

## RAPID POPULATION DIFFERENTIATION IN A MOSAIC ENVIRONMENT

### III. MEASURES OF SELECTION PRESSURES

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#### SUMMARY

1. Reciprocal transplants were made of pairs of contrasting populations of *Anthoxanthum odoratum* collected from the Park Grass Experiment at Rothamsted.
2. In most cases, plants survived longer, produced more tillers and produced more dry matter when transplanted into their native plots than when transplanted into ecologically contrasting plots.
3. The average half-life of plants transplanted into contrasting plots was 8 months, that of plants in their native plots was about 2 years.
4. Selection coefficients against "alien" populations based on survival after 18 months ranged from 0.09 to 0.77 with a mean value of 0.36. Similar coefficients of selection were calculated for tiller number and plant weight.
5. The coefficients of selection on the various plots were correlated with both the yield of herbage on the plots and the vegetation height on the plots, this is discussed in relation to the observed pattern of differentiation of *A. odoratum* on the plots.
6. We conclude that selection pressures acting upon *A. odoratum* in the mosaic of environments that occur on the Park Grass Experiment are large and sufficient to account for the morphological and physiological differences that have been observed between closely adjacent populations of *A. odoratum* on the plots.

#### 1. INTRODUCTION

MORPHOLOGICAL and physiological differences have evolved between populations of *Anthoxanthum odoratum* L. on the Park Grass Experiment within a period of less than 60 years and over distances of less than a metre (Snaydon, 1970; Snaydon and Davies, 1972, 1976; Davies and Snaydon, 1973a, 1973b, 1974; Davies, 1975). The differences between populations are apparently adaptive and are seed transmitted. If the differences arose as a result of natural selection acting upon genetic variation within the original population, then selection must be intense and the potential store of genetic variation large.

We have no measure of the amount of genetic variability within the original population but the present populations are genetically very variable (Davies and Snaydon, in preparation). Other studies, such as those by Cooper (1959) have shown that large amounts of potential genetic variation are present even within individual plants of perennial outcrossing species and that this variation is susceptible to recombination and artificial selection. The large amount of genetic variation within populations of grass species in the field is also subject to natural selection, and large changes in the genetic structure of populations can occur within a few years (Charles, 1961, 1964; Brougham and Harris, 1967; Crossley and Bradshaw, 1968).

In mosaic environments, such as the Park Grass Experiment, where the boundaries between environments are sharp and the area of each environment is relatively small, population differentiation will depend largely upon the relative magnitude of the opposing forces of selection and gene flow; Wright (1951), Mather (1955), Stebbins (1964), and Jain and Bradshaw (1966) have discussed the interaction of these forces. Intense artificial selection can outweigh the effects of high gene flow (Thoday and Boam, 1959; Streams and Pimental, 1961; Paterniani, 1969), though other workers (Robertson, 1970) have not been able to demonstrate population divergence under conditions of high gene flow. However, gene flow in the field may not be as large as has been previously assumed (Bateman, 1947; Griffiths, 1950; Copeland and Hardin, 1970; Gleaves, 1973), whilst recent estimates of selection coefficients (Jain and Bradshaw, 1966; Cook, Lefebvre and McNeilly, 1972) indicate that selection may be much more intense than envisaged by Haldane (1948) and Fisher (1950) in their early mathematical analysis of selection.

This study is an attempt to measure the magnitude of selection pressures operating within the species *A. odoratum* on some plots of the Park Grass Experiment in order to assess whether these were sufficient to account for the rapid changes in population structure that have occurred, both in time and space, in the area. A reciprocal transplant technique was used, plant survival and performance was followed over a period of 18 months. Unfortunately, because of the nature of the experimental area, no estimate of the reproductive performance of the transplants could be obtained.

