

COMPETITION AND THE FORMATION OF SPATIAL PATTERN IN SPACING GRADIENTS: AN EXAMPLE USING *KOCHIA SCOPARIA*

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SUMMARY

(1) The presence of pattern in the distribution of dominant and suppressed individuals of the annual plant *Kochia scoparia* was studied under greenhouse conditions.

(2) The experimental design consisted of plants positioned in a polar coordinate grid with eleven arcs and nineteen rays. The distance between arcs increased exponentially from 2.3 cm to 11.1 cm. Rays were separated by an angle of 10°. A superimposed triangular array determined that plants were always surrounded by six neighbours.

(3) The average size (stem height, stem sectional area and total weight) of plants varied in a regular fashion both across and along arcs. Spatial autocorrelation of the average weight of plants in each arc showed a negative correlation when the lag was one, three or five arcs and a positive correlation when the lag was an even number. When comparisons were made between plants along each arc a negative correlation between a plant and its most immediate neighbour was consistently found. In contrast, the correlations with a lag greater than one did not reveal a consistent pattern.

(4) The relationship between mean plant size and spacing did not follow a monotonic function, but showed fluctuations up and down the expected trend. This indicated that interference in this kind of design is not a monotonic function of inter-plant distance. Hierarchy, as measured by the coefficient of variation of plant size in each arc, increased with time, but at a higher rate in inner arcs. For a given recording date, hierarchy within an arc was inversely related to mean plant size.

(5) The results suggest that the formation of pattern in the distribution of dominant and suppressed plants is a consequence of a strong 'edge effect' whose transmission proceeds in the preferential direction of the spacing gradient. The overall effect can be described by a kind of wave of constant period (though this constancy need not be the case in every instance). This 'competition-effect wave' makes the definition of individual plant density impossible: the degree of interference experienced by each individual in the design depends on the degree of interference its neighbours have themselves experienced.

(6) It is recommended that spatial gradients should not in general be used to calculate yield-density relationships. Plants create their own 'density' according to the space that they capture. Because the emergence of spatial pattern in plant populations is the rule, we suggest the use of spacing gradients to study the transmission of interference effects in modular, sessile organisms.

INTRODUCTION

In recent years there has been a growing interest in developing methods for the study of plant interference which consider the importance for a plant of its fixed position. Because plants cannot escape the effects of interference from neighbours by changing their position, 'movement' is restricted to the plasticity of growth of the population of meristems present in different parts of the individual plant (Jones 1985; Franco 1986). If

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space (as a source of light, water, nutrients, etc.) is limiting plant growth, each individual plant should grow until its weight is proportional to the size of its immediate, available space. This has led to the development of neighbourhood models of plant performance (Mead 1966; Opie 1968; Bella 1971; Moore, Budelsky & Schlesinger 1973; Mack & Harper 1977; Alemdag 1978; Adlard & Smith 1981; Waller 1981; Weiner 1984; Pacala & Silander 1985; Silander & Pacala 1985).

Spacing gradients of the kind known as fan designs (Nelder 1962) have been used, particularly in agricultural practice, as a means of studying the effect of inter-plant spacing on the growth of individual plants in a reduced space and with equal or almost equal sample size (number of plants) for each spacing. In these gradients, the space allocated to each plant is clearly defined at the beginning of the experiment. In theory, neighbourhood models of plant performance should be able to predict the results obtained from such gradients. In practice, however, because neighbourhood models of plant performance assume a monotonic relationship between plant yield and inter-plant spacing, they would fail to account for the regularity in the pattern of dominance and suppression generated in such designs.

It is known that when plants compete they develop a hierarchy of dominance and suppression (Koyama & Kira 1956; Obeid, Machin & Harper 1967; Ford 1975; Rabinowitz 1979; Turner & Rabinowitz 1983; Weiner & Solbrig 1984; Weiner 1985). That the spatial distribution of dominant and suppressed plants is not random but can show a great regularity has been shown in experiments where the distribution of plants is itself highly regular (Hozumi, Koyama & Kira 1955; Yoda, Kira & Hozumi 1957; Laessle 1965; Kitamoto & Shidei 1972; Cannell *et al.* 1977). The emergence of spatial pattern when individual plants are equally spaced has been studied by means of the statistical technique known as spectral analysis (Renshaw & Ford 1983, 1984; Ford & Renshaw 1984; Renshaw 1984). The development of spatial pattern occurs not only when plants are equally spaced, but whenever plants compete, regardless of the planting regime (e.g. Simons, Davies & Troughton 1973; Assemat & Oka 1980; Antonovics & Fowler 1985, for spacing gradients; and Zeide 1972, 1975, for natural forests in the U.S.S.R.).

In particular, the formation of pattern in spacing gradients allows the investigation of the transmission of competition effects as plants along the gradient start interfering with their neighbours at different times. On the basis of what is known about inter-plant competition, one may predict: (i) a negative correlation in the growth of neighbouring plants, and (ii) an increase in plant size with increasing available area. From what is known about the formation of hierarchies and spatial pattern in plant populations, however, one may speculate that, because plants on the edge of the design have more space to develop and behave as dominants over their most immediate neighbours, this dominance releases their neighbours' neighbours from competition, thus producing a periodic distribution of dominant and suppressed plants.

From the results of an experiment in which the annual plant *Kochia scoparia* was grown in a spacing gradient, we discuss the emergence of spatial pattern in plant populations. We propose the use of spacing gradients as a means to study the way in which interference effects are transmitted in populations of sessile, modular organisms.

