

INTERFERENCE IN DUNE ANNUALS: SPATIAL PATTERN AND NEIGHBOURHOOD EFFECTS

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SUMMARY

Interference among four autumn-germinating annuals (*Cerastium atrovirens*, *Mibora minima*, *Phleum arenarium* and *Vulpia fasciculata*) native to the stabilized dunes near Aberffraw, Anglesey, North Wales, was examined at the individual plant level in monocultures, in all combinations of two species in mixture, and in a mixture of all four species. Frequency histograms of individual plant weights for each species from the four-species mixtures became skewed through time. Species with low competitive ability had a larger proportion of the cohort in the smaller size classes. Density is a crude abstraction of the precise neighbourhood relationship of individuals: up to 69% of variance in individual plant weight and fecundity is accounted for by linear regression on a measure of neighbourhood effects that takes into account the weight, distance and angular dispersion of neighbours within 2 cm.

INTRODUCTION

Plants interfere with each others' activities when their density is high enough for individuals to enter into and modify the environment of each other. For sedentary organisms, 'density' is a shorthand that summarizes the spatial relationships of individuals and, as interplant distances in nature are scarcely ever regular, 'density' is a very crude measure of the state of a population or the conditions met by the individuals. The individual plant does not react to the density of its population but to the activity of some of its neighbours. Certainly the major negative activity of neighbours is interference or competition which has been defined as, 'those hardships caused by the proximity of neighbours' (Harper 1961). The pattern and arrangement of individuals, therefore, takes on a potential importance that animals would rarely experience.

The effect of proximity and pattern is recognized by agronomists who have been concerned to find the optimum sowing distances between rows and between individuals in a row (Ralston 1953; Boswell *et al.* 1970). Nevertheless, the concept has not been applied extensively, for competition is still regarded as a density-dependent phenomenon for broadcast-sown crops such as cereals (Donald 1963). Indeed when the concern is with production per unit area of land, density remains an effective way of describing the state of a population because individuals tend through their plasticity to fill the space (i.e. exploit the resources) available to them. A plant that is unusually far from its neighbours usually reacts by making a disproportionately large amount of growth and contributes disproportionately to the yield of the crop—hence variations in the arrangement of

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individuals can contribute strongly to individual plant performance but are relatively unimportant in determining yield per unit area. Vegetation is usually interpreted holistically as the plants that occupy areas of land rather than as individuals assembled in populations (Harper 1976) and the role of interference has generally been measured as a mean or average response, e.g. by de Wit (1960). In fact, the vigour and abundance of individuals within a population appears to be a complex function of the age and arrangement of its members (Harper 1961). Analysis of the behaviour of individuals is particularly important for the understanding of evolutionary biology, because natural selection operates at the level of the individual; it is therefore important to know the sources of variation in fecundity. In biometrical genetics, environmental sources of variation are measured as a remainder after estimation of the part attributable to heredity. An ecologist may well attempt the reverse procedure and attempt to account for the components of environmental variance.

Even when variation in individual plant weight has been studied within populations it has generally been interpreted in terms of overall density. Obeid, Machin & Harper (1967) found that individuals of *Linum usitatissimum* L. developed a log-normal frequency distribution of weight which became exaggerated with increasing density and the passage of time. Hozumi, Koyama & Kira (1955) and White & Harper (1970) have shown a similar effect. Thus, there are important changes in the frequency distribution of individual plant weights within populations and statements about mean performance hide the nature and even existence of such hierarchies. Sakai (1957) showed that the biomass of a rice seedling was depressed by increasing the number of neighbours at the loci of a surrounding hexagon. The depression of the central plant was a function of the number (0–6) of neighbours. Goodall (1960) found that in mangolds the effect of intraspecific competition on individual plant yield was inversely proportional to the cube of the distance from a neighbour and Mead (1966) found that the growth of individual carrots was proportional to the area of the irregular polygon of open space around each individual and to its degree of excentricity within this space. A similar effect occurs in even-aged tree plantations and significant correlations have been found between individual plant size (i.e. basal area) and the size and distance away of the neighbours of each tree (e.g. by Bella 1971). The seedling growth of individual grasses was shown by Ross & Harper (1972) to be a function of the biological space available to each individual. This biological space was defined not only by the position but also by the stage of growth of neighbours. The ability of an individual plant to exploit its biological space was shown to be a function of its position within the area defined by its neighbours and also its time of emergence and stage of development relative to these neighbours.

Interference between plants may have three different consequences: (i) failure to germinate; (ii) death; (iii) survival and a plastic development (Harper 1964). However, interference both in plant and animal populations is a notoriously elusive phenomenon to demonstrate, and the ecological literature holds many more cases of circumstantial evidence than of irrefutable proof (Elton 1958). This paper describes experiments in which the design is a variant of that outlined by Williamson (1972) for the formal demonstration of competitive interaction. If altering the number of one species, either up or down, alters the vigour, vitality or mortality of its possible competitors, respectively down or up, and if the experiment also works the other way round, interference has been demonstrated.

For the present study five autumn-germinating annuals native to coastal dune vegeta-

tion in North Wales were chosen to determine whether the biological expression of interference is a diffuse phenomenon spread through the community or produces locally defined special interactions at the level of the individual. The main aim of the experiment was to determine how much of the total plant-to-plant variation in biomass and fecundity could be related to subtle differences in the species proximity and pattern of arrangement of neighbours. An extension of this aim was to determine whether final biomass and fecundity can be predicted by a mathematical expression of the summed activity of each plant's neighbours.

MATERIALS AND METHODS

Biological

The five species chosen for these experiments (*Cerastium atrovirens* Bab., *Mibora minima* (L.) Desv., *Phleum arenarium* L., *Saxifraga tridactylites* L., *Vulpia fasciculata* (Forskål) Samp.) are autumn-germinating annuals found on a series of stabilized low-lying inland dunes at Aberffraw, Anglesey (Nat. Grid ref. SH 3568). Of these plants *Vulpia fasciculata* is by far the largest, while *Phleum arenarium* is usually the second largest species. The species form mixed populations in an association that also includes the perennials *Festuca rubra* L., *Galium verum* L. and *Thymus drucei* Ronn. (Pemadasa & Lovell 1974a). The pattern in this dune community has been described quantitatively by Pemadasa, Grieg-Smith & Lovell (1974c). Seed of the five species from this habitat tend to germinate synchronously (Pemadasa & Lovell 1974a). Watkinson (1975) has shown that field densities of *Vulpia fasciculata* are such that interference from individuals is likely to be common, and Mack (1976) has shown that at field densities *Cerastium atrovirens* is very much suppressed compared with its growth on the dune sand as spaced individuals. The five species were therefore chosen for a study of the role of spatial arrangement in the interference that occurs within and between individuals.

Interference in two-species mixtures

Seed was collected from natural populations in the dune system at Aberffraw in the spring of 1972 and 1973 and stored in paper envelopes under laboratory conditions prior to use.

In order to test the response of the species in all possible pairings, seeds of each of the five species were sown broadcast in October 1973 at 3700/m² on separate flats (30 × 38 cm) of sterilized sand from the Aberffraw site. Each flat was divided lengthwise into two rows of three evenly spaced squares each 9 × 9 cm (see Fig. 1) and four of the squares received an equal density of one of the four remaining species. The fifth square remained a monoculture of the background species while the sixth square received an equal additional allotment of the background species. Thus each flat contained a square with the background species at density x , a square with the background species at density $2x$ and squares in which the background species was in equi-proportioned mixture with each of the other four species in turn. After the seed was sown, a 1-mm deep layer of sand was added through a fine mesh sieve. The experimental design gave a mechanical diallel (Harper 1964) with all five species alternately used as the background organism (Fig. 1(a)). Immediately after germination the mixtures were thinned so that their final density was forty plants per square (twenty background and twenty alternate species). The fifth square was thinned to twenty plants and the sixth was thinned to forty plants. In the thinning operation the plants were removed at random by placing a punched paper disc

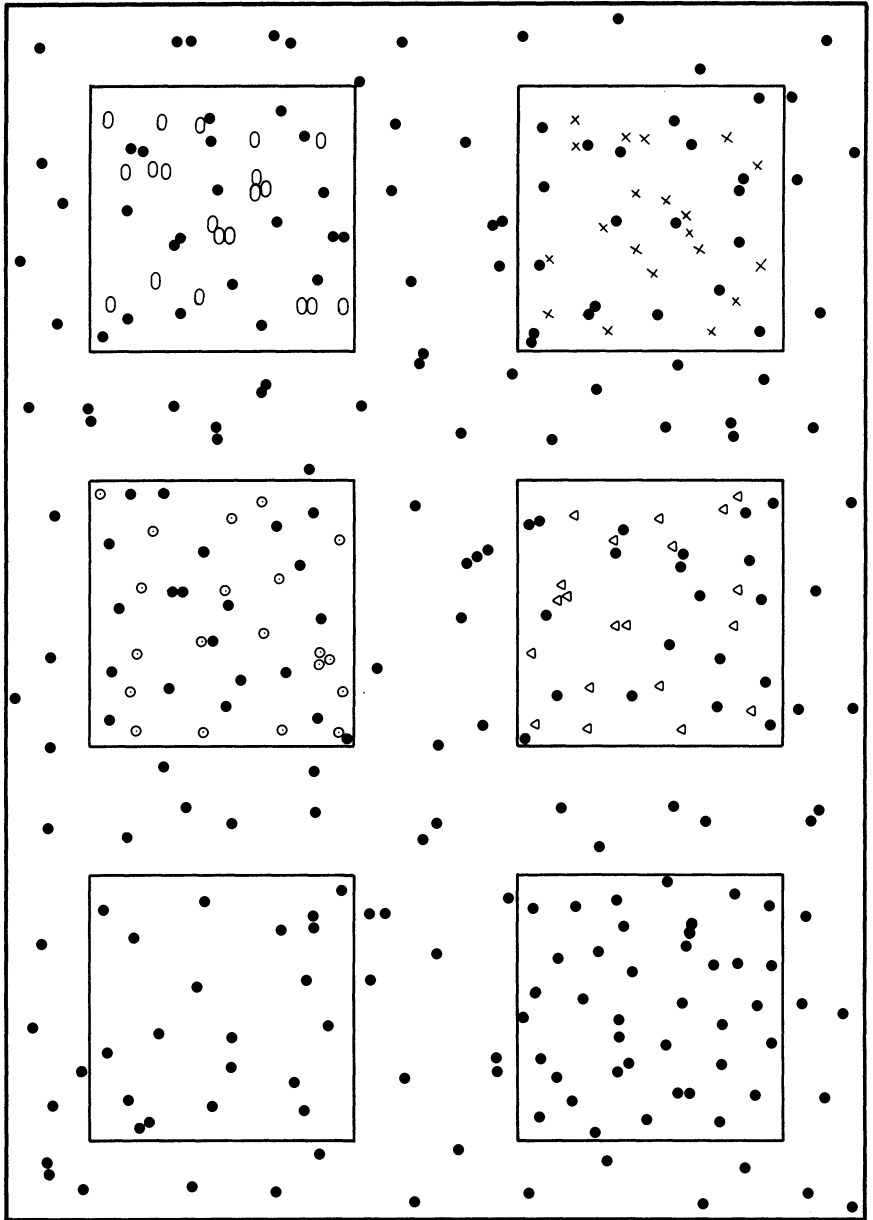


FIG. 1. Broadcast sowing pattern used for six squares (9×9 cm) within each flat for the substitutive experiment. The different symbols represent plants of different species. For explanation see text.

of random holes over each square in turn. In the text and tables this experiment is referred to as a substitutive experiment.

Interference in a five-species mixture

The same general sowing procedure and sowing time was used to assess the nature and extent of interference among the five species grown together in a mixture. Seed of all five

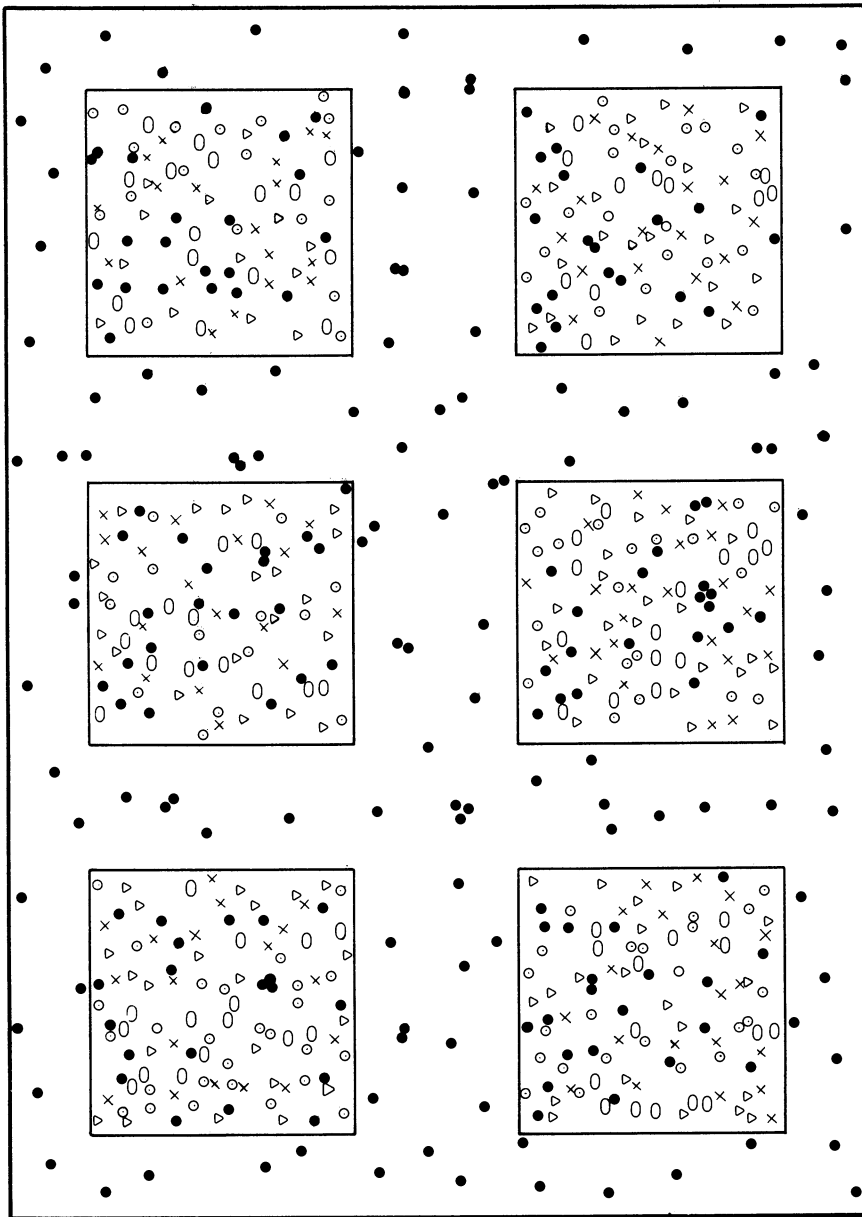


FIG. (1b) Broadcast sowing pattern used in the multiple-species experiment.

species was sown so that the final density (after random thinning) was a total of 100 individuals (twenty of each species) per square. Five treatments were prepared in which all five species alternatively were used as the background organism (Fig. 1(b)). This experiment is referred to subsequently as the 'multiple-species experiment'. Both the substitutive and the multiple-species experiment were sown with three replicates giving a total of thirty flats in all.

The flats were placed on benches in an unheated Dutch light structure at the Pen-y-Ffridd Experimental Field Station of the University College of North Wales. Doors and ridge ventilators were opened as needed to avoid overheating. The flats were arranged in a randomized block design and were rotated within blocks each week. The flats were watered approximately every other day.

All the individuals in each flat (except for some background individuals) were mapped within a month from sowing the experiments and thereafter at roughly monthly intervals. The maps were made by means of a glass table to which transparent acetate sheets could be attached. A sighting tube, fitted with three pairs of cross hairs to eliminate parallax error, was free to move across the levelled mapping table. Maps were made by aligning each individual within the cross hairs and then placing an ink dot in the line of sight on the transparent acetate. Permanent vertical wooden stakes in each flat were used to align successive maps so that these could be superimposed with high precision (resolution: 1 mm). At the time of mapping, phenologic events and mortality were recorded. Records from the acetate sheets were reproduced onto permanent paper maps. Each plant was assigned a serial number which was also marked on the map prepared at harvest time. The above-ground parts of each plant were then individually oven-dried for 48 h at 70 °C, removed to a desiccator and weighed separately to the nearest 0.1 mg.

In December, March and May one replicate of the whole experiment was harvested (ten flats per harvest). The number of seeds produced by each plant of the early-maturing *Mibora minima* was counted under magnification after the March harvest and that of the other species after the May harvest. The May harvest was completed on 26 May 1974. The minute *S. tridactylites* showed very sporadic and generally poor germination in all treatments and it was not considered in the neighbourhood analyses.

The position of each of the approximately 13 000 plants harvested during the experiment was described by x , y co-ordinates to the nearest millimetre. The serial number, harvest date, biomass, seed production, and location (in terms of x , y co-ordinates) were then put into computer storage.

Statistical methods

A statistical analysis was designed to expose relationships between individual plant weight and the spatial relationships of each individual with its neighbours. Neighbourhood relationships were described in terms of (i) the size of neighbours, (ii) the distance separating plants from their neighbours, and (iii) the pattern or dispersion of neighbours.

(i) *The size of neighbours.* Size is a convenient although rough index of the impact that any plant might have on its immediate neighbours. Zinke (1962) found that trees influence the spatial pattern of soil mineral nutrients around them in direct proportion to their size. Such a relationship would be particularly strong in low-nutrient soils, such as the sandy soil of Aberffraw where most nutrients are in short supply (Pemadasa & Lovell 1974b). It was hypothesized that the biomass of each plant might be inversely proportional to some weighted accumulated biomass of its neighbours.

(ii) *The distance between neighbours.* The competitive stress between individual plant competitors has been reported to be inversely related to their distance apart in a variety of agronomic and natural situations. Ross & Harper (1972) found the relationship to be inversely proportional to the cube of the separating distance (x^3), implying that interference in *Dactylis glomerata* L. was three-dimensional. In cases where there is no demonstrable interference for light, the relationship between distance and the degree of

interference is probably dependent on the nature of the neighbour's rooting systems and on the soil type, i.e. the relationship might be expected to be different between two fibrous-rooted plants from that between two tap-rooted individuals or a mixture of plants with the two root forms.

Among plants developing from a broadcast sowing there will be an infinite number of unique patterns of neighbour relationships which must be incorporated into any generalized model. To this end, three categories of neighbours were recognized for each plant according to their distance: for each plant neighbours were counted in three concentric annuli around each plant. For *Vulpia* the annuli were: 0-0.5, 0.51-1.0, and 1.01-2.0 cm. Thus, neighbours found at 0.56 and 0.75 cm away from a plant at the centre of this ring were included in the 0.51-1.0 cm ring. The annuli used for the other (smaller) species were 0-0.5, 0.51-1.0, and 1.01-1.5 cm. The sum of the biomasses (b_1, b_2, b_3, b_4) of the neighbours by species in each annulus are three of the terms used in a polynomial expression of the neighbourhood effect.

$$\text{Biomass (any individual)} = \sum_{0-0.5 \text{ cm}} \text{biomass} + \sum_{0.51-1.0 \text{ cm}} \text{biomass} + \sum_{1.01-2.0 \text{ cm}} \text{biomass}$$

(iii) *Pattern effect and angular dispersion.* Plants were smaller when completely surrounded by a given number of neighbours than when the same number of neighbours was aggregated on one side of the annulus. Ross & Harper (1972) found that a plant will make its greatest growth in the direction of least interference. The well-known 'edge effect' in plant populations can be thought of as occurring because the edge plants have 180° of an annulus unoccupied by neighbours.

In the experiments involving pairs of species the angular dispersion of neighbours was estimated by using a transparent plexiglass template etched with three concentric annuli with each of the outer two annuli divided into four equal sectors (see Fig. 2). The centre of the template was superimposed on each plant's position on the map and rotated about its centre so that the minimum number of vacant sectors was obtained: the number of neighbours was then counted in each of the sectors of the second and third annulus. The accumulated biomass of neighbours in the second and third annuli was divided by the proportion of quadrants in which they occurred (1.00, 0.75, 0.5, or 0.25). The growth of *Phleum* and *Vulpia* appeared to be affected only by the pattern of neighbours of other *Phleum* or *Vulpia* plants. Consequently, *Cerastium* and *Mibora* were ignored in assessing the pattern effect on the two larger species. *Cerastium* and *Mibora* were affected by all neighbours regardless of species. No allowance was made for angular dispersion of neighbours in the innermost ring, as it seemed unlikely that the mutual position of neighbours less than 0.5 cm apart was very important.

For the calculation of angular dispersion of neighbours in the five-species mixtures, only *Phleum* and *Vulpia* neighbours were considered as they contributed overwhelmingly to the competitive interaction. Angular dispersion, δ , was calculated as:

$$\delta = \sqrt{x^2 + y^2}$$

$$x = \frac{\sum_{i=1}^n \sin \theta}{n} \quad \text{and} \quad y = \frac{\sum_{i=1}^n \cos \theta}{n}$$

where

This calculation gives values varying from 1.0 to 0 as the neighbours in any annulus vary from tightly clumped to regularly dispersed (Zar 1974). In these experiments the

minimum value of δ was set at 0.25 and the inverse of angular dispersion is such that it varies from a minimum of 0.25 (high aggregation of the plants in an annulus) to 1.0 (low aggregation).

In addition it was necessary to calculate the mean direction from which interference originates in each annulus. It was found empirically that the effect of neighbours decreased progressively as the mean direction of this interference in the two outer annuli came from opposite sectors, adjacent sectors, or the same sector of the surrounding circle. The mean direction is measured as the mean angle, \bar{a} , of the *Phleum* and *Vulpia* neighbours in each annulus by the expression:

$$\text{Tan } \bar{a} = \frac{y}{x}$$

A correction factor was computed for each plant based on these calculations, where z is 1.0, 0.75 or 0.5 when the mean angles of the second and third annuli come from the opposite, adjacent, or the same quadrant, respectively. Of the many expressions incorporating the above points which were constructed, those giving best fit to the data are as follows:

Monocultures and substitutive experiments

(1) The biomass of any *Vulpia* individual is proportional to:

$$-\log \left\{ \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \frac{1}{\delta} \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \frac{1}{\delta} \sum_{i=1}^n \left(\frac{b_1 + b_2 + b_3 + b_4}{5} \right) \right\}$$

(2) The biomass of any *Phleum* or *Cerastium* individual is proportional to:

$$-\log \left\{ 3 \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \frac{3}{\delta} \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \frac{1}{\delta} \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) \right\}$$

Multiple-species mixtures

(3) The biomass of any *Vulpia* individual is proportional to:

$$-\log \left\{ \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \delta \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \delta z \sum_{i=1}^n \left(\frac{b_1 + b_2 + b_3 + b_4}{5} \right) \right\}$$

(4) The biomass of any *Phleum* or *Mibora* individual is proportional to:

$$-\log \left\{ \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \delta \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \delta z \sum_{i=1}^n \left(\frac{b_1 + b_2 + b_3 + b_4}{3} \right) \right\}$$

(5) The biomass of any *Cerastium* individual is proportional to:

$$-\log \left\{ 3 \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + 3\delta \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) + \delta z \sum_{i=1}^n (b_1 + b_2 + b_3 + b_4) \right\}$$

The influence of neighbours decreases with distance and this has been taken into account by dividing the accumulated biomass in the third annulus by 5 in expressions (1) and (3), multiplication of the biomass in the first and second annulus by 3 in expressions (2) and (5) and division of the accumulated biomass by 3 in expression (4).

The following exemplifies calculation of the interference expression for a neighbourhood about a *Vulpia* plant as illustrated in Fig. 2.

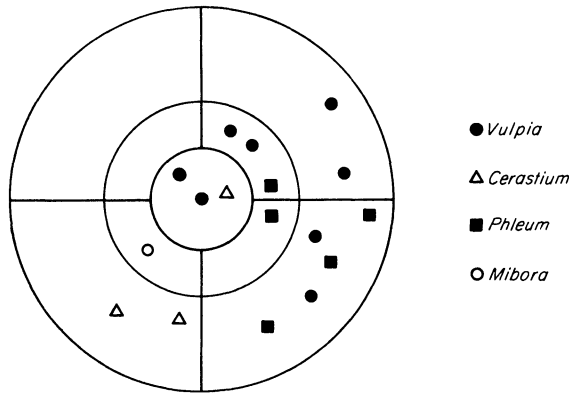


FIG. 2. Neighbourhood about a *Vulpia* plant with annuli and quadrants used in the calculation of the interference expression. See text for explanation.

Neighbours' biomass (g) and angle with respect to centre plant.

Annulus (cm)	<i>Vulpia</i>	(angle)	<i>Phleum</i>	(angle)	<i>Mibora</i>	<i>Cerastium</i>
0-0.50	0.011					0.001
0.51-1.00	0.017	25°	0.0056	82°	0.0011	
	0.0156	46°	0.0037	105°		
1.01-2.0	0.010	55°	0.0030	96°		0.0006
	0.011	81°	0.0020	117°		
	0.018	109°	0.0011	154°		
	0.009	132°				

Annulus (0-0.50): no angular dispersion correction.

Annulus (0.51-1.00):

$$\delta = \sqrt{0.774^2 + 0.37^2} = 0.857$$

$$\text{Sin (mean angle)} = \frac{0.774}{0.857} = 0.903$$

$$\text{Mean angle} = 65^\circ$$

Annulus (1.01-2.0):

$$\delta = \sqrt{-0.246^2 + 0.8313^2} = 0.866$$

$$\text{Sin (mean angle)} = \frac{0.8313}{0.866} = 0.9589$$

$$\text{Mean angle} = 106^\circ$$

The mean angle of both the second and third annuli fall in the same quadrant, therefore $z = 0.5$. Combining the above information into expression (3) for *Vulpia* in a mixture we see that the interference expression of this neighbourhood is as follows:

$$-\log\left\{\frac{\Sigma(0.011 + 0.001) + 0.857\Sigma(0.017 + 0.0156 + 0.0056 + 0.0037 + 0.0011 + 0.01 + 0.011 + 0.018 + 0.009 + 0.003 + 0.002 + 0.0011 + 0.0006 + 0.0005)}{5}\right\}$$

$$= -\log(0.0904)$$

Thus the interference expression = 1.0438.

RESULTS

Interference in the substitutive and multiple-species mixtures

A gross measure of interference within and between species was obtained by comparing the biomass and seed number produced by each species at high density in monoculture (2x) with its performance at low density (1x), and comparing the performance of each species when sown in equal proportions with each of the others. Comparisons were tested using Student's *t* test (Table 1). Both the biomass and seed production of *Phleum* and *Mibora* were significantly depressed when they were grown in mixture with equal numbers of *Vulpia*. The biomass of *Cerastium* was also significantly lower when it was grown in mixture with *Vulpia*. In addition, the biomass per plant of *Vulpia* was depressed by doubling the density of *Vulpia*, but there did not appear to be any comparable intra-specific interference within high-density populations of *Phleum*, *Mibora* or *Cerastium*. Even at the highest density of sowing, individuals of these small species apparently failed to interfere significantly with each other's development.

The competitive ability of each species was measured as the average depression in biomass produced by the presence of each of the other three species (Table 2). The values are based on six trials (3 species \times 2 replicates). While little confidence can be placed on the absolute differences between these values, they allow a ranking of relative competitive

Table 1. *Depression in each species' biomass and seed production at maturity in May in all possible pairings versus performance in low density (approximately twenty plants) monoculture; each test based on composite performance of any pair used alternatively as test and background organism with each other*

(a) Biomass				
Plants affected	Plants having effect			
	<i>Cerastium</i>	<i>Vulpia</i>	<i>Phleum</i>	<i>Mibora</i>
<i>Cerastium</i>	—	+	+	+
<i>Vulpia</i>	—	+	+	+
<i>Phleum</i>	—	+	—	—
<i>Mibora</i>	—	+	+	—

(b) Seed production				
Plants affected	Plants having effect			
	<i>Cerastium</i>	<i>Vulpia</i>	<i>Phleum</i>	<i>Mibora</i>
<i>Vulpia</i>	—	+	+	+
<i>Phleum</i>	—	+	—	—
<i>Mibora</i>	—	+	+	—

Table 2. *Average depression (\bar{x}) in biomass (at maturity in May) due to the presence of each species on the other three species in mixtures of equal proportions and high density monoculture as compared with those species' performance in low density monoculture (with approximately twenty plants)*

Plants affected	Plants having effect			
	<i>Vulpia</i>	<i>Phleum</i>	<i>Mibora</i>	<i>Cerastium</i>
<i>Vulpia</i>	0.74	0.73	0.63	—
<i>Phleum</i>	0.35	0.06	—	—
<i>Mibora</i>	0.50	0.41	0.31	0.32
<i>Cerastium</i>	0.77	0.87	0.32	0.31
\bar{x}	0.59	0.52	0.31	0.11

ability *Vulpia* > *Phleum* > *Mibora* > *Cerastium* > *Saxifraga*. The plant weight of *Saxifraga* was so small that it was not possible to obtain meaningful results for this species from the analyses of its neighbourhood pattern. *Vulpia* appeared to be the most competitive species in the group and this agrees with the findings of Pemadasa & Lovell (1974c). The poor performance of *Cerastium* in competition with the grasses may reflect its relatively small root system.

An analysis of variance was made of the dry matter produced by each species among the squares in each multiple-species flat. The primary purpose of this analysis was to identify those squares in which factors other than interference, such as variation in micro-habitat within the box, might appear. Approximately 30% of the squares (as subsequently identified by a Newmann-Keuls test) were omitted from the modelling of individual plant response in the multiple-species mixtures.

The correlation of individual plant biomass and seed production

There was a significant correlation ($P < 0.05$) between individual plant biomass and seed number for *Vulpia* ($r = 0.96$), *Phleum* ($r = 0.94$) and *Mibora* ($r = 0.79$). The erratic and generally sparse flowering of *Cerastium* in all flats (both in the sown squares and in the background areas) provided insufficient individuals for an accurate relationship to be established between seed number and biomass for this species. Nevertheless, for the grass species the larger the individual the more seed produced, and May biomass alone can be used to predict reproductive output with some precision. The stress produced by the proximity of neighbours was reflected in smaller plants with lower reproductive output. The possibility that density also had an effect on the mean weight of individual seeds was tested (ANOVA) in *Vulpia* by comparing the biomass of the proximal seed for 138 plants with 1–6 seeds produced. There was no significant difference ($P > 0.01$).

The frequency distribution of individual plant weights

Frequency histograms of individual plant weights were constructed for the four species (Fig. 3) based on the combined measurements of all individuals in the multiple-species mixtures at the three harvests. As the shape of a curve can be an artifact of the size and number of class intervals chosen, care was taken that the same number of classes was used in the histograms for each species. Skewness was apparent in the distributions in December and became increasingly pronounced as the plants matured from March to late May, resulting in a highly asymmetric distribution of weight similar to that found in monocultures (Obeid *et al.* 1967). It appears that the interference detected with pooled data (see above) is exerted disproportionately among members of a population rather than being equally shared. The relative degree of skewness among the species' histograms for May corresponds to the order of competitive ability indicated above with *Vulpia*, *Phleum*, *Mibora* and *Cerastium* having, in that order, progressively larger proportions of the cohort in the smaller size classes.

It is difficult to divide continuous data objectively into unbiased size-classes. However, where seed production per plant bears a close correlation with plant biomass (as in *Vulpia*) these discrete data provide a biologically sound basis for such divisions. The results of such a separation of individuals of *Vulpia* in the five-species population is shown in Fig. 4. Even the relatively vigorous *Vulpia* was apparently under considerable stress in these flats as the majority of the individuals produced three or less seeds.

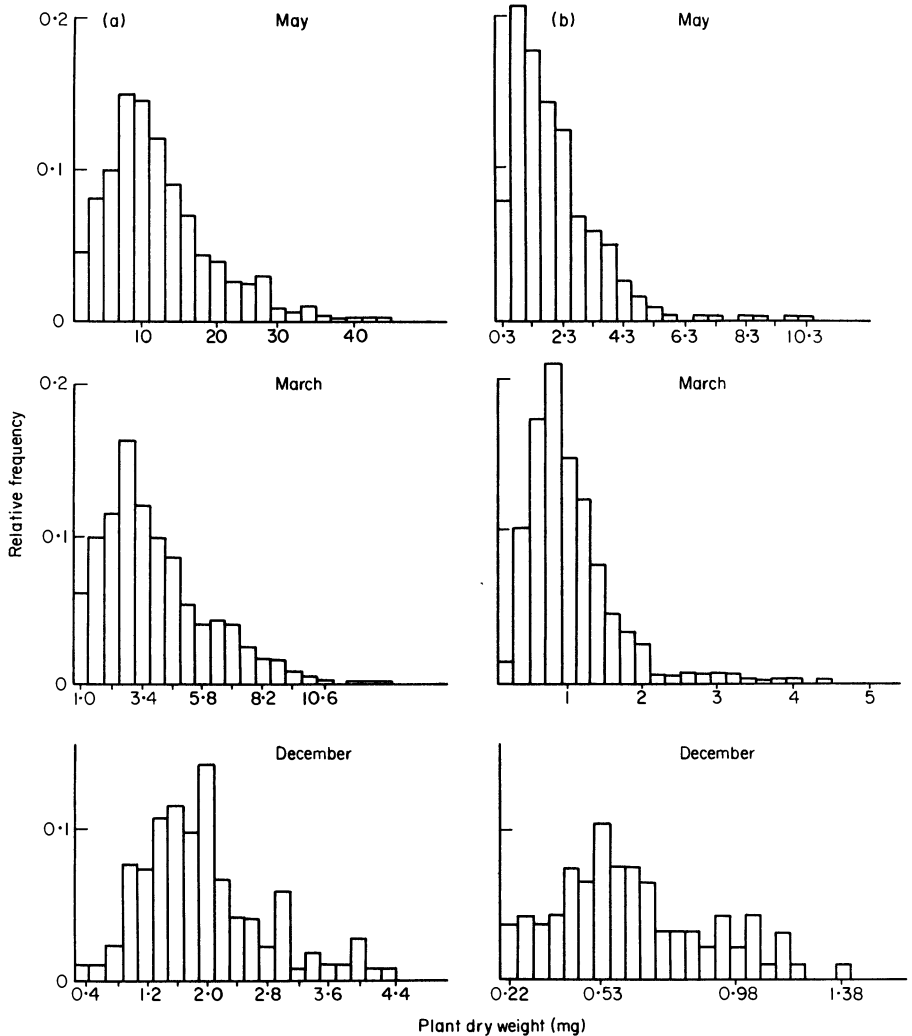


FIG. 3. Frequency histograms of the dry weights of individual plants from the five-species mixture flats in December, March, and May. (a) *Vulpia fasciculata*, (b) *Phleum arenarium*, (c) *Mibora minima*, (d) *Cerastium atrovirens*.

The correlation of individual plant biomass with the proximity and arrangement of neighbours

The results of the linear regressions between individual plant biomass and the derived expression for neighbour effects are shown in Fig. 5. The biomass of *Vulpia* (and its seed production) is significantly correlated with neighbourhood effects as modelled by expression (1). The expression appears to be equally satisfactory for describing the response

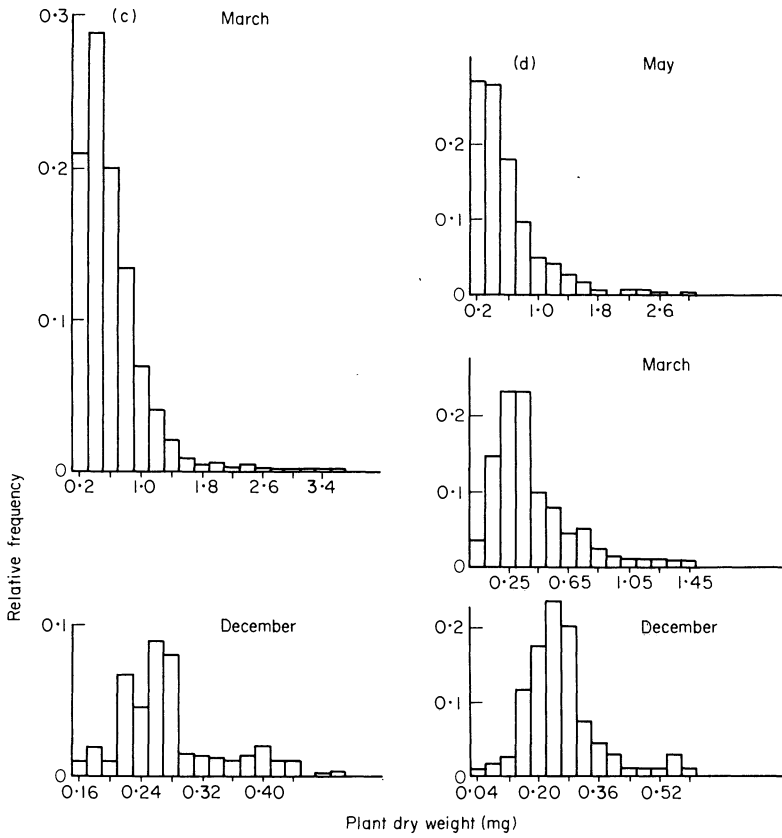


FIG. 3 (c) and (d)

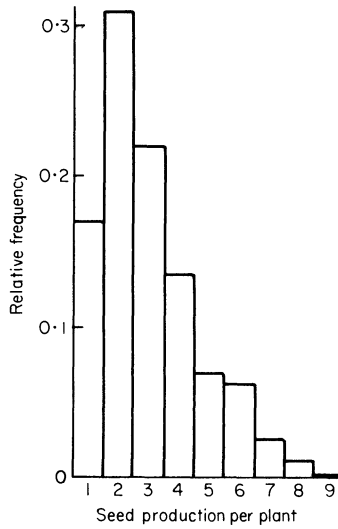


FIG. 4. Frequency histogram of seed production per plant for 700 individuals of *Vulpia fasciculata*.

Interference in dune annuals

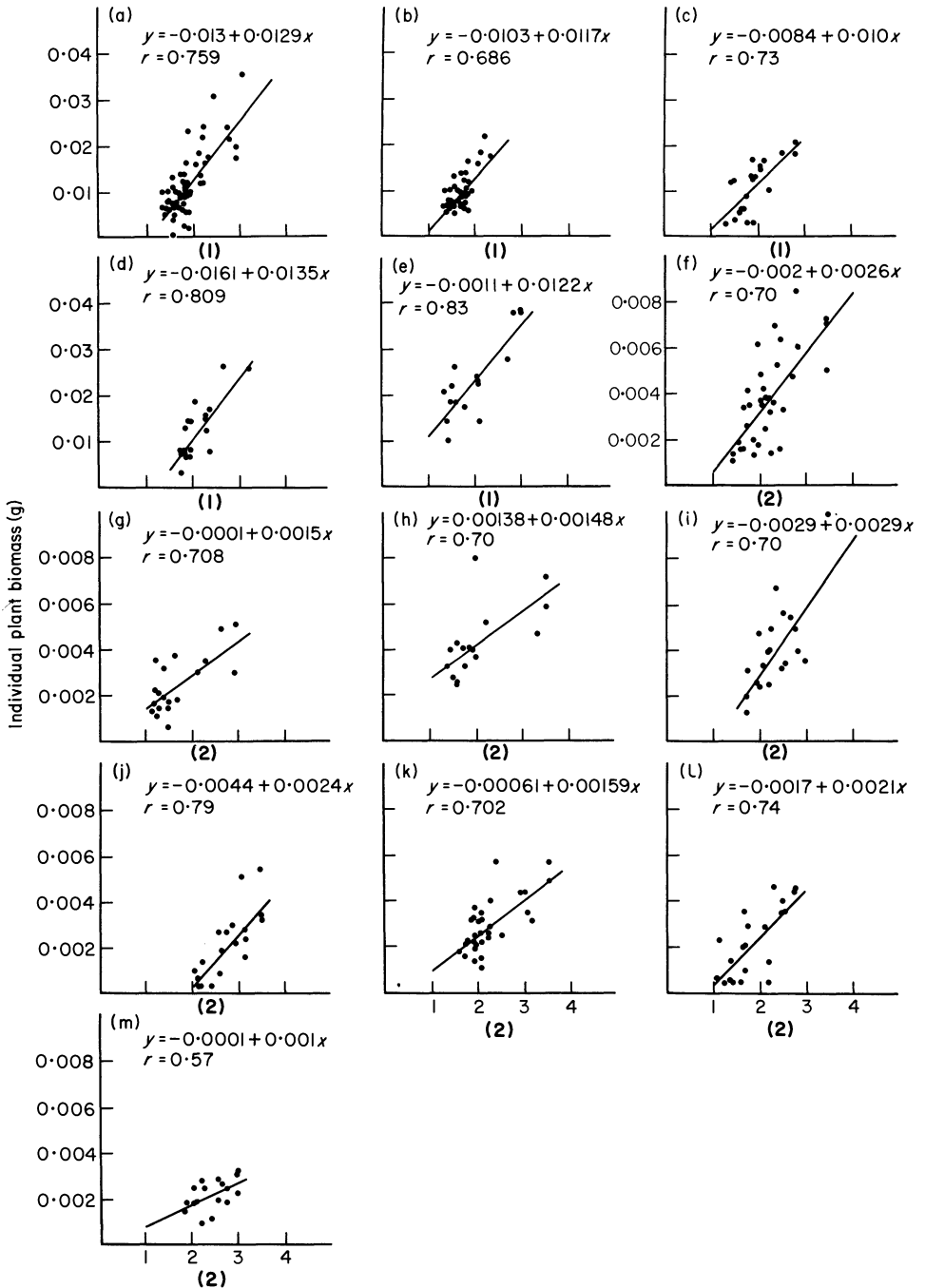


FIG. 5. The relationship between the biomass of individuals for each species of dune annual (in monocultures and two-species mixtures) and a measure of neighbourhood interference: (a) *Vulpia* in pure stands (data for density x and $2x$ pooled), (b) *Vulpia* in pure stands at density $2x$, (c) *Vulpia* in mixtures of *Vulpia* and *Phleum*, (d) *Vulpia* in mixtures of *Vulpia* and *Mibora*, (e) *Vulpia* in mixtures of *Vulpia* and *Cerastium*, (f) *Phleum* in pure stands at density $2x$, (g) *Phleum* in mixtures of *Phleum* and *Vulpia*, (h) *Phleum* in mixtures of *Phleum* and *Mibora*, (i) *Phleum* in mixtures of *Phleum* and *Cerastium*, (j) *Cerastium* in pure stands at density x , (k) *Cerastium* in pure stands at density $2x$, (l) *Cerastium* in mixtures of *Cerastium* and *Phleum*, and (m) *Cerastium* in mixtures of *Cerastium* and *Mibora*. (1), Interference expression (1); (2), interference expression (2).

of *Vulpia* in mixtures with each of the other three species. Pemadasa & Lovell (1974c) have concluded from the study of mixed populations of annuals that interspecific interference has little effect on *Vulpia*. Self-crowding, especially in the populations of high density, resulted in the most severe depression of the dry weight of *Vulpia*. The detailed analyses of individual neighbourhood effects reveals the same order of species aggressiveness (as measured by dry weight or seed output): *Vulpia* > *Phleum* > *Cerastium* = *Mibora* as was obtained by studying population biomass. The biomasses of *Phleum* plants are also significantly correlated with the descriptions of their neighbourhoods modelled by expression (2), and the same expression appears to be satisfactory in explaining neighbourhood effects on *Cerastium* but not on *Mibora*. The analysis of data collected in this experiment failed to provide a statistically significant model to account for plant-to-plant variation in the biomass of *Mibora*. In general, although *Mibora* plants reached their maximum size when growing in comparative isolation, and were much smaller when surrounded by close neighbours, there was erratic and large plant-to-plant variation in intermediate conditions. The failure of the analysis to account for variation between plants of *Mibora* may arise because the demonstration of a correlation requires an adequately wide range of values. The individual biomasses of *Mibora* did not form a continuum of changing values and for this reason a correlation would be harder to detect.

The results of the correlations for the four species in the multiple species mixtures are: *Vulpia*, $y = 0.0141 + 0.0154x$ ($r = 0.657$); *Phleum*, $y = 0.0016 + 0.0019x$ ($r = 0.630$); *Cerastium*, $y = 0.0004 + 0.00083x$ ($r = 0.643$); *Mibora*, $y = 0.000737 + 0.00093x$ ($r = 0.610$). While less of the plant-to-plant variation is accounted for than in the simpler monocultures and pairings, the interference expressions (3, 4) are significantly correlated with individual plant biomass for both of these grasses. The problems of predicting the final biomass of very small plants such as *Cerastium* and *Mibora* are compounded in the multiple-species mixtures.

DISCUSSION

The experimental results suggest that the effects of the presence of neighbours are not diffused through a population but involve rather precise, quantifiable local interactions. The size and the distance and pattern of distribution of neighbours together account for up to 69% of the variation in individual plant weight. The responses to interference were mainly through plasticity: fewer than 5% of the individuals that germinated in October died before reaching maturity. Individual plant weight was inversely proportional to increasing neighbourhood effects (see Fig. 5) and individual fecundity was closely correlated with plant weight.

It has already been shown (Pemadasa & Lovell 1974b) that the annual species of this dune system have a relatively high tolerance to soil moisture stress, and are very sensitive to the addition of nitrogen and phosphate fertilizer. It seems very probable that the neighbour effects in these experiments are produced by demands on nutrients in excess of the ability of the sand dune soil to provide.

White & Harper (1970) pointed out that there is a connection between Yoda's $3/2$ law ($w = Cp^{-3/2}$) and the formula $r = C/p^2$ that related individual plant weight (w) to the distance to nearest neighbour, r (Clark & Evans 1954), where p is the density of plants and C is a constant. They showed that, provided the space available to each plant is such that neighbours interfere with each other's growth and zones of influence overlap, a

series of transformations of Clark and Evans' expression to $r = Cp^{-1/2}$ yielded an equation formally identical to that of Yoda *et al.* or $w = Kp^{-3/2}$, where K is a constant depending on the space available to each plant under competitive conditions, and average plant volume (and in turn its weight) is directly proportional to r^3 .

The constant, K , depends on planting pattern, density, and the genetic properties of the plant. Attainment of the maximum value for K in any population is reflected in changes in w and p , but not in K (White & Harper 1970). We believe that some of the elements of K are those modelled here and that within limits it may be possible to determine K for each species in a mixture. It might be argued that as thinning (i.e. a mortal response) was not common amongst these species, then K and the neighbourhood interference expressions are not related. On the other hand, the parameters incorporated here may prove more useful as they describe not just the mean response, but predict the responses of all individuals in a population.

This model of interference omits a number of other known sources of plant-to-plant variation.

(i) *Timing of emergence.* All germination occurred within two weeks from sowing, but there was considerable variation within and between species in the date of seedling emergence. Early emergence tends to give a seedling a pre-emptive control of resources. This may explain those situations in which a few plants reached large biomass in spite of numerous close neighbours. The effect of the time of seedling emergence could be added to the present model by treating cohorts of individuals that emerge on successive days as separate categories in a way comparable to the procedure that Ross & Harper (1972) applied to neighbouring individuals of grasses.

(ii) *Genetic variability within each species.* The seed used in these experiments was collected as bulk samples from the field and the extent of genetic variability within the populations is known only for *Vulpia fasciculata* (Watkinson 1975). The dune populations of *V. fasciculata* contain many small sub-populations that have been shown to differ genetically in the characteristics that affect their growth rate and reproductive output. The large plants that develop in some of the neighbourhood experiments may represent more vigorous genotypes.

(iii) *Undetected micro-environmental variation.* Although the sand used in the experiments was thoroughly mixed, gradients in nutrient concentration could have existed from point to point in the same flat. More likely is the differential effect of temperature and light intensity due to the position of the flats in the glasshouse. The aberrant plant responses caused by such environmental gradients in the glasshouse are minimized by the 'blocking factor' (Zar 1974) in most analyses of interference. But when it is plant-to-plant rather than plot-to-plot variation that is studied, these errors must be eliminated by careful rotation of the flats through the design, or by limiting each correlation to plants which grew in relatively close proximity to each other (i.e. the same flat or square). The nature of the analyses and controls employed in these experiments goes a long way to minimizing the effects of such micro-environmental variation.

(iv) *Unaccounted spatial effects.* Undoubtedly interference does not exert itself in quantum jumps as modelled by using concentric rings of neighbours. Instead each neighbour must exert an influence proportional to its unique distance from other plants, and the nature of the interference will be complicated by the varying form of the root and shoot systems.

(v) *Interference by neighbours which died before May.* The individuals of *Vulpia*, *Phleum*

and *Cerastium* which died before the May harvest are neglected in this experimental model. As mortality was less than 5%, the error is likely to be small. *Mibora* is a very tiny plant and matures early but nevertheless depresses the yield of its neighbours. Presumably nutrients removed by *Mibora* are not immediately re-available for other plants when it matures and dies. Neighbours may benefit from the early death of neighbours if the environment is limited by light—more is then available for the surviving plants—but this will not be the case where it is nutrients that are limited.

The effects of varying patterns of arrangement of neighbours may not be limited to terrestrial plants. Stimson (1974) found that the accumulated size (sum of diameters) of two neighbouring corals was directly proportional to their distance apart and agreed with Pielou's (1969) suggestion that this indicates interference for a resource. Space competition in etching bivalves may also be related to the spatial pattern of the neighbours (Kleeman 1974). Termite colonies may also be viewed as sessile animals which partition a territory among the resident colonies in a pattern dependent on the resources available (Wood & Lee 1971). In this case the foraging behaviour of termites is analogous to a plant root system foraging out from a central point.

The organisms and environment chosen here are somewhat specialized for modelling interference as a spatial problem; the species are annuals, generally germinate and die synchronously, there is no clonal growth and no known root grafting, there is little or no population of buried viable seeds, and the response of individuals to interference is consistently plastic rather than mortal. The species all have a simple leaf morphology and live in an environment in which they seem scarcely ever to shade each other. The soil is infertile and interference is most likely to be concentrated in mutual demand for nutrients. In contrast, in plant populations in which there are overlapping leaves or in which leaf area index is >1 , correlations between individual plant performance and the pattern of neighbours may be more complicated. Nevertheless, in the case of interference for light among plants with multilayers of leaves, the phenomenon is basically three-dimensional, and interference may be explained in spatial terms where the volume of the canopy of neighbours is substituted for their biomass as the main statistic in a model.

It is quite likely that the four-dimensional biological space (including time) occupied by any plant is subject to considerable fluctuation, dependent on variation in the availability of resources. The dune annuals are capable of demonstrating even greater vigour at higher density than employed in these experiments if the nutrient levels in the sand are artificially raised (Pemadasa & Lovell 1974b).

In spite of its apparent competitive superiority, *Vulpia* has not excluded other small annual species from the natural sand dune community (Pemadasa 1973). A partial explanation may lie in the predation of *Vulpia* by rabbits which seem not to eat the other annuals that have been studied in this experiment (Watkinson 1975). It is easy to envisage situations in which *Vulpia* fails to fill its fundamental niche because of predation, leaving unoccupied niche space for other, weaker species (Harper 1969).

Intra- and interspecific sociability, where it is defined as the relationship of individuals to each other, has not progressed much beyond describing random and non-random (contagious and sometimes regular) patterns for species during the course of succession. While it has been widely observed that contagions progressively break down as succession proceeds (Daubenmire 1968), there is little understanding of the mechanisms or the manner in which this is accomplished. The explanation of such a complicated process must include many agents, but the use of procedures aimed at plotting the spatial pattern, fate

and performance of individuals through time, may demonstrate the factors that are responsible. Thus, there is considerable potential benefit to be derived both in synecology as well as demography from detailed mapping of individuals.

Regardless of any other implications of these experiments, they emphasize the limitation of evaluating plant response to interference as a mean or group effect. Individual plants respond to subtle changes in the proximity and pattern of their neighbours. These effects significantly influence the size of the plant's vegetative body, and more important its fecundity. The crude analysis of density response would seem to be a necessary limitation for ecologists who study mobile animals but an unnecessary handicap in studying interference amongst terrestrial plants, whose neighbours can be defined with precision. Even in the case of mobile animals it is becoming clear that an individual may maintain its position within a flock and reacts to its position relative to neighbours, rather than to the density of the flock; (an example is seen in Murton's account of the feeding behaviour of the woodpigeon (Murton, Isaacson & Westwood 1966)). It would seem prudent for both ecologists and evolutionary biologists to evaluate their experiments at the level of the individual, particularly as biological phenomena demand an evolutionary interpretation and natural selection acts on individuals.

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