## 2. MATERIALS AND METHOD

Approximately 25 plants, ranging in size from 2-6 tillers were collected at random from each of plots 3U, 1U, 7U, 9L, 1L and 8L in November 1967. Plants were grown in boxes filled with John Innes No. 1 potting compost until May 1968 when they were planted as spaced plants in a garden bed. Material was collected from these plants in November 1968 for reciprocal transplants. For the purposes of the transplant experiment, the populations were grouped into pairs from contrasting plots; thus population 9L was paired with population 3U on the basis of the contrasting fertiliser treatments on their source plots (table 1), though the soil pH of the two plots was similar. Population 1L was paired with population 1U because of the widely different soil pH brought about by the contrasting liming treatment, though similar fertiliser treatment, on the two plots. Population 8L was paired with population 7U, again on the basis of contrasting liming and fertiliser treatment but in this case the unlimed plot had a greater yield of herbage.

One hundred rametes, each of two tillers, were collected at random from each population accession, 50 of these rametes were transplanted into the native plot of the population and the other 50 were transplanted into the plot of the contrasting paired population. The rametes of the two populations were planted alternately, at 0.3 m intervals along two rows, which were located 0.5 m and 1 m respectively from the edge of the plot. Each plant was marked with coloured wire, so that it could be easily located. Plants which had failed to establish 3 weeks after the initial planting were replaced.

Plant survival and numbers of tillers per plant were measured in May 1969, October 1969 and May 1970. The vegetation on the plots is normally

environmental conditions on the source plots from the Park Grass Experiment, Rot.

Population pairs	Fertiliser treatment	Mean annual yield of vegetation (kg, ha <sup>-1</sup> ) (1920-59)
9L	N <sub>2</sub> P, K, Na, Mg	5613
3U	unfertilised	1475
1L	N <sub>1</sub>	2363
1U	N <sub>1</sub>	1700
8L	P, Na, Mg	2150
7U	P, K, Na, Mg	3650

— unlimed plots, L = limed plots (225 annual applications: N<sub>1</sub> = 48 kg, N<sub>2</sub> = 34 kg, P, ha<sup>-1</sup>, Mg = 11 kg, Mg,

\* Suspension  
† Extracted in  
‡ Extracted in

cut twice annually, in June and a few weeks before these cuts. when dry weight yield per recorded.

The number of plants surviving for each population on After 18 months the average s native plots was 65 per cent an plots was 40 per cent. The lar tion was for population 3U; survived but on plot 9L only 1. At the same time, 60 per cent survived on its native plot and

The surviving plants of po generally grew more rapidly th: For example, after 18 months into their native plots average alien plots, they averaged only mean dry weight yield of survi was 470 mg, but that of tran difference of 36 per cent (table was found for population 9L only 364 mg on plot 3U, a dif nounced differences occurred i

TABLE 1

Environmental conditions on the source plots of the three reciprocal pairs of populations of *Anthoxanthum odoratum* from the Park Grass Experiment, Rothamsted. (Park Grass data from Warren and Johnson, 1964)

Population	Fertiliser treatment	Mean annual yield of vegetation (kg, ha <sup>-1</sup> ) (1920-59)	Vegetation height 1969 (mm)	Soil* pH	Soil† P (mg/100 g)	Soil‡ K (mg/100 g)	% N in surface soil
9L	N <sub>2</sub> P, K, Na, Mg	5613	580	5.3	10.0	7.7	0.31
3U	unfertilised	1475	110	5.2	0.5	1.1	0.27
1L	N <sub>1</sub>	2363	160	7.2	1.0	0.5	0.30
1U	N <sub>1</sub>	1700	120	4.0	0.5	1.2	0.24
8L	P, Na, Mg	2150	230	7.0	11.0	0.5	0.31
1U	P, K, Na, Mg	3650	270	4.9	13.0	11.3	0.23

\* Unlimed plots, L = limed plots (2250 kg CaO/ha every 4 years since 1903)

† Soil applications: N<sub>1</sub> = 48 kg, N, ha<sup>-1</sup>      N<sub>2</sub> = 96 kg, N, ha<sup>-1</sup>  
 P = 34 kg, P, ha<sup>-1</sup>      K = 225 kg, K, ha<sup>-1</sup>  
 Mg = 11 kg, Mg, ha<sup>-1</sup>      Na = 16 kg, Na, ha<sup>-1</sup>

\* Suspension 1 : 2.5 in water.