MATERIALS AND METHODS

Plant species

We used a horticultural variety (*culta*) of the annual plant *Kochia scoparia* (L.) Schrad (Chenopodiaceae), sold commercially under the incorrect name of *Kochia trichophylla*

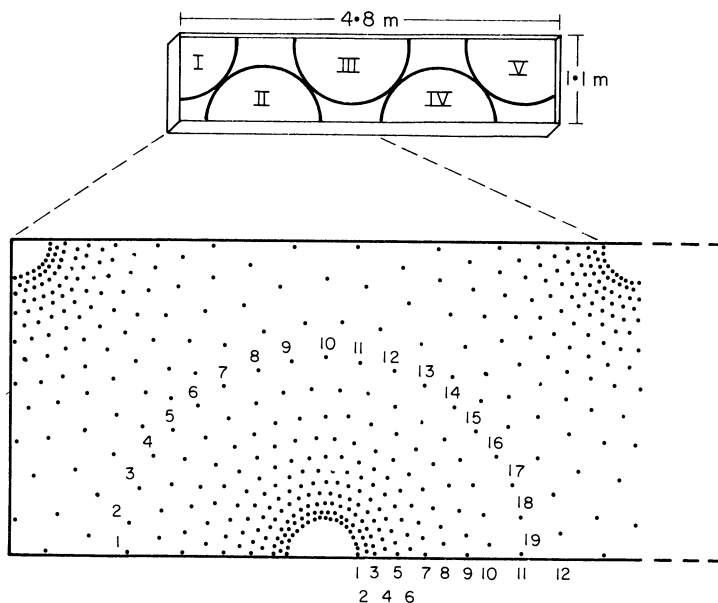


FIG. 1. Layout of the gradient used to investigate the effect of inter-plant spacing on the growth of individual plants of *Kochia scoparia* var. *culta*. The upper part shows the arrangement of fans (I-V) on the soil bed. The lower part illustrates the ordering of arcs (I-11) and plants in arc 11 (1-19) of fan II.

(Hitchcock *et al.* 1964). When growing under good conditions *Kochia scoparia* var. *culta* develops a cypress-like appearance. It produces a main stem with secondary thickening and with branches arranged in a $2/5$ spiral phyllotaxis. *Kochia* resembles a tree not only in its overall shape and secondary thickening, but also because, in contrast to other annual plants with secondary thickening, it produces several orders of branching (a maximum of five when it grows in isolation from other plants). A more complete description of the plant can be found in Franco (1985).

Experimental layout

Seeds of *Kochia scoparia* var. *culta* were germinated on 1 June 1982. On 20 June seedlings of approximately 10 cm height were transplanted on to a 25-cm deep soil bed (4.8 m long \times 1.1 m wide) containing John Innes No. 2 compost enclosed in a wooden frame 30-cm high (Fig. 1). Care was taken to ensure that the scar left by the cotyledonary leaves was positioned at surface ground level. This gave a standard point from which to measure plant height, stem diameter 1 cm above it, and separation of aerial and root parts at harvest.

The position of each plant was located in a polar co-ordinate grid with arcs and rays (fan design type I; Nelder 1962). The position of each arc is defined by an exponential function ($r_i = r_0 \alpha^i$) that describes its distance from the origin of the grid (r_i) as a function of the arc number, i . The function has two parameters: the distance, somewhat arbitrarily defined, of the first arc (r_0) and a coefficient (α) that defines the speed with which the distance between arcs increases. This parameter is necessarily greater than one. The angular distance between plants in an arc (distance between rays: θ) was arbitrarily

TABLE 1. Initial available space per plant and calculated density in experimental density gradient.

Arc number	Radial distance from origin (cm)	Area per plant (cm ²)	Density (plants m ⁻²)
1	12.11	4.48	2232
2	14.41	6.35	1575
3	17.16	9.00	1111
4	20.42	12.75	784
5	24.31	18.07	553
6	28.94	25.61	390
7	34.45	36.30	275
8	41.01	51.44	194
9	48.82	72.89	137
10	58.12	103.30	97
11	69.19	146.38	68

defined to be 10° or 0.1745 radians. One more parameter of this fan design, called eccentricity (τ), is defined as the symmetry, (or departure from it) of the space available to each plant, and is characterized by the ratio between inter-arc distance and inter-ray distance. Clearly, when this quotient is equal to one the space available to each plant is symmetrical. Having chosen θ to be 10° , and in order for the value of eccentricity to be equal to one, the parameter α was calculated from the formulae presented in Nelder (1962) as 1.19 and the distance to the first arc as 12.11 cm.

Arcs were numbered from 1 to 12. Plants were arranged in a triangular array superimposed on the 'rectangular' fan design giving either nineteen or eighteen plants per arc (Fig. 1). Plants in each arc were numbered clockwise. Three fans of 180° and two fans of 90° each were intercalated, as illustrated in Fig. 1.

Immediately after transplanting, the seedlings lost turgor and remained wilted for one or two days. Turgor recovery was then a clear sign of seedlings having established firmly in the soil. Seedlings that had not recovered turgor on the third day after transplanting (never more than three per fan) were replaced by seedlings from the same stock. Therefore, seedling establishment amounted to 100%.

The total height of plants and diameter of the stem 1 cm above the node of the cotyledonary leaves were recorded on days 15, 29, 50, 71 and 100 after planting. In some of the figures we refer to these dates, on an arbitrary time scale, as recording dates 2, 3, 4, 5 and 6; 1 being the date when plants were transplanted. Height was measured to the nearest centimetre and diameter to the nearest tenth of a millimetre, using a metallic measuring tape and a Vernier calliper, respectively. Because some stems were not completely circular, care was taken to measure their diameter in the same direction at each recording date. Cross-sectional area of the stem base was calculated from the diameter measured, assuming a circular transverse section.

On day 100, plants were harvested at ground level and dried in an oven at 50°C for two weeks. Because of their small size, it was impossible to separate seeds from leaves. Therefore, each plant was divided into leaves and seeds, branches, and stem, and these three weighed separately to the nearest mg.

Analysis of data

Because plants in arc 12 and beyond were common to two or more fans (see Fig. 1), only plants in arcs 1-11 were taken into account. The allocated space per plant and the

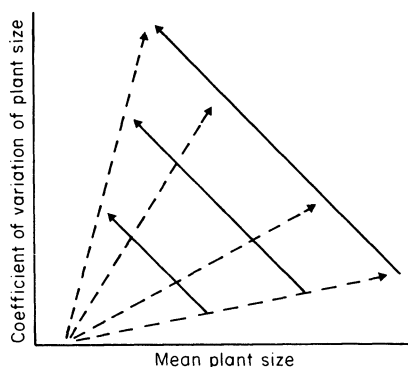


FIG. 2. A graphic model of intra- and inter-arc hierarchy in a spacing gradient (fan design). Intra-arc hierarchy (---) is measured by the coefficient of variation of plant size (height, mass, etc.) within an arc as it changes through time. Inter-arc hierarchy (—) is estimated by the relative position of each arc in the scatter plot at a single time.

calculated corresponding 'density' (i.e. plants m^{-2}) are shown in Table 1. Notice, however, that the available space must necessarily be greater for plants at the edge of the design (all plants in arc 1, and plants 1 and either 19 or 18 in the other arcs). As this produces a strong 'edge effect', analyses were made on: (i) the whole data set (all plants in arcs 1–11); (ii) the central part of the design (plants 3–17 in arcs 1–11) including those that died at some time during the experiment; (iii) the central part of the design (plants 3–17 in arcs 1–11) excluding plants that had died before each recording date; (iv) the central part of the design (plants 3–17 in arcs 1–11) considering only those plants that remained alive throughout the experiment.

Except where stated, the analyses presented here correspond to this last set, because the results for the four data sets were similar and showed little variation among themselves. Similarly, because the results were similar in all fans, only the analyses performed on one of the 180° fans (fan III in Fig. 1) are shown.

In order to assess the presence of patterns of dominance and suppression, we investigated both the formation of size hierarchies and the correlation in the size of neighbour plants. The former was done by calculating the coefficient of variation (Zar 1974) of stem height, stem cross-sectional area and final total plant weight within each arc, and plotting it against their corresponding means. We hypothesized that hierarchy, as measured by the coefficient of variation, should increase with both the size of the average plant (time of development) (Koyama & Kira 1956) and the intensity of competition (Weiner 1985). Although the Gini coefficient (an index of inequality from the literature on economics) has previously been suggested as a measure of hierarchy in plant populations (Weiner & Solbrig 1984; Weiner 1985), we preferred the coefficient of variation because it is easier to calculate and because it is obvious that both are correlated: the coefficient of variation is a measure of deviation of all the members of the sample from the mean, divided by the mean, while the Gini coefficient is a measure of deviation of every pair of individuals in the sample (each pair is taken twice) divided by twice the mean. There were two ways of comparing inequality of plant size (or hierarchy) in the design: by focusing on one arc at different times of development, and by comparing different arcs on the same date. These will be referred to as intra- and inter-arc hierarchy, respectively (Fig. 2).

Correlation of plant size between neighbours, on the other hand, was estimated by means of the correlation of mean plant size in different arcs, i.e. by means of an autocorrelogram. This analysis was also performed, within each arc, for individual plants along it. In order to make the respective variation (across and along the arcs) homogeneous, the data were first transformed logarithmically. Furthermore, to remove the trend from the series, these were differenced once, i.e. each series was constructed by taking the difference between two successive elements of the original, logarithmically transformed series. Considering the assumptions of this statistical technique, these results must be taken with reservations and only as a visual aid to the kind of pattern generated in the spacing gradient.

Finally, regression between logarithmically transformed data of mean plant weight and the estimated 'densities' were calculated. In these regressions, a measure analogous to the coefficient of determination was obtained. This is the percentage of variance accounted for by the regression (% var.), calculated as:

$$100 \times (\text{total MS} - \text{residual MS}) / \text{total MS}$$

Mean squares (MS), instead of sum of squares (SS), are used, thus taking into account the number of parameters in the model (Alvey *et al.* 1977).

RESULTS

Survivorship

No mortality occurred before recording date 3. After this date seventeen out of 204 plants in the eleven arcs died before the end of the experiment. Mortality was most likely due to competition with neighbours, both because it was delayed until the canopy was completely closed and because it was limited to the centre of suppressed arcs 2, 3, 5, 7 and 9 (see next section).

Height and cross-sectional area increment

Mean height and cross-sectional area of central plants in the design (plants 3–17) that remained alive until the end of the experiment increased with both time and spacing (Fig. 3a, b). The increase with spacing, however, did not occur monotonically; instead, the figures show a series of ridges and furrows which suggests that some arcs dominated over neighbouring arcs. Hierarchy (as measured by the coefficient of variation), on the other hand, increased also with time but more slowly at wider spacings (Fig. 3c, d). Not only do the graphs of plant height and cross-sectional area show ridges and furrows perpendicular to the spacing axis, but their corresponding coefficients of variation do so also, but in 'mirror image'.

Plotting the coefficient of variation against their corresponding means (Fig. 4) reveals the hypothesized intra- and inter-arc hierarchies of Fig. 2, particularly for plant height. Assuming a positive correlation between the degree of interference experienced by plants in an arc and the development of hierarchy (Weiner 1985), these results support our suspicion that some arcs suffer stronger interference while others undergo weaker interference than that expected by their position in the gradient. Therefore, the degree of interference is not a monotonic function with respect to inter-plant spacing. It is suggestive that the greatest neighbour effects in the design (as measured by the between-arc inequality) occurred in arc 3, and the smallest neighbour effects were found in arc 10. This order was determined very early in the development of the stand and, given its

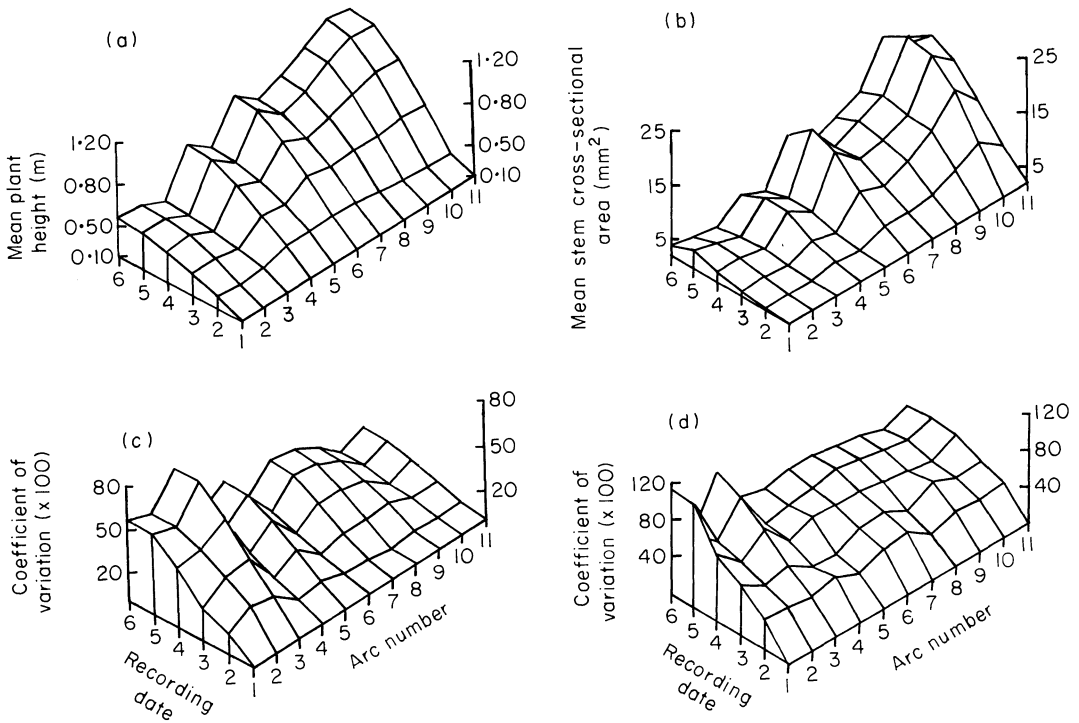


FIG. 3. The response of *Kochia scoparia* to inter-plant spacing as measured by its increase in height (a) and stem cross-sectional area (b), and their corresponding coefficients of variation (c and d). Spacing increases from arc 1 to arc 11. Only central plants (3–17) that remained alive throughout the experiment in arcs 1–11 were considered. Notice that time is represented in an arbitrary, not absolute, scale (see text).

regularity when one considers the height of the plants, suggests that early differences in total height determine the differential success of neighbouring individuals. Within-arc inequality increases with time in all arcs but at a higher rate in arcs with a greater between-arc hierarchy. The pattern of arc dominance and suppression appears more clearly when one considers the whole data set (all plants in arcs 1–11, including dead ones, Fig. 5). The exclusion of dead plants (Fig. 4) reduces the calculated intra-arc hierarchy. Death of suppressed plants presumably relaxes inter-plant competition and this is reflected as a change in the relative position of an arc in the scatter plot.

Final size of individual plants

Leaf and seed, branch, stem and total weight of individual plants at the end of the experiment showed the same kind of spatial periodicity as height and stem cross-sectional area. This periodicity occurred not only along the spacing axis, but also across it, along each arc.

An indication of the kind of spatial pattern present is suggested by the correlation of the difference of the logarithm of total final weight of neighbouring plants. This was done (i) across arcs, i.e. considering the series formed by the average weight of plants in arcs 1–11 (Fig. 6), and (ii) separately for each arc considering the series of individual weights along

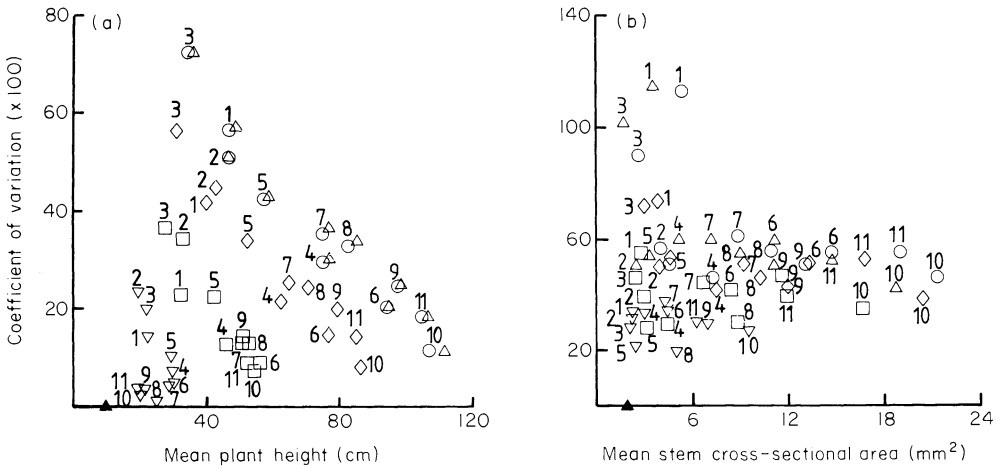


FIG. 4. The development of intra- and inter-arc hierarchy of *Kochia scoparia* in a spacing gradient (fan design), as estimated by (a) plant height (cm) and (b) stem cross-sectional area (mm²). Only central plants (3–17) in the design that remained alive until the end of the experiment were included. Numbers represent arcs. Recording periods: 1(▲); 2(▽); 3(□); 4(◊); 5(○); 6(△).

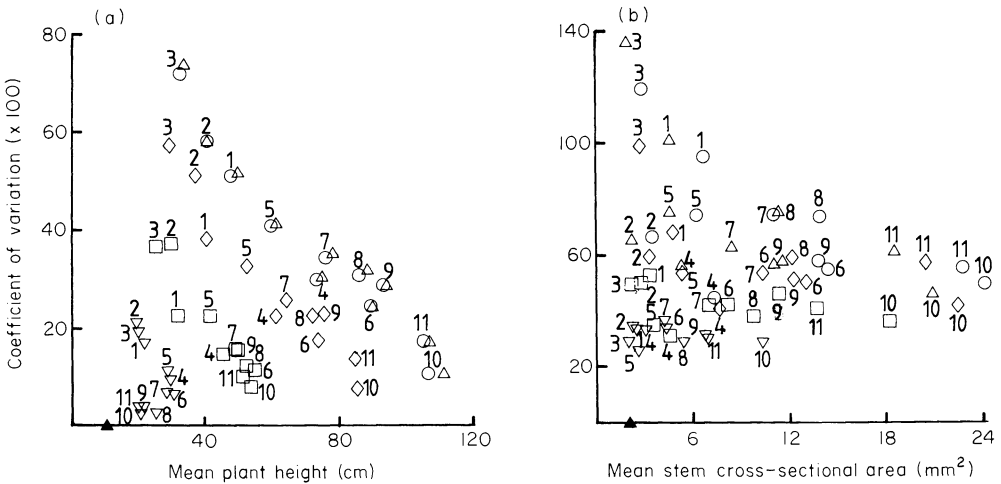


FIG. 5. Intra- and inter-arc hierarchy of *Kochia scoparia* plants in a fan design as estimated by (a) plant height and (b) stem cross-sectional area. All plants, including dead ones, were used. Numbers represent arcs. Recording periods: 1(▲); 2(▽); 3(□); 4(◊); 5(○); 6(△).

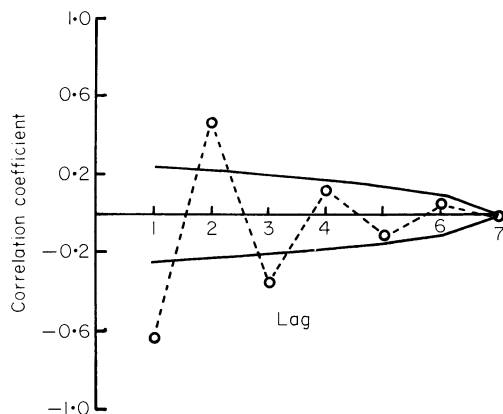


FIG. 6. The response of *Kochia scoparia* plants to the presence of neighbours as estimated by the autocorrelation of the logarithm of mean plant weight per arc. The continuous curves on each side of the x axis represent twice the standard error limits. The trend in the data was removed by first-order differencing of the series (Box & Jenkins 1970).

the arc (Fig. 7). In the first case, there is a negative correlation between plants separated by a distance of 1, 3 and 5 arcs, and a positive correlation between plants separated by a distance of 2, 4 and 6 arcs. The correlation damps down very rapidly, so that one would attach more significance to the correlation in the size of plants situated in adjacent arcs (lag 1, strongly negative) and to that of plants separated by one intermediate arc (lag 2, strongly positive). In the case of the analysis along each arc, there is a consistent negative correlation between the size of a subject plant and the size of its closest neighbour (lag 1), but no clear pattern between a subject plant and farther neighbours. Except for the pattern of dominance and suppression between adjacent individuals, the pattern along arcs seems to be obliterated by the stronger pattern in the direction of the spacing gradient.

An attempt to measure between-arc inequality using the final weight of the plants (Fig. 8) shows that this variable yields more unexplained variation than plant height (Figs 4 and 5). This again suggests that height of the plant is more important in the determination of the ecological success of the individual (as measured by its probabilities of survival and reproduction) than its absolute size (this is also suggested, for example, by the results of Kuroiwa 1960; Kitamoto & Shidei 1972; Trenbath & Harper 1973; Trenbath 1974; Hutchings & Barkham 1976; Cannell *et al.* 1977). The absolute size of a plant is a measure of its potential reproductive output, but this potential is only realized if the plant can avoid being overtopped and shaded by neighbours. Small differences in the height of adjacent plants became exaggerated with time, and were probably decisive in the final outcome of dominance and suppression. 'The plants may be so nearly the same height that the difference is only a millimetre, yet this may be decisive since one leaf overlaps the other' (Clements, Weaver & Hanson 1929).

Relationship between yield and inter-plant spacing

Given the strong spatial autocorrelation in the growth of individual plants, it is not surprising to find a periodicity in the average yield values between successive arcs (Fig. 9).

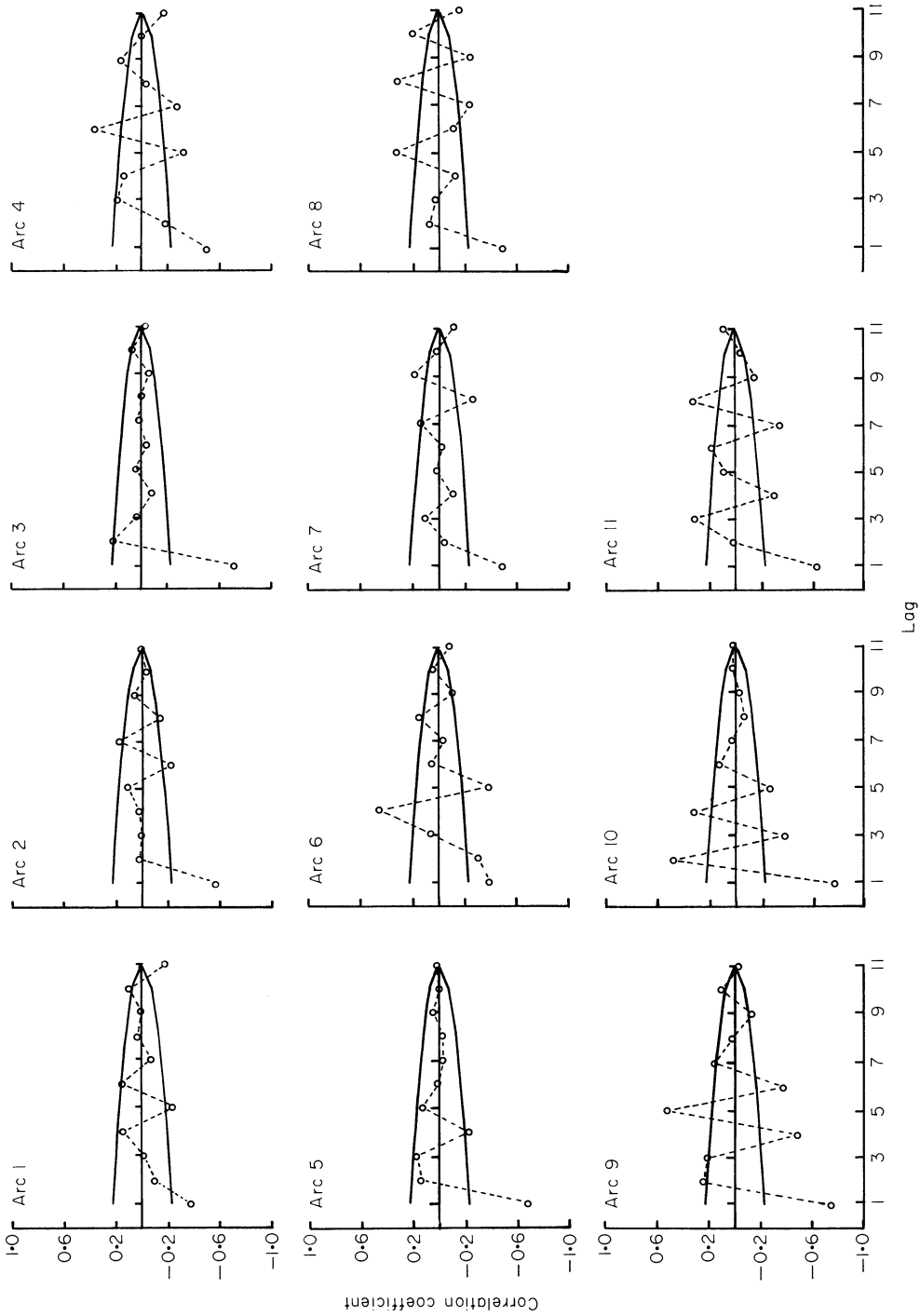


FIG. 7. The response of *Koehia scoparia* plants to the presence of neighbours, estimated by the autocorrelation of the logarithm of plant weight along each arc (1-11). The continuous curves on each side of the x axis represent twice the standard error limits. The trend in the data was removed by first-order differencing of the series (Box & Jenkins 1970).

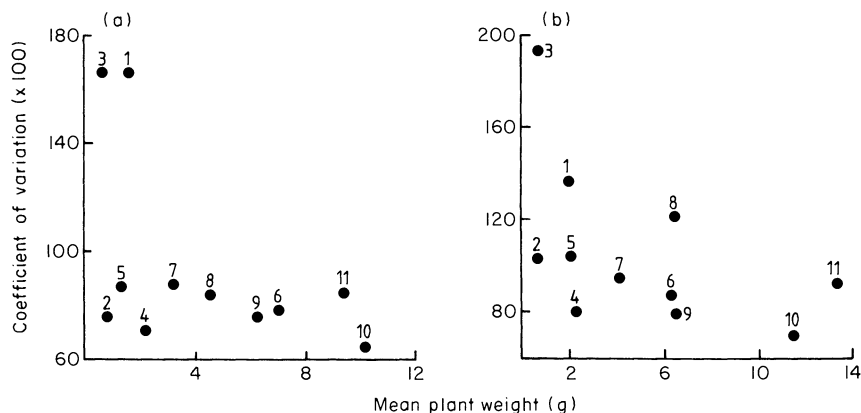


FIG. 8. The hierarchy-size relationship of *Kochia scoparia* plants in a spacing gradient (fan design) estimated by the total final mass per plant. (a) Only central plants that remained alive until the end of the experiment. (b) All plants, including dead ones. Numbers represent arcs.

Fitting a linear model to the logarithmic transformation of average weight per plant against the estimated 'density' produced values of the slope smaller than 1 for all but one of the variables recorded (Table 2). The only exception, branch mass, occurred because plants did not produce substantial branching except at the wider spacings. In density experiments where each point in the graph of yield against density comes from an independent experimental plot, the fitting of this model can be interpreted in terms of the value of the slope (Kira, Ogawa & Sakazaki 1953)*. The model has the form: $\log w = \log k - a \log n$ or, $w = k n^{-a}$. Given sufficient time, and when the range of spacings is such that plants occupy the whole surface of the ground, the parameter a increases from zero to a maximum of 1. Similarly, the parameter k increases from the initial average weight per plant (seed or seedling weight) when a is equal to zero, to the final predicted seasonal yield of a plant covering one unit of ground surface, once a reaches a value of 1. Because yield per unit area is defined as $y = w n$, it follows that $y = k n^{1-a}$, and, once $a = 1$, $y = k$, i.e. yield per unit area is constant and independent of the initial average spacing or density.

Two interpretations of the results presented in Fig. 9 are possible: either the plants do not reach final constant yield, even at the narrower spacings (Antonovics & Fowler 1985), or the plants attain constant final yield, but this is obscured in the results by the way we have defined density, as the inverse of the average available space per plant in each arc at the beginning of the experiment. From what we have shown about the non-independence of arcs and the presence of autocorrelation, we believe the first conclusion is unwarranted. The 'densities' calculated on the basis of the initial space potentially available to each plant in the design do not provide enough information on the dynamic nature of space occupation. Some arcs produce plants that spread beyond their initial allocated space while others obviously surrender part of their space to these dominant plants.

Assuming the central part of the design (plants 3-17 in arcs 3-11) has reached constant final yield, a slope equal to -1 is expected. In order to calculate the line describing this function we calculated the average weight of these plants, and the area of ground between

* Other models that fit the data outside the range of spacings or time of development at which plants compete have been proposed (Shinozaki & Kira 1956; Bleasdale & Nelder 1960; Holliday 1960; Watkinson 1980), but they are not relevant to the point made here.

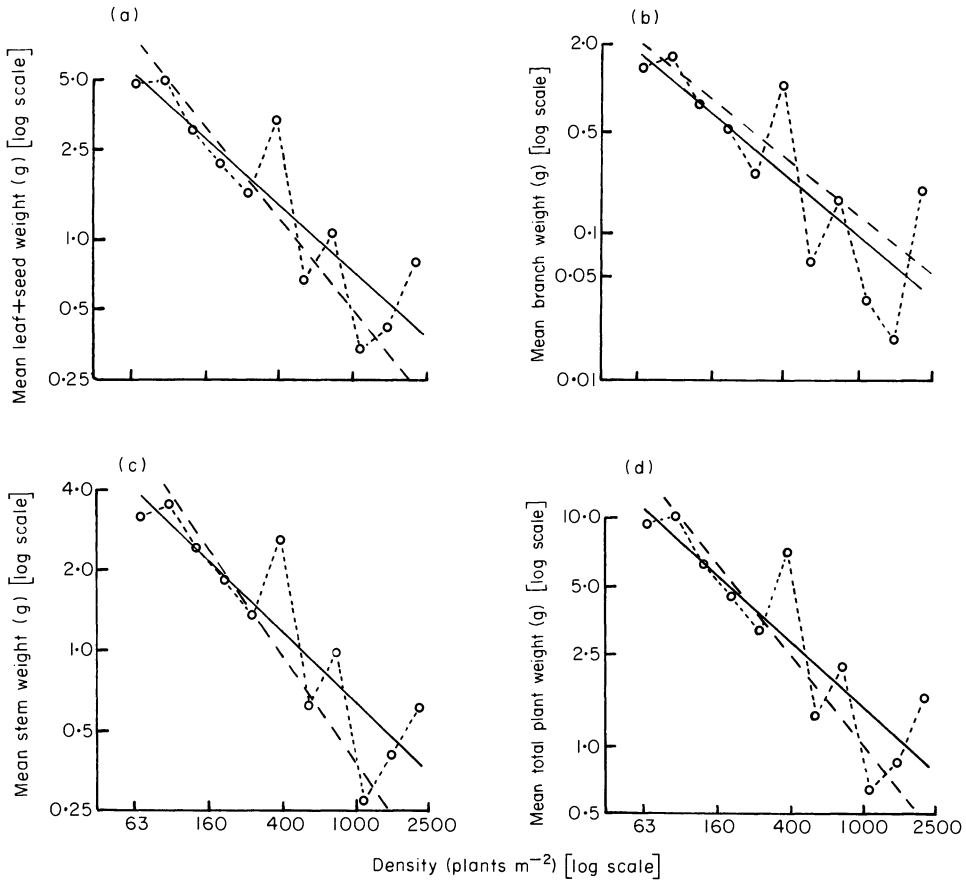


FIG. 9. The effect of inter-plant spacing on the mass-density relationship of *Kochia scoparia* plants estimated by (a) mean leaf and seed weight, (b) mean branch weight, (c) mean stem weight and (d) mean total weight per plant. Only central plants in the design (plants 3–17) that remained alive until the end of the experiment were used in the calculation of the mean values on which the regressions were performed. The dashed line is a theoretical line of slope -1 calculated on the basis of the mass present in arcs 3–11, considering the area of ground between 'arcs' 2.5 and 11.5 and the initial number of plants in it. The continuous line corresponds to the regression performed on the eleven points of the gradient (full data set; see also Table 2).

'arcs' 2.5 and 11.5 was used to calculate the average density (plants m^{-2}). This predicted function is shown for comparison as a dashed line in Fig. 9. The position of each arc with respect to these regression lines (e.g. Fig. 9d) is somehow reminiscent of the order of inter-arc hierarchy revealed in Figs 4a and 5a. Notice, however, how, when excluding the edge arc 1, the percentage of variance accounted for by the regression is greater and the slopes are not significantly different from 1 (Table 2). The periodicity along the spacing gradient cancels itself out. We must stress, however, the inappropriateness of using regression methods to calculate mass-density relationships in this kind of design. Given the fact that this is a single density plot with a peculiar distribution of individuals, regression analysis and analysis of residuals could only be used to gain an insight into the strength with which plants in different arcs invade their neighbour's space or surrender their own. Only in the hypothetical situation where this does not occur can the slope of the regression be equal to

TABLE 2. Results of the regressions between leaf plus seed mass, branch mass, stem mass, and total mass per average plant (w), respectively, and estimated plant density (n) when arcs 1, and 1 and 2, were excluded from the analyses. The model used was: $\log w = \log k - a \log n$. Values in parentheses represent the standard error of the estimate above. % var., percentage of variance accounted for by the regression; * $P < 0.05$; N.S., not significantly different from 1.

	Leaf + seed mass	Branch mass	Stem mass	Total mass
Full data set (arcs 1-11)				
$\log k$	2.044 (0.349)	2.140 (0.679)	1.792 (0.320)	2.352 (0.360)
a	0.724 (0.133)	1.050 (0.258)	0.661 (0.121)	0.725 (0.137)
$t(a < 1)$	2.079*	0.195 N.S.	2.790*	2.014*
% var.	74.3	61.0	74.2	73.1
Restricted data set (arcs 2-11)				
$\log k$	2.331 (0.347)	2.827 (0.596)	2.004 (0.341)	2.638 (0.362)
a	0.850 (0.136)	1.350 (0.233)	0.754 (0.133)	0.850 (0.142)
$t(a < 1)$	1.105 N.S.	1.501 N.S.	1.844 N.S.	1.057 N.S.
% var.	80.9	78.3	77.4	79.5
Restricted data set (arcs 3-11)				
$\log k$	2.341 (0.421)	2.552 (0.689)	2.026 (0.413)	2.647 (0.440)
a	0.854 (0.171)	1.227 (0.279)	0.764 (0.167)	0.854 (0.178)
$t(a < 1)$	0.856 N.S.	0.815 N.S.	1.414 N.S.	0.821 N.S.
% var.	75.1	69.7	71.3	73.4

– 1 and deviations from the line be close to zero. In general, a tendency for all plants to grow towards the part of the design with the widest spacing will produce a line whose slope will tend to a value of zero. On the other hand, spatial autocorrelation will produce greater values of the residuals.

DISCUSSION

The emergence of spatial pattern in density gradients has been observed in other studies (e.g. Assemat & Oka 1980; Chang 1982; Gessesse 1983; Aziz 1984; Antonovics & Fowler 1985) but its importance has not been sufficiently emphasized. The emergence of spatial pattern is not, however, a feature unique to spatial gradients. Hozumi, Koyama & Kira (1955) and Yoda, Kira & Hozumi (1957) showed similar autocorrelations to the ones presented here along rows of plants sown at equal, regular spacings. The main limitation of the use of autocorrelations along one spatial dimension is that this direction has to be known in advance. The emergence of two-dimensional spatial pattern as a result of inter-plant competition has been observed in other studies (e.g. Cooper 1961; Laessle 1965; Kitamoto 1972; Ford 1976; Cannell *et al.* 1977) and competition models that generate similar patterns have been produced (Diggle 1976; Ford & Diggle 1981; Buzikin *et al.* 1985). To study the formation of spatial pattern in two dimensions, Renshaw and Ford have introduced the statistical technique known as spectral analysis (Renshaw & Ford 1983, 1984; Ford & Renshaw 1984; Renshaw 1984). This technique, however, cannot yet be applied to spacing gradients because the theoretical spectrum for the kind of spatial distribution of plants in these designs is not known (E. Renshaw, pers. comm.).

Zeide (1972, 1975) studying natural forests in the U.S.S.R. observed that around a dominant tree there is usually a ring of suppressed trees. In turn, trees in the next concentric ring behave as dominants and so on. The overall effect can be described by a 'density wave' that damps down with distance, propagating in all directions from dominant trees. Our results suggests that in spacing gradients 'density waves' are transmitted along the rays of the design and away from the origin of the polar co-ordinate grid (Fig. 6), as interference between neighbours follows this direction with time. The presence of negative correlation in the growth of adjacent plants along arcs (Fig. 7) suggests that 'density waves' are also transmitted in this direction. The strength of the wave propagating along the rays, however, obscures the presence of waves propagating in other directions. As shown by Renshaw & Ford (1984), directionality (anisotropy) may be responsible for the accentuation of pattern. Under field conditions, further complications arise because of directionality of crown growth (Jones 1985) which may itself depend on the specific nature of the neighbours (Franco 1986).

From what we have said, it seems that the formation of spatial pattern is a consequence of asymmetrical occupation of space. Because spatial pattern is always produced irrespective of the actual distribution of the plants, asymmetric competition must be an essential feature of plant competition. Spacing gradients provide a strong initial asymmetry because plants in the first arc, where inter-plant distance is shortest, are at the edge of the design and can, temporarily, escape the effects of competition and suppress their neighbours in the next arc. This early asymmetry propagates with time through the whole spacing gradient and is almost certainly a consequence of a strong 'edge effect'.

Given the fact that asymmetrical competition occurs whenever an individual gains some advantage over its neighbours, we suggest that 'edge effects' and resource pre-emption (Ross & Harper 1972) are in essence the same phenomenon. In this respect, asymmetric competition occurs when a plant dies leaving a gap in the canopy into which already existing neighbours or newly recruited plants can invade, or whenever an individual acquires an advantage over its neighbours (a richer patch of soil, an earlier germination, some resistance to pathogens or herbivores, etc.).

Spacing gradients have been used to predict mass-density relationships by excluding from the analyses plants on or near the edges (e.g. Simons, Davies & Throughton 1973; Assemat & Oka 1980; Aziz 1984). This is done in the hope that the 'jumps' up and down the mass-spacing scatter plot cancel each other out. Nelder (1962) pointed out that this assumption might be valid in gradients whose steepness (the difference in spacing between successive arcs defined by the parameter α) is not too great. As shown by our results, however, in general this assumption is not tenable. The above arguments do not imply, however, that spacing gradients have no use in the study of neighbour effects. Although we do not recommend them for calculating mass-density relationships, they may be a useful design for studying the way in which neighbour effects are transmitted in populations of organisms that cannot move away and escape from each other.

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