

# THE DEMOGRAPHY OF A SAND DUNE ANNUAL: *VULPIA FASCICULATA*

## I. THE NATURAL REGULATION OF POPULATIONS

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### SUMMARY

(1) The population dynamics of the winter annual grass *Vulpia fasciculata* on two dune systems in North Wales is described. Permanent quadrats were mapped frequently to obtain data on the fates of seedlings and the reproductive performance of each individual. The role of density in the regulation of populations was assessed by the manipulation of natural densities in the field.

(2) The behaviour of populations of *V. fasciculata* on the fixed dunes of the two dune systems studied was remarkably similar. The probability of a seedling surviving to maturity was high, but the potential seed rain on some plots was considerably reduced by rabbit grazing at or just before flowering. There was a peak of mortality during inflorescence development. The causes of mortality during the life cycle were various.

(3) There was no evidence for any density-dependent mortality, but above a density of 100 flowering plants per 0.25 m<sup>2</sup> it was found that there was a significant negatively density-dependent relationship between the number of spikelets per plant and the density of flowering plants. A simple model which describes the population dynamics of *V. fasciculata* in terms of the density-dependent regulation of spikelet number and the density-independent mortality is presented.

(4) The reasons for the stabilization of the density of *V. fasciculata* at different levels in different areas on the two dune systems and the reasons for the annual fluctuations in population density within these areas are discussed.

### INTRODUCTION

There are four parameters which govern the population size of any species of plant or animal, and these are the numbers of births, deaths, immigrants and emigrants. Any attempt to understand the population dynamics of a species must, therefore, involve measuring, describing and explaining changes in these four parameters throughout the life cycle of the species. Those populations that persist are sooner or later subject to density-dependent regulation, and several authors (e.g. Harper & White 1971; Sagar 1970) have pointed to the phases of the life cycle when the regulation of numbers in a plant population can occur and to the agents involved in regulation. There have also been numerous studies on various aspects of the population dynamics of particular plant species during specific parts of the life cycle in the field and under controlled experimental conditions, but there has been little attempt to synthesize the whole from the parts or

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to make complete studies on the population dynamics of single species in the field.

Until recently almost all our knowledge of the population dynamics of annual plants has come from species of agronomic interest. Species that are rare or locally abundant and that are restricted to non-agricultural ecosystems have received little attention. Fortunately, two detailed studies have recently been made on the population dynamics of non-weedy annuals: by Sharitz & McCormick (1973) on *Minuartia uniflora* (Walt.) Mattf. and *Sedum smallii* (Britt.) Ahles, and by Symonides (1974a, b) on *Spergula vernalis* Willd. *Minuartia uniflora* and *Sedum smallii* have high reproductive potentials, and in populations of both species there was extremely high mortality during the seed and seedling establishment phases of the life cycle. The individuals that survived past seedling establishment had relatively high expectations of completing their life cycle. From a series of experimental studies in the field and under controlled environmental conditions, Sharitz & McCormick (1973) concluded that varying soil depths, soil moisture and interspecific competition were the primary factors controlling the density and distribution of both species on granite outcrops in Georgia, U.S.A. Symonides (1974a) found that there was fairly intensive auto-regulation of the number of flowering individuals in populations of *Spergula vernalis* in a variety of dune habitats in Poland: mortality rather than plasticity was important in this regulation. There were, however, distinct differences in population behaviour in different habitats on the same dune system. The population dynamics of a species in different habitats, and in similar habitats in different areas, are two aspects of population biology that have received little attention.

The present paper forms part of a study on the population biology of the winter annual grass *Vulpia fasciculata* (Forskål) Samp. (previously known as *V. membranacea* auct.; see Stace & Cotton (1976)), and is concerned with the ways in which the population size of *V. fasciculata* is determined on the fixed dunes of two dune systems in North Wales. Permanent quadrats have been mapped in detail to obtain data on the fate and reproductive performance of individual plants, and seedling densities in the field have been manipulated to various levels to determine the role of plant density in the regulation of populations.

The choice of material suitable for an investigation of this type is of paramount importance. *V. fasciculata* possesses several characteristics which make it especially suitable for a study of population dynamics. The individuals are discrete, they have a short life cycle, the development of individuals is roughly synchronous and the seeds are large and conspicuous. Furthermore, on the two dune systems where the studies were made the species was widespread, the density of individuals was high, their distribution (on the scale studied) was relatively uniform and individual plants did not vary greatly in size.

The life cycle of *V. fasciculata* is characterized by autumn germination and late spring flowering. Seed dispersal occurs during early summer, and the seeds remain dormant until the autumn when germination occurs.

## THE STUDY AREAS

Studies were made on two similar groups of low fixed dunes 8 km apart in Anglesey, U.K., at Aberffraw (National Grid reference SH 357682) and at Newborough Warren (National Grid reference SH 424640). At both sites the low fixed dunes supported an open community of plants, with a range of small annual and prostrate perennial species.

These included, in addition to *Vulpia fasciculata*, *Cerastium atrovirens* Bab., *Lotus corniculatus* L., *Mibora minima* (L.) Desv., *Phleum arenarium* L., *Sedum acre* L. and *Thymus drucei* Ronn. The populations of *Vulpia fasciculata* at Aberffraw and Newborough Warren have been in existence since the nineteenth century, and have been at relatively high densities for at least 10 years on the fixed dunes chosen for this study.

The fixed dunes studied at Aberffraw form a network of small hummocks in a slack about 400 m from the sea, between two ridges of yellow dunes. *V. fasciculata* formed large uniform populations over extensive areas of these dunes. At Newborough Warren the study area was sited between two wet slacks about 1600 m from the sea. The vegetation cover was sparser than at Aberffraw, and the distribution of species, including *V. fasciculata*, was less uniform.

Newborough Warren is a National Nature Reserve with restricted access to the public. Aberffraw is common land and a popular holiday area. Rabbits were found in both areas, although they were far more numerous on Newborough Warren. More detailed descriptions of Newborough Warren and Aberffraw have been given by Ranwell (1955) and Pemadasa (1973) respectively.

## MATERIALS AND METHODS

A series of permanent plots was chosen subjectively, to include a range of the population densities at which *Vulpia fasciculata* is commonly found on the fixed dunes. The chosen sites included a variety of aspects and vegetation types. Six 40 × 40 cm plots were sited at Aberffraw (A–F) and six at Newborough (1–6). Each plot was marked by two 30 × 0.5 cm metal rods sunk into the ground, on to which an aluminium frame 50 × 50 cm could be fitted when observations were made. A mapping table locked into holes in the frame, so that four areas of 20 × 20 cm could be mapped in each plot.

On each sampling date the position of every plant of *V. fasciculata* in each 20 × 20 cm sub-plot was recorded on a cellophane sheet by direct overhead mapping. Records were also made for each plant of the date of germination and of death, of the number of spikelets, and of whether or not the developing inflorescence or the flowering inflorescence had been eaten. Observations were started at the end of August 1973 and made at intervals until the end of flowering in July 1974. The most frequent mapping, on average every fortnight, was made during the period of germination from September to December.

In order to assess the relationship between the number of spikelets and the number of seeds per plant, 350 individual plants with maturing seeds were collected in July 1974 from around the permanently mapped plots at Aberffraw and Newborough and 120 from around a rabbit burrow at Aberffraw where larger plants predominated. The numbers of spikelets and seeds were counted for each plant.

In order to investigate the effect of plant density on mortality and fecundity, thirty-seven permanent plots were set up in five areas on various parts of the fixed dunes at Aberffraw on 7 September 1973. Each plot was marked by two 30 × 0.5 cm metal rods sunk into the ground. The seedlings of *V. fasciculata* on twelve 50 × 50 cm plots were thinned in November and January, to give a range of approximately uniform seedling densities of 100, 200 and 400 plants per 0.25 m<sup>2</sup>. Seed collected from the fixed dunes in July was added to a further twenty-five 30 × 30 cm plots, to give seedling densities of approximately 800, 1600, 3200, 4800, 6400, and 8000 plants per 0.25 m<sup>2</sup>. On 14 July

1974 the numbers of flowering plants and the numbers of spikelets per flowering plant were counted within the central area (40 × 40 cm or 20 × 20 cm) of each plot.

## RESULTS

### Germination

In 1973 germination started in the last week of August, and continued until February (Fig. 1). Germination was, on average, slightly later at Newborough than at Aberffraw,

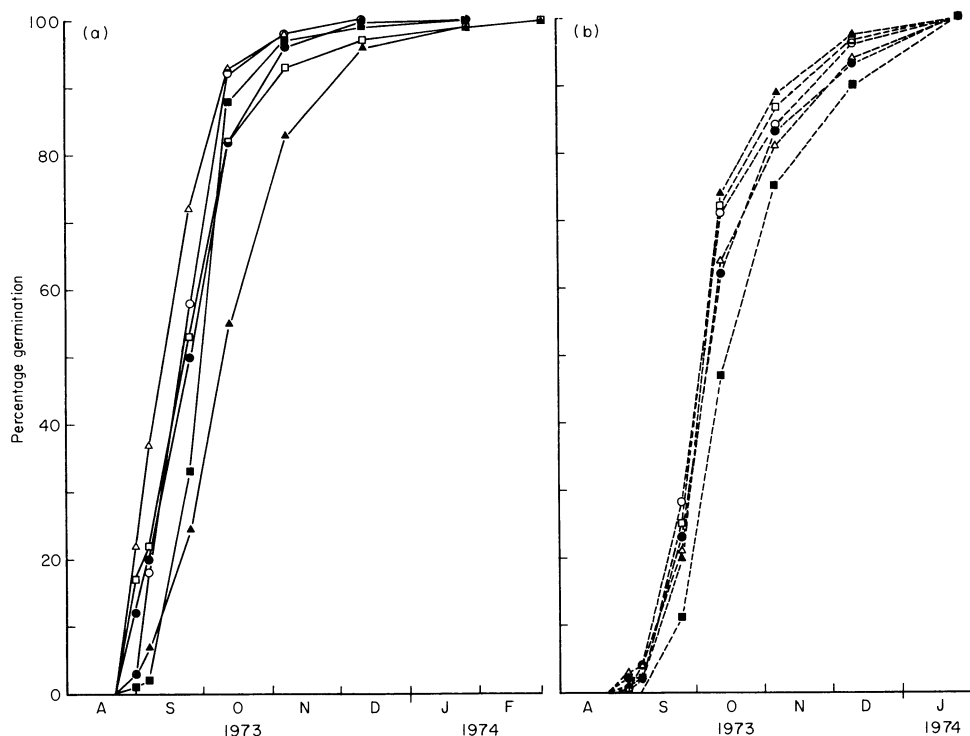


FIG. 1. Progress curves of germination of seeds of *Vulpia fasciculata* on the twelve permanent plots at Aberffraw and Newborough. (a) Aberffraw: plot A, ○—○; B, ▲—▲; C, ●—●; D, □—□; E, ■—■; F, △—△. (b) Newborough: plot 1, ▲---▲; 2, ○---○; 3, □---□; 4, △---△; 5, ■---■; 6, ●---●.

but on all the plots most seeds (75–99%) germinated during September and October. At both Aberffraw and Newborough germination was slightly later on those plots which were higher, more exposed and where the vegetation cover was sparse, e.g. plots 5 and B.

### Survivorship

In these field studies we know only about individuals that produce an emerged coleoptile. The survivorship curves omit any pre-emergence mortality of seeds and seedlings.

The total percentage mortality of individuals between coleoptile emergence and the flowering period varied between 7 and 41% (Table 1). The survivorship curves (Fig. 2) for the seedlings on the nine plots where the percentage mortality was less than 22% are very similar, with little or no mortality during the autumn and winter. Most of the plants that died did so in May and June, when the plants were at maximal size and the inflorescences were developing. The survivorship curves of the populations on the remaining three plots (B, 4, 5) are all similar in having a higher rate of mortality during the autumn and winter. However, if survivorship is examined in each of the four sub-plots of each plot, it can be seen that the overall survivorship curve is a composite of a range of survivorship curves (Fig. 3), some of which are similar to those found from the plots with a percentage mortality of less than 22%.

Some of the causes of mortality were identified as follows:

(a) The high level of spring mortality on plot 4a was due to the death of plants whose developing inflorescences had been eaten by rabbits.

(b) The high level of mortality on plot 5 during the same period was due to desiccation.

(c) Some of the small plants on other plots (e.g. A and F) died because they were

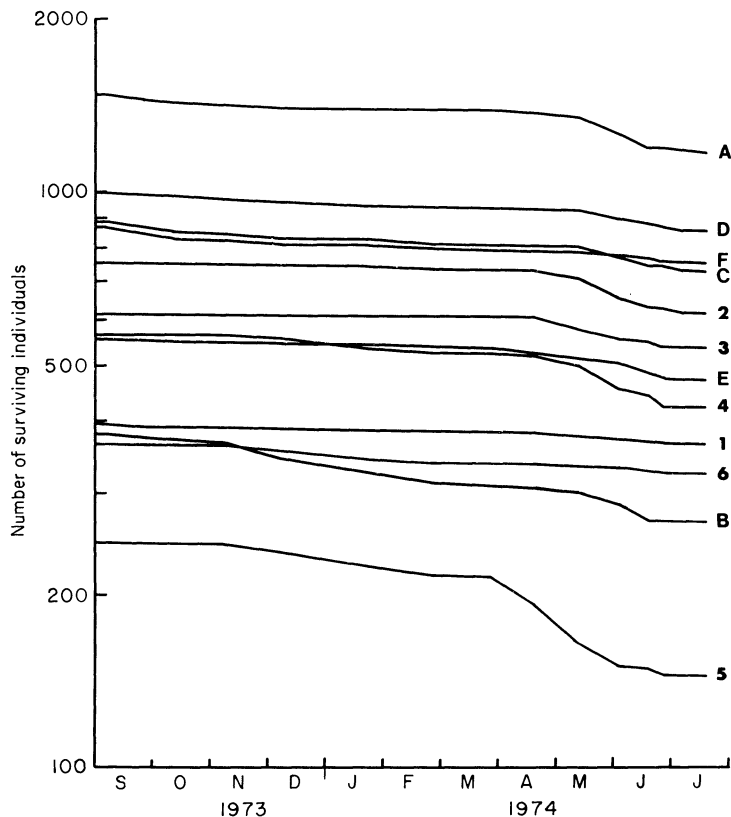


FIG. 2. Survivorship between the period of seedling emergence and flowering of twelve sub-populations of *Vulpia fasciculata* (number of individuals per 0.25 m<sup>2</sup>) at Aberffraw (A-F) and Newborough (1-6).

completely shaded by perennials (e.g. *Anthyllis vulneraria* L. and *Lotus corniculatus*), which began growth during the spring.

(d) Mortality during the autumn and winter was generally due to wind-drag on seedlings. Seedlings on exposed plots (e.g. 5 and B) and late-germinating individuals were particularly vulnerable to this hazard.

(e) There was considerable mortality amongst the very early-germinating individuals, which were liable to desiccation due to fluctuations in the moisture level of the sand during late summer.

#### Reproductive capacity

The mean spikelet production per plant on the different plots varied from 1.94 to 3.37 (Table 1). Only 2.3% of the plants produced more than one inflorescence, and most plants (91%) produced less than five spikelets, although one plant produced twenty.

On the fixed dunes around the permanently mapped plots the number of seeds per spikelet was proportional to the number of spikelets per plant (Fig. 4), although few spikelets contained more than one seed. In a more fertile region around a rabbit burrow the situation was similar, although the number of seeds per spikelet was higher than around the permanent plots. Most spikelets contained at least one seed, and several contained two or three if the spikelet number per plant was greater than five.

#### Rabbit grazing

Rabbits grazed the developing inflorescences of plants prior to emergence of the ears, and took whole inflorescences from flowering plants before the seeds had ripened and

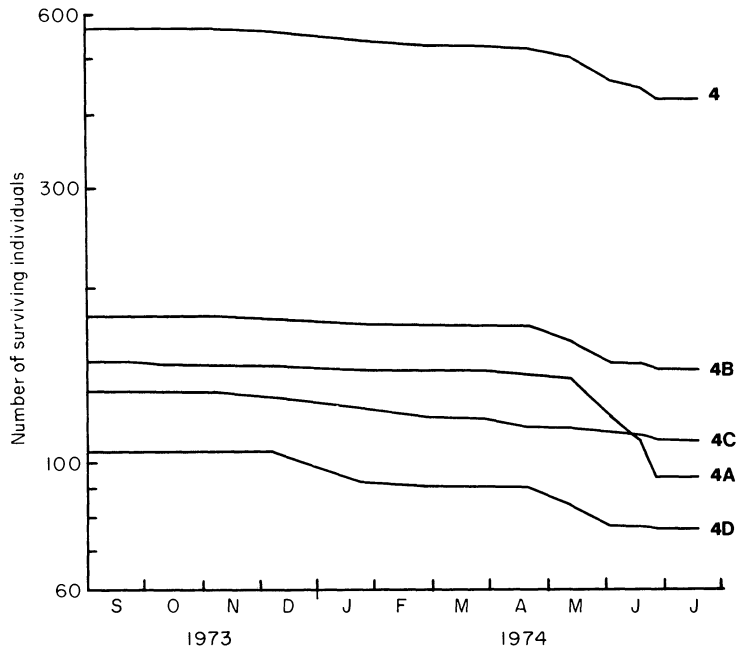


FIG. 3. Survivorship between the period of seedling emergence and flowering of individuals of *Vulpia fasciculata* in the four sub-plots of plot 4 (number of individuals per 0.0625 m<sup>2</sup>), and in plot 4 as a whole (number of individuals per 0.25 m<sup>2</sup>).

the awns had stiffened. The extent of both types of grazing was extremely variable from plot to plot (Table 1), and even between adjacent plots (cf. C and D).

Some of the plants (8–74%) that were grazed before the inflorescence emerged were subsequently found to have died, but others succeeded in flowering by early July if all of the spikelet primordia had not been eaten or damaged. These grazed plants produced 27% fewer spikelets per plant than the ungrazed plants. When a whole flowering inflorescence was eaten, the plant then died. Three plots were unaffected by either type of grazing, but on the other nine the potential seed production was reduced by 4–31%.

#### Density

On the permanent plots the total percentage mortality was dependent upon the specific characteristics of each individual plot and not upon the density of *Vulpia fasciculata* (Fig. 5). The risk of death tended to be slightly greater on the low density plots, because they were the most open and exposed and the plants were more susceptible to wind-drag. Over the eighty-four-fold range of plant densities obtained by thinning or supplementing natural populations in the experimental plots there was no evidence of density-dependent mortality. However, above a density of 100 plants per 0.25 m<sup>2</sup> the number of spikelets per plant was dependent upon plant density (Fig. 6). The relationship between the number of spikelets per plant and plant density on the permanent plots at Aberffraw was the same as that on the experimental plots. Spikelet production

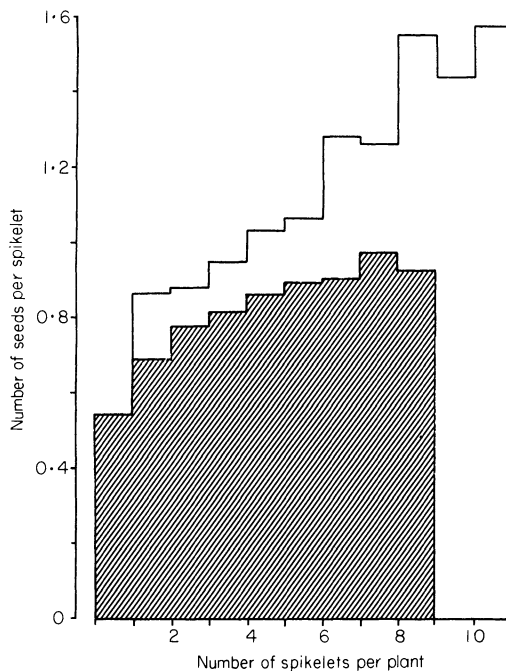


FIG. 4. The relationship between the number of seeds per spikelet and the number of spikelets per plant, based on 350 plants from the fixed dunes around the permanent plots at Aberffraw and Newborough (shaded area) and 120 plants from near a rabbit burrow on the fixed dunes at Aberffraw (unshaded area).

TABLE 1. A summary of the data on the fate and reproductive performance of sub-populations of *Vulpia fasciculata* in twelve permanent plots

	Aberffraw						Newborough					
	A	B	C	D	E	F	1	2	3	4	5	6
(a) Number of seedlings per 0.25 m <sup>2</sup>	1478	380	888	998	555	870	394	756	617	567	245	364
(b) Number of flowering plants per 0.25 m <sup>2</sup>	1175	267	730	856	475	747	366	619	539	422	145	322
(c) Percentage mortality: (b)/(a) × 100	20.5	29.6	17.8	14.2	14.4	14.2	7.1	18.2	12.7	25.6	40.8	11.6
(d) Individuals grazed at stage of inflorescence development (%)	21.0	0	39.2	0	0	13.6	0	0	0	8.1	0	0.9
(e) Individuals grazed at stage of flowering (%)	0	0	0.2	0	0	0	2.6	5.1	19.4	18.9	14.0	15.1
(f) Number of spikelets per flowering plant	2.32	3.37	2.25	2.63	2.95	2.67	2.66	1.94	2.32	2.37	2.65	2.68



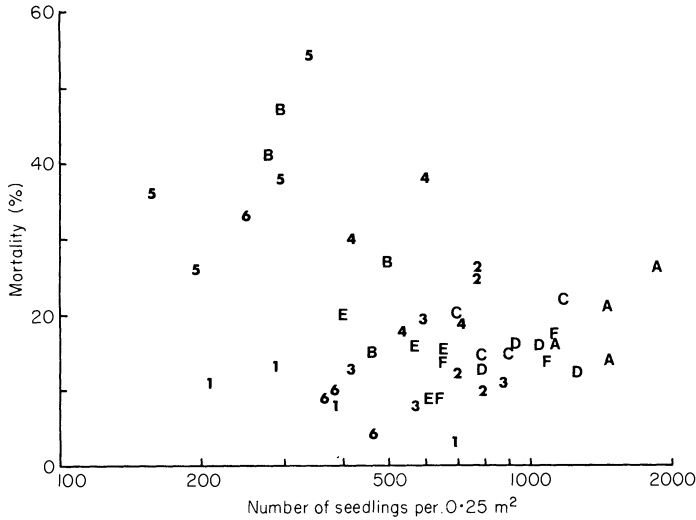


FIG. 5. The relationship between the percentage mortality of individuals between seedling emergence and flowering, and the density of seedlings (number per 0.25 m<sup>2</sup>) in the four sub-plots of each of the permanent plots at Aberffraw (A-F) and Newborough (1-6).

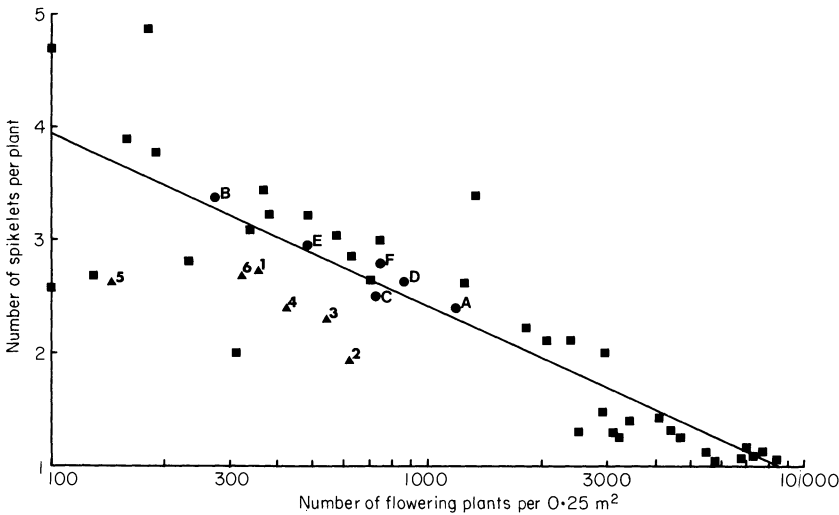


FIG. 6. The relationship between the number of spikelets per flowering plant and the density of flowering plants (number per 0.25 m<sup>2</sup>) on the experimental plots at Aberffraw (■), the permanent plots at Aberffraw (●) and the permanent plots at Newborough (▲). The values for the number of spikelets per flowering plant on the permanent plots do not include those flowering plants the developing inflorescence of which had been grazed. The regression line is for the Aberffraw data only. Regression equation:

$$y = 7.020 - 1.531 \log_{10} x \quad (P < 0.001).$$

per plant at any given density was lower at Newborough than at Aberffraw, but the density-dependent regulation of spikelet production appeared to be the same at both sites.

## DISCUSSION

The loss of individuals from a population can be represented by a survivorship curve. In the case of perennial plants, where populations commonly have a mixed-age structure, a number of authors have recorded individuals present at a point in time, and, ignoring age structure and new recruits to the population, have recorded the rate of disappearance of these individuals from the population. The graph of numbers obtained in this way, plotted as their logarithms against time, has been called a 'depletion curve' (Harper 1977), to distinguish it from a 'survivorship curve' in which the fate of specific age groups or cohorts is plotted. In the case of annual organisms, with a well-defined time of birth, depletion and survivorship curves are the same. However, 'birth' (the time of release from maternal tissue = germination in plants) is a rather arbitrary point in a life cycle. The mortality risk of a genet begins with the formation of a zygote, but the mortality risks in the phase between zygote formation and seed ripening have rarely been studied. Various arbitrary points have been chosen by different authors for the start of the survivorship curve—the ripe seed on the parent (Sharitz & McCormick 1973), dispersed seeds, emerged seedlings (Mack 1976) and clonal modules (Sarukhán & Harper 1973). The time chosen for the beginning of a survivorship curve will be particularly important if some seeds remain viable but dormant from year to year. Seeds in the soil have their own survivorship curves (Roberts 1958, 1962; Sarukhán 1974). Sharitz & McCormick have suggested that the earlier the chosen starting point of the survivorship curve, the more concave it is likely to be.

From the data in this paper, taken together with those obtained from a study of seed-population dynamics (Watkinson 1978), it is possible to construct a generalized survivorship curve for natural populations of *Vulpia fasciculata* from the time of seed maturation to flowering (Fig. 7). The risk of mortality prior to flowering is extremely low, but a peak of mortality occurs during inflorescence development. On the fixed dunes at Aberffraw and Newborough each plant of *V. fasciculata* on average produced 1.7 mature seeds, of which 90% germinated. Sixty-nine percent of the seedlings survived to flowering, and those individuals which flowered died immediately afterwards.

The shape of the survivorship curve for *V. fasciculata* is markedly different from the concave or positively-skewed survivorship curves of *Minuartia uniflora* and *Sedum smallii* given by Sharitz & McCormick (1973). These two species are also winter annuals, but produce a much larger number of seeds than *Vulpia fasciculata* (on average 305 and 114 respectively). Sharitz & McCormick have suggested that the survivorship curves of most plant populations will be positively skewed (Deevey Type III), and that this will be especially true of colonizing species. It might generally be expected that annuals which produce a large number of small seeds will suffer extremely high juvenile mortality, and will, therefore, exhibit positively-skewed survivorship curves, the degree of skewness depending on the reproductive potential. However, populations of annual species with low reproductive potentials must presumably give negatively skewed (Deevey Type I) survivorship curves, as the level of mortality in populations of such species which are relatively stable in time must be low in comparison with that of species which produce a large number of seeds.

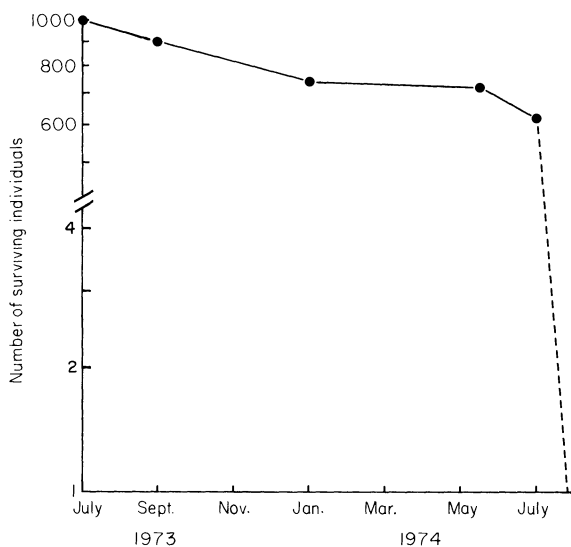


FIG. 7. Survivorship of natural populations of *Vulpia fasciculata* from seed production to flowering. Those individuals which flowered died immediately afterwards.

Salisbury (1942) gives the average seed output for a range of annual species from various habitats, and these values range from 39 to 176 000 seeds per plant. The seed output of *V. fasciculata* is beyond the lowest extremity of this range, and the population behaviour of *V. fasciculata* cannot, therefore, be expected to be typical of many annual species. There are, however, some other annuals which produce a relatively low number of seeds. The mean seed production per plant of *Cerastium atrovirens* at Aberffraw was 7.3, and populations exhibited negatively-skewed (Deevey Type 1) survivorship curves (Mack 1976), as would be expected; no direct measurements were made of the mortality between seed maturation and germination, but it was found that only about 40% of seedlings died without flowering. Marshall & Jain (1967) found that the average number of seeds produced per plant by both *Avena fatua* L. and *A. barbata* Brot. over a number of sites ranged from six to thirty-six, and on some of the sites they studied the overall mortality between the seed and adult stages in both species was as low as 41%.

Fundamental to the study of population dynamics is the understanding of the ways in which population size is determined. In environments in which there is a recurrence of disasters, the size of a population may frequently be a function of the magnitude of the last disaster and the time available for recovery (Harper 1967). Prior to myxomatosis in 1954 the population densities of *Vulpia fasciculata* on some British dune systems were very low (A. J. Willis, personal communication) and in these areas it is possible that the population densities were then determined entirely by the intensity of rabbit grazing and the time available for the recovery from such damage. *V. fasciculata* is grazed at both Aberffraw and Newborough, and it is possible that the density of some of the local populations within these areas, which had recently been subject to rabbit grazing, was also a function of the intensity of grazing and the time available for recovery. However, the population densities in the permanent plots in 1974 were similar to those in 1973, and

none of the plots was grazed to any great extent in 1973. The population densities were, therefore, at a level which could not be explained by disasters alone.

The results from the permanent plots and the experimental plots at Aberffraw indicated that above a density of 100 plants per  $0.25 \text{ m}^2$  there was a significant negative relationship between the number of spikelets produced per plant and the density of reproducing plants. In formulating the relationship between the number of spikelets per plant and the density of flowering plants of *V. fasciculata*, it was not necessary to take account of differences in the 'carrying capacity' of each site. This indicates that the carrying capacity of the environment was relatively uniform over the studied areas of the fixed dunes, despite a range of topography and vegetation types. Below a density of 100 plants per  $0.25 \text{ m}^2$  it is probable that the number of spikelets produced per plant was entirely independent of density. Evidence for this comes from six other plots at Aberffraw where the vegetation cover was very sparse, and which were not, therefore, directly comparable with the experimental plots. In these plots the natural density of plants ranged from 12 to 98 plants per  $0.25 \text{ m}^2$ , and the mean number of spikelets produced per plant ranged from 3.0 to 4.2 (overall mean = 3.6). There was no evidence from these data of a correlation between spikelet number per plant and plant density.

The density response at Newborough was similar to that at Aberffraw, although the number of spikelets produced per plant at any given density was lower at Newborough (probably due to the slightly lower nutrient status of the sand and the later germination at Newborough). The vegetative growth of *V. fasciculata* is greatly reduced in the presence of *Festuca rubra* L. (Pemadasa & Lovell 1974a), and this reduction is intensified by increasing soil fertility or the density of both species. It is likely, therefore, that in certain situations the density response of *Vulpia fasciculata* will be complicated by the relative frequency of the interacting species. The vegetation cover on all plots examined at both sites was sparse, and it is unlikely that competition for light was the causal factor in the density response. The nutrient levels (especially of nitrogen and phosphorus) severely limit plant growth on the fixed dunes (Pemadasa & Lovell 1974b), and competition for nutrients is probably the causal factor in the density response of *V. fasciculata*.

Plants generally respond to increasing density through an increase in mortality and/or a plastic response in the reproductive capacity of individuals. The plastic response in reproductive capacity (through the number of spikelets produced per plant) was the only density-dependent regulator observed in *V. fasciculata*: there was no evidence of density-dependent mortality. Mortality occurred at various stages throughout the life cycle (Table 2), and is regarded here as being density-independent, though the possibility of some of this mortality being weakly density-dependent cannot be completely ignored.

Williamson (1972) has shown that an interaction between a density-independent death rate and a negatively density-dependent birth rate will lead to an equilibrium population density, and that, in general, any change in the birth or death rates, which are functions of the physical and biotic conditions, will produce a corresponding change in population size. The flux of population size may also be affected by the numbers of immigrants and emigrants. However, the dispersal of seeds of *V. fasciculata* from the infructescence and subsequent movement on the ground is restricted to a few centimetres, and the rates of immigration and emigration can be assumed to be equal for most sub-populations (Watkinson 1975). A simple model to describe the population dynamics of *V. fasciculata* need, therefore, include only density-independent mortality and density-dependent

regulation of reproductive capacity. *V. fasciculata* has virtually no bank of survivable seed (Watkinson 1978), and this effectively allows a model of discrete, non-overlapping generations to be developed.

The relationship between the number of seeds per flowering plant and the density of flowering plants (Fig. 8) can be calculated from the data of Figs 4 and 6. The relationship approximates to a straight line, and the average seed output per flowering plant (for densities greater than 100 plants per 0.25 m<sup>2</sup>) can be calculated from the linear

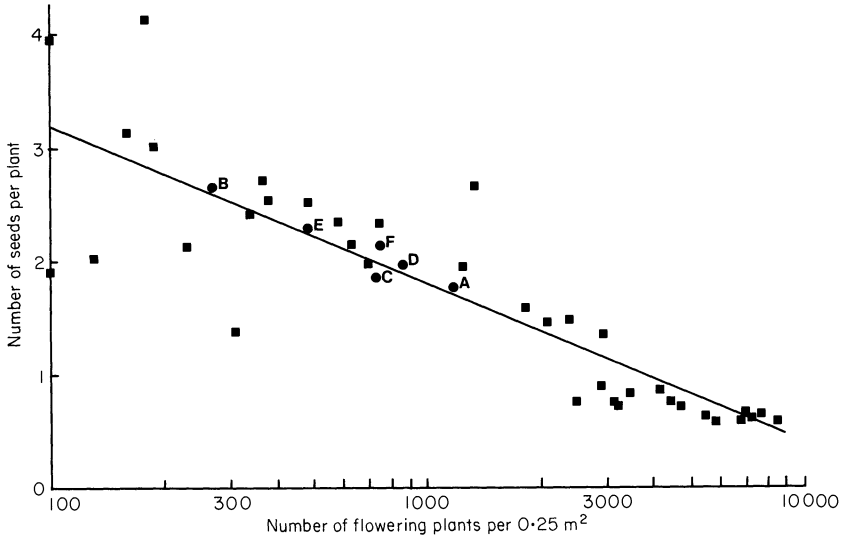


FIG. 8. The relationship between the number of seeds per flowering plant and the density of flowering plants (plants per 0.25 m<sup>2</sup>) on the experimental plots at Aberffraw (■) and the permanent plots at Aberffraw (●).

regression of seed output per flowering plant on flowering density (using Aberffraw values only):

$$\frac{N_s}{N} = -1.406 \log_{10} N + 6.012 \quad (1)$$

where  $N_s$  is the number of seeds produced, and  $N$  is the number of flowering plants in an area of 50 cm square. The number of seeds produced is thus given by

$$N_s = (-1.406 \log_{10} N + 6.012) N \quad (2)$$

and the general relationship between the number of seeds produced in any given area and the density of flowering plants is

$$N_s = (-c \log_{10} N + k) N \quad (3)$$

where  $c$  and  $k$  are both constants.

It is assumed, for the purpose of this model, that the number of seeds produced per plant is independent of density below a density of 100 plants per 0.25 m<sup>2</sup>. The threshold

density at which seed production becomes dependent upon plant density is  $N_{\min}$ . The mean number of seeds produced per plant at or below this density is  $S_m$ .

If  $N_{t-1}$  is the number of flowering individuals at time  $t-1$ , measured in years, then the population number at time  $t$  can be expressed in terms of the number in the previous year,  $t-1$ , as a function of the number of seeds produced at time  $t-1$  (see equation (3)) and the probability,  $P$ , of an individual surviving from seed production to maturity:

$$N_t = (-c \cdot \log_{10} N_{t-1} + k) P \cdot N_{t-1} \quad (4)$$

where  $N_{t-1} > N_{\min}$ .

Assuming that  $P$  is constant from year to year and that  $N > N_{\min}$ , then at equilibrium

$$N = (-c \cdot \log_{10} N + k) P \cdot N \quad (5)$$

and

$$\log_{10} \hat{N} = \frac{k}{c} - \frac{1}{c \cdot P} \quad (6)$$

where  $\hat{N}$  is the equilibrium density.

There is no equilibrium population density below a density of  $N_{\min}$ . Below this density the number of individuals in a population is given by

$$N_t = S_m \cdot P \cdot N_{t-1}. \quad (7)$$

The density of a population will decrease when  $S_m \cdot P < 1$ , and will increase when  $S_m \cdot P > 1$ . In populations of *V. fasciculata*  $S_m = 3.2$ , and a population will, therefore, decline to extinction if the probability of an individual attaining maturity is less than 0.31.

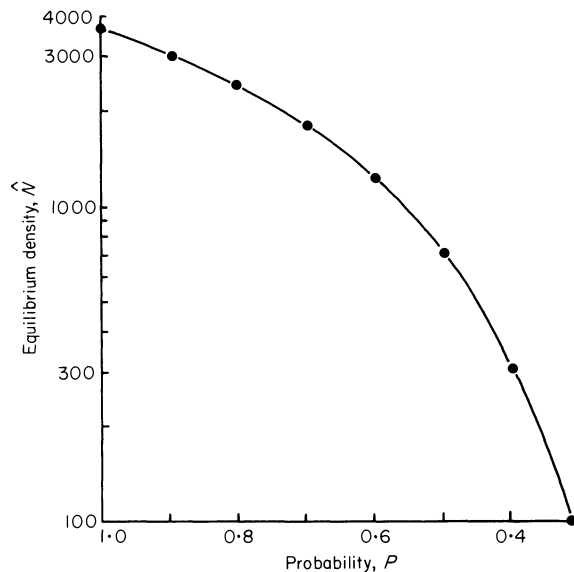


FIG. 9. The relationship between the equilibrium density of flowering plants,  $\hat{N}$  (plants per 0.25 m<sup>2</sup>), and the probability of an individual surviving from seed production to flowering,  $P$ .

Substituting the values of  $c$  and  $k$  from eqn (2) into eqn (6) gives the equilibrium population density for an area of 50 cm square where  $P > 0.31$ .

$$\log_{10} \hat{N} = 4.276 - \frac{0.711}{P}. \quad (8)$$

The equilibrium population density becomes increasingly sensitive to a decrease in the probability of survival from seed production to maturity (Fig. 9). With density-dependent regulation of seed production alone (i.e. when  $P = 1$ ), the population density of *V. fasciculata* equilibrates at approximately 3700 flowering plants per 0.25 m<sup>2</sup>, a density which is three times that of the highest density in any permanent plot (A), and 1.33 times that of the highest natural density observed in the field. This equilibrium density is halved when the value of  $P$  is reduced from 1.0 to 0.7, and quartered when  $P$  is reduced to 0.54.

If it is assumed that the population density on each of the permanent plots is at equilibrium and that the value of  $P$  is a constant for each plot, then the estimated values of  $P$  (calculated from equation (8)) which correspond to the observed densities on the permanent plots range from 0.39 to 0.59 for the populations at Aberffraw, and from 0.34 to 0.48 for the populations at Newborough. These values correspond approximately to the estimates of  $P$  derived from observations in the field, which range from 0.50 to 0.67 for the populations at Aberffraw and from 0.31 to 0.55 for the populations at Newborough (Table 2). It should be noted that the estimates of  $P$  for the Newborough plots calculated from equation (8) are slight overestimates, as equation (8) is derived from Aberffraw data only.

Although it is naïve to expect the observed flowering densities in one year to be at equilibrium, and the level of mortality to be constant from year to year, it can nevertheless be concluded from the above that the densities of populations of *V. fasciculata* are largely a function of a density-dependent birth rate and a density-independent death rate.

The variations in population density between the plots within Aberffraw and Newborough can largely be explained by differences in the levels of the various types of mortality (Table 2). The low densities on the exposed plots on which the vegetation cover was sparse (e.g. B and 5) are due to the high levels of mortality between germination and flowering. The differences between Aberffraw and Newborough can be explained in part by the higher levels of rabbit grazing and seed predation at Newborough, and in part by the lower density response.

It has already been shown that the population density is extremely sensitive to changes in the level of mortality, especially within the range of mortalities found in the field. Annual variations in population density can, therefore, readily be explained by the fact that all the parameters of population growth will normally vary with the physical and biotic conditions in which the population finds itself each year. Rabbit grazing and the predation of seeds by invertebrates will vary in intensity from year to year. Loss of seed viability during the summer will depend on the weather conditions during the later stages of inflorescence development, seed maturation and dormancy. Seedling establishment and the survival of individuals to flowering will depend on the weather conditions, and especially the run of wind. During the period of study the winters were very mild, and mortality during the winter was low. There may, however, be heavy mortality during severe winters. Symonides (1974a) found that severe frosts caused considerable mortality in populations of *Spergula vernalis* on dunes in Poland. The density-dependent regulation

TABLE 2. A summary of the data on the probability of an individual of *Vulpia fasciculata* surviving from seed maturation to maturity (and through the intervening parts of the life cycle)

Period of mortality	Cause of mortality	Aberffraw						Newborough							
		A	B	C	D	E	F	1	2	3	4	5	6		
(a) Spikelet or inflorescence development*	Rabbit grazing	0.96	1.00	0.90	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	0.98	1.00	0.99
(b) Seed maturation	Rabbit grazing	1.00	1.00	0.99	1.00	1.00	1.00	0.95	0.92	0.69	0.72	0.79	0.78		
(c) Seed dissemination to germination†	Loss of viability	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
(d) Seed dissemination to germination†	Seed predation	1.00	0.94	1.00	0.97	1.00	1.00	0.85	0.87	0.98	0.87	0.95	0.92		
(e) Post-emergence† to establishment	Wind-drag	0.88	0.72	0.80	0.80	0.73	0.80	0.76	0.81	0.81	0.76	0.72	0.76		
(f) Post-establishment to flowering	Desiccation	0.83	0.78	0.87	0.90	0.88	0.91	0.95	0.83	0.88	0.76	0.61	0.91		
	Various (see text)														
Complete life cycle		0.67	0.50	0.59	0.66	0.61	0.66	0.55	0.51	0.46	0.34	0.31	0.47		

\* This category represents the reduction in potential seed output of those plants which produced seeds but which were grazed during spikelet or inflorescence development. Individuals that were grazed and died before flowering are included in (f).

† Data from Watkinson (1978). The estimate of post-germination to establishment mortality for each of the permanent plots is from observations made on similar sites on the fates of seedlings, the seeds of which were radioactively-labelled. An estimate from the mapped individuals would be an underestimate, as seedlings which died and failed to produce a coleoptile or which were blown away between mapping sessions were not recorded.



of spikelet number in *Vulpia fasciculata* will also be sensitive to annual changes in the physical environment; for example, a dry autumn causes later germination (Pemadasa & Lovell 1975) and consequently fewer spikelets per plant.

Although there have been numerous studies on density-dependence, it has proved difficult to show the quantitative relationships of various factors to population density, and the relation of population size to physical factors (Williamson 1972). Comparisons with the dynamics of *V. fasciculata*, are, therefore, difficult. For plant populations the evidence for density-dependent regulation of natural populations is especially poor. The most detailed field studies on population regulation are on animals, but again there is a lack of information on the factors affecting the stabilization and fluctuation of numbers in time and space.

One of the most detailed studies on population behaviour is that for the great tit, *Parus major* L. Krebs (1970) summarized: 'Clutch size and hatching success are density-dependent and sufficiently so to regulate the population of great tits at the observed level assuming there is in addition a fairly large density-independent mortality. . . . The density-dependent variations in clutch size are probably in the main due to shortage of available food and density-dependent hatching failure is caused by predation. . . . There may also be some weak, density-dependent mortality outside the breeding season'. Lack (1966) stressed that the critical factor influencing the annual fluctuations of the breeding population of the great tit in Marley Wood was the level of juvenile mortality. It would, therefore, appear that the regulation of population density and the reasons for annual fluctuations in population density of the great tit are essentially the same as in *Vulpia fasciculata*, with 'food' the ultimate controlling density-dependent factor, and density-independent mortality determined by the physical and biotic environment each year responsible for annual fluctuations in the population density.

The model developed to describe the population dynamics of *V. fasciculata* is based on an empirical relationship between seed output and the density of flowering plants.

$$N_s = f(N)$$

where  $f(N)$  is a function describing seed output in terms of flowering density.

The field situation is obviously more complex. The number of spikelet primordia is in fact determined very early in the life cycle of an annual grass, although the chance of a primordium producing a floret can be affected by various factors, including changes in density, up to the time of inflorescence emergence (Puckridge 1968), just as the chance of a floret producing a caryopsis is not unity. There is evidence from cereals that soil-moisture stress at anthesis results in a reduction in grain-filling and in the production of smaller and sometimes shrivelled grains (Aspinall, Nicholls & May 1964). However, Newman (1967) found that the seed production in the winter annual *Aira praecox* L. was unaffected by soil-moisture stress if confined to the period after inflorescence emergence. Severe soil-moisture stress during emergence of the inflorescence reduced both that emergence and seed production. Observations on *Vulpia fasciculata* suggest that periods of soil-moisture stress during the spring may reduce both inflorescence emergence and the number of seeds produced.

The number of seeds produced in a given area by *V. fasciculata* is, therefore, likely to be a function of (a) the density of plants during the period of regulation of the number of spikelet primordia; (b) the probability of an individual surviving from the period of regulation to maturity; and (c) the number of seeds produced per flowering plant. The

last function will be a complex one dependent upon several factors, including the weather conditions, the number of spikelets per plant, the density of plants between regulation and maturity, and the extent of rabbit grazing. A further understanding of population regulation in *V. fasciculata* will, therefore, need additional experiments on the regulation of the number of spikelets per plant and the factors affecting seed production.

An interaction between a density-dependent birth rate and a density-independent death rate is only one of the ways in which population size can be determined. Populations may react to density-independent and density-dependent factors through mortality or plasticity, and the possible causal factors of density-dependence are various. In order to determine the method of regulation of plant populations and the reasons for the flux in population density in both time and space, it is necessary to consider all the factors which affect the four parameters (i.e. the births, deaths, immigrants and emigrants) that determine the size of populations. These aims can only be achieved by making detailed observations on the fates of individuals in both the vegetative and seed phases of the life cycle, and by identifying the agents which cause mortality and the various factors which affect both seed reproduction and clonal spread. It is particularly necessary through observations and experiments in the field to determine the roles of density, the spatial distribution of individuals, associated plant species, plant/animal interactions and weather in the mortality and reproduction of that population.

The contrast between the population dynamics of *V. fasciculata* and some other annuals is at least as striking as that between annuals and perennials. There is a very strong case to be argued for detailed studies on the population dynamics of many more species of plants. Until these studies are made there is a constant danger that generalizations about population dynamics will prove false. Few species can afford so few problems for this type of study as *V. fasciculata*, and the elucidation of the population dynamics of most other species will undoubtedly prove to be more difficult.

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