† Extracted in 0.5M sodium bicarbonate.

‡ Extracted in water.

cut twice annually, in June and in autumn, and measurements were made a few weeks before these cuts. The plants were finally removed in May 1970 when dry weight yield per plant, plant height and tiller number were recorded.

### 3. RESULTS

#### (i) Plant survival

The number of plants surviving, expressed as a percentage of the total planted for each population on each plot, decreased rapidly with time (fig. 1). After 18 months the average survival of populations transplanted into their native plots was 65 per cent and of populations transplanted into contrasting plots was 40 per cent. The largest difference in survival for any one population was for population 3U; on its native plot 55 per cent of the plants survived but on plot 9L only 14 per cent survived after 18 months (table 2). At the same time, 60 per cent of the plants of the reciprocal population (9L) survived on its native plot and 50 per cent on the alien plot 3U.

#### (ii) Plant growth

The surviving plants of populations transplanted into their native plots generally grew more rapidly than those transplanted into alien plots (table 2). For example, after 18 months' growth plants of populations transplanted into their native plots averaged 8.8 tillers per plant, but transplanted into alien plots, they averaged only 5.8 tillers (fig. 2 and table 2). Similarly the mean dry weight yield of surviving plants transplanted into their native plot was 470 mg, but that of transplants into alien plots was only 345 mg, a difference of 36 per cent (table 2). The largest difference for any population was found for population 9L which yielded 614 mg on its native plot but only 364 mg on plot 3U, a difference of 69 per cent. Similar but less pronounced differences occurred in other populations.

Experiment, where the area of each environment depend largely upon selection and gene flow; and Bradshaw (1966) artificial selection can Boam, 1959; Streams workers (Robertson, on divergence under the field may not be as 947; Griffiths, 1950; t recent estimates of efebvre and McNeilly, use than envisaged by hematical analysis of

of selection pressures of the Park Grass ent to account for the ed, both in time and ue was used, plant f 18 months. Unfor- a, no estimate of the obtained.

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ted at random from ansplanted into the lanted into the plot he two populations rows, which were ot. Each plant was ated. Plants which were replaced. : measured in May he plots is normally

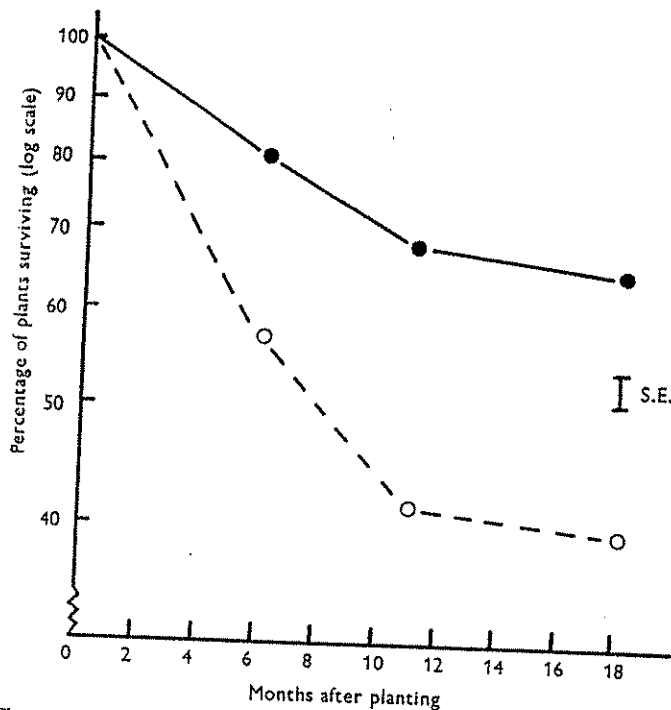


FIG. 1.—The mean survival (percentage) of plants transplanted into their native plots (—) and into contrasting plots (-----), 6, 11 and 18 months after planting.

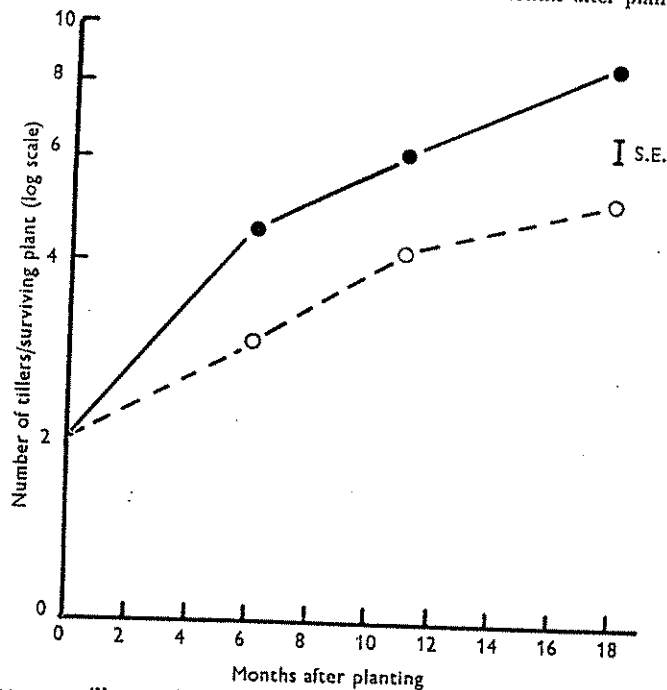


FIG. 2.—The mean tiller number per surviving plant of plants transplanted into their native plots (—) and into contrasting plots (-----) 6, 11 and 18 months after planting.

plant survival, mean number of tillers, 18 months after being to

Population	Survival %	
	Native	Contrasting
{ 9L	60	50
{ 3U	55	14
{ 1L	82	54
{ 1U	61	49
{ 8L	76	54
{ 7U	69	38
Mean	67.1	43.2
S.E.	3.4	

Coefficients of selection from the survival, tiller measurement date (table) population was calculated

$$1.0 - \frac{\text{Per}}{\text{Per}}$$

The coefficients of selection greatest on plot 9L and less were also greater on lime (mean = 0.21).

The mean coefficient of the mean annual yield of the vegetation on the plots (r

Coefficients of selection against the

Plot	Survival %	
	May 1969	Oct. 1969
{ 9L	0.67	0.74
{ 3U	0.08	0.07
{ 1L	0.29	0.42
{ 1U	0.12	0.10
{ 8L	0.31	0.50
{ 7U	0.15	0.22
Mean of limed plots	0.42	0.55
Mean of unlimed plots	0.12	0.13

TABLE 2

Plant survival, mean number of tillers, mean plant height and mean plant weight of six populations of *A. odoratum*, 18 months after being transplanted into their native plots and into contrasting plots

Population	Survival %		Tiller number		Plant height (mm)		Plant weight (mg)	
	Native	Contrasting	Native	Contrasting	Native	Contrasting	Native	Contrasting
9L	60	50	10.4	6.4	114	85	614	364
3U	55	14	8.5	4.5	87	100	451	491
1L	82	54	8.3	7.1	84	82	476	395
1U	61	49	9.4	6.4	80	78	491	310
8L	76	54	7.8	4.9	78	88	391	264
7U	69	38	8.4	5.4	94	84	395	248
Mean	67.1	43.2	8.8	5.8	89.5	86.2	496.7	345.3
S.E.		3.4		0.30		4.8		28.4

(iii) Selection coefficients

Coefficients of selection against the "alien" population were calculated from the survival, tiller number and plant yield data on each plot at each measurement date (table 3). The coefficient of selection against the alien population was calculated as

$$1.0 - \frac{\text{Performance of the alien population}}{\text{Performance of the native population}}$$

The coefficients of selection against the alien population were invariably greatest on plot 9L and least on plot 3U (table 3). Coefficients of selection were also greater on limed plots (mean = 0.44) than on unlimed plots (mean = 0.21).

The mean coefficient of selection on each plot was correlated with both the mean annual yield of the plots ( $r = 0.90, P < 0.05$ ) and the height of the vegetation on the plots ( $r = 0.95, P < 0.01$ ).

TABLE 3

Coefficients of selection against the "alien" population on six plots of the Park Grass Experiment

Plot	Survival %			Tiller number			Dry matter yield	
	May 1969	Oct. 1969	May 1970	May 1969	Oct. 1969	May 1970	May 1970	Mean
9L	0.67	0.74	0.77	0.58	0.55	0.57	0.60	0.64
3U	0.08	0.07	0.09	0.17	0.17	0.25	0.20	0.15
1L	0.29	0.42	0.40	0.42	0.23	0.23	0.35	0.33
1U	0.12	0.10	0.12	0.29	0.26	0.25	0.20	0.19
8L	0.31	0.50	0.54	0.24	0.20	0.31	0.39	0.36
7U	0.15	0.22	0.22	0.29	0.33	0.42	0.36	0.28
							S.E. = 0.05	
Mean of limed plots	0.42	0.55	0.57	0.41	0.33	0.37	0.41	0.44
							S.E. = 0.03	
Mean of unlimed plots	0.12	0.15	0.14	0.25	0.25	0.31	0.25	0.21
							Mean of all plots 0.33	

## 4. DISCUSSION

Each population generally performed best in its native plot, though the superiority was not consistent across all measured attributes. Indeed there was some evidence that if a population performed better in one attribute it might be compensated by a relatively poorer performance in another. For example, in the reciprocal pair of populations 9L and 3U, there was little difference in survival of plants of population 9L on native and alien plots (table 2) but a large difference in dry weight yield; conversely there was a large difference in the survival of population 3U but no significant difference in yield (table 2).

Observation was not continued for long enough to adequately determine the half-life of populations on both native and alien plots. On alien plots, populations had an average half-life of 8 months (fig. 1). Extrapolation of the data for native plots (fig. 1) indicates a probable average half-life of 2 years; this is similar to the value obtained by Antonovics (1972) for *A. odoratum* growing on zinc contaminated mine waste.

The coefficients of selection against alien populations measured here are relatively large, with a mean value of 0.33. These values are not as large as those obtained in more extreme habitats, such as heavy metal contaminated spoil heaps, where selection coefficients of 0.9 and more seem normal (Jain and Bradshaw, 1966).

The largest coefficients of selection occurred on plots characterised by large annual yield and tall vegetation in summer. These plots have received heavy applications of fertiliser and lime (table 1). The lowest selection coefficients occurred on plots with small annual yield and short vegetation. The correlation between selection coefficient and vegetation height ( $r = 0.95$ ) may reflect the role of competition for light as a selective force. Populations of *Anthoxanthum odoratum* collected from plots with tall vegetation are taller (Snaydon and Davies, 1972) and more tolerant of low light conditions (Davies, 1970) than populations from plots with short vegetation.

The greater selection coefficients against alien populations on limed plots (table 3) may be partly associated with the generally greater height and yield of the vegetation (table 1), but populations of *A. odoratum* collected from limed and unlimed plots of the Park Grass Experiment also differ in response to acid and calcareous soils (Snaydon, 1970) and in response to a number of specific soil nutrient factors (Davies and Snaydon, 1973a, 1973b, 1974).

The selection coefficients against alien populations on limed plots were greater when calculated on the survival data than when calculated on the growth performance of surviving plants, tiller number and dry weight yield; on unlimed plots the reverse was true. This indicates that the mechanism of selection may be different on the various plots.

The technique used here to estimate the magnitude of selection operating *in situ* on the Park Grass Experiment is subject to several major criticisms. Firstly, the estimate of the selection coefficient on each plot is directly dependent upon the particular alien population transplanted into that plot, the greater the contrast between the native and alien population, the greater the estimated selection coefficient on that plot. Ideally, all populations should be transplanted into all plots, though this would have tripled the size of the present experiment. Secondly, selection acting upon germinating and

establishing seedlings was not estimated on the basis of surviving plants which failed to establish. Selection during seedling establishment. For example, Charles (1961) found differences in survival of grasses in survival during t. Thirdly, no measures were taