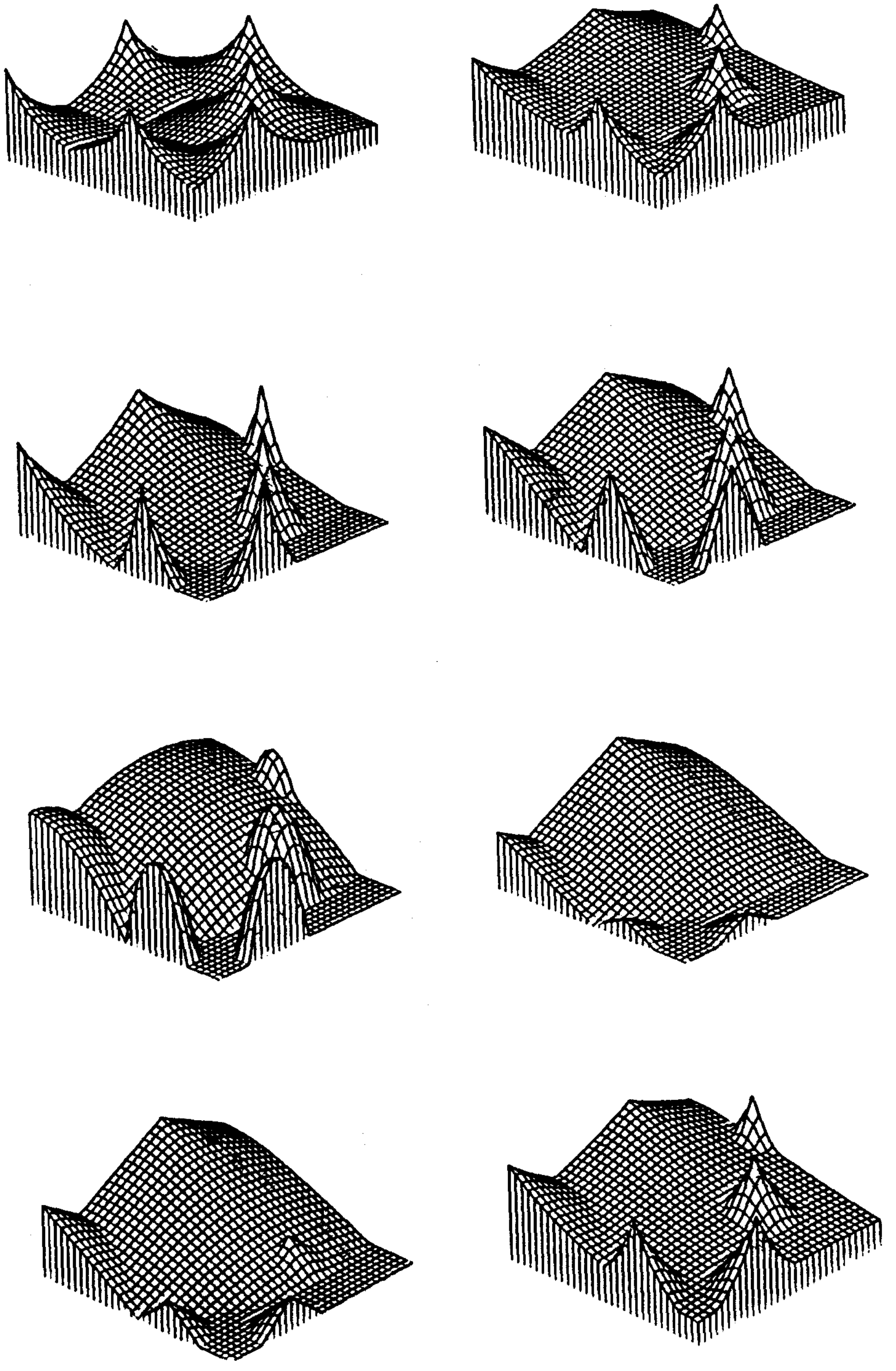

Fig. 4. Realizations of scores for each location on a map grid containing six individuals of varying sizes implementing each of the eight rules. The boundaries are represented by intersections of the conic-like sections centered on each individual. Note the disappearance of some small individuals under Rules 6 and 7.

Rules 2 through 5 and 8 are placing boundaries between unequal size individuals such that the distances from any point on the boundary to the two neighbors are in the same proportion as the sizes of the two neighbors.

After all cells have been assigned, the following parameters are accumulated for each individual (Fig. 2, Module C):

(a) Total area of cells assigned to this individual.

(b) Sum of all scores in cells assigned to this individual.

(c) Coordinates (x,y) of the geometric center of the assigned area.

(d) Eccentricity - distance from individual to geometric center.

(e) Maximum distance to an assigned cell.

(f) Number of neighbors sharing a common boundary.

(g) Identification number for each neighbor.

Individuals that are assigned cells at an edge of the mapped space are flagged for omission from portions of the analysis. Since their complete boundary is unknown, their total area and neighbor contacts are unknown. They are still available as neighbors of individuals in the interior of the map.

Using the accumulated parameters about each individual, linear regressions are calculated for area=f(size) and scores=f(size); then observed distributions of number of neighbors, scaled distances, and angles are reported and compared with the expected distributions for a random point dispersion (Vincent *et al.* 1976) using a Kolmogorov-Smirnov goodness of fit test (Zar 1974) (Fig. 2, Module D).

Additional regression analysis of the summary information generated by SPACE was accomplished with MINITAB (Ryan, Joiner & Ryan 1976) and SPSS (Nie *et al.* 1975), primarily to examine additional relationships between parameters found for each individual and transformations of those parameters. In particular, non-linear relationships between size and area or total score suggested more appropriate transformations of size to use in a reanalysis. The command file for these analyses is included in Appendix B.

A sequence of analyses was established for examination of a data set. The data set was first analyzed using Rule 1 to test for departure from randomness using the Vincent *et al.* (1976) method. Rule 2 was then applied to each of the measures of size as well as any desired transformations of size for each data set. The various measures of size are not expected to be independent. The rank order of individuals by size would be similar for any measure of size. However, one measure will perform better than the rest as measured by the coefficient of determination, r^2, of a linear regression of assigned area on the square of individual size. That measure of size will be selected for use in further analyses with Rules 3 through 8.

In an attempt to parameterize rules that go to zero at some distance (Rules 3-7), a linear regression is calculated for size versus maximum distance assigned. The resulting linear equation in expected to have a positive slope and a negative intercept. The parallel equation passing through the origin is taken as the upper limit of desired assignment distances so the slope of that equation is used as the multiplicative factor for successive runs of Rules 3 through 7.

In general, unassigned space is not desirable. If it occurs as a few isolated patches in the map space, it may be indicating space that is unoccupied due to a recent individual's death and/or colonization failure or space that is sparsely occupied due to a local violation of the homogeneity requirement of the model. If unassigned space occurs as a buffer between many plants that had been designated as neighbors under Rule 2, then it is probable that the multiplicative factor, determined above, is too small.

Several natural and synthetic data sets were examined:

(a) Synthetic data from Fig. 6 of Vincent *et al.* (1976) consisting of coordinates without any size measure.

(b) Corn data from a high density experimental garden plot consisting of coordinates, height, total fresh weight, and leaf fresh weight.

(c) Four desert shrub data sets obtained from aerial photographs near Pine Valley, Utah, consisting of coordinates and shrub diameters.

(d) Three lodgepole pine data sets obtained from 20 by 25 m stem maps from the Utah State University Forest, Cache County, Utah, consisting of coordinates and diameter breast height (d.b.h.).

(e) Artificial Population Sampler data (Schultz, Gibbens & Debano 1961) consisting of four selected species codes (colors), coordinates, and cover.

The data set of Vincent *et al.* (1976) was included as a test of the algorithm using Rule 1. Comparison of the frequency distribution produced by the algorithm with those published in Vincent *et al.* (1976) showed some discrepancies of method for removal of edge effects.

The corn data set was intended to test the advantages of biomass metrics as a measure of size as well as to provide an example with the smallest amount of unused space possible. A one meter by three meter plot was carefully marked out with one seed planted at each intersection of a decimeter grid in the plot. The soil had been pretreated with a balanced fertilizer, was watered twice a week, and was supplementally fertilized with ammonium sulfate every two weeks.

After germination results were apparent, some additional seedlings were removed to provide a variation in space available to some remaining individuals. About 80% of the initial planting became established.

The treatment was designed to provide abundant nutrient resources so that competition for light would be as great as possible. By the time vegetative growth had ceased, the canopy had thoroughly closed and no sunflecs were observed on the ground.

Stalks were individually cut just above the prop roots, measured, weighed, stripped of leaves, and reweighed. Part of the plot was vandalized so that only about a third was undisturbed and recorded.

The desert shrub and lodgepole pine data were used to test the suitability of the simple size metrics available with those types of mapping as well as possible transformations of those metrics. For the aerial photos, the space assignments of the models could be plotted to a matching scale and compared directly with the photos for subjective comparisons.

Results using the Artificial Population Sampler data could be compared to the tabulated results of a variety of traditional dispersion indices applied to the same data by Goodall & West (1979). The description of the techniques used to locate individuals of various sizes does not indicate any interdependence between size and location.

RESULTS

Sixty-three analyses were examined using various combinations of data sets, size metrics, and assignment rules (Table 2). The sequence of analyses, previously described, was continued for each data set only so long as the analyses continued to have interpretable results. A brief summary of each analysis listed in Table 2 is given in Table 3.

Vincent data set

The data set (VHGC) obtained from Fig. 6 of Vincent *et al.* (1976) was analyzed only with Rule 1 since no varying size measure was given. An exceptionally small increment size was used to improve the resolution of the analysis since it was noted from their Fig. 7 that some neighbors shared very small borders. Fig. 5 shows the resulting tesselation and Simplicial graph which matches their Fig. 7 quite closely.

There were major discrepancies between the frequency distributions produced by the analysis and those presented in their Table 2. Some discrepancies, especially in numbers of neighbors, are clearly due to inaccuracies in mapping the data from their figure. A Kolmogorov-Smirnov test comparing the relative frequency distributions shows no significant difference at α=0.2 probability level. However, the total counts of distances and angles are far from agreement. Their summary includes more angles and fewer distances due to some disparate membership rules for each distribution in an attempt to avoid edge or boundary effects.

Using each non-boundary individual as a reference, program SPACE

Table 2. Number of analyses run for each combination of eight rules and 13 data sets.

Dataset	Rule Number 1	2	3	4	5	6	7	8	Comments
VHGC.DAT	1								no measure of size
CORN.DAT	1	5	4	1	1	1	1	1	five measures of size
LPO.DAT	1	1							only six nonboundary individuals
LPM.DAT	1	1	1	1	1	1	1	1	mature stand with some invasion by other species
LPY.DAT	1	1	1						young stand
DER2.DAT	1	2	1	1	1	1	1	1	cover also used as size once
DATR.DAT	1	1	1						relatively high abundance of *Atriplex confertifolia*
DCER.DAT	1	1	1	1	1	1	1	1	relatively high abundance of *Ceratoides lanata*
DLOW.DAT	1	1	1						relatively low total density
PWHI.DAT	1	1							size was very poorly correlated with assigned space. No mechanism for selecting size was reported by the originators of these artificial populations
PIVO.DAT	1	1	3						
PYEL.DAT	1	1							
PRED.DAT	1	1							
COLUMN TOTALS	13	17	13	4	4	4	4	4	63 total

Table 3. Summary of results of the 63 analyses.

Rule used	Measure of Size	N	# of cells: Assigned	# of cells: Empty	Maximum Distance	r^2: Area	r^2: Score	Kolmogorov-Smirnov Test: Distance	Kolmogorov-Smirnov Test: (#)	Kolmogorov-Smirnov Test: Angle	Kolmogorov-Smirnov Test: Neighbors	Slope of Distance Regression
1[a]	(no size)	54	83190	-	5.04	-	-	0.15	(312)	0.10	0.10	-
1[b]	(height)	56	6950	-	15.81	0.00	0.00	0.44	(308)	0.33	0.13	0.01
2	height	56	6605	-	20.62	0.68	0.76	0.44	(314)	0.27	0.19	0.07
	tot wt	60	5602	-	35.81	0.60	0.67	0.44	(256)	0.27	0.46	0.06
	leaf wt	59	6523	-	25.00	0.72	0.78	0.44	(312)	0.21	0.29	0.25
	$\sqrt{\text{leaf wt}}$	56	6611	-	19.65	0.59	0.69	0.44	(319)	0.31	0.09	1.40
	$\sqrt[3]{\text{leaf wt}}$	56	6748	-	18.68	0.46	0.57	0.44	(323)	0.32	0.05	2.64
3	leaf wt (0.20)	61	5749	1421	20.52	0.83	0.97	0.44	(205)	0.40	0.55	0.19
	leaf wt (0.25)	60	6559	366	20.52	0.74	0.93	0.44	(281)	0.27	0.34	0.22
	leaf wt (0.30)	60	6791	79	22.36	0.70	0.89	0.44	(309)	0.23	0.31	0.24
	leaf wt (0.35)	59	6523	7	25.00	0.72	0.87	0.44	(312)	0.21	0.29	0.25
4	leaf wt (0.25)	60	6559	366	20.52	0.74	0.90	0.44	(281)	0.27	0.34	0.22
5	leaf wt (0.25)	60	6559	366	20.52	0.74	0.86	0.44	(281)	0.27	0.34	0.22
6	leaf wt (0.25)	51	6011	366	26.40	0.62	0.75	0.44	(244)	0.28	0.33	0.23
7	leaf wt (0.25)	60	6523	366	24.76	0.74	0.90	0.44	(280)	0.27	0.34	0.22
8	leaf wt (0.25)	59	6523	0	25.00	0.72	0.81	0.44	(312)	0.21	0.29	0.25
1[c]	(DBH)	6	4140	-	78.49	0.21	0.19	0.31	(37)	0.13	0.21	0.45
2	DBH	6	827	-	125.18	0.82	0.84	0.45	(16)	0.50	0.71	1.08
1[d]	(DBH)	65	7539	0	48.17	0.21	0.24	0.08	(373)	0.06	0.10	0.44
2	DBH	60	4882	0	76.06	0.80	0.83	0.17	(295)	0.15	0.41	1.43
3	DBH	61	5276	79	76.06	0.80	0.88	0.15	(298)	0.15	0.40	1.43
4	DBH	61	5276	79	76.06	0.80	0.86	0.15	(298)	0.15	0.40	1.43
5	DBH	61	5276	79	76.06	0.80	0.84	0.15	(298)	0.15	0.40	1.43
6	DBH	30	4226	79	77.83	0.70	0.75	0.44	(151)	0.17	0.31	1.74
7	DBH	61	5236	79	76.06	0.80	0.87	0.16	(298)	0.15	0.37	1.43
8	DBH	60	4882	0	76.06	0.80	0.84	0.17	(295)	0.15	0.41	1.43

Table 3. Continued.

Rule Used	Measure of Size	N	# of cells		Maximum Distance	r^2		Kolmogorov-Smirnov Test				Slope of Distance Regression
			Assigned	Empty		Area	Score	Distance	(#)	Angle	Neighbors	
1[e]	(DBH)	135	8986	-	31.02	0.11	0.13	0.03	(792)	0.03	0.04	0.34
2	DBH	116	6829	-	38.60	0.67	0.72	0.12	(622)	0.10	0.25	1.42
3	DBH	116	6787	108	29.97	0.68	0.79	0.12	(620)	0.11	0.25	1.39
1[f]	(diameter)	317	8429	-	32.57	0.04	0.05	0.08	(1837)	0.05	0.07	0.25
2	diameter	320	7979	-	58.26	0.79	0.83	0.08	(1719)	0.10	0.31	3.92
	cover	268	9783	-	620.61	0.26	0.44	0.07	(1215)	0.18	0.51	0.72
3	diameter	323	8046	220	50.22	0.80	0.91	0.07	(1672)	0.11	0.33	3.69
4	diameter	323	8046	220	50.22	0.80	0.89	0.07	(1672)	0.11	0.33	3.69
5	diameter	323	8046	220	50.22	0.80	0.87	0.07	(1672)	0.11	0.33	3.69
6	diameter	243	7917	220	50.22	0.79	0.83	0.17	(1294)	0.10	0.29	3.78
7	diameter	323	8036	220	50.22	0.80	0.90	0.07	(1662)	0.12	0.34	3.73
8	diameter	321	8052	0	58.26	0.79	0.85	0.08	(1727)	0.10	0.31	3.93
1[g]	(diameter)	181	7834	-	44.42	0.11	0.11	0.05	(1047)	0.04	0.06	0.53
2	diameter	182	7478	-	68.41	0.60	0.67	0.11	(1020)	0.09	0.21	4.17
3	diameter	184	7247	505	58.03	0.65	0.84	0.07	(957)	0.12	0.30	3.95
1[h]	(diameter)	196	7752	-	56.01	0.05	0.04	0.05	(1135)	0.03	0.04	0.34
2	diameter	204	7108	-	88.42	0.58	0.62	0.15	(1030)	0.15	0.39	5.96
3	diameter	208	7158	746	59.54	0.63	0.76	0.10	(961)	0.18	0.48	5.43
4	diameter	208	7156	746	59.54	0.63	0.73	0.10	(962)	0.18	0.48	5.43
5	diameter	208	7156	746	59.54	0.63	0.70	0.10	(962)	0.18	0.48	5.43
6	diameter	132	6531	746	59.54	0.65	0.73	0.27	(602)	0.20	0.48	5.71
7	diameter	208	7142	746	59.54	0.63	0.73	0.10	(962)	0.18	0.48	5.47
8	diameter	204	7108	0	88.46	0.58	0.65	0.15	(1030)	0.15	0.39	5.96
1[i]	(diameter)	77	7026	-	81.44	0.09	0.08	0.10	(451)	0.04	0.06	1.25

Table 3. Continued.

Rule Used	Measure of Size	N	# of cells: Assigned	# of cells: Empty	Maximum Distance	r^2: Area	r^2: Score	Kolmogorov-Smirnov Test: Distance	(#)	Angle	Neigh-bors	Slope of Distance Regression
2	diameter	82	6566	-	114.06	0.61	0.67	0.20	(391)	0.16	0.45	5.42
3	diameter	82	6340	500	96.83	0.65	0.80	0.18	(368)	0.18	0.46	4.88
1[j]	(diameter)	94	27059	-	149.60	0.00	0.00	0.03	(535)	0.05	0.09	0.32
2	diameter	94	21682	-	224.20	0.69	0.75	0.13	(446)	0.17	0.47	10.71
1[k]	(diameter)	56	19056	-	460.80	0.03	0.05	0.30	(316)	0.07	0.11	1.61
2	diameter	56	17191	-	768.21	0.30	0.33	0.29	(297)	0.13	0.39	13.61
3	diameter (3.3)	74	8474	31059	59.84	0.72	0.90	0.33	(234)	0.28	0.64	3.37
3	diameter (5.0)	73	12720	26241	89.99	0.52	0.77	0.36	(284)	0.20	0.56	4.69
3	diameter (6.7)	69	15658	21600	119.97	0.42	0.64	0.36	(292)	0.18	0.51	6.18
1[l]	(diameter)	106	15613	-	577.70	0.00	0.00	0.32	(593)	0.11	0.18	-2.05
2	diameter	124	18631	-	605.70	0.25	0.32	0.42	(535)	0.21	0.54	13.17
1[m]	(diameter)	118	20998	-	347.80	0.02	0.03	0.27	(677)	0.11	0.13	2.09
2	diameter	123	20228	-	451.07	0.52	0.56	0.34	(555)	0.21	0.51	11.99

	Population Size	Total Cells
[a] VHGC.DAT	80	144,508
[b] CORN.DAT	90	10,000
[c] LPO.DAT	20	12,500
[d] LPM.DAT	98	10,000
[e] LPY.DAT	191	12,500
[f] DER2.DAT	486	10,000
[g] DATR.DAT	276	10,000

	Population Size	Total Cells
[h] DCER.DAT	314	10,000
[i] DLOW.DAT	143	10,000
[j] PWHI.DAT	128	40,000
[k] PIVO.DAT	77	40,000
[l] PYEL.DAT	145	40,000
[m] PRED.DAT	153	40,000

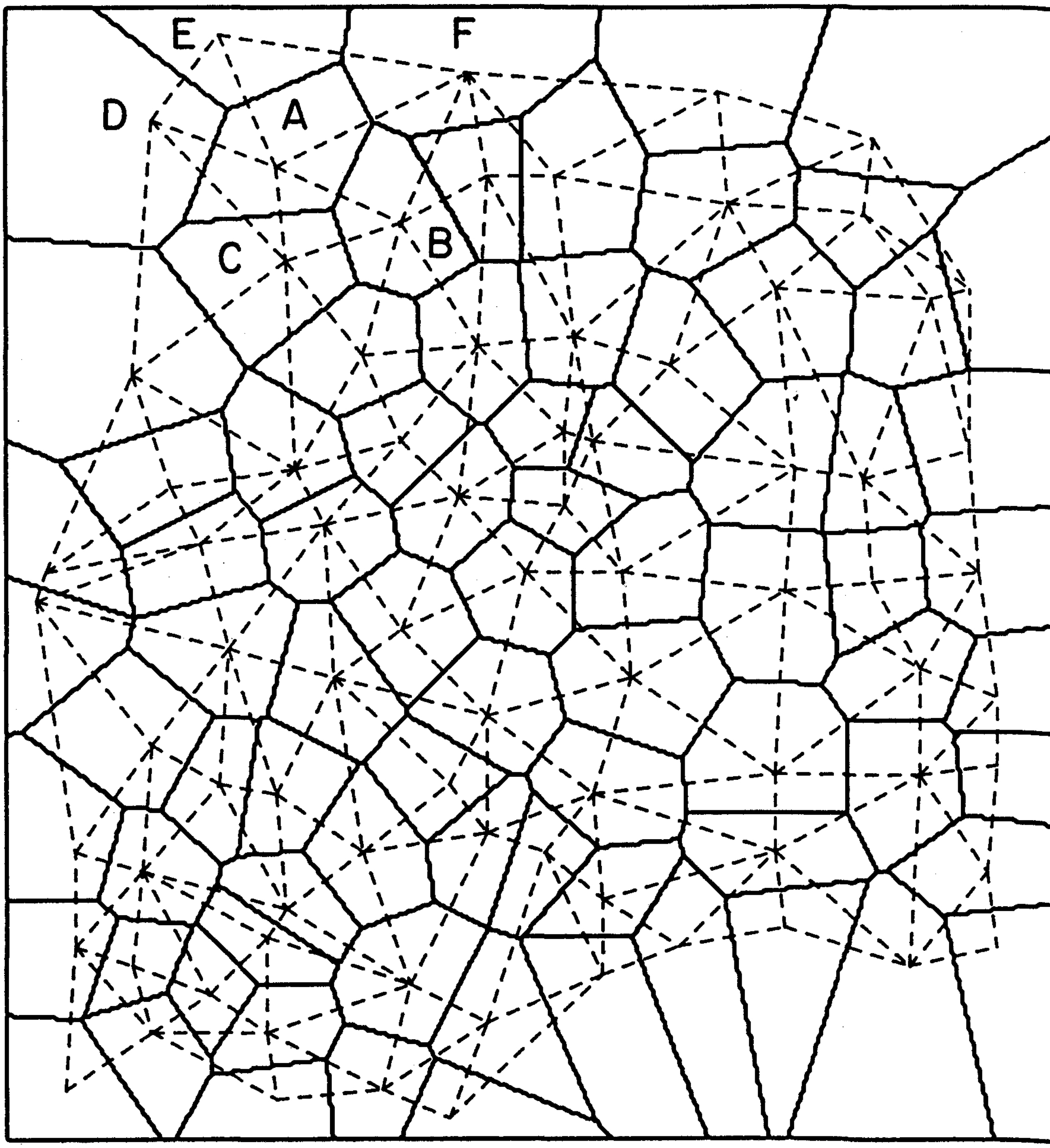

Fig. 5. Map of space assignments (solid lines) and neighbor identification (dashed lines) resulting from the application of Rule 1 (no size effect) to the point pattern presented in Fig. 6 of Vincent *et al.* (1976). Letters identify individuals discussed in the text.

counts number of neighbors (regardless of their boundary status) and measures a distance and an angle for each of those neighbors. Vincent *et al.* (1976) count the same neighbors but include distances only to nonboundary neighbors while including angles in all completed triangles of the Simplicial graph. For example, the nonboundary reference plant 'A' in Fig. 5 has five neighbors for which SPACE would measure five distances and angles. Vincent *et al.* (1976) would count only the distances to nonboundary neighbors 'B' and 'C' but include three angles from plant 'D', two angles from plant 'E', and five angles from plant 'F'. The membership criteria used in SPACE is more parsimonious computationally since entries in all three frequency distributions can be generated by examination of the neighbor list of each nonboundary individual.

Corn data set

The corn data set, analyzed first with Rule 1, showed no correlation of assigned area with size measured by height. The frequency distribution tests confirmed that the regular planting scheme was far from random except for the number of neighbors distribution. Rule 1 yielded no relationship between size (height) and maximum distance of assignment.

All five measures of size (height, total fresh weight, leaf weight, square root and cube root of leaf weight) were examined with Rule 2. Leaf weight produced the highest correlation with assigned area and total score (Fig. 6 & 7) and was selected for use with Rules 3 through 8. Examination of the regression of maximum distance versus size suggested a size multiplier of 0.25 for succeeding analyses. That value was compared with neighboring values of 0.20, 0.30, and 0.35 using Rule 3

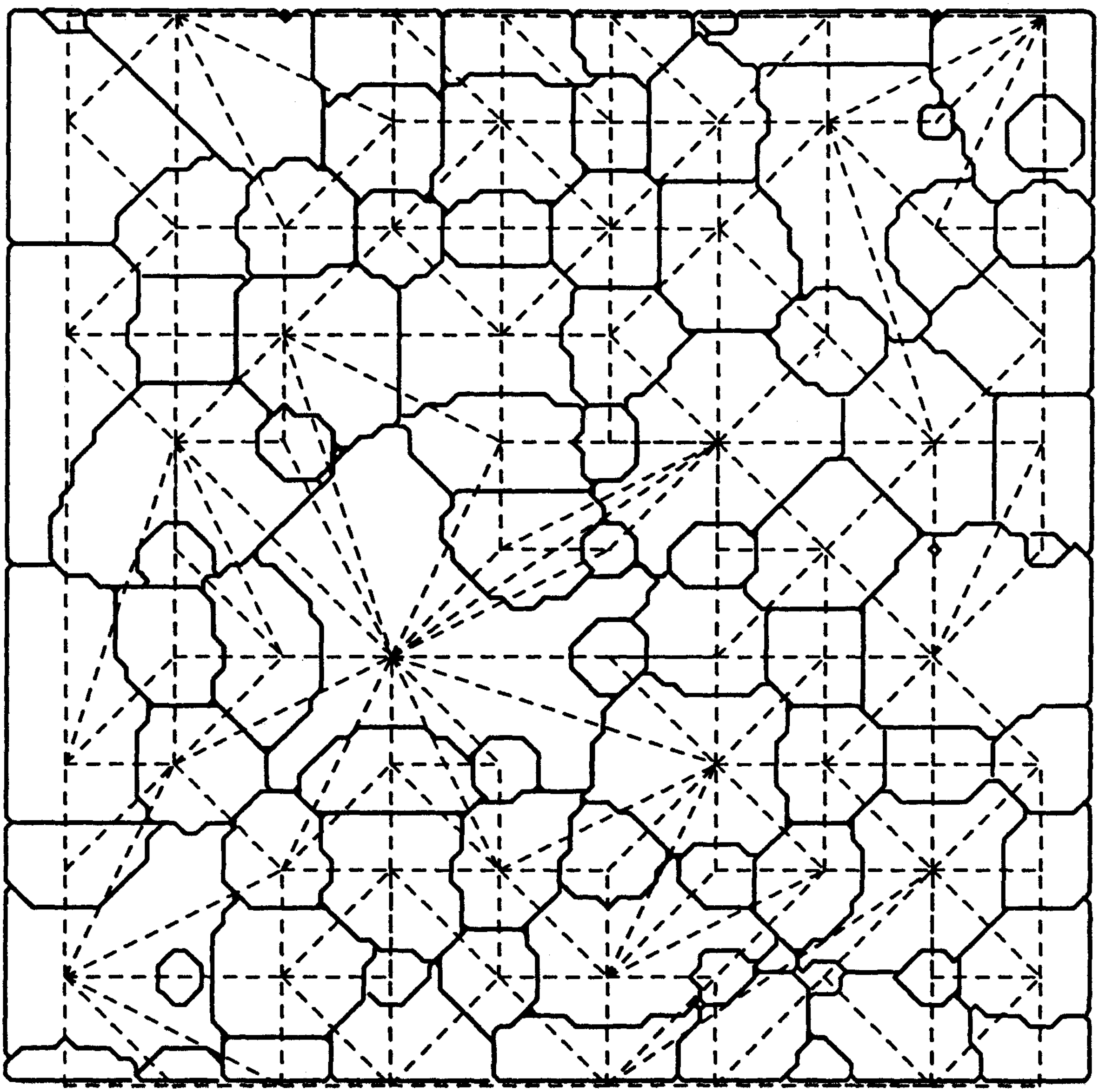

Fig. 6. Map of space assignments (solid lines) and neighbor identifications (dashed lines) resulting from the application of Rule 2 to the corn data set using leaf weight as a measure of size.

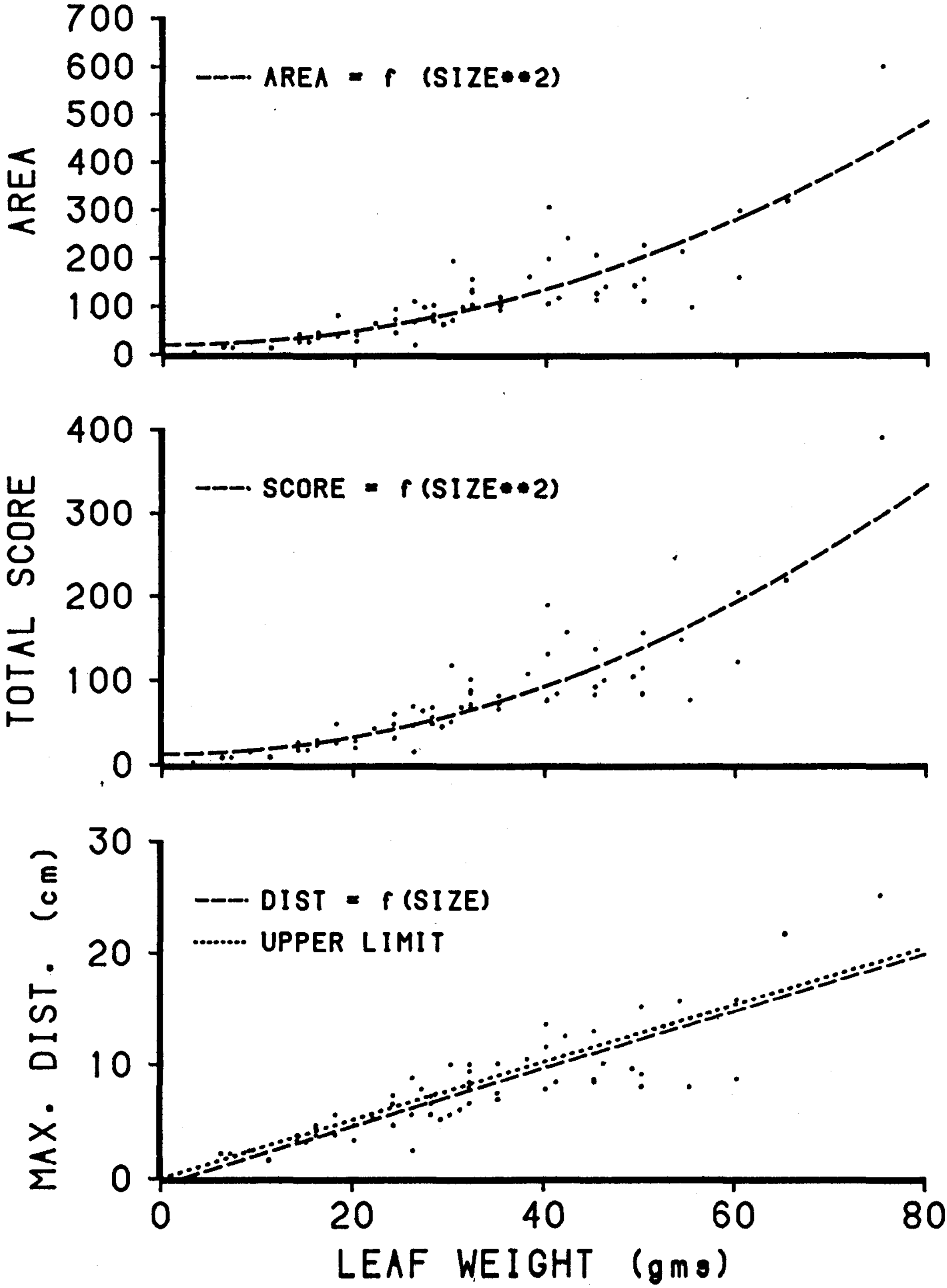

Fig. 7. Results of application of Rule 2 to the corn data set using leaf weight as a measure of size.

only (since Rules 3 through 7 will all leave the same amount of unassigned space given the same multiploer). It was of some concern that the intercept of the maximum distance versus size regression was very close to zero and application of a parallel upper limit through the origin would truncate a large portion of the population (Fig. 7). A stepwise multiple regression of maximum distance using SPSS (Nie *et al.* 1975) showed a significant contribution of the x-coordinate in helping size to predict maximum distance. Distance from a plot border on the 1 m^2 plot did not contribute to the prediction of maximum distance.

This effect was taken as an indication of a bias in weights due to the sequence in which the data were collected (low to high x-coordinate) and a decrease in water content of plants weighed last. A map of space assignments using Rule 3 and the recommended multiplier shows most of the unassigned space at high x-coordinates (Fig. 8 & 9).

An analysis using a smaller multiplier (0.20) showed a marked increase in unassigned space, a decrease in total number of neighbors, and increasing correlations of size with area and total score.

The decrease in unassigned space with larger multipliers was appealing in view of the closed corn canopy and complete lack of light penetration. However, since at least some of the unassigned space appeared to be due to the bias in plant weights, it was determined to continue the analysis with the original recommended multiplier.

Rules 4 and 5 produce the same space assignments as Rule 3, differing only in the total score, a measure of area weighted by distance according to the rule used. Rule 3 appeared to be the best rule in terms of the correlation of size and total score. This effect is expected in part simply from the nature of the Rules. Rule 3 produces

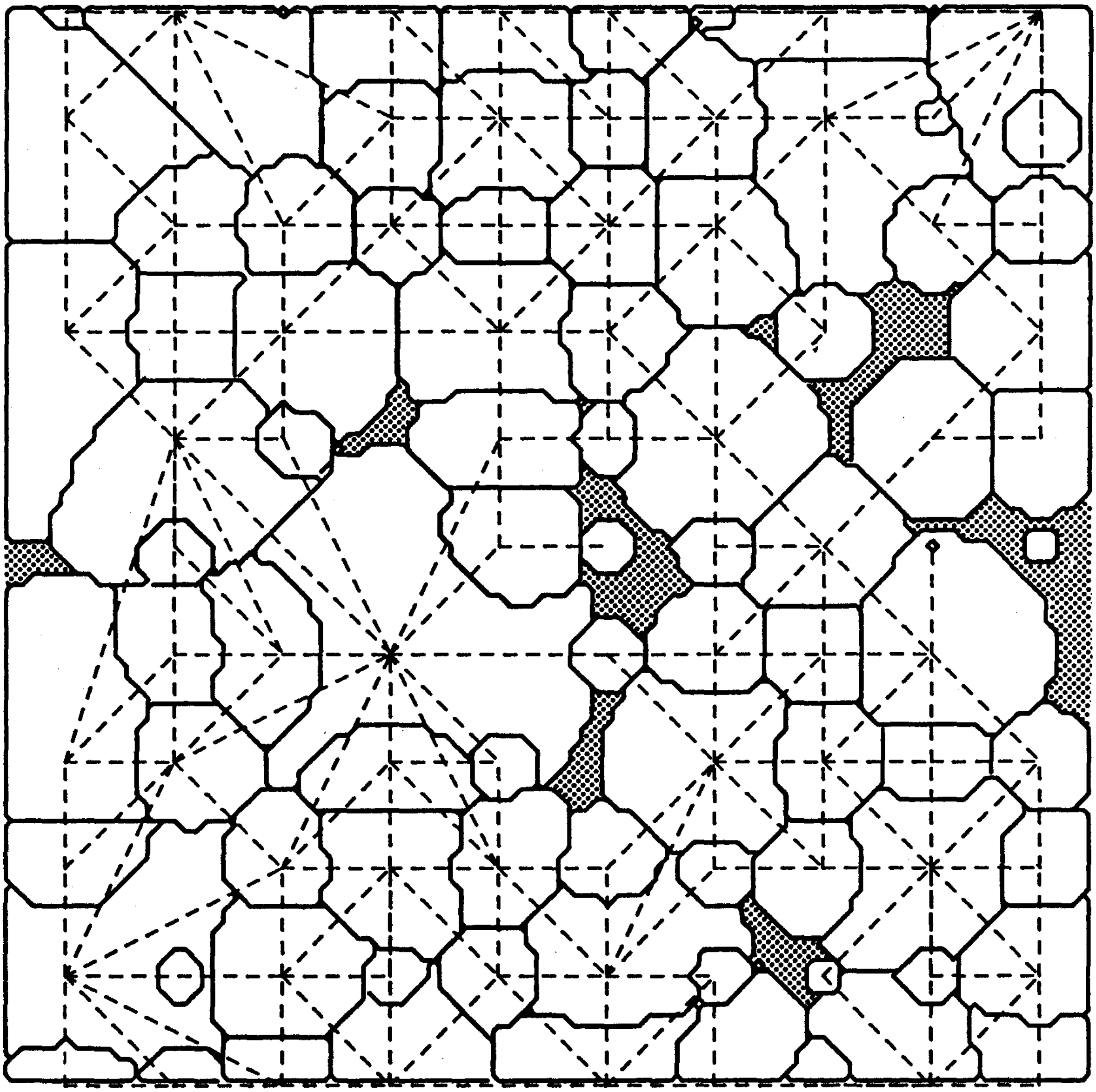

Fig. 8. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 3 to the corn data set using leaf weight as a measure of size.

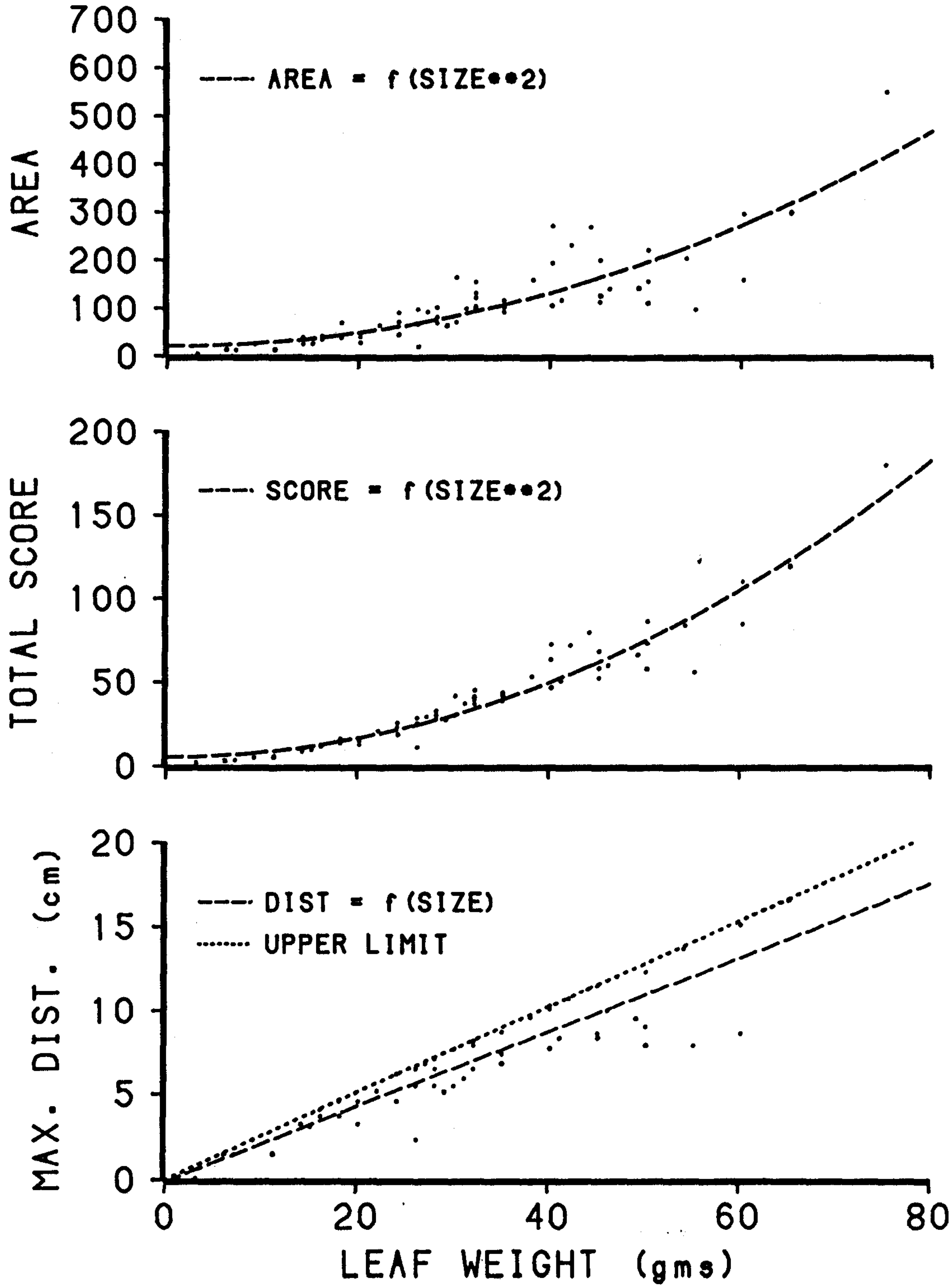

Fig. 9. Results of application of Rule 3 to the corn data set using leaf weight as a measure of size.

a lower score at a distance than other rules so that the total score for an individual is influenced less by variability in area. Rules 6 and 7 leave the same unassigned area as Rule 3 because the maximum possible assignment distance for a given size is not changed. However, these rules require a minimum distance between nearby individuals of differing sizes to allow the smaller individual to be assigned any space at all. Boundaries between different size neighbors are located closer to the smaller neighbor than under Rule 3. One indication of the inappropriateness of Rule 6 or 7 is the portion of individuals which are deleted from the population for lack of assigned space. Rule 6 deleted nine individuals from the corn data set; Rule 7 deleted none.

Rule 8 (normal curve) does not allow unassigned space, but produces the same boundaries as Rule 2. It differs from Rule 2 only in the weighting of area by distance summarized in total scores. It requires the multiplier suggested by Rule 2 to define the distance of a standard deviation. The correlation of size and score was slightly higher for Rule 8 (r^2=0.814) than for Rule 2 (r^2=0.783).

Lodgepole pine data

The lodgepole pine (*Pinus contorta* Dougl.) data set provided a natural population with some characteristics analogous to the corn data set. The data were originally collected as part of a spruce-fir succession study in 1976-1978 (Schimpf, Henderson & MacMahon 1980). They represent a nearly monospecific canopy stage in the successional process investigated by that study. The three stands, all within a kilometer of each other, are here designated as 'old' (LPO), 'mature' (LPM), and 'young' (LPY) as suggested by the size distributions found for each data set. The stands were presumed suitable for analysis because of the accuracy with which individuals could be identified, located, and measured. They were analyzed using Rule 1 and correlating the assignments to diameter breast height (d.b.h.) as a measure of size. Correlations of size with assigned area and total score were very poor as were correlations of size and maximum distance assigned. The frequency distributions suggested that the LPO data set was the only one with a dispersion that was significantly nonrandom. Rule 2 was applied, resulting in a marked increase in correlation of size with area, score, and maximum distance, although the LPY data set still had relatively low correlations (Fig. 10 & 11, Table 3).

Of the 20 individuals in the LPO data set, 14 were lost from the analysis as boundary individuals, so analysis of that data set was discontinued. Application of Rule 3 to the LPY and LPM data sets using the multiplier indicated by the Rule 2 analysis resulted in a small amount of unassigned space and small increases in correlations (e.g., Fig. 12 & 13, Table 3).

Only the LPM data set was subjected to analyses using Rules 4 through 8. Rules 4 and 5 did not perform as well as Rule 3. Rule 6 deleted about half the population through failure to assign any space. Rule 7 actually performed slightly better than Rule 3 while Rule 8, calibrated by the results of Rule 2, had a slightly increased correlation of size with total score (Table 3).

Examination of Fig. 10 shows that the multiplier suggested by the Rule 2 analysis did not truncate many maximum distances. Comparison of the maps for Rules 2 and 3 (Fig. 11 & 13) shows only two patches of unassigned space, one on the boundary and possibly assignable to an

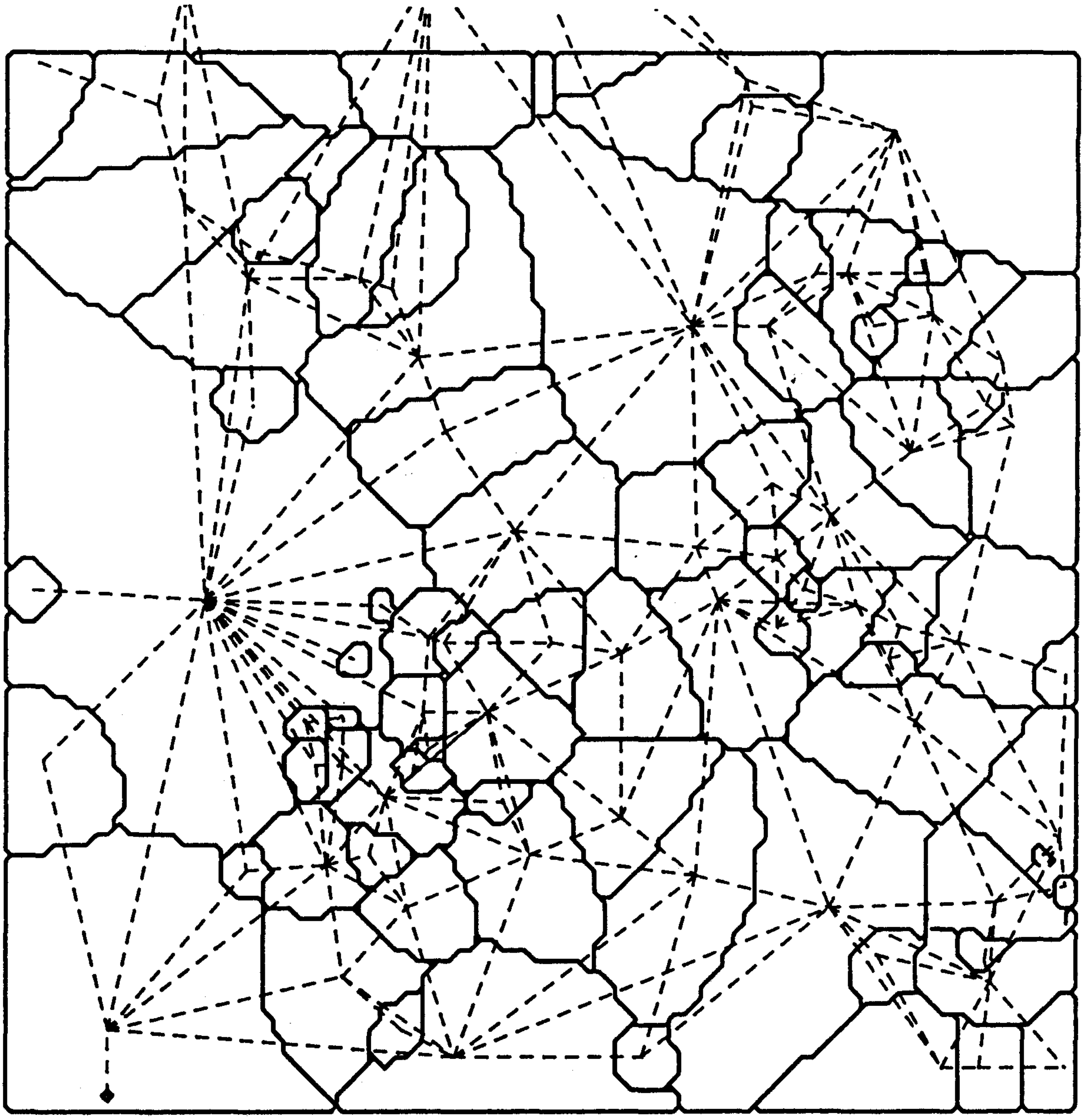

Fig. 10. Map of space assignments (solid lines) and neighbor identifications (dashed lines) resulting from the application of Rule 2 to the LPM data set using d.b.h. as a measure of size.

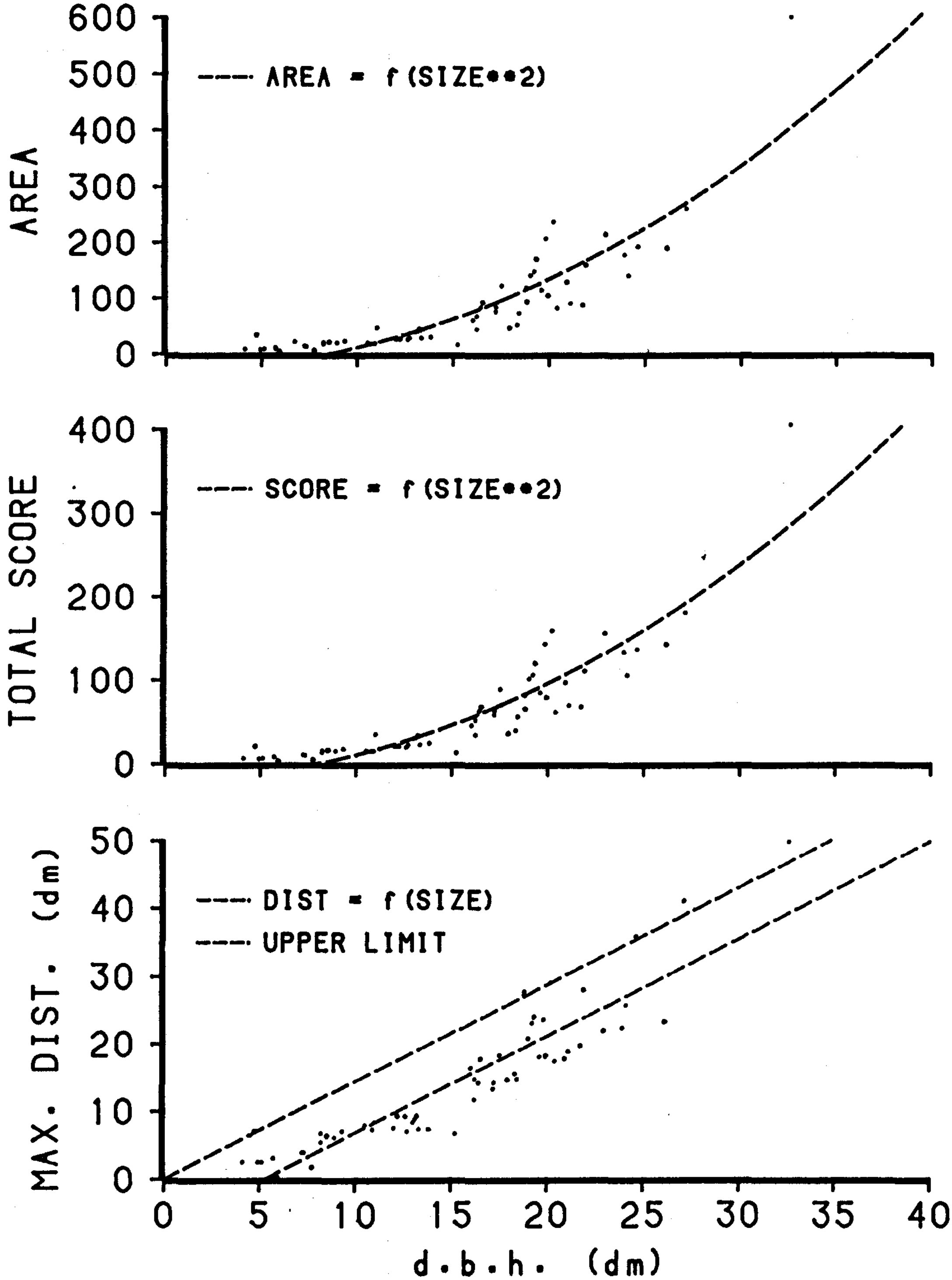

Fig. 11. Results of application of Rule 2 to the LPM data set using d.b.h. as a measure of size.

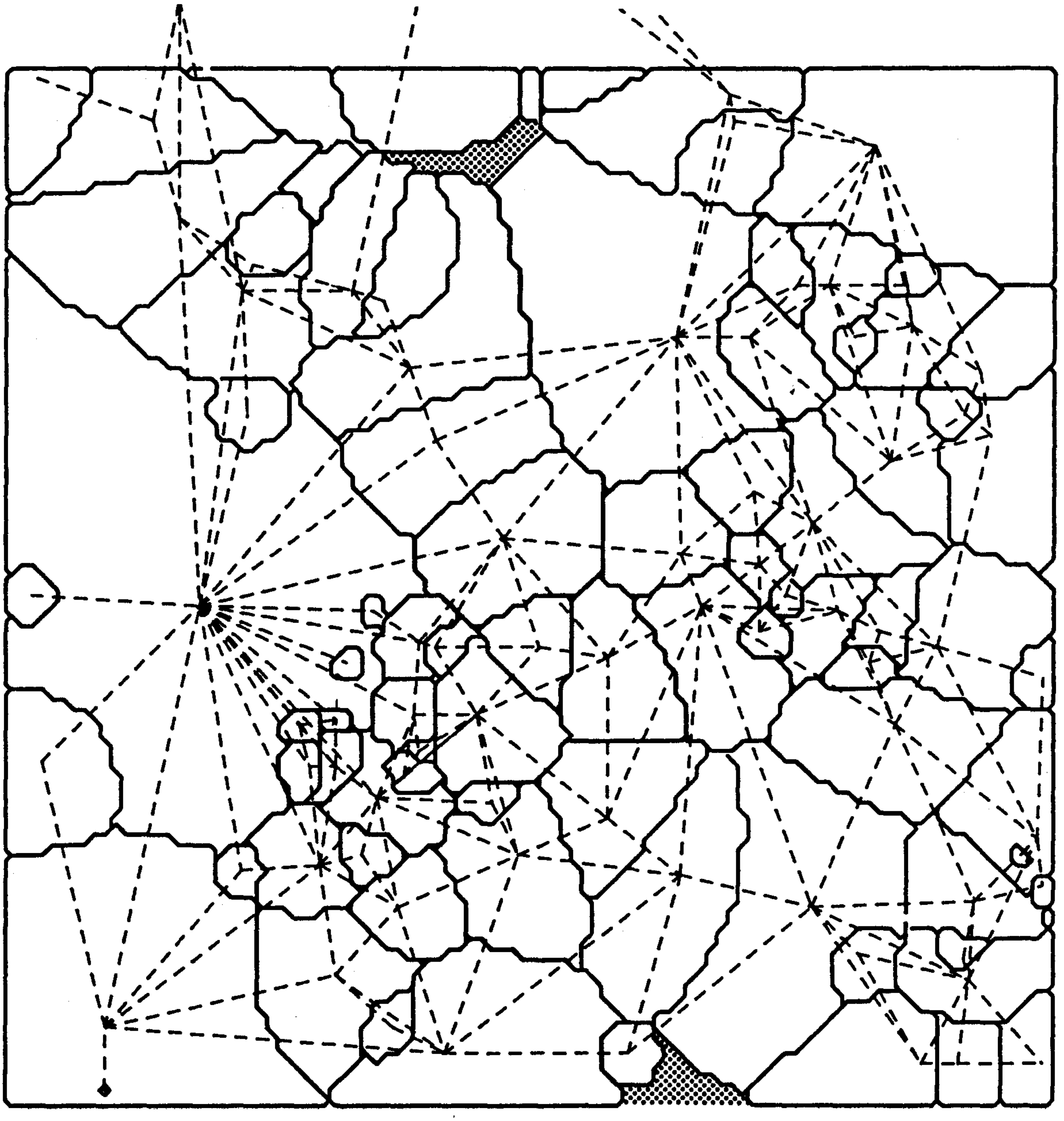

Fig. 12. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 3 to the LPM data set using d.b.h. as a measure of size.

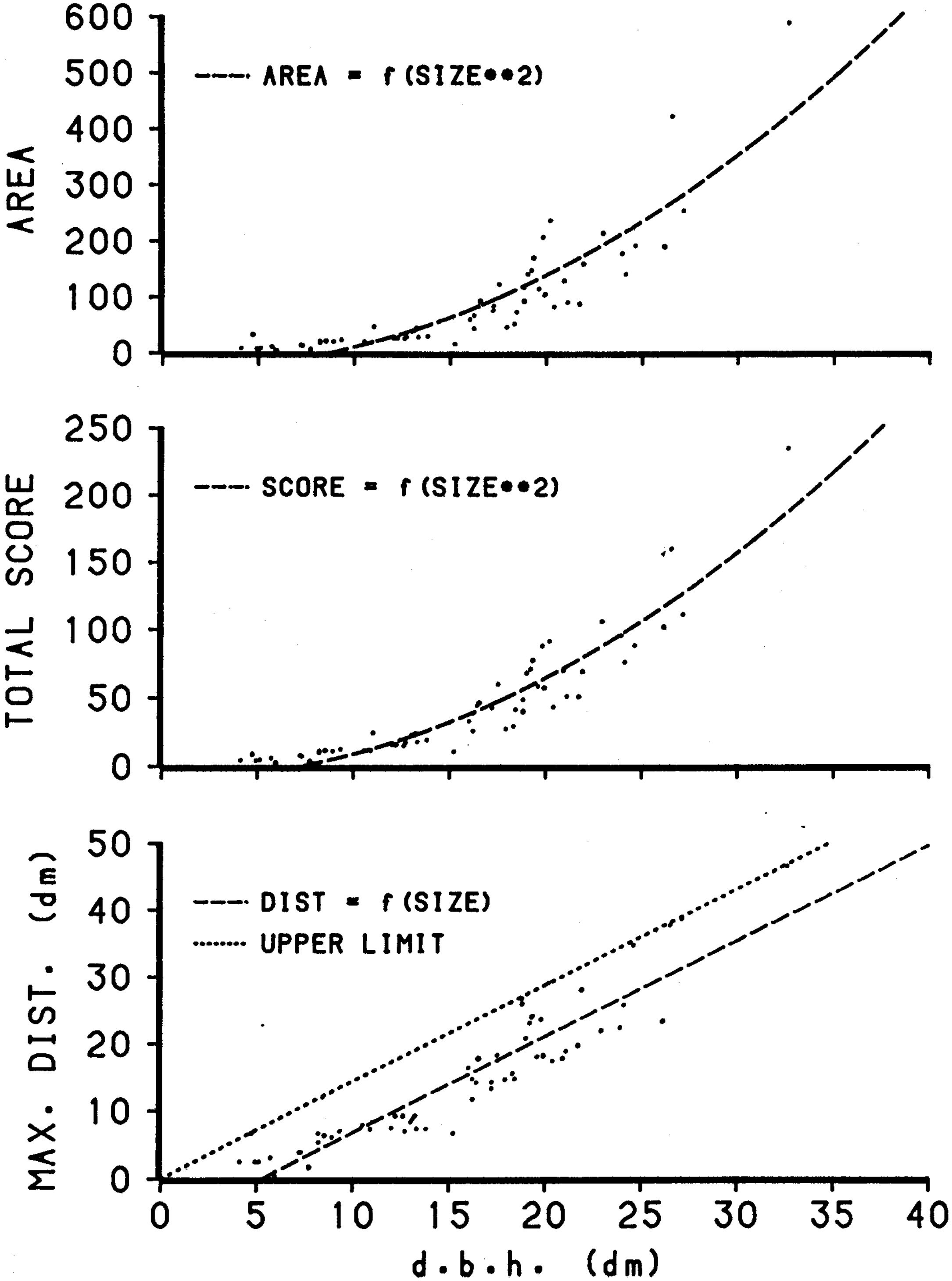

Fig. 13. Results of application of Rule 3 to the LPM data set using d.b.h. as a measure of size.

individual outside the mapped area. Comparison of the maps for Rules 3 and 6 (Fig. 13 & 14) show the same unassigned patches but the loss of many small individuals near the largest individual (left center). Although Fig. 14 (Rule 6) does not clearly depict the parabolic shape of boundaries, it is clear that there are no 'island' individuals imbedded completely within the space of a single neighbor. The maps for Rules 3 and 7 (Fig. 13 & 15) are nearly identical.

Desert shrub data

The four desert shrub data sets were examined ignoring any distinction between the two dominant perennial shrubs (*Atriplex confertifolia* and *Ceratoides lanata*). Three of the data sets were selected from a transect of aerial photos at one site near Cow Camp Wells, Pine Valley, Utah (designated DER#16). One data set (DATR) was selected for its relatively high abundance of *Atriplex*. A second set (DCER) was selected for relatively high abundance of *Ceratoides*. The third set (DLOW) was selected for its low total shrub abundance. The final data set (DER2) was selected from another site in Pine Valley, Utah (DER#2) for the high resolution of the photograph, especially suited to direct comparison with an analysis output map.

The original data set contained two diameters (d_1,d_2) (maximum and perpendicular) measured on the photographs. Two measures of size were constructed: (a) elliptic cover ($\pi d_1 d_2/4$) and (b) geometric mean diameter ($\sqrt{d_1 d_2}$).

Rule 1 was applied to each data set with the resulting assignments compared to diameter as a measure of size. As with the other real population data, correlations were near zero. In all four cases the

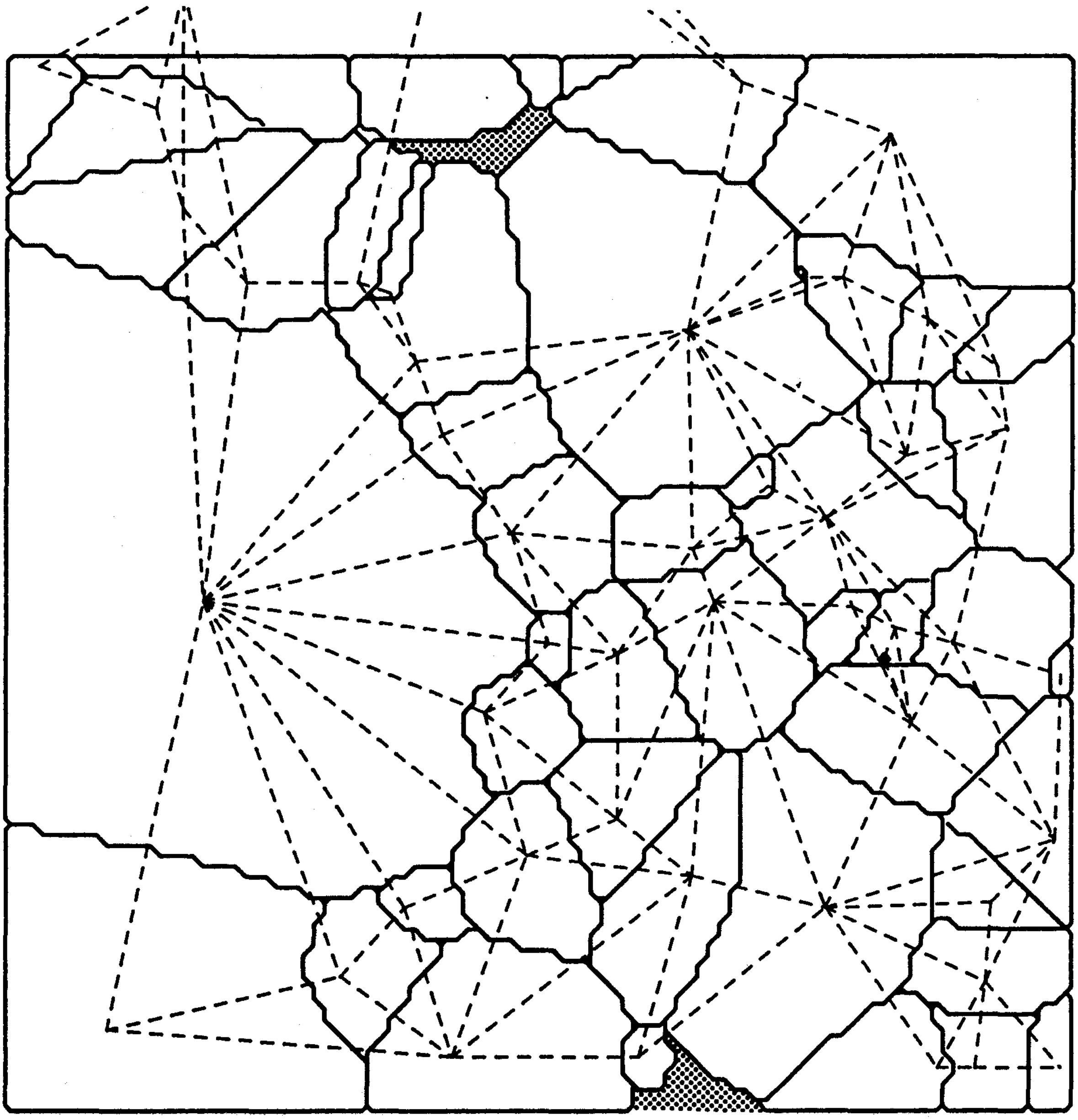

Fig. 14. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 6 to the LPM data set using d.b.h. as a measure of size.

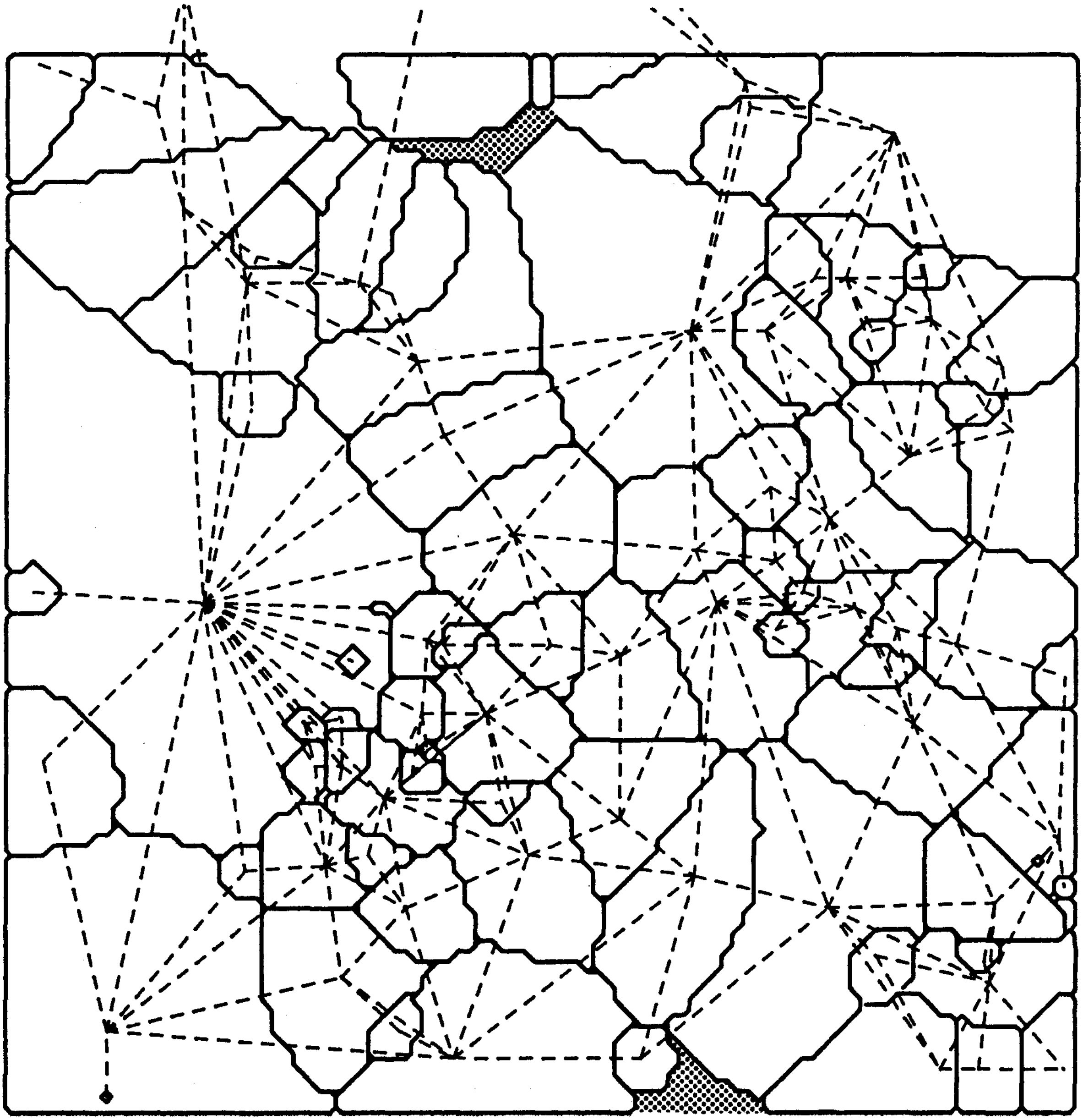

Fig. 15. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 7 to the LPM data set using d.b.h. as a measure of size.

frequency distributions did not differ significantly from random (Table 3).

Diameter was used as a measure of size under Rule 2 for all data sets with a comparison analysis for cover using only the DER2 data set. Correlations were fair ($r^2 \approx 0.6$) for diameters and very poor ($r^2 = 0.263$) for cover versus assigned area. Imprecision of size measurement from the aerial photo as well as errors due to the assumption of elliptic cover might be responsible for the variability seen in the graphs of size versus area, score, and maximum distance (Fig. 16 through 18) and indicated by the correlation coefficients (Table 3).

Interestingly, the correlation was best for the DER2 data set which was photographed from a higher altitude than the other location, so that a more dense population of smaller individuals was mapped from the photograph with lower resolution.

Cover was rejected as a suitable measure of size and further analyses were restricted to diameter.

The intercepts of the size versus maximum distance regressions were quite close to zero (Table 3). The wide variation above and below that line (Fig. 17 & 19) indicated that a small portion of the population would be markedly constrained by applying the prescribed distance limit by Rule 3. Many other individuals would not be affected at all.

Rule 3 resulted in modest improvements in the correlations. Acceptable amounts of unassigned space occurred in a few patches (Fig. 20 through 23). Rules 4 through 8 were examined in the two data sets with the greatest difference in unassigned space: DER2 (220 units) and DCER (746 units). As before, none of the other bounded rules (4 through 7) performed any better than Rule 3 as measured by correlations with

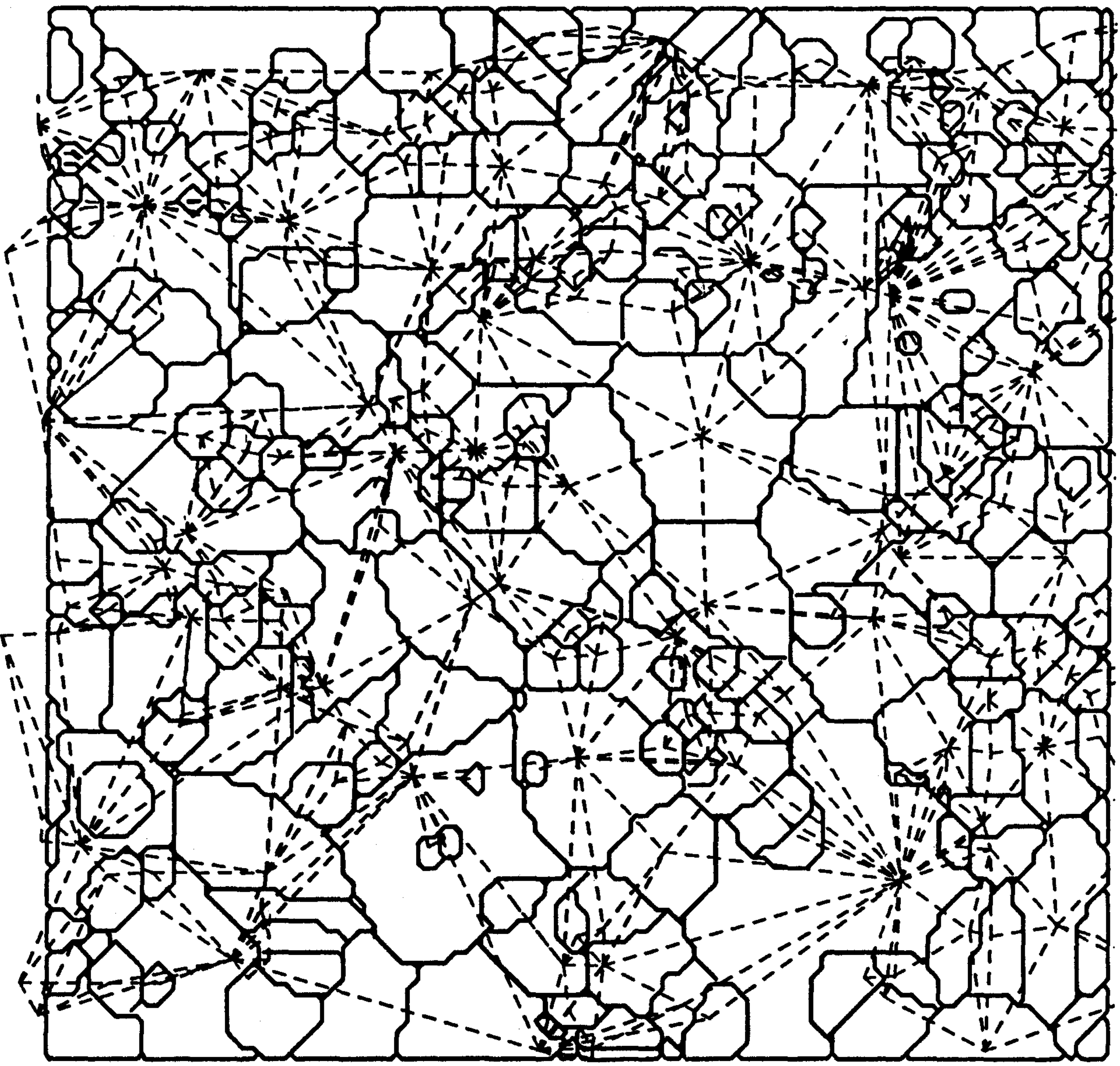

Fig. 16. Map of space assignments (solid lines) and neighbor identifications (dashed lines) resulting from the application of Rule 2 to the DCER data set using diameter as a measure of size.

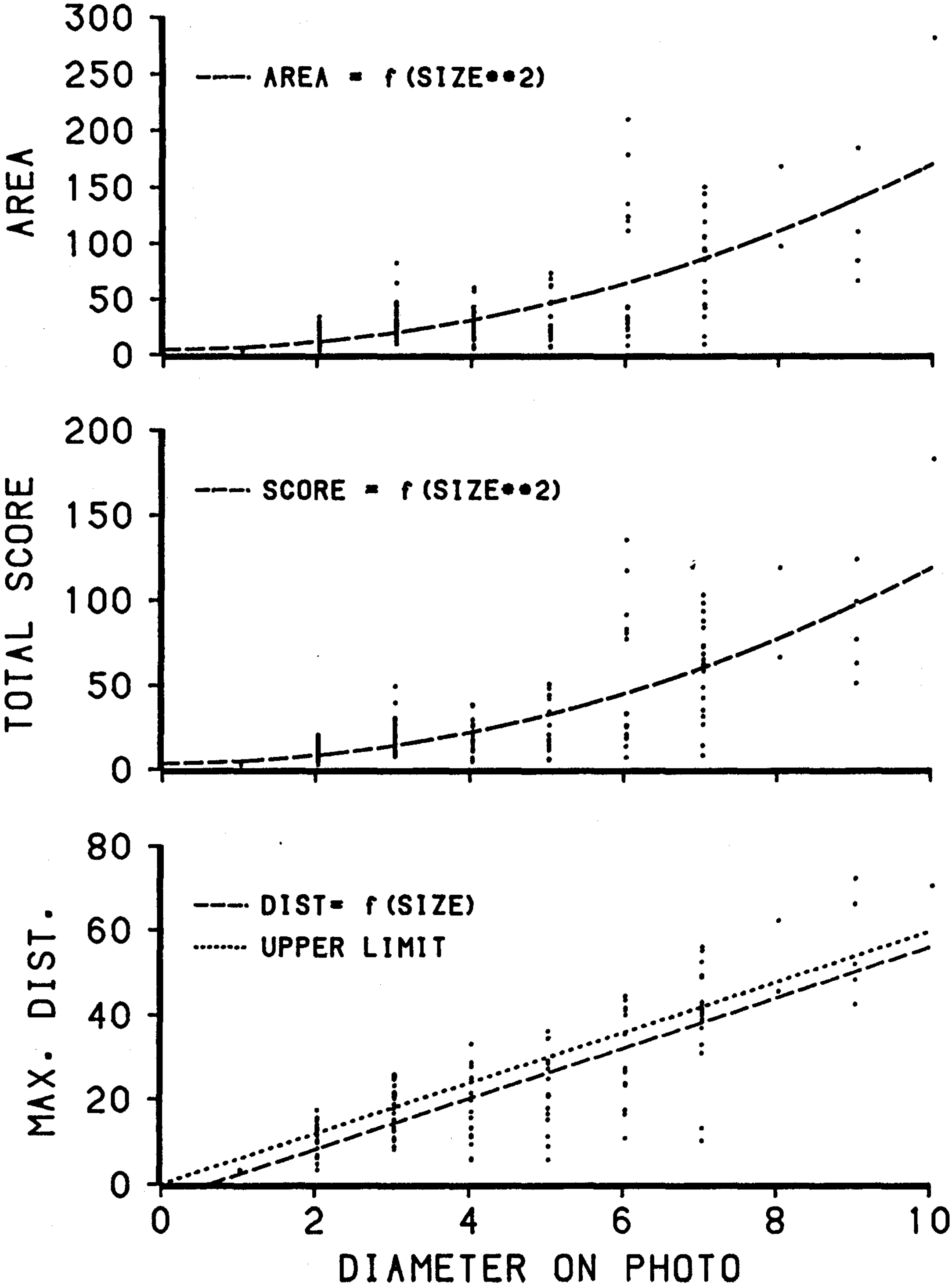

Fig. 17. Results of application of Rule 2 to the DCER data set using diameter as a measure of size.

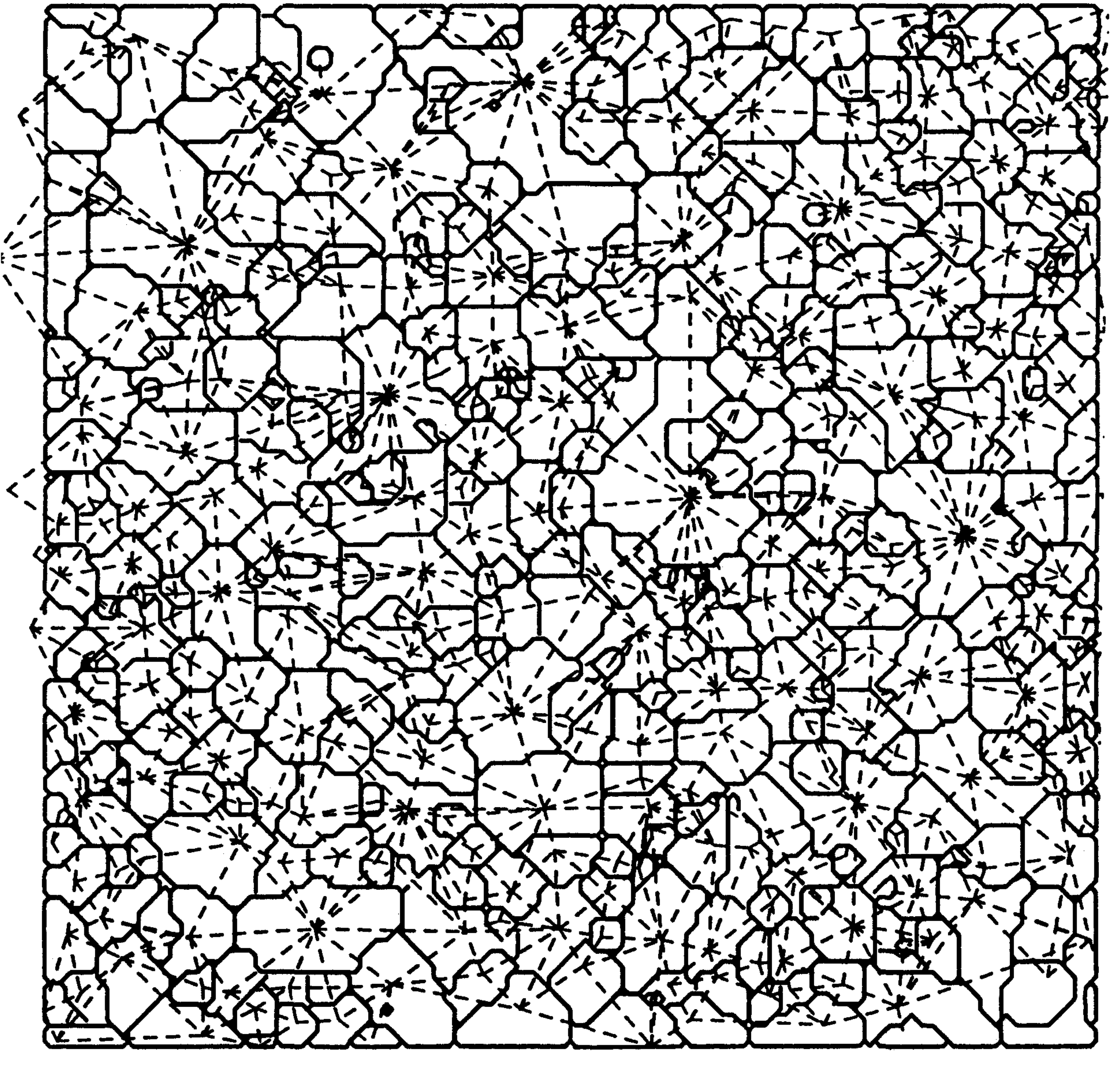

Fig. 18. Map of space assignments (solid lines) and neighbor identifications (dashed lines) resulting from the application of Rule 2 to the DER2 data set using diameter as a measure of size.

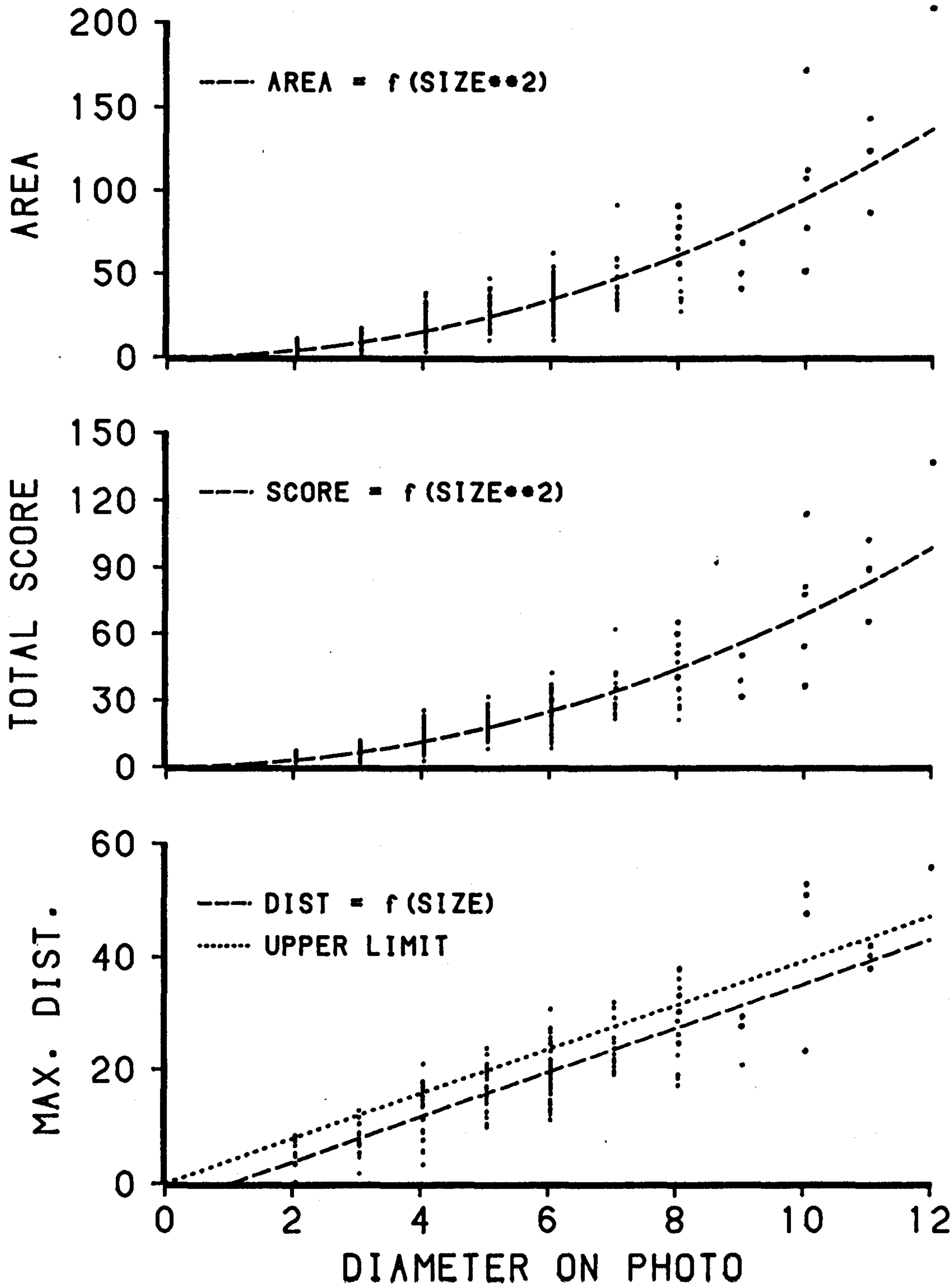

Fig. 19. Results of application of Rule 2 to the DER2 data set using diameter as a measure of size.

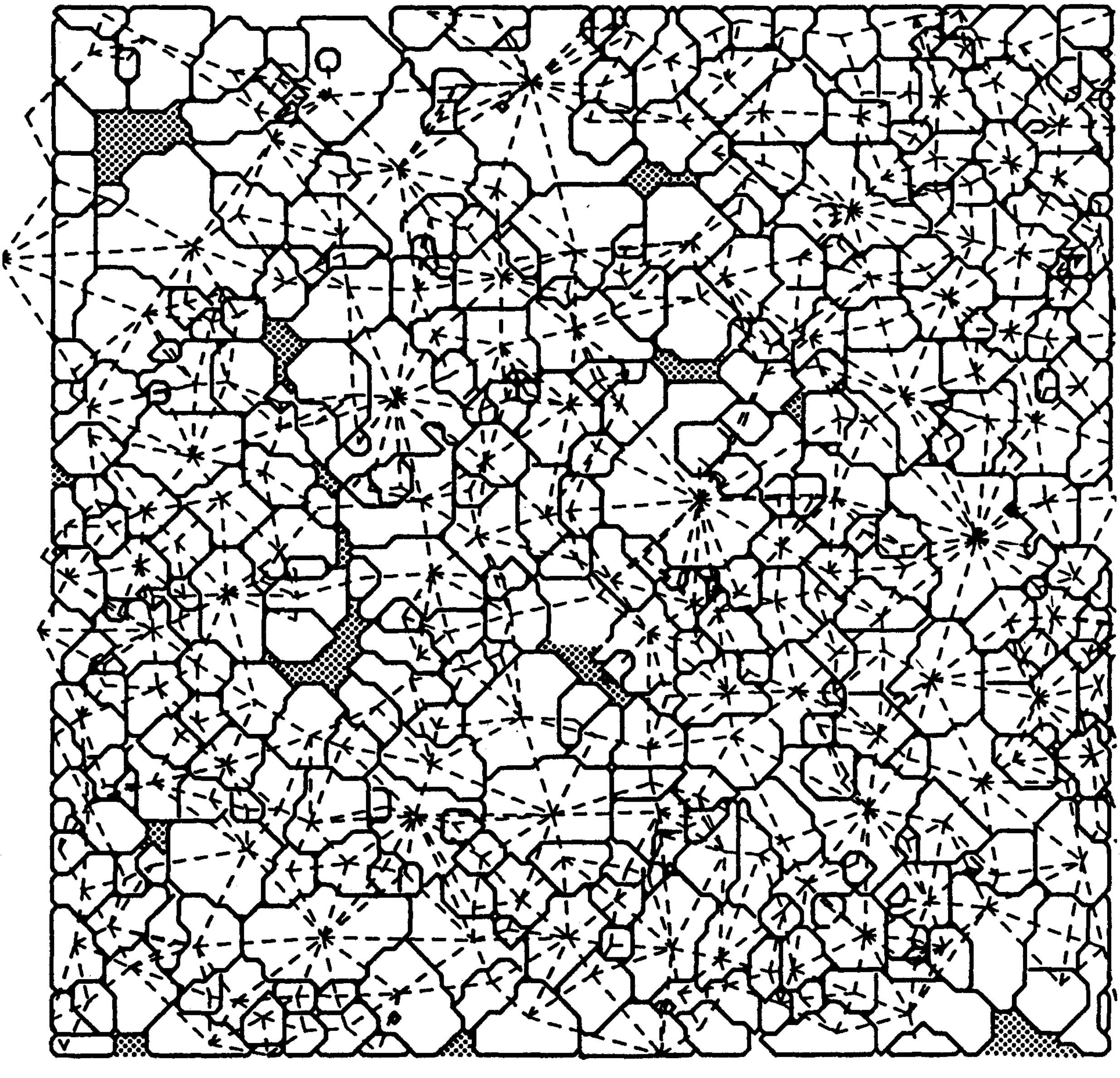

Fig. 20. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 3 to the DER2 data set using diameter as a measure of size.

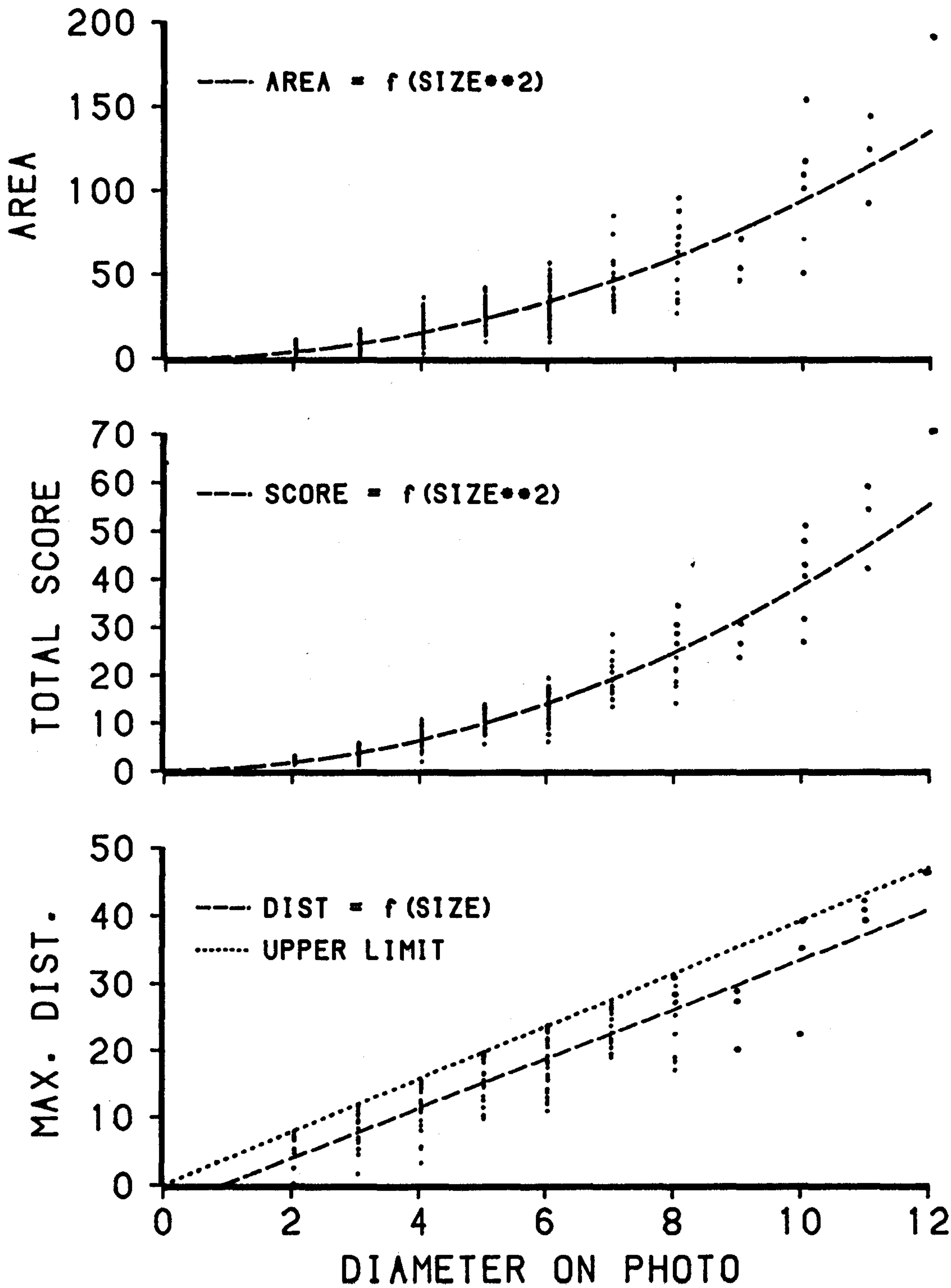

Fig. 21. Results of application of Rule 3 to the DER2 data set using diameter as a measure of size.

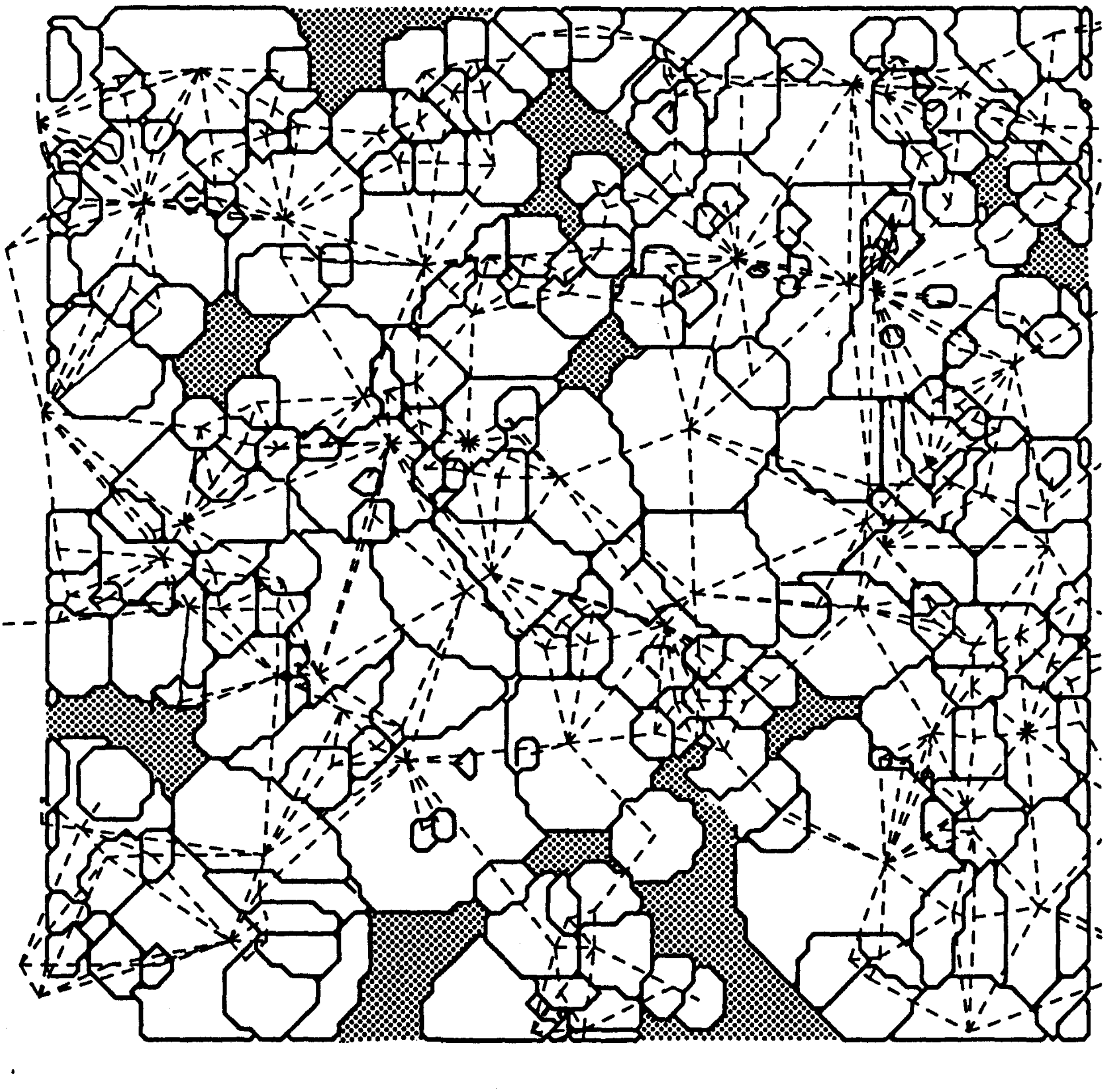

Fig. 22. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 3 to the DCER data set using diameter as a measure of size.

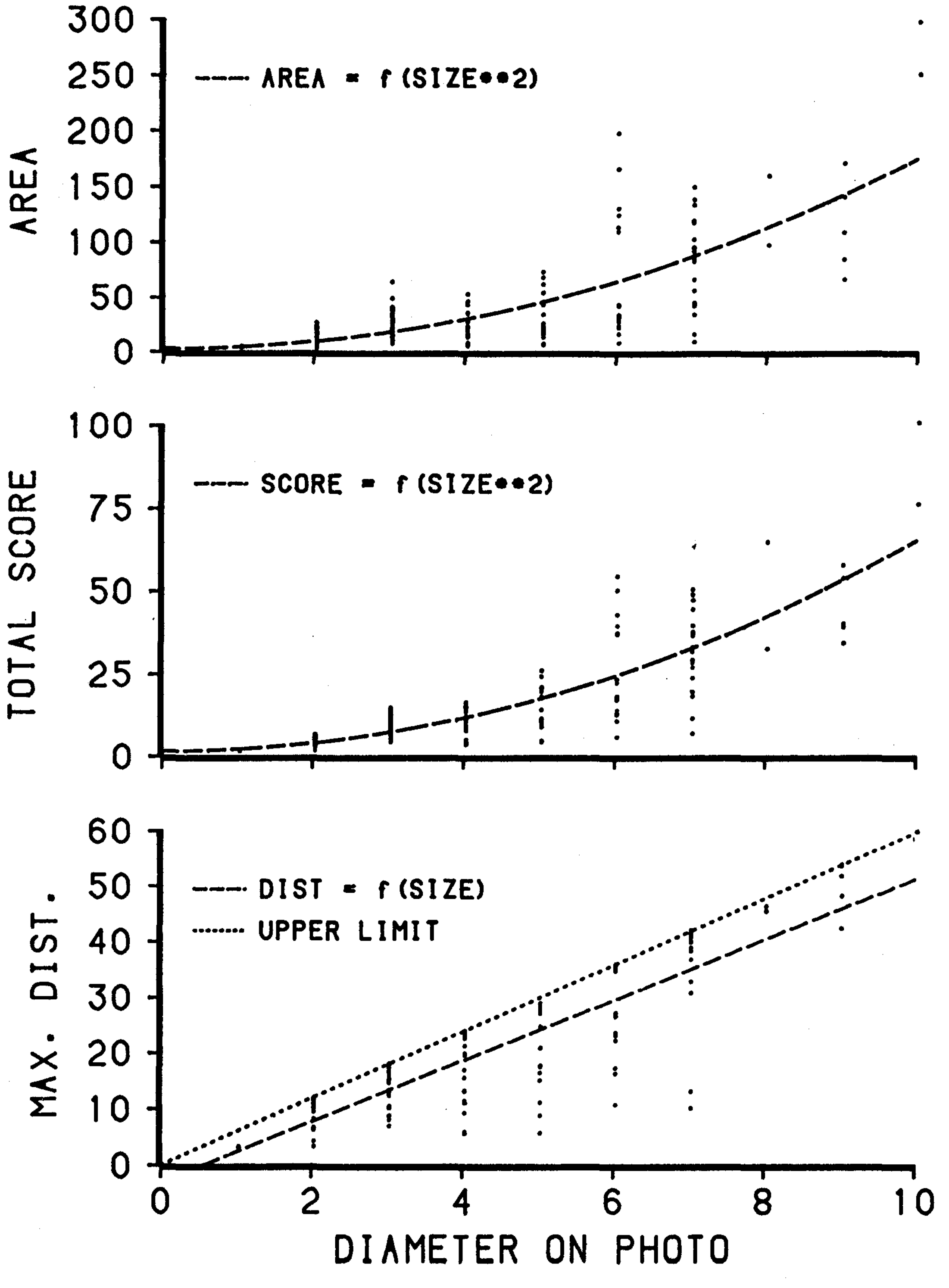

Fig. 23. Results of application of Rule 3 to the DCER data set using diameter as a measure of size.

size. Rule 6 omitted a large portion of each population which Rule 7 did not. Rule 8 produced a marginally better correlation of size and total score than Rule 2 did (Table 3).

Artificial Population data

Four color 'species', previously examined by Goodall & West (1979) from the 'Artificial Population Sampler' (Schultz, Gibbens & Debano 1961), were selected for analysis. The white population (PWHI) consists of 128 individuals in a random pattern. The ivory population (PIVO) consists of 87 individuals in a large scale aggregation consisting of five randomly placed stands about 30 cm in diameter. The yellow population (PYEL) consists of 145 individuals in clusters of one to 16 concentrated toward one corner of the map space. The red population (PRED) consists of 153 individuals in small scale aggregations of one to eight concentrated toward one corner of the map space. Six size classes are represented, although Schultz, Gibbens & Debano (1961) do not report how they determined which individuals would be which size. The four populations were analyzed independently.

The four populations were analyzed using Rules 1 and 2. Rule 1 produced no correlations of size with assigned area, total score, or maximum distance. Test statistics for the frequency distributions agree that the white population is not significantly different from random. The departures from random by the other populations (all reported to be aggregated) are most strongly reflected in significant deviations of the frequency distributions of distance (Table 3).

Rule 2 revealed the poor relationship between size and area, score and distance for all of the populations except PWHI, the random population. However, the intercept of the regression line for size versus distance of PWHI is so far negative that none of the individuals would be affected by a parallel limit on maximum distance that passes through the origin. That is, application of a bounded rule with the suggested upper limit would produce no unassigned space.

For the three aggregated artificial populations, Rule 3 could be quite appropriate because a large amount of empty space may be desirable. The ivory population, by definition, is contained within five circles, each with an area of about 700 cm^2 out of the total map area of 10,000 cm^2. This suggests that about 6500 cm^2 or 26,000 units of empty space should be expected from a suitable assignment rule. The ivory population was examined with three trials of Rule 3 using as multipliers: 3.33, 5.00, and 6.67. The second multiplier (5.00) yielded approximately the expected amount of empty space with fair correlations of size with assigned area (r^2=0.523) and with total score (r^2=0.768). The resulting map for the best multiplier is shown in Fig. 24. It is clear from the map that the amount of space assigned to most individuals is influenced largely by the boundary with unassigned space, rather than any size dependent interaction between neighbors.

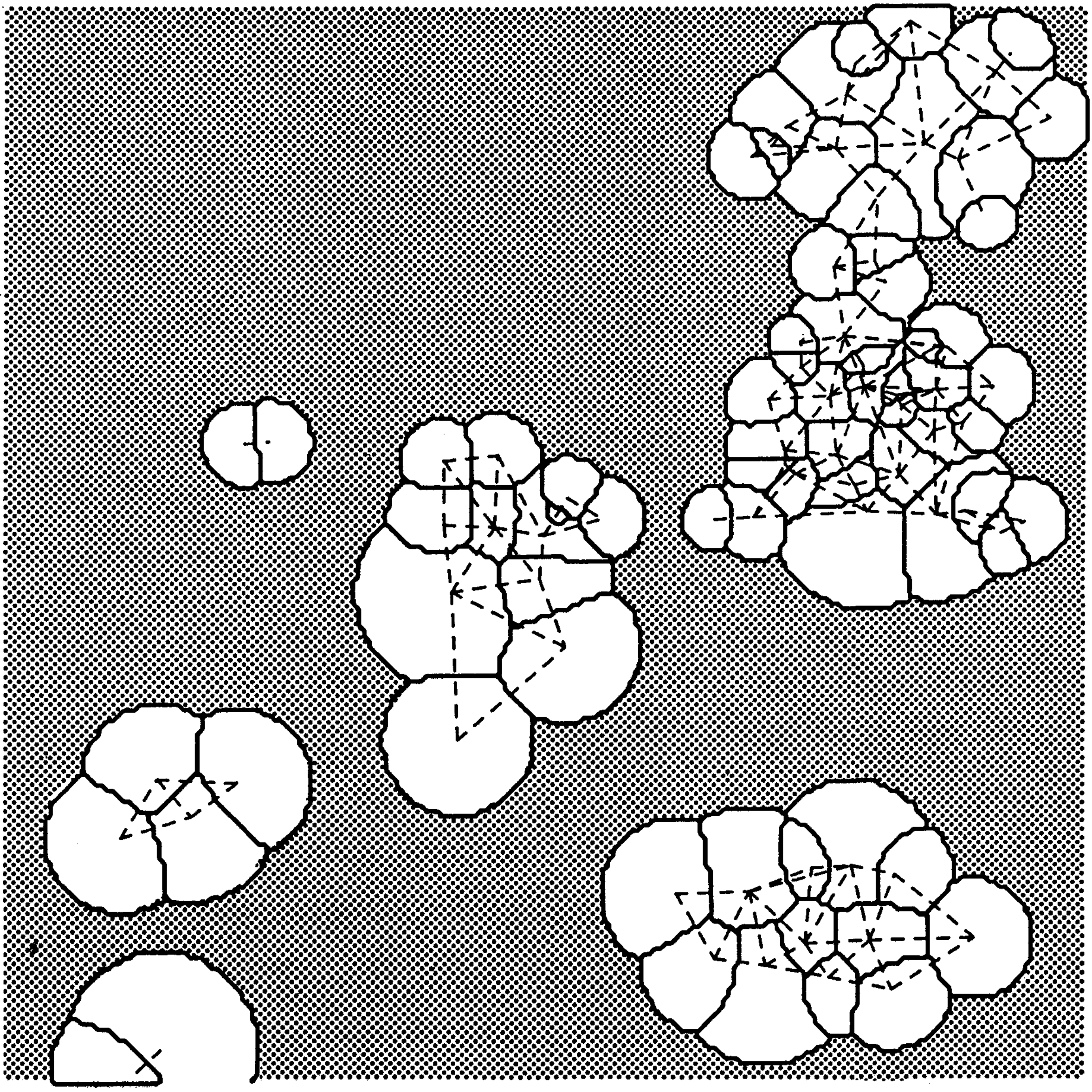

Fig. 24. Map of space assignments (solid lines), neighbor identifications (dashed lines) and unassigned space (cross-hatched) resulting from the application of Rule 3 to the PIVO data set using diameter as a measure of size.

DISCUSSION AND CONCLUSIONS

In an environment in which a limiting resource is uniformly distributed, an individual may claim 'quanta' of that resource by preempting parcels of space. In such a case, the size of the individual is correlated with the amount of space preempted. The location of that space relative to the point of establishment of the individual may also influence ultimate size. This effect might be expected if the cost of producing and maintaining structures to preempt or exploit space (roots, stems, or leaves) were significant relative to the benefits (resources) to be extracted from that space as with annuals or herbaceous perennials preempting aerial space. The cost of occupying space with perennial (woody) structures is generally amortized over a sufficiently long term, which may make the increased cost with distance insignificant.

As a result of examination of several plant populations believed to be in that circumstance, several generalizations can be made about models ('rules') for the preemption ('assignment') of space as a function of size and distance. An individual will always be constrained by some maximum distance at which it can search or preempt space for a limiting resource. That maximum distance is typically a linear function of some measure of size. For modelling purposes, if individuals are located such that all available space is closer than the maximum distance to some individual, then a model rule that simply decreases with distance will be adequate for defining the boundaries of space preemption. However, if there is a time lag between release of space with an individual death and colonization of that space by a new individual or invasion of that space by a neighbor, then a bounded model rule is required for definition of boundaries shared with unassigned space.

Rule 3 (Fig. 2) consistently performed as well or better than the other bounded rules based on the correlations of size with the areas, total scores, and maximum distances generated by the rules on the several real data sets examined. Rule 3 is the only one of the bounded rules examined that is composed of a family of curves (hyperbolas) of the same shape as an unbounded rule. Rules 4 and 5 produced the same boundaries but generated a poorer correlation between size and total score, a measure of area weighted by distance. Rules 6 and 7 produced different boundaries and had different maximum scores for different sizes. Rule 6 consistently omitted smaller individuals from the population by failing to assign any space to them. Rule 7, quite unexpectedly in view of its apparent similarity to Rule 6, performed about as well as Rule 3, rarely omitting individuals in spite of the variable maximum score it allowed. Rule 7 is a case of a more general rule for which separate parameters define the point of intersection of all sizes (at x=-Dmax, y=2.0 for Rule 7).

In spite of a hint of circularity in the method, examination of artificial data sets shows that use of size to locate boundaries between individuals does not insure that the space assigned to an individual will be highly correlated with its size. This method extends the pairwise examination of size to distance relationships used by many workers to the identification and simultaneous consideration of all interacting neighbors.

The analysis used could be made more efficient and robust by developing an algorithm tailored to a single partitioning rule and generating boundaries with smooth functions (probably arcs of circles) rather than by assigning increments of area from a grid. Some errors are detectable in the maps of space assignments due to the inclusion or exclusion of an individual based on contact at a single cell. Some four-way intersections were noted (for which neither of the diagonal pairs were counted as neighbors) that could be resolved into two three-way interactions.

Analogous to the overlapping cell model of interference between neighbors (Pielou 1960 and others), a measure of interference could be deduced from the model presented here. The matrix of cell assignments and scores can be visualized as a solid mosaic (Fig. 4) of blocks with a horizontal shape of the space assigned each individual and a vertical dimension defined by the score at each point in the assigned space. The relative amount of interference between two neighbors would be indicated by the area of the vertical surface of contact of the two blocks (that is, the length of the boundary times the height of the score surface above the boundary). This interpretation of the model could presumably be tested by applying the model to a mapped population, as before. Selected individuals could then be physically removed. Neighbors of the removed individuals would subsequently be examined for changes due to the decrease in competitive interference from the removed neighbor. The change might be expressed by individual water status or amount of new growth. If the model had placed the boundaries appropriately, then the individual changes subsequently recorded would be expected to be proportional to the relative contribution that the removed individual had made to the total neighbor boundary length or boundary surface of each of its neighbors. Such an experiment could look like the converse of the Fonteyn & Mahall (1981) experiment in which they removed all possible neighbors of an individual and monitored its subsequent water status compared to unaltered controls.

The model, as currently presented, assumes homogeneity of space over the area mapped. That is, a unit of space has a score value based only upon its distance from an individual, not on some measure of its value as a container of a resource. For purposes of boundary location, only fine grained homogeneity is required. So long as the substrate does not change much within the space assigned to neighbors, correction for that change will not move the boundary much. Therefore, the model is expected to be robust in its boundary assignments in the face of large scale or gradient changes in the substrate. Such heterogeneity would affect the size versus area regressions because individuals of the same size in different portions of the area would tend to have different amounts of unassigned space. If a heterogeneous space could be modeled by some gradient function or an application of regionalized variable theory (David 1977), then a weighting factor for relative value (or relative size) might be incorporable into the model, relaxing the homogeneity requirement.

This model does not accommodate different size to area relationships for each species of a multi species mix. An independent means of selecting a size to distance conversion would need to be developed to permit analysis of multispecies mixes for cases in which a common conversion factor was considered inappropriate. It was hoped that the desert shrub data sets examined (with two species included) did not suffer too greatly from this effect. Plots were selected for their dominance by one species to minimize this effect. Although the *Atriplex* and *Ceratoides* plots were in close proximity, comparison of results is confounded by the very good possibility of local differences in the substrate. Different species, or even different age classes of the same species may get more space, with less interference by exploiting different vertical strata, either above or below ground, in their search for resources. In this dimension, it is not always appropriate to model an assignment score as a decreasing function of distance from the mapped point of origin, which would be at the surface. This effect was minimized by omitting very small individuals that would be assigned very little space in any case and examine only mature members of the population (e.g., canopy members of lodgepole pine).

The modification presented here defines a network of neighbors that no longer has the mathematical properties of a Simplicial graph. This is because of the possibility of individuals having two, one, or no neighbors due to curved boundaries or unassigned space. As a result, the dispersion test presented by Vincent *et al.* (1976) cannot be applied to the results of this modification. However, two real populations could be examined by the model and compared with a goodness of fit test for similarity in their neighbor/distance/angle frequency distributions.

In summary, a size sensitive modification of the Dirichlet tessellation has been examined. The new model is useful for identifying neighbors that may be interacting directly due to their proximity to each other. Means of examining the suitability of a measure of individual size were presented. A size dependent function for maximum distance of space utilization can be generated. Various functions relating size to distance were examined with one (Rule 3) consistently superior in tests with several diverse sets of real plant size and location data.

An application for the simultaneous quantification of interference of all neighbors was presented. An extension of the model was suggested which relaxes the requirement of homogeneity of space.

REFERENCES

Barbour, M. G., MacMahon, J. A., Bamberg, S. A. & Ludwig, J. A. (1977). The structure and distribution of *Larrea* communities. *Biology and Chemistry of Larrea in New World Deserts* (Ed. by T. J. Mabry, J. H. Hunziker & D. R. Difeo, Jr.), pp. 227-255. Dowden Hutchinson & Ross Inc., Stroudsburg, PA.

Clark, P. J. & Evans, F. C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, 35, 445-453.

Cormack, R. M. (1979). Spatial aspects of competition between individuals. *Spatial and Temporal Analysis in Ecology* (Ed. by R. M. Cormack & J. K. Ord), pp. 151-212. International Co-operative Publishing House, Fairland, MD.

David, M. (1977). *Geostatistical Ore Reserve Estimation.* Elsevier Scientific Publishers, New York.

Diggle, P. J. (1979). On parameter estimation and goodness-of-fit testing for spatial point patterns. *Biometrics*, 35, 87-101.

Fonteyn, P. J. & Mahall, B. E. (1981). An experimental analysis of structure in a desert plant community. *Journal of Ecology*, 69, 883-896.

Goodall, D. W. (1960). Quantitative effects of intraspecific competition: an experiment with mangolds. *Bulletin of the Research Council of Israel, Section D*, 8, 181-194.

Goodall, D. W. & West, N. E. (1979). Comparision of techniques for assessing dispersion patterns. *Vegetatio*, 40, 15-27.

Grieg Smith, P. (1952). The use of random and continuous quadrats in the study of the structure of plant communities. *Annals of Botany, London N.S.*, 16:293-316.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.

Harper, J. L. (1977). *Population Biology of Plants.* Academic Press, New York.

Liddle, M. J., Budd, C. S. J. & Hutchings, M. J. (1982). Population dynamics and neighbourhood effects in establishing swards of *Festuca rubra*. *Oikos*, 38, 52-59.

MacMahon, J. A., Schimpf, D. J., Andersen, D. C., Smith, K. G. & Bayn, R. L. Jr. (1981). An organism-centered approach to some community and ecosystem concepts. *Journal of Theoretical Biology*, 88, 287-307.

MacNally, R. C. (1979). Social organization and interspecific interactions in two sympatric species of Ranidella (Anura). *Oecologia*, 42, 293-306.

Matern, B. (1960). Spatial variation. Stochastic models and their applications to some problems in forest surveys and other sampling investigations. *Medd. fran Statens Skogsforsknings-institut.*, 49, 1-144.

Mead, R. (1966). A relationship between individual plant spacing and yield. *Annals of Botany, London N.S.*, 30, 301-309.

Mead, R. (1967). A mathematical model for the estimation of interplant competition. *Biometrics*, 23, 189-205.

Morisita, M. (1954). Estimation of population density by spacing methods. *Mem. Fac. Sci. Kyushu U. Series E (Biology)*, 1, 187-197.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. (1975). *SPSS, Statistical Package for the Social Sciences*, 2nd edn. McGraw-Hill Book Co., New York.

Nobel, P. S. (1981). Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida*. *Journal of Ecology*, 69, 735-742.

Phillips, D. J. & MacMahon, J. A. (1981). Competition and spacing patterns in desert shrubs. *Journal of Ecology*, 69, 97-116.

Pielou, E. C. (1959). The use of point-to-plant distances in the study of pattern of plant populations. *Journal of Ecology*, 47, 607-613.

Pielou, E. C. (1960). A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology*, 49, 255-269.

Pielou, E. C. (1961). Segregation and symmetry in two-species populations as studied by nearest-neighbor relationships. *Journal of Ecology*, 49, 255-269.

Pielou, E. C. (1977). *Mathematical Ecology*, 2nd edn. Wiley Interscience Publishers, New York.

Ripley, B. D. (1981). *Spatial Statistics*. Wiley Interscience Publishers, New York.

Ross, M. A. (1968). *The establishment of seedlings and the development of pattern in grassland.* Ph.D. thesis. University of Wales.

Ryan, T. A., Joiner, B. L. & Ryan, B. F. (1976). *Minitab Student Handbook*. Duxbury Press, North Scituate, MA.

Schultz, A. M., Gibbens, R. P. & Debano, L. (1961). *Artificial Population Sampler. Instruction Manual*. Schultz Developments, Walnut Creek, CA.

Schimpf, D. J., Henderson, J. A. & MacMahon, J. A. (1980). Some aspects of succession in the spruce-fir forest zone of northern Utah. *The Great Basin Naturalist*, 40, 1-26.

Vincent, P. J., Haworth, J. M., Griffiths, J. G. & Collins, R. (1976). The detection of randomness in plant patterns. *Journal of Biogeography*, 3, 373-380.

Yeaton, R. I. (1978). Competition and spacing in plant communities: Differential mortality of White Pine (*Pinus strobus* L.) in a New England woodlot. *American Midland Naturalist*, 100, 285-293.

Yeaton, R. I. & Cody, M. L. (1976). Competition and spacing in plant communities: the northern Mohave Desert. *Journal of Ecology*, 62, 689-696.

Yeaton, R. I., Travis, J. & Gilinsky, E. (1977). Competition and spacing in plant communities: the Arizona Upland association. *Journal of Ecology*, 65, 587-595.

Zar, J. H. (1974). *Biostatistical Analysis*. Prentice-Hall Inc., Englewood Cliffs, NJ.

APPENDICES

Appendix A. Program listing of SPACE.FOR

```
      PROGRAM SPACE
C-     This program produces a partition of a rectangular map space
C-     containing individuals of known size. Borders are produced
C-     placing one individual in each cell according to the Rule
C-     selected.  This program is intended for exploration of the
C-     properties of a variety of Rules and is not expected to be
C-     efficient at applying any one Rule for production runs of
C-     many data sets.  The boundaries are approximated at boundaries
C-     of cells of a fine grid rather than being the smooth functions
C-     that the Rules would actually develop. This incremental approach
C-     may cause minor errors in identification of 'minor' neighbors
C-     that contact or miss at only one cell boundary; however, it
C-     allows the examination of a variety of different Rules producing
C-     different shaped boundaries.


C-     This program developed on the USU VAX11/780 by R. Bayn
C-     in partial fulfillment of the requirements for the PhD.
C-     in Biology Ecology.


      COMMON NHASH,H(2,0:32000)
      COMMON /PARAM/ ZB, IFUNC
C-
C-     As currently dimensioned the following limits apply:
C-        maximum population size: 1000 individuals
C-        maximum number of increments in y direction: 32000
C-        maximum number of increments in x direction: unlimited
C-        maximum number of neighbors per individual : 30
C-


      DIMENSION X(0:1000),Y(0:1000),N(0:1000),SIZE(0:1000),IROW(0:1000),
     *    S(2,0:32000),D(0:32000),FMT(10),NBR(0:30,0:1000)
      DIMENSION ANG(30),RANDI(0:13),RANCR(0:13),RANNB(0:13)
      INTEGER DI(0:40),CRCL(0:40),NAB(0:40),AREA,
     *       T(2,0:32000),TT,TJ1,TJ2,01,02
      INTEGER TIND,TAREA,H  ! hash storage array
      REAL JX,IY
      LOGICAL*1 FLAG
      EQUIVALENCE (S,NBR)  ! NBR IS FOR USE AFTER CELL ASMTS ARE COMPLETE
      EQUIVALENCE (DI,N),(CRCL,N(100)),(NAB,N(200))  ! DI,CRCL,NAB USED LATER
      CHARACTER*60 NAME1,NAME6,FUNCS(8)
      CHARACTER*80 LINE
      DATA RANDI/ .0209,.0827,.1809,.3059,.4439,.5800,.7016,  ! Expected
     *           .8009,.8753,.9267,.9596,.9791,.9898,.9953/  ! distributions
      DATA RANCR/ .0163,.0637,.1380,.2328,.3408,.4540,.5652,  ! for
     *           .6682,.7585,.8333,.8908,.9389,.9680,.9862/  ! Kolmogorov-
      DATA RANNB/ .0000,.0000,.0000,.0107,.1260,.3907,.6865,  ! Smirnov test
     *           .8789,.9638,.9920,.9985,.9997,.9998,.9999/  !
      DATA FUNCS/
     * 'SCORE=1.0/(DIST+1.0)    <no size effect,SIZE=1.0>          ',
     * 'SCORE=SIZE/(DIST+SIZE)  <hyperbolic function of size>      ',
     * 'SCORE=((Z+1)*SIZE/(SIZE+DIST))-Z <SCORE=0 when DIST=SIZE/Z> ',
     * 'SCORE=1-(DIST/(SIZE)) <flat slope, max=1.0>                ',
     * 'SCORE=1-(DIST/(SIZE))**2 <convex up; max=1.0>              ',
     * 'SCORE=SIZE-DIST        <flat slope, max=f(SIZE)>           ',
     * 'SCORE=2*(1-(DIST+Z)/(SIZE+Z))  <diff.flat slopes,max=f(SIZE)',
     * 'SCORE=EXP(-((DIST/(SIZE))**2)/2.0)  <normal curve>         '/
```

```
C-                   * * * * * * MODULE A * * * * * *
C-       Scan the data file, describe its extent, suggest parameters,
C-       accept Rule selection and parameters, print sample of SCOREs
C-       over expected range of SIZEs and DISTances.
C-

      CALL CPUTIME(TIME1)
      INQUIRE(FILE='INPDATA',EXIST=FLAG)
      IF(FLAG) THEN
         OPEN(1,STATUS='OLD',FILE='INPDATA')
         INQUIRE(1,NAME=NAME1)
      ELSE
         TYPE 10       ! PROMPT FOR FILENAME
         READ(5,20) NAME1
         OPEN(1,STATUS='OLD',FILE=NAME1)
      END IF
      READ(1,20) LINE
      REWIND 1
      TYPE 30, NAME1,LINE  ! PROMPT
      READ (5,40) FMT
      OPEN(6,STATUS='NEW',FILE='SPACEOUT')
      INQUIRE(6,NAME=NAME6)
      WRITE(6,50) NAME1,FMT,NAME6
      READ(1,FMT) XIN,YIN,SIN
      XMIN=XIN
      YMIN=YIN
      SMIN=SIN
      SMAX=SIN
      M=1
      READ(1,FMT,IOSTAT=IOS) XIN,YIN,SIN
      DO WHILE (IOS.EQ.0)
         SSUM=SSUM+SIN*SIN      ! accumulate sum of squares of sizes
         IF(YMAX.LT.YIN) THEN
              YMAX=YIN
              ELSE IF(YMIN.GT.YIN) THEN
                   YMIN=YIN
              ELSE
              END IF
         IF(SMAX.LT.SIN) THEN
              SMAX=SIN
              ELSE IF(SMIN.GT.SIN) THEN
                   SMIN=SIN
              ELSE
              END IF
         M=M+1
         READ(1,FMT,IOSTAT=IOS) XIN,YIN,SIN
         END DO
      XMAX=XIN   ! since the input file is ordered by x


      REWIND 1
```

```
      TOTAR=(XMAX-XMIN)*(YMAX-YMIN)
      XINC=SQRT(TOTAR/M)/10.0     ! recommended increment size
      YINC=XINC
      ZA=SQRT(TOTAR/(0.785398*SSUM))  ! recommended size:area conversion
      TYPE 32, M,XMIN,XMAX,YMIN,YMAX,SMIN,SMAX,XINC,ZA
   15 TYPE 60   ! request input parameters
      READ (5,*) XMIN,XMAX,XINC,YMIN,YMAX,YINC,DMAX,INTRVL,ZA,ZB,IFUNC
      IF(IFUNC.LE.2) ZB=0.0
      IF(ZA.EQ.0) ZA=1.0      ! don't change all sizes to zero
      IF(IFUNC.EQ.0) THEN
         TYPE 62, (I,FUNCS(I),I=1,8)
         GOTO 15
      END IF
      IF(IFUNC.GE.3 .AND.IFUNC.LE.7 .AND. DMAX.EQ.0.0) DMAX=SMAX*ZA
      IF(IFUNC.EQ.3 .AND. ZB.EQ.0) ZB=1.0
      IF(IFUNC.EQ.7 .AND. ZB.EQ.0) ZB=DMAX
      NHASH=M*32*MIN(1.0,(XMAX-XMIN)*(YMAX-YMIN)/TOTAR)  ! scale down by portion used
      YDELTA=(YMAX-YMIN)/YINC + 1
      XDELTA=(XMAX-XMIN)/XINC + 1
      WRITE(6,33) IFIX(XDELTA),XINC,XMIN,XMAX,IFIX(YDELTA),YINC,
     *              YMIN,YMAX,DMAX,INTRVL,ZA,ZB,NHASH
      OPEN(2,STATUS='NEW',CARRIAGECONTROL='LIST',FILE='CELLASMTS')
      OPEN(3,STATUS='NEW',CARRIAGECONTROL='LIST',FILE='REGDATA')
      OPEN(4,STATUS='NEW',CARRIAGECONTROL='LIST',FILE='NABRPAIRS')
   75 CONTINUE
      IF(SMAX.LT.(SMAX-SMIN)*1.2) THEN                          !
         SMIN=IFIX(SMAX/10.0+1.0)                                !
         SMAX=SMIN*11.0                                          !
      END IF                                                     ! write a
      SDELTA=(SMAX-SMIN)/10.0000001                              ! table of
      WRITE(6,130) FUNCS(IFUNC),ZB,(SI,SI=SMIN,SMAX,SDELTA)      ! sample
      SMAX=SMAX*ZA                                               !
      SMIN=SMIN*ZA                                               !
      SDELTA=(SMAX-SMIN)/10.0000001                              !
      IF(SMAX.GT.SMIN .AND. IFUNC.GT.1) THEN                     ! scores
         WRITE(6,140)                                            ! for the
         I=0                                                     ! expected
   80    J=0                                                     ! range of
            DO 70 SI=SMIN,SMAX,SDELTA                            ! sizes and
               J=J+1                                             ! distances
   70          X(J)=SCORE(0.0,0.0,SI,FLOAT(I),0.0,DIST)          !
            WRITE(6,150) I,(IFIX(1000.0*X(K)),K=1,J)             !
            I=I+(1+I/5)                                          !
            IF(I.LT.DMAX) GOTO 80                                !
      END IF


   10 FORMAT(' ENTER FILENAME.EXT FOR MAP DATA')
   20 FORMAT(A)
   30 FORMAT(' ENTER FORMAT OF MAP DATA IN ',A/
     *        ' FIRST LINE IS  ',A)
   32 FORMAT(X,I6,' INDIVIDUALS WERE FOUND BETWEEN X=',F,' AND ',F/
     *        7X, '                                AND Y=',F,' AND ',F/
     *        7X,  '              WITH SIZES RANGING FROM ',F,'  TO ',F/
     *        7X,  '              RECOMMENDED INCREMENT : ',F/
     *        7X,  '   RECOMMENDED AREA:SIZE FACTOR : ',F)
   33 FORMAT(' MAPPED AREA:'/
     * 6X,'X:',I6,' UNITS,',F,' INCREMENT FROM ',F,' TO ',F/
     * 6X,'Y:',I6,' UNITS,',F,' INCREMENT FROM ',F,' TO ',F/
     * 6X,'THE MAX DISTANCE OF INFLUENCE IS:',F/
     * 6X,'# OF INCREMENTS IN A SORTING INTERVAL IS:',I/
     * 6X,'SIZE:AREA FACTOR IS: ',F/
     * 6X,'CONSTANT FUNCTION COEFFICIENT IS: ',F/
     * 6X,'SIZE OF NEIGHBOR HASHING ARRAY IS:',I)
   40 FORMAT(10A4)
   50 FORMAT(' FILE: ',A,' FORMAT:',10A4/' OUTPUT: ',A)
   60 FORMAT
     *(' ENTER XMIN MAX INC,YMIN MAX INC,DMAX,INTRV,ZA,ZB,FUNC(1>6)'/)
   62 FORMAT(' AVAILABLE FUNCTIONS ARE:'/8(I6,':= ',A/))
  130 FORMAT('OSCORE. FUNC. VALUES FOR VARIOUS SIZES AND DISTANCES'/
     *        X,A,'  Z=',F8.3/
     *        35X,'- - - INDIVIDUAL SIZE - - -'/
     *        ' DIST. ',11F6.1)
  140 FORMAT(7X,11(' -----'))
  150 FORMAT(I5.2X.11I6)
```

```
C-                * * * * * * MODULE B * * * * * *
C-       Make the cell assignments column by column (i.e. all increments
C-       of y for each increment of x).  Store the cell assignments in
C-       file CELLASMTS and neighbor contacts in file NABRPAIRS.

      85 DIJX=(DMAX*2.0)+(INTRVL*XINC)+XMIN  ! check adequacy of dmax
         M=0
         CALL CPUTIME(TIME2)
      90 READ(1,FMT,END=100) XIN,YIN,SIN    ! Read entries (x,y,size)
            M=M+1                           ! until an entry with
            X(M)=XIN                        ! an x-coordinate
            Y(M)=YIN                        ! greater than
            N(M)=M                          ! DIJX is encountered
            SIZE(M)=SIN*ZA                  !
            IF(XIN.LT.DIJX) GOTO 90         !
     100 CONTINUE                           !
         NIND=M                             ! NIND= #ind in x,y,size list
         CALL SORTY (X,Y,N,SIZE,NIND)       ! sort the NIND entries by y value
         JX=XMIN
         TYPE *, ' PROCESSING X=',JX,' WITH',NIND,' INDIVIDUALS'
         IND=1
         DMX=0.0
         J1=1
         J2=1

C-       Begin processing the current column JX

     160 KMIN=1
         KX=KX+1
         IY=YMIN-YINC
         DO I=1,YDELTA   ! find winners for each cell (1 to YDELTA)
            IY=IY+YINC                                        !
            S(J1,I)=0                                         !
            T(J1,I)=0                                         !
            C=SCORE(X(IND),Y(IND),SIZE(IND),JX,IY,DIST)       !
            IF(C.GT.0) THEN                                   !
               S(J1,I)=C                                      !
               DIS=DIST                                       !
               T(J1,I)=N(IND)                                 !
            END IF                                            !
            DO K=KMIN,NIND       ! this includes the range IY+/- DMAX     !
               IF(Y(K).GT.IY+DMAX) GOTO 200  ! don't search any farther   !
               IF(Y(K).GE.IY-DMAX) THEN                                   !
                  C=SCORE(X(K),Y(K),SIZE(K),JX,IY,DIST)                   !
                  IF(C.GT.S(J1,I)) THEN                                   !
                        S(J1,I)=C                                         !
                        T(J1,I)=N(K)                                      !
                        DIS=DIST                                          !
                        IND    = K                                        !
                  END IF                                                  !
               ELSE                                                       !
                  KMIN=K+1                                                !
               END IF                                                     !
            END DO                                                        !
     200    CONTINUE                                          !
            D(I)=DIS              ! save winning distance !
            IF(DIS.GT.DMX) THEN   ! need to increase DMAX ?
               DMX=DIS                                        !
               IF(DMX.GE.DMAX) THEN                           !
                  DMAX=DMX*1.1                                !
                  TYPE *, 'DMAX INCREASED TO ',DMAX           !
               END IF                                         !
            END IF                                            !
         END DO ! I=1,YDELTA                                  !
         WRITE(2,410)              ! id#,x,y,score,dist
        *     ((T(J1,I),JX,((I-1)*YINC)+YMIN,S(J1,I),D(I)),I=1,YDELTA)
```

```
C-           --- now look for neighbor boundaries:

        O1=T(J1,1)
        O2=O1
        DO K=1,YDELTA
           TJ1=T(J1,K)
           TJ2=T(J2,K)
           IF(TJ1.NE.O1) THEN
              CALL HASH(TJ1,O1)                ! neighbors in same col
              IF(TJ1.NE.TJ2) CALL HASH(TJ1,TJ2)  ! neighbors in same row
           ELSE IF(TJ2.NE.O2) THEN
              IF(TJ2.NE.TJ1) CALL HASH(TJ1,TJ2)  ! neighbors in same row
           END IF
           O2=TJ2
           O1=TJ1
           END DO

C-      SWITCH J1 & J2 TO ACCUMULATE NEXT ROW OF WINNERS WHILE SAVING
C-      THE PREVIOUS ROW FOR NEIGHBOR COMPARISONS NEXT TIME
        J2=J1
        J1=J1+1
        IF(J1.GT.2) J1=1    ! SWITCH J1 AND J2



        JX=JX+XINC
        IF(JX.GT.XMAX) GOTO 310          ! goto MODULE C >>>>>>>>>>>>>>>
        IF(KX.LT.INTRVL) GOTO 160

C-      AFTER DOING 'INTRVL' ROWS OF CELL ASSIGNMENTS, ITS TIME TO
C-      REVISE THE LIST OF INDIVIDUALS TO CONSIDER.  DELETE THOSE TO
C-      LEFT THAT ARE NO LONGER WINNING CELLS AND ADD THOSE TO THE
C-      RIGHT UP TO DMAX+NINTRVL AWAY.  THEN SORT THE REVISED LIST
C-      BY Y-COORDINATE.

        KX=0
        OT=0
        NROW=0
        DIJX=DMAX+(INTRVL*XINC)+JX       ! max x-coord to include
        DO  K=1,YDELTA                  ! make a list in IROW(*) of all
           IF(T(J2,K).NE.OT) THEN       ! winners found in the current
              OT=T(J2,K)                ! column so that individuals
              NROW=NROW+1               ! to the left that didn't win
              IROW(NROW)=OT             ! any space this time can be
           END IF                       ! deleted from the search
           END DO                       ! list.
        K=1
    225 CONTINUE
           IF(X(K).GE.JX) GOTO 270               ! scan the search list,
           DO KK=1,NROW                          ! deleting individuals
              IF(N(K).EQ.IROW(KK)) GOTO 270      ! to the left of the
              END DO                             ! current column (JX)
           DO  KK=K,NIND-1                       ! that didn't win
              X(KK)=X(KK+1)                      ! any space this time
              Y(KK)=Y(KK+1)                      ! and move the remaining
              N(KK)=N(KK+1)                      ! individuals up in the
              SIZE(KK)=SIZE(KK+1)                ! list.
              END DO                             !
           NIND=NIND-1                           !
           K=K-1                                 !
    270    K=K+1
        IF(K.LE.NIND) GOTO 225
    280 READ(1,FMT,ERR=310,END=290) XIN,YIN,SIN   ! add new individuals
           NIND=NIND+1                            ! to the end of the
           M=M+1                                  ! list until one is
           X(NIND)=XIN                            ! found to the right
           Y(NIND)=YIN                            ! of x=DIJX
           N(NIND)=M                              !
           SIZE(NIND)=SIN*ZA                      !
           IF(XIN.LT.DIJX) GOTO 280               !
    290 CONTINUE
        TYPE *, ' PROCESSING X=',JX,' WITH',NIND,' INDIVIDUALS'
        CALL SORTY(X,Y,N,SIZE,NIND)    ! sort the new entries by y-coord
        GOTO 160
    300 FORMAT(2I6)
```

```
C-              * * * * * * MODULE C * * * * * *

      310 CONTINUE
          CALL CPUTIME(TIME3)
          TYPE *,' ELAPSED TIME CELL ASMTS:',TIME3-TIME2
          WRITE(6,*) ' ELAPSED TIME CELL ASMTS:',TIME3-TIME2
          REWIND 2       ! cell assignments
          REWIND 4       ! neighbor pairs
          TYPE *,' END OF CELL ASSIGNMENTS, SUMMARY BEGINS'
          DO  I=0,M      !
             IROW(I)=0   ! zero some
             SIZE(I)=0   ! storage
             X(I)=0      ! for reuse
             D(I)=0      !
             Y(I)=0      !
             N(I)=0      !
             END DO
          M=0  ! FIND MAX INDIVIDUAL # IN FOLLOWING LOOP
      330 READ(2,410,END=340) TT,XX,YY,SS,DD  ! id#,x,y,score,dist
             IF(TT.GT.M) M=TT                 !
             IF(TT.EQ.0) THEN                 !
                N(0)=N(0)+1                   !
             ELSE IF(XX.LE.XMIN.OR.XX.GT.XMAX-XINC  .OR.
     *              YY.LE.YMIN.OR.YY.GT.YMAX-YINC) THEN
                N(TT)=-1000000000             ! flag a boundary individual
             ELSE                             !
                N(TT)=N(TT)+1                 ! accumulate area,
                X(TT)=X(TT)+XX                ! x-coord,
                Y(TT)=Y(TT)+YY                ! y-coord,
                SIZE(TT)=SIZE(TT)+SS          ! total score
                IF(DD.GT.D(TT)) D(TT)=DD      ! and max distance for
             END IF                           ! each individual
             GOTO 330
      340 WRITE(6,430)      ! HDG
      350 READ(4,300,END=360) IH1,IH2                   !
             IF(IROW(IH1).LT.30) THEN                   !
                IROW(IH1)=IROW(IH1)+1                   !
                NBR(IROW(IH1),IH1)=IH2                  ! accumulate ID#s of
             ELSE                                       ! up to 30 neighbors
                IF(IH1.NE.0)TYPE *,                     ! of each individual
     *                IH1,' HAS OVER 30 NEIGHBORS' ! in NBR(*,*)
             END IF                                     !
             IF(IROW(IH2).LT.30) THEN                   !
                IROW(IH2)=IROW(IH2)+1                   !
                NBR(IROW(IH2),IH2)=IH1                  !
             ELSE                                       !
                TYPE *, IH2,' HAS OVER 30 NEIGHBORS'!
             END IF                                     !

             GOTO 350
      360 CONTINUE     ! now IROW(*) has # of neighbors
```

```
         REWIND 1   ! raw datafile: x,y,size
         IF(N(0).NE.0) WRITE(6,460) N(0)
         DO I=1,M
            READ(1,FMT,END=390) XIN,YIN,SIN      !
               NN=N(I)    ! NN = # of cells assigned
               IF(NN.LE.0) THEN                 !
                  NN=-99          ! flag boundary !
                  XX=-99.0        ! individual    !
                  YY=-99.0        ! with 99's     !
                  ECCEN=-99.0     ! for all       !
                  D(I)   =-99.0   ! incomplete    !
                  SIZE(I)=-99.0   ! parameters    !
               ELSE                             !
                  XX=X(I)/NN                    ! for each individual
                  YY=Y(I)/NN                    ! accumulate some
                  SIN2=SIN*SIN     !size squared ! statistics
                  SX =SX +SIN2                  ! and write a summary
                  SXX=SXX+SIN2*SIN2             ! line to file
                  SYARE =SYARE +NN              ! REGDATA
                  SYYARE=SYYARE+NN*NN           !
                  SXYARE=SXYARE+SIN2*NN         !
                  SYCOM =SYCOM +SIZE(I)         !
                  SYYCOM=SYYCOM+SIZE(I)*SIZE(I) !
                  SXYCOM=SXYCOM+SIN2*SIZE(I)    !
                  NSAMP=NSAMP+1                 !
                  XE=XX-XIN    ! eccentricity   !
                  YE=YY-YIN    ! coordinates    !
                  ECCEN=SQRT(XE*XE+YE*YE)       !
               END IF                           !
            WRITE(3,440) I,XIN,YIN,SIN,NN,XX,YY,ECCEN,SIZE(1),IROW(I),D(I),
     *                  (NBR(J,I),J=1,IROW(I))
            END DO
     390 CONTINUE
         EXX=SXX-(SX*SX/NSAMP)                       !
         IF(EXX.GT.0.0) THEN                         !
            EXYARE=SXYARE-(SX   *SYARE/NSAMP)        !
            EYYARE=SYYARE-(SYARE*SYARE/NSAMP)        !
            EXYCOM=SXYCOM-(SX   *SYCOM/NSAMP)        !
            EYYCOM=SYYCOM-(SYCOM*SYCOM/NSAMP)        ! calculate and
            BARE=EXYARE/EXX                          ! report regressions
            BCOM=EXYCOM/EXX                          ! of total score
            RARE=BARE*EXYARE/EYYARE                  ! and total area
            RCOM=BCOM*EXYCOM/EYYCOM                  ! against size squared
            AARE=(SYARE/NSAMP)-BARE*(SX   /NSAMP)   !
            ACOM=(SYCOM/NSAMP)-BCOM*(SX   /NSAMP)   !
            TYPE 470, RCOM,BCOM,ACOM, RARE,BARE,AARE
            WRITE(6,470) RCOM,BCOM,ACOM, RARE,BARE,AARE
            WRITE(6,480) SX,SXX,SXYCOM,SYYCOM,SYCOM,
     *                           SXYARE,SYYARE,SYARE,NSAMP
         END IF ! EXX.GT.0.0
         WRITE(6,490) NSAMP,IFIX(SYARE),DMX
         TYPE 490, NSAMP,IFIX(SYARE),DMX
         CALL CPUTIME(TIME4)
         TYPE *,' ELAPSED CPU TIME FOR SUMMARY:',TIME4-TIME3
         WRITE(6,*) ' ELAPSED CPU TIME FOR SUMMARY:',TIME4-TIME3
     410 FORMAT(I4,4A4)  ! id#,x,y,score,dist
     430 FORMAT(/' IND#     X-COORD-Y     SIZE     AREA      X-CENTER-Y',
     *          '    ECCEN. SCORE. NAB MAXDIST')
     440 FORMAT(I4,3F8.2,I8,4F8.2,I4,F8.2/12X,30I4)
     460 FORMAT(3X,'0',24X,I8)    ! unassigned area (ind# 0)
     470 FORMAT('  SCORE: RSQ=',F6.3,'     SCORE=',F,'*SIZE**2+',F/
     *         '  AREA : RSQ=',F6.3,'      AREA=',F,'*SIZE**2+',F)
     480 FORMAT(10X,'SX',9X,'SXX',9X,'SXY',9X,'SYY',10X,'SY',11X,'N'/
     *       5F12.2/24X,3F12.2,I12)
     490 FORMAT(/I6,' INDIVIDUALS ENTIRELY WITHIN BOUNDARY PREEMPTED',
     *       I10,' UNITS OF SPACE'/' MAX DIST OF INFLUENCE FOUND WAS',
     *       F8.2)
```

```
C-                    * * * * * * MODULE D * * * * * *

      500 CONTINUE
          CALL CPUTIME(TIME5)
          REWIND 3  ! contains all the plant coords,sizes and neighbor i.d.s
          M=0
          DO I=0,40
             DI(I)=0
             CRCL(I)=0
             NAB(I)=0
             END DO
      505 CONTINUE
             M=M+1
             READ(3,510,END=507)
     *          X(M),Y(M),SIZE(M),NBR(0,M),(NBR(J,M),J=1,NBR(0,M))
             GOTO 505
      507 M=M-1  ! subtract the read when EOF occurred
          DCELL=2.5*SQRT(3.141592654*M/(XINC*YINC*SYARE))
          DO I=1,M                        ! find dist and angles for each plant
             IF(SIZE(I).NE.-99.0) THEN ! omit plants at boundary
                XI=X(I)
                YI=Y(I)
                NN=NBR(0,I)               ! # of neighbors recorded
                NNB=0                     ! number of 'real' neighbors (not #0)
                DO J=1,NN
                   NJ=NBR(J,I)            ! ID# of J-th neighbor
                   IF(NJ.NE.0) THEN
                      NNB=NNB+1
                      XJ=X(NJ)
                      YJ=Y(NJ)
                      XD=XI-XJ
                      YD=YI-YJ
                      DIST=SQRT(XD*XD+YD*YD)
                      ANGLE=ASIN(YD/DIST)  ! radians
                      IF(XJ.LT.XI) ANGLE=3.141592654-ANGLE
                      IF(ANGLE.LT.0.0) ANGLE=ANGLE+6.2831853
                      ANG(NNB)=ANGLE   ! angle to NNB-th real neighbor
                      ID=DIST*DCELL    ! convert distance to freq class
                      IF(ID.GT.40) ID=40
                      DI(ID)=DI(ID)+1
                   END IF !NJ.NE.0
                   END DO
                NTOT=NTOT+NNB
                DO K=1,NNB-1                        ! now sort angles in ANG(*)
                   DO J=1,NNB-K                     !
                      IF(ANG(J).GT.ANG(J+1)) THEN!
                         TEMP=ANG(J)                !
                         ANG(J)=ANG(J+1)            !
                         ANG(J+1)=TEMP              !
                      END IF                        !
                      END DO                        !
                   END DO                           !
                DO K=1,NNB-1
                   IA=(ANG(K+1)-ANG(K))*6.3662            ! calculate angles
                   CRCL(IA)=CRCL(IA)+1                    ! between successive
                   END DO                                 ! real neighbors and
                IA=(6.2831853-ANG(NNB)+ANG(1))*6.3662     ! increment the
                CRCL(IA)=CRCL(IA)+1                       ! frequency class in
                NAB(NNB)=NAB(NNB)+1                       ! CRCL(*)
             END IF ! SIZE(I).NE.-99
             END DO ! I=1,M for each plant
```

```
          WRITE(6,520)  ! heading for freq distributions
          DO I=0,13
             WRITE(6,530)                                    !
     *           I*DCELL,(I+1)*DCELL,DI(I),I*9,(I+1)*9,CRCL(I),I,NAB(I)
             CUMDI=CUMDI+DI(I)                               !
             CUMCR=CUMCR+CRCL(I)                             ! accumulate
             CUMNB=CUMNB+NAB(I)                              ! totals for the
             DMAXDI=MAX(DMAXDI,ABS(CUMDI/NTOT -RANDI(I)))    ! Kolmogorov-
             DMAXCR=MAX(DMAXCR,ABS(CUMCR/NTOT -RANCR(I)))    ! Smirnov test
             DMAXNB=MAX(DMAXNB,ABS(CUMNB/NSAMP-RANNB(I)))    ! over I=0,13
             END DO                                          !
          DO I=14,40
             WRITE(6,530)
     *           I*DCELL,(I+1)*DCELL,DI(I),I*9,(I+1)*9,CRCL(I),I,NAB(I)
             END DO
          WRITE(6,550) DMAXDI,NTOT,DMAXCR,NTOT,DMAXNB,NSAMP
          TYPE 550,    DMAXDI,NTOT,DMAXCR,NTOT,DMAXNB,NSAMP
          CALL CPUTIME(TIME6)
          TYPE *,' ELAPSED CPU TIME FOR FREQ DIST:',TIME6-TIME5
          WRITE(6,*) ' ELAPSED CPU TIME FOR FREQ DIST:',TIME6-TIME5
          TYPE *,' TOTAL CPU TIME FOR RUN:',TIME6-TIME1
          WRITE(6,*) ' TOTAL CPU TIME FOR RUN:',TIME6-TIME1
          STOP
      510 FORMAT(4X,2F8.2,40X,F8.2,I4/12X,30I4)  ! REREAD FILE3
      520 FORMAT('0FREQUENCY DISTRIBUTIONS:'/
     *     ' =======DISTANCES=======      =====ANGLES=====      NEIGHBORS'/
     *     '     INTERVAL        COUNT     INTERVAL    COUNT      #  COUNT')
      530 FORMAT(X,F7.2,' -',F7.2,I7.0,5X,I3,' - ',I3.3,I7.0,5X,I2,I7.0)
      540 FORMAT(I4,2F6.1,(T20,10F6.1))
      550 FORMAT(' KOLMOGOROV-SMIRNOV TEST STATISTICS COMPARING THE 3'/
     *          ' FREQUENCY DISTRIBUTIONS TO THE RANDOM DISTRIBUTIONS:'/
     *          ' DISTANCE    D=',F6.4,'  N=',I4/
     *          ' ANGLE       D=',F6.4,'  N=',I4/
     *          ' # NEIGHBORS D=',F6.4,'  N=',I4)
          END
```

```
      FUNCTION SCORE(X,Y,SIZE,XI,YJ,DIST)
      COMMON /PARAM/ Z,I
      DIST2=((X-XI)*(X-XI) + (Y-YJ)*(Y-YJ))   ! calculate distance and
      DIST=SQRT(DIST2)                        ! branch to appropriate
      GOTO (10,20,30,40,50,60,70,80),I        ! rule
   10 SCORE = 1.0/(DIST+1.0)             ! no size effect
      RETURN
   20 SCORE = SIZE / (DIST + SIZE)       ! hyperb. sect. always pos.
      RETURN
   30 SCORE = ((Z+1.0)*SIZE/(SIZE+DIST))-Z ! y=0 at DIST=SIZE/Z
      RETURN
   40 SCORE = 1.0 -(DIST/(SIZE))         ! flat slope; max=1
      RETURN
   50 SCORE = 1.0 -(DIST/(SIZE))**2      ! convex up; max=1
      RETURN
   60 SCORE = SIZE - DIST                ! flat slope; max=f(SIZE)
      RETURN
   70 SCORE = 2.0*(1.0-((DIST+Z)/(SIZE+Z)))  ! different slopes & intercepts
      RETURN
   80 SCORE=EXP(-((DIST/(SIZE))*2)/2.0)  ! normal curve
      RETURN
      END
```

```
      SUBROUTINE SORTY (X,Y,N,SIZE,NIND)
      DIMENSION X(0:1000),Y(0:1000),N(0:1000),SIZE(0:1000)
      LOGICAL FLAG

C-        a slightly modified 'bubble sort' for a partially sorted
C-        list with random entries at the bottom.

      DO 20 I=2,NIND
         FLAG=.TRUE.
         DO 10 KK=-NIND,-I,1
            K=-KK
            IF(Y(K).GT.Y(K-1)) GOTO 10
               FLAG=.FALSE.
               TEMP=X(K)
               X(K)=X(K-1)
               X(K-1)=TEMP
               TEMP=Y(K)
               Y(K)=Y(K-1)
               Y(K-1)=TEMP
               TEMP=N(K)
               N(K)=N(K-1)
               N(K-1)=TEMP
               TEMP=SIZE(K)
               SIZE(K)=SIZE(K-1)
               SIZE(K-1)=TEMP
   10       CONTINUE
         IF(FLAG) RETURN
   20    CONTINUE
      RETURN
      END
```

```
      SUBROUTINE HASH(TI1,TI2)
C-        store the neighbor pairs TI1 and TI2
      INTEGER TI1,TI2,H
      COMMON NHASH,H(2,0:32000)
      J=TI1
      K=TI2
      IF(J.GT.K) GOTO 10
      J=TI2
      K=TI1
   10 IHASH=MOD(J+K,NHASH)+1
      JHASH=IHASH
   20 IF(H(1,IHASH).EQ.J) GOTO 30
      IF(H(1,IHASH).NE.0) GOTO 40
      H(1,IHASH)=J
      H(2,IHASH)=K
      WRITE(4,200) J,K
      RETURN

   30 IF(H(2,IHASH).EQ.K) RETURN  ! ALREADY RECORDED
   40 IHASH=IHASH+1
      IF(IHASH.GT.NHASH) IHASH=1
      IF(IHASH.EQ.JHASH) GOTO 50
      GOTO 20

   50 CONTINUE
      WRITE(6,100) NHASH
      RETURN
  100 FORMAT(' HASH ARRAY FILLED TO CAPACITY WITH ',I6,' NEIGHBORS')
  200 FORMAT(2I6)
      END
```

Appendix B. Command files for MINITAB and SPSS analyses of REGDATA output from program SPACE

```
$ ASSIGN/USER_MODE MINIOUT FOR006
$ RUN MINITAB
DIMENSION 500
FREAD 'REGDATA' INTO C1-C11
(F4.0,8F8.0,F4.0,F8.0/)     ! ALTERNATE LINES CONTAIN NEIGHBOR LIST
NAME C1 'ID',C2 'X',C3 'Y',C4 'SIZE',C5 'AREA',C6 'X-C',C7 'Y-C'
NAME C8 'ECCEN',C9 'SCORE',C10 'NABRS',C11 'MDIST'
OMIT -99.0 IN C5,C1-C4,C6-C11 PUT INTO C5,C1-C4,C6-C11
DESCRIBE C2-C11
BRIEF 1
MULTIPLY 'SIZE' BY 'SIZE' PUT INTO C12
NAME C12 'SIZE2'
REGRESS Y IN 'MDIST' USING 1 PREDICTOR 'SIZE'
REGRESS Y IN 'AREA'  USING 1 PREDICTOR 'SIZE'
REGRESS Y IN 'AREA'  USING 1 PREDICTOR 'SIZE2'
REGRESS Y IN 'SCORE' USING 1 PREDICTOR 'SIZE'
REGRESS Y IN 'SCORE' USING 1 PREDICTOR 'SIZE2'
PLOT 'MDIST'   VS 'SIZE'
PLOT 'AREA'    VS 'SIZE'
PLOT 'SCORE'   VS 'SIZE'
STOP
```

```
RUN NAME          SPACE ANALYSIS
PAGESIZE          NOEJECT
PRINT BACK        CONTROL
FILE NAME         REGDATA
VARIABLE LIST     ID,X,Y,SIZE,AREA,XC,YC,ECCEN,COMPET,NABRS,MDIST
MISSING VALUES    AREA,XC,YC,ECCEN,COMPET,NABRS (-99.0)
COMPUTE           S2=SIZE*SIZE
COMPUTE           S3=S2*SIZE
COMPUTE           SLOG=LG10(SIZE)
INPUT MEDIUM      REGDATA
COMMENT           FMT INCLUDES SLASH TO SKIP NEIGHBOR LIST ON ALT. LINES
INPUT FORMAT      FIXED(F4.0,8F8.0,F4.0,F8.0/)
N OF CASES        UNKNOWN
REGRESSION        VARIABLES=X,Y,SIZE,S2,S3,SLOG,AREA,XC,YC,ECCEN,COMPET,NABRS/
                  REGRESSION=AREA(1) WITH SIZE,S2,S3,SLOG (1),ECCEN,NABRS,
                            X,Y (0) RESID=0/
STATISTICS        1,2
OPTIONS           7
READ INPUT DATA
REGRESSION        VARIABLES=X,Y,SIZE,S2,S3,SLOG,ECCEN,COMPET,NABRS/
                  REGRESSION=COMPET(1) WITH SIZE,S2,S3,SLOG (1),ECCEN,NABRS,
                            X,Y (0) RESID=0/
OPTIONS           7
REGRESSION        VARIABLES=X,Y,SIZE,S2,S3,SLOG,ECCEN,COMPET,NABRS,MDIST/
                  REGRESSION=MDIST(1) WITH SIZE,S2,S3,SLOG (1),ECCEN,NABRS,
                            X,Y (0) RESID=0/
OPTIONS           7
FINISH
```