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# INTERFERENCE IN POPULATIONS OF SOME DUNE ANNUALS

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## INTRODUCTION

The ecological affinities of *Aira caryophyllea*†, *A. praecox*, *Cerastium atrovirens* and *Vulpia membranacea* growing in the dune system at Aberffraw, Anglesey, have been clearly indicated by the investigations discussed in previous papers (Pemadasa, Greig-Smith & Lovell 1974; Pemadasa & Lovell 1974a,b). Not only is the timing of the life-cycle of all the four annuals generally synchronous, but also the overall distributional pattern of different species within the dune system and their response to various environmental factors such as soil moisture and inorganic nutrients are remarkably similar. Moreover, two of the species, *Aira caryophyllea* and *A. praecox*, are closely related systematically. The available evidence indicates that the majority of the seeds of these annuals are deposited in the immediate vicinity of the parent plants (Pemadasa & Lovell 1974a), and that most of them germinate more or less simultaneously (Pemadasa 1973). Clearly, individuals with such similar ecological requirements are likely to compete for the limited available resources.

In the drier areas of the dune system, where most of these annuals are common, the dominant perennial species is *Festuca rubra*. Pattern analysis showed that the annual species examined are negatively correlated with *F. rubra*, and it was tentatively suggested that some form of interference is operating to exclude them from the places where the representation of *F. rubra* is high (Pemadasa *et al.* 1974).

The low vigour and sparseness of dune vegetation have been attributed to low nutrient status of the sand (Pemadasa & Lovell 1974b; Willis 1963, 1965; Willis & Yemm 1961). The sparseness of perennial plants is thought to favour the continued persistence of the annuals in dune habitats (Willis 1963). If this is the case, perennials should be able to eliminate the annuals when the nutrient deficiencies are made good. Unfortunately, little published information is available regarding the effect of soil fertility on the interference between species.

In the present investigation two experiments were performed, one to examine specifically the reaction of different annuals to their own density and to compare this with their reaction to the density of associated annual species, and the other to determine the influence of *F. rubra* on the performance of the annuals. A further aim of the experiments was to study the effect of contrasting nutrient regimes on the interference between species.

## EXPERIMENTAL METHODS

Seed was collected from natural populations in the dune system at Aberffraw in the spring

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† Nomenclature follows Clapham, Tutin & Warburg (1962).

and stored in paper envelopes under laboratory conditions for about eight months prior to use to reduce dormancy problems (Pemadasa 1973). In January 1972 the seeds were sown in Aberffraw dune sand in plastic pots of 15 cm diameter in a heated glasshouse with supplementary lighting from Philips 400W mercury vapour lamps giving a 16 h day-length. Two nutrient regimes were investigated. The plants grown under the low nutrient regime received only de-ionized water while those subjected to high nutrient regime received a balanced nutrient solution (Hewitt 1966, pp. 434–6) once a week. Usually the pots were watered twice a week.

### *Interference between annuals*

The four annuals were grown at four densities (2, 6, 18 and 54 plants per pot) in pure stands and at three densities (6, 18 and 54 plants per pot) in mixtures of ratio 1:1. The four densities are subsequently referred to as lowest, low, medium and high respectively. In the lowest density regime the two plants were grown at an inter-plant spacing of 8 cm. For the low density regime, the plants were arranged in a hexagonal pattern, at an inter-plant spacing of 4 cm. In mixtures each alternate corner of the hexagon was occupied by an individual of the same species; thus, on either side of each plant there were two plants of the other species. For the medium and high density regimes, the plants were arranged in a square pattern, at an inter-plant spacing respectively of 2 and 1 cm. In mixtures a central plant was immediately surrounded by two plants of its own species and two of the other. The experiment ran for twelve weeks.

### *Influence of* Festuca rubra *on populations of annuals*

In the present investigation the reaction of annuals to already established populations of *F. rubra* was studied. 'Seed' of *F. rubra* was sown four weeks before that of the annuals so that populations of sufficiently established plants of *F. rubra* were obtained. At each of three overall densities (6, 18 and 54 plants per pot, referred to as low, medium and high densities respectively) all the five species were grown in pure stands, and each of the annuals was grown with *F. rubra* in mixtures of ratio 1:1. The planting patterns were similar to those used in the previous experiment. The experiment ran for sixteen weeks so that the annuals had a growing period of twelve weeks.

All treatments were replicated three times and experiments were of randomized block design. Seedling counts were taken for all pots two weeks after sowing. Since the position of seeds in the planting grid was known, it was possible to make separate seedling counts for each species. At the end of the experiments the above-ground parts of plants were harvested for dry weight determination. Records were also made of tiller production in the grasses.

## RESULTS

### *Interference between annuals*

#### *Pure stands*

The data on seedling emergence in pure stands are summarized in Table 1. It is clear that essentially more than 90% of the seeds of all the species produced seedlings. An analysis of variance of the transformed data (angular transformation) indicated no significant effect of either density or soil nutrient regime on seedling emergence, neither was there any significant difference between different species.

Table 2 summarizes the data on seedling establishment. In all the species the proba-

Table 1. *Seedling emergence (expressed as a percentage of the number of seeds sown) in pure stands of annuals under different density and nutrient regimes*

| | Low nutrient regime | | | | High nutrient regime | | | |
|---|---|---|---|---|---|---|---|---|
| Density (plants/pot) | 2 | 6 | 18 | 54 | 2 | 6 | 18 | 54 |
| *Aira caryophyllea* | 100·0 | 100·0 | 96·3 | 98·7 | 100·0 | 100·0 | 98·1 | 97·5 |
| *A. praecox* | 100·0 | 100·0 | 92·6 | 97·5 | 100·0 | 100·0 | 94·5 | 96·3 |
| *Cerastium atrovirens* | 100·0 | 100·0 | 90·8 | 96·3 | 100·0 | 100·0 | 88·8 | 95·6 |
| *Vulpia membranacea* | 100·0 | 100·0 | 100·0 | 100·0 | 100·0 | 100·0 | 100·0 | 100·0 |

Table 2. *Effect of density and nutrient regime on seedling establishment (expressed as a percentage of the number of seedlings emerged) in pure stands of annuals*

| | Low nutrient regime | | | | High nutrient regime | | | |
|---|---|---|---|---|---|---|---|---|
| Density (plants/pot) | 2 | 6 | 18 | 54 | 2 | 6 | 18 | 54 |
| *Aira caryophyllea* | 100·0 | 100·0 | 96·1 | 96·5 | 100·0 | 100·0 | 97·5 | 95·3 |
| *A. praecox* | 100·0 | 100·0 | 92·0 | 93·0 | 100·0 | 100·0 | 94·1 | 94·3 |
| *Cerastium atrovirens* | 100·0 | 100·0 | 87·7 | 91·0 | 100·0 | 100·0 | 89·7 | 93·6 |
| *Vulpia membranacea* | 100·0 | 100·0 | 100·0 | 97·4 | 100·0 | 100·0 | 100·0 | 96·3 |

bility of an emerged seedling surviving to maturity was extremely high (>90% overall). Neither density nor nutrient regime had any significant effect on the seedling establishment of any of the species, nor was there any significant interaction between different treatments.

As can be seen from Fig. 1, the mean plant dry weight was significantly reduced with increasing density ($P<0{\cdot}001$) and decreasing soil fertility ($P<0{\cdot}001$). Moreover, the density × nutrient regime interaction was also highly significant ($P<0{\cdot}001$), indicating that the effect of density is dependent on the nutrient status of the soil. The differing response of different species to soil nutrient level is indicated by the significant interaction between

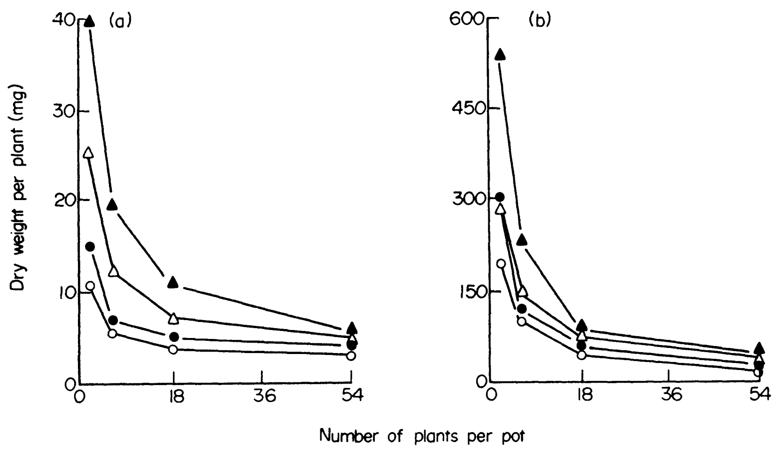



FIG. 1. Effect of density and nutrient regime on dry weight per plant in pure stands of annuals: *Aira caryophyllea* (●), *A. praecox* (○), *Cerastium atrovirens* (△), *Vulpia membranacea* (▲). (a) Low nutrient regime; (b) high nutrient regime; note the difference in scale on the vertical axis in (a) and (b).

species and nutrient regime ($P<0{\cdot}001$). Although the species × density and species × density × nutrient regime interactions were also statistically significant, their effects were relatively less important than the main effects and the other interactions.

The effect of density and of nutrient regime on the tiller production of *Aira caryophyllea*, *A. praecox* and *Vulpia membranacea* was essentially similar to that for dry matter described above (Table 3).

In addition to the quantitative information already presented, the following visual observations were made. Firstly, leaf production was markedly reduced with increasing density and decreasing soil fertility. Secondly, leaf senescence was hastened at medium and high densities under both nutrient regimes. In *Cerastium atrovirens* branch production was markedly improved by the nutrient enrichment of dune sand, particularly at the lowest and low densities.

*Mixed stands*

Seedling emergence in mixed stands was essentially similar to that in the pure stands described above, and so no detailed data are included. In all the species more than 90% of the seeds produced seedlings irrespective of the density, nutrient regime, and associated species.

Table 3. *Effect of density and nutrient regime on the mean number of tillers per plant in pure stands of the three grasses*

| | Low nutrient regime | | | | High nutrient regime | | | |
|---|---|---|---|---|---|---|---|---|
| Density (plants/pot) | 2 | 6 | 18 | 54 | 2 | 6 | 18 | 54 |
| *Aira caryophyllea* | 7·2 | 6·1 | 3·8 | 2·0 | 28·1 | 19·2 | 12·3 | 5·3 |
| *A. praecox* | 6·9 | 4·6 | 3·1 | 2·1 | 24·5 | 17·9 | 12·9 | 7·2 |
| *Vulpia membranacea* | 3·5 | 2·4 | 1·3 | 1·1 | 18·2 | 11·2 | 7·5 | 3·2 |

As seen from Fig. 2, seedling establishment in all the species except *Vulpia membranacea* was considerably affected by both the density and the associated species. In *V. membranacea* the percentage seedling establishment was extremely high (95% overall), and was not appreciably affected by any of the experimental treatments. On the other hand, in the other three species the probability of an emerged seedling surviving to maturity decreased significantly with increasing overall density ($P<0{\cdot}001$), and this was, to a certain extent, aggravated under the high nutrient regime. The establishment of all the other species was severely hampered by *V. membranacea* especially at medium and high densities under the high nutrient regime. The suppression by *V. membranacea* was highest in *Aira praecox* while the other two species were somewhat less affected. Both *A. caryophyllea* and *A. praecox* were more or less equally suppressed by *Cerastium atrovirens* which failed to influence *Vulpia membranacea.* There was hardly any effect of *Aira caryophyllea* and *A. praecox* on establishment of each other or on the establishment of *Cerastium atrovirens* and *Vulpia membranacea.* The effect of increasing overall density was to aggravate the influence of the associated species as shown by the significant density × associated species interaction ($P<0{\cdot}001$).

The effects of various treatments on tiller production by *Aira caryophyllea*, *A. praecox* and *Vulpia membranacea* are illustrated in Fig. 3. There was a significant reduction in both the number of tillers per plant and the size of tillers in all the species with increasing density ($P<0{\cdot}001$) and decreasing soil fertility ($P<0{\cdot}001$). Again the response to the associated species differed. Tiller production in the two *Aira* species was severely

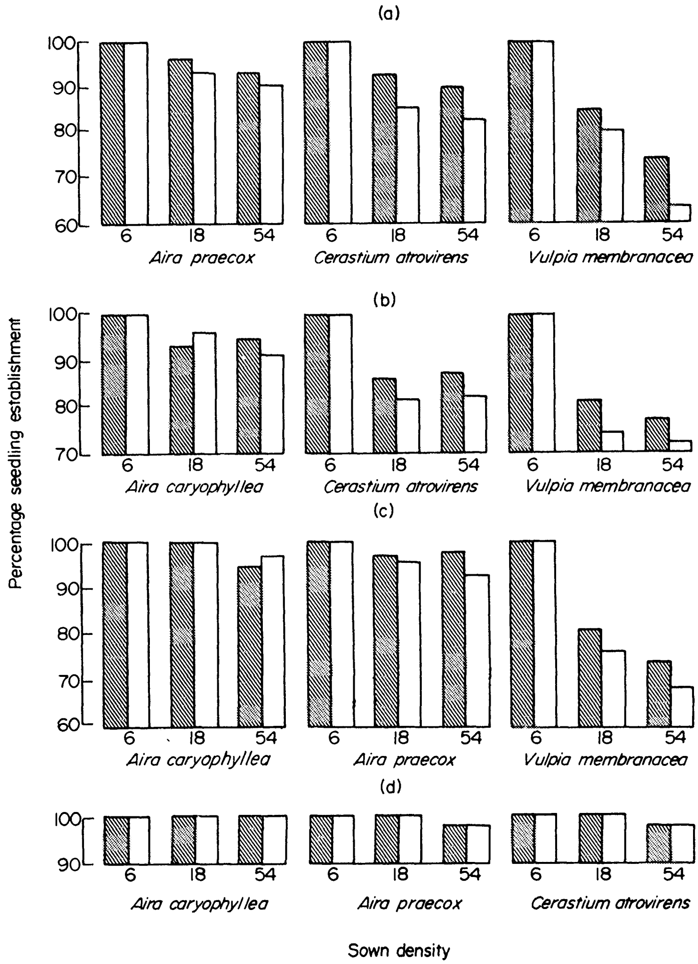



FIG. 2. Effect of density, nutrient regime, and of associated species (given under each set of six histograms) on the seedling establishment of (*a*) *Aira caryophyllea*, (b) *A. praecox*, (c) *Cerastium atrovirens*, and (d) *Vulpia membranacea* (expressed as a percentage of the number of seedlings emerged) in mixed stands of annuals. The figures on the horizontal axis give the number of seeds sown per pot. Open columns represent the high nutrient regime and stippled columns the low nutrient regime.

restricted by both *Cerastium atrovirens* and *Vulpia membranacea*; however, the presence of *V. membranacea* led to the more marked detrimental effect. These effects were further aggravated under the high nutrient regime.

*Replacement series*

The relationship between the total dry matter production, in both pure and mixed stands under the different nutrient regimes, and the proportion of seeds sown at each density is shown in Fig. 4 in a set of replacement series graphs. A detailed account of the rationale for this method of data presentation is given by de Wit (1960). It was apparent that the performance of the two *Aira* species under different density and nutrient regimes was generally similar (Fig. 4a). The curves for these two species were markedly concave in the replacement series graphs showing their response to *Cerastium atrovirens* (Fig.

4b, 4d) and *Vulpia membranacea* (Fig. 4c, 4e). However, there was a general tendency for this concavity to become more pronounced with increasing overall density and soil fertility. The degree of concavity was somewhat higher in the presence of *V. membranacea.* The curve for *Cerastium atrovirens* was generally convex in the presence of *Aira caryophyllea* (Fig. 4b) and *A. praecox* (Fig. 4d), but was markedly concave in the presence of *Vulpia membranacea* (Fig. 4f). This concavity also became relatively more pronounced

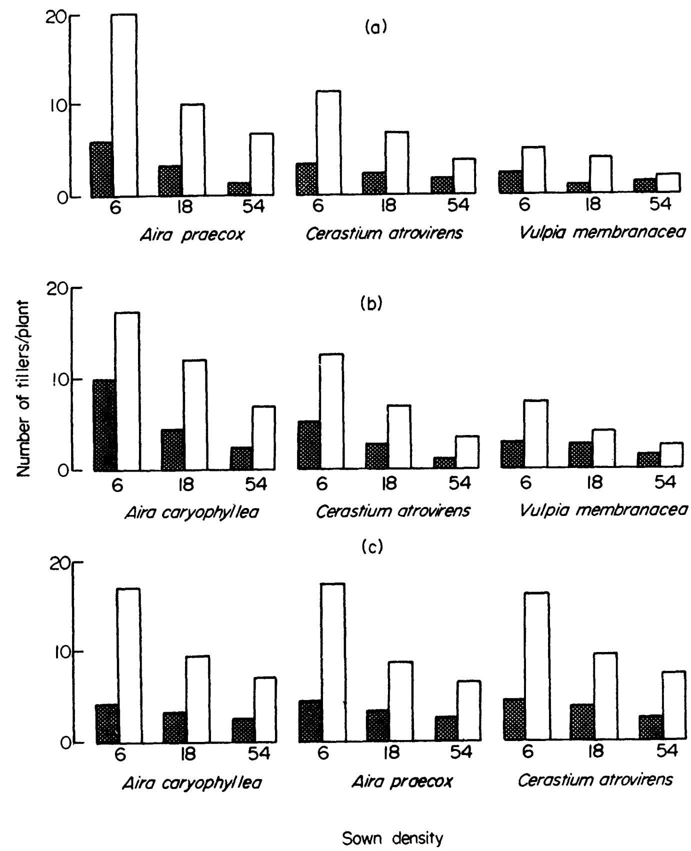



FIG. 3. Effect of density, nutrient regime, and of associated species (given under each set of six histograms) on the number of tillers per plant of (a) *Aira caryophyllea*, (b) *A. praecox*, and (c) *Vulpia membranacea* in mixed stands of annuals. The figures on the horizontal axis give the number of seeds sown per pot. Open columns represent the high nutrient regime and the stippled columns the low nutrient regime.

with increasing density and soil fertility. The curve for *V. membranacea* was generally convex in the presence of any of the other three species, and the degree of convexity intensified with increasing density and soil fertility.

Comparison of the observed total dry matter production in mixtures with the expected values, calculated on the assumption that the two species are independent or show no interference, revealed several important points. In mixtures containing all the possible pairs of the three species *Aira caryophyllea, A. praecox* and *Cerastium atrovirens*, the observed dry weights did not differ significantly from the expected values. On the other hand, the total dry matter production in mixtures containing *Vulpia membranacea* and

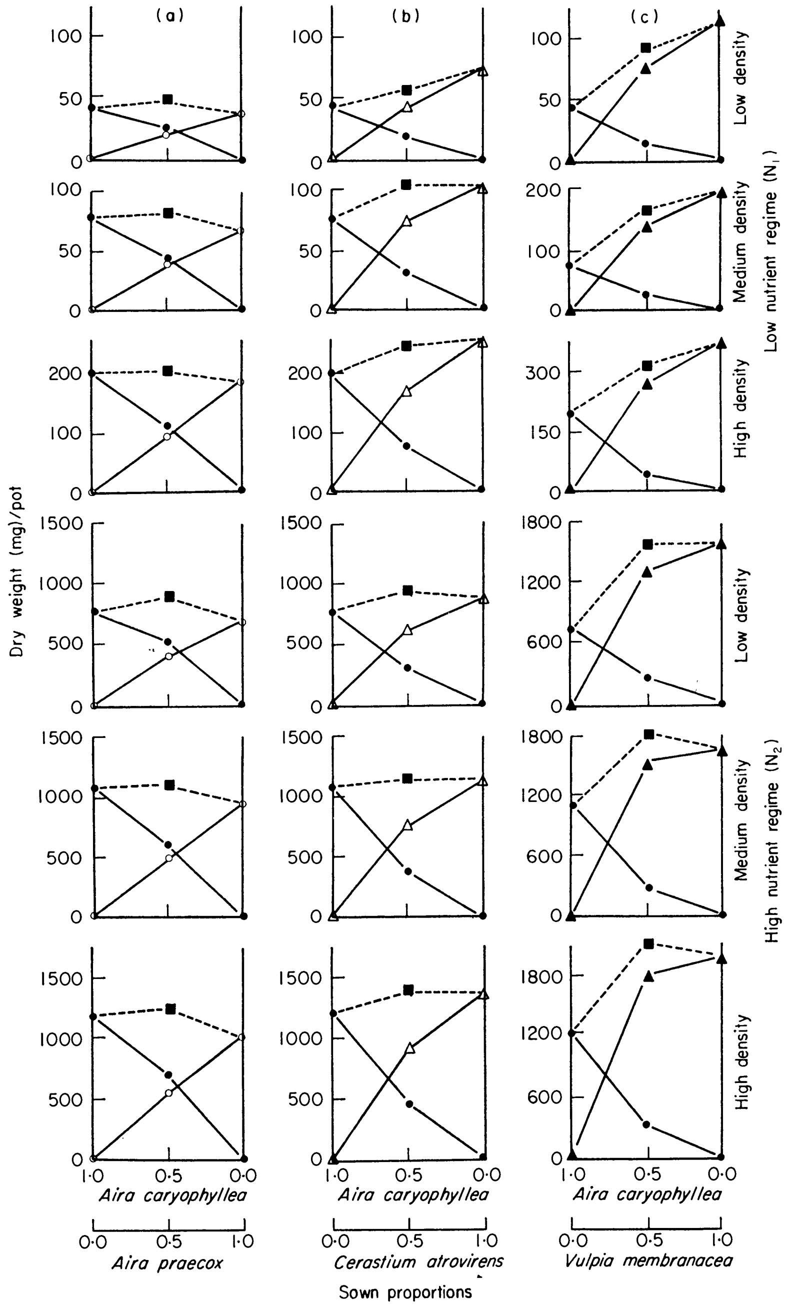
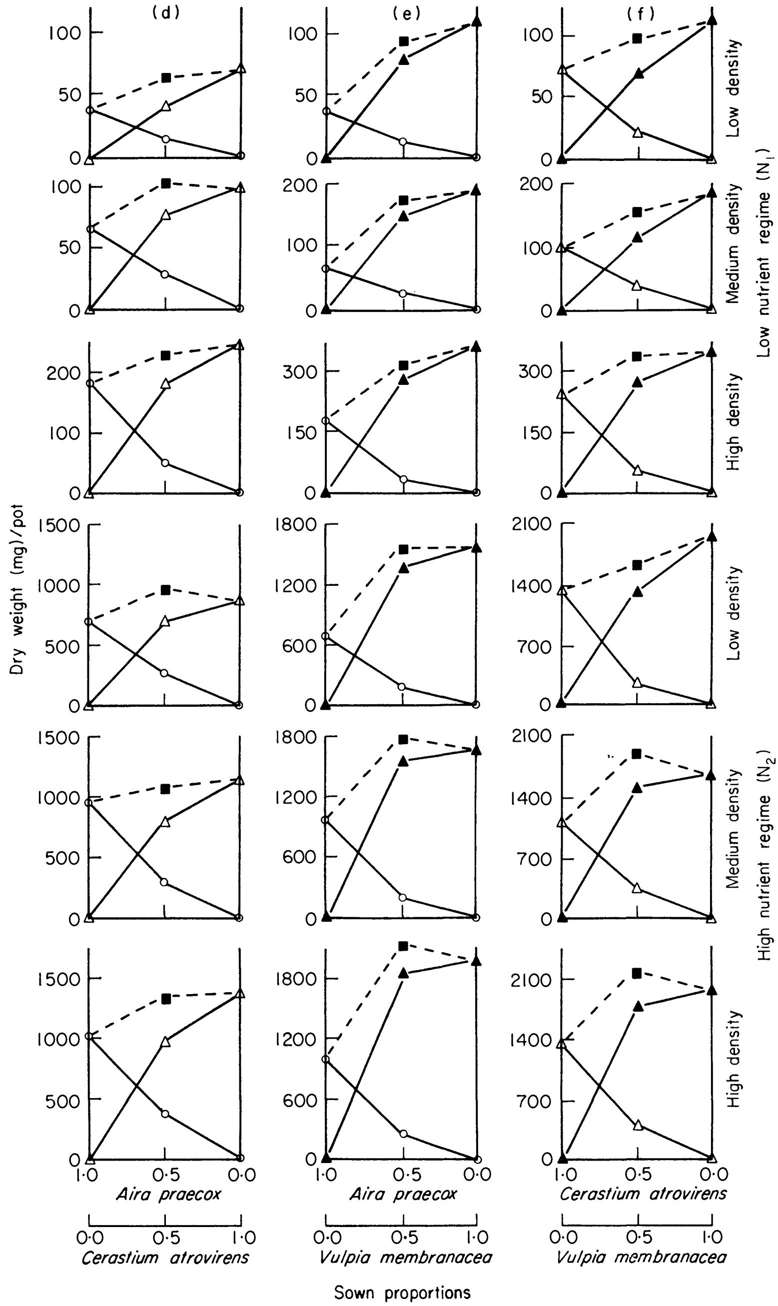



FIG. 4. Replacement series graphs showing the interrelationships between the dry matter production of annuals in pure and mixed stands at various density and low and high nutrient regimes. (a) *Aira caryophyllea: A. praecox*, (b) *A. caryophyllea: Cerastium atrovirens*, (c) *Aira caryophyllea: Vulpia membranacea*, (d) *Aira praecox: Cerastium atrovirens*, (e) *Aira praecox: Vulpia membranacea*, (f) *Cerastium atrovirens: Vulpia membranacea*.


(d)
(e)
(f)
Dry weight (mg)/pot
Low density
Medium density
High density
Low nutrient regime ($N_1$)
High nutrient regime ($N_2$)
1·0 0·5 0·0
Aira praecox
Cerastium atrovirens
0·0 0·5 1·0
Cerastium atrovirens
Vulpia membranacea
Sown proportions

each of the other three species was generally higher than the expected values. This increase in dry matter production in mixtures was owing mainly to the improved growth of *V. membranacea*.

### *Influence of* Festuca rubra *on populations of annuals*

Since seedling emergence in the annuals was essentially similar to that observed in the previous experiment, detailed data are not presented. In all the species seedling emergence was more than 90% regardless of the density, soil fertility and the presence of established plants of *F. rubra*.

As can be seen from Fig. 5, the probability of an emerged seedling surviving to maturity was considerably reduced by the presence of *F. rubra*, and this reduction was particularly significant in the nutrient-enriched dune sand at medium and high densities, and was slightly less pronounced in *Vulpia membranacea* than in the other three species.

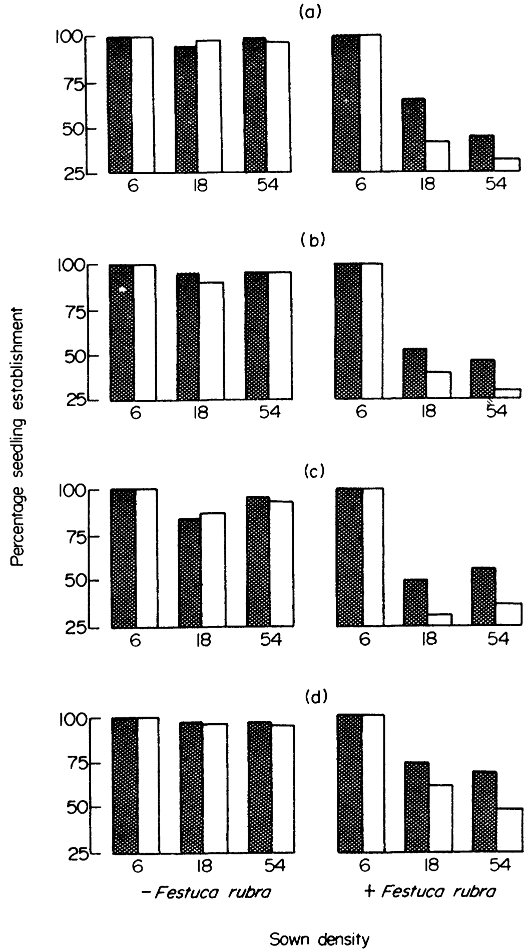



FIG. 5. Effect of density, nutrient regime, and of *Festuca rubra* on seedling establishment (expressed as a percentage of the number of seedlings emerged) of (a) *Aira caryophyllea*, (b) *A. praecox*, (c) *Cerastium atrovirens*, and (d) *Vulpia membranacea*. The figures on the horizontal axis give the number of seeds sown per pot. The open columns represent the high nutrient regime and stippled columns the low nutrient regime.

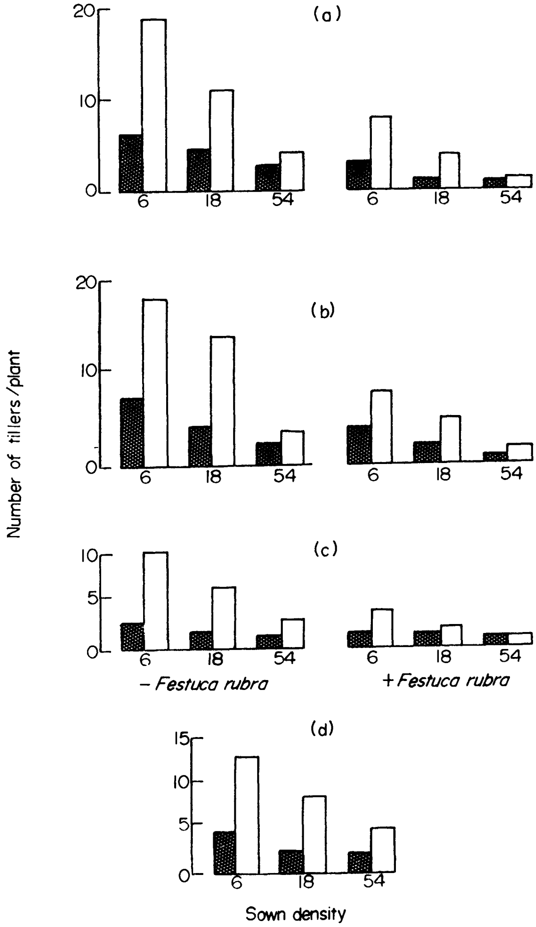



FIG. 6. Effect of density, nutrient regime, and of *Festuca rubra* on the number of tillers per plant in (a) *Aira caryophyllea*, (b) *A. praecox* and (c) *Vulpia membranacea*. Open columns represent the high nutrient regime and stippled columns the low nutrient regime. The tiller production in pure stands of *Festuca rubra* (d) is also illustrated.

Tiller production in *Aira caryophyllea*, *A. praecox* and *Vulpia membranacea* was significantly reduced with increasing overall density ($P<0{\cdot}001$) and decreasing soil fertility ($P<0{\cdot}001$), and, most interestingly, by the presence of *Festuca rubra* ($P<0{\cdot}001$). The nutrient enrichment of dune sand resulted in an increase in the effect of *F. rubra* (Fig. 6).

The replacement series graphs (Fig. 7) clearly illustrate the relationship between dry matter production of different species in pure and mixed stands under the two nutrient regimes and the proportion of seeds sown at each density. In general, the curves for all the annuals were concave and those for *F. rubra* were markedly convex. The degree of concavity became increasingly pronounced with increasing overall density under the high nutrient regime. On the other hand, the convexity of curves for *F. rubra* was more or less similar under different nutrient and density regimes and in the presence of different companion species.

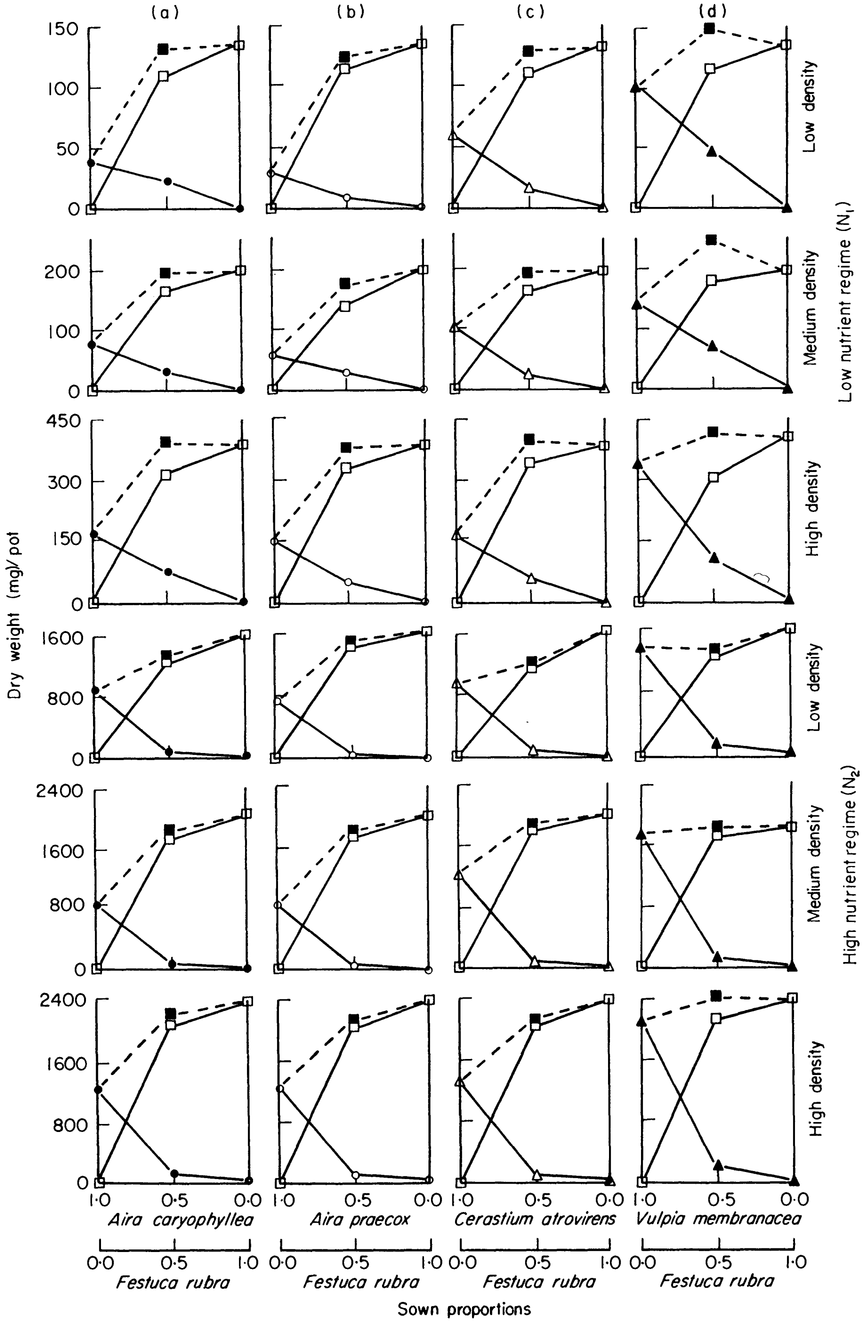



FIG. 7. Replacement series graphs showing the interrelationships between the dry matter production of annuals in pure stands and mixtures with *Festuca rubra* at various density and nutrient regimes. (a) *Aira caryophyllea*: *Festuca rubra*, (b) *Aira praecox*: *Festuca rubra*, (c) *Cerastium atrovirens*: *Festuca rubra*, (d) *Vulpia membranacea*: *Festuca rubra*.

The observed total dry matter production in mixtures was generally higher than the expected values irrespective of the companion pair of species. This increase was primarily owing to better growth of *F. rubra*.

The performance of *F. rubra* in pure stands also merits some consideration. Both the emergence and establishment of seedlings were extremely high (90% overall), and neither was significantly affected by any of the experimental treatments. There was a marked reduction in the size and vigour of plants with decreasing soil fertility and increasing density. The nutrient enrichment of dune sand resulted in a considerable increase of tiller production (Fig. 6). On the other hand, there was a significant decline in the degree of tillering with increasing density, and this was especially pronounced under the high nutrient regime. Thus the response of *F. rubra* to an increase in its own density and to soil fertility observed during this experiment was basically comparable to that of the annuals.

## DISCUSSION

The size of plant populations may be regulated either by a mortal response, where the chance of survival of individuals is reduced, or a plastic response, where the reproductive capacity of individuals is reduced, to increasing density (Harper 1960, 1961; Harper & Gajic 1961). There are two ways in which the mortal response can be expressed; the biological mortality, where the individuals are removed from populations owing to the failure of either seedling emergence or seedling establishment, and the genetic mortality, where the individuals are able to survive but fail to produce effective propagules. Both the mortal and plastic responses may be modified by both the physical and biological components of the environment.

Seedling emergence of all the species examined was extremely high (>90%) in both pure and mixed populations irrespective of the density and nutrient regimes, and this suggests that differential seedling emergence is unlikely to confer any important regulating properties on their populations.

In pure populations more than 90% of the seedlings of all the species were able to survive regardless of the density and nutrient regimes. However, they all showed a remarkable plastic response to increasing density. This strongly suggests that under the experimental conditions used in the present study, regulation in pure populations operated primarily through a plastic response to density as opposed to a mortal response involving changes in surviving rates. Similar predominantly plastic responses to density have been observed by Harper & Gajic (1961) in *Agrostemma githago*, and Marshall & Jain (1969) in *Avena barbata* and *A. fatua*. Unfortunately, since no information is available regarding the reproductive capacity of individuals at different densities, it is not possible to infer whether the species under study show any genetic mortality in response to increasing density.

In mixed stands the performance of different species was clearly different. Both the seedling establishment and dry matter production of *Aira caryophyllea* and *A. praecox* were generally similar in pure and mixed stands, suggesting that their reaction to intra-specific and inter-specific interference did not differ significantly. However, they both were markedly suppressed by *Cerastium atrovirens*. The results of pattern analysis also indicated that the representation of *Aira praecox* is relatively low in places where the density of *Cerastium atrovirens* is high (Pemadasa *et al.* 1974). At the other extreme was *Vulpia membranacea*, which was remarkably effective in suppressing the other three annuals, and was hardly affected by any of them. Obviously it had a greater 'competitive advantage' over all the others. When *V. membranacea* was grown with each of the other three annuals, the observed total dry matter production was markedly higher than the expected, and this was primarily due to improved growth of *V. membranacea.* Clearly it suffered more in pure stands than in mixtures.

In the presence of *V. membranacea* the growth of *Aira caryophyllea*, *A. praecox* and *Cerastium atrovirens* was no better under the high nutrient regime than under the low nutrient regime. Apparently, these three species failed to obtain their share of nutrients. The reduction in their growth caused by *Vulpia membranacea* was proportionately higher in nutrient-enriched sand, suggesting that the 'competitive advantage' of *V. membranacea* is greater when the soil fertility is high.

The experimental results clearly indicate that a vigorously growing dense population of established plants of *Festuca rubra* is quite effective in reducing the chance of survival of the annuals examined. The pattern analysis also showed that these annuals are relatively rare in places where the density of *F. rubra* is high (Pemadasa *et al.* 1974).

The vegetative growth of all the four annuals was greatly reduced in the presence of *F. rubra*, and this reduction was intensified with increasing density and soil fertility. Their performance was no better under the high nutrient regime than under the low nutrient regime in the presence of *F. rubra.* Clearly, the improved vigour of the perennial in response to the nutrient enrichment of dune sand has greatly increased its 'competitive power'. It seems not unreasonable, therefore, to suppose that if the nutrient level of dune sand is raised *F. rubra* could suppress these annuals under natural conditions. In fact, Willis (1963) found in Braunton Burrows that the increased dominance of this perennial in response to the addition of nutrients resulted in severe suppression and sometimes even complete elimination of several annuals, e.g. *Aira praecox*, *Arenaria serpyllifolia* and *Phleum arenarium*.

From the preceding discussion it is clear that the established plants of *Festuca rubra*, and probably most other perennials too, have greater 'competitive advantage' over the annuals. Thus, for continued existence these annuals require habitats where the 'competitive pressure' of perennials is low. This may be one of the reasons why these species are not very abundant in closed communities. It should, however, be emphasized that the situation in the field is in all likelihood far more complicated than indicated by the present observations.

## SUMMARY

The effects of density and soil nutrient regime on interference between individuals in pure and mixed populations of four dune annuals, *Aira caryophyllea*, *A. praecox*, *Cerastium atrovirens* and *Vulpia membranacea*, and the perennial *Festuca rubra* were studied in two pot experiments. The reactions of all the species to increasing density took the form of increasing mortality and plastic reduction in the size of individuals. In mixed populations of annuals, *Vulpia membranacea* suppressed all the other species while *Cerastium atrovirens* suppressed the two *Aira* species which reacted to the presence of each other much as they reacted to their own. The effect of *Festuca rubra* and high soil fertility was to intensify the degree of both mortality and plasticity of annuals. The results are discussed with reference to the regulation of populations of these species in the field.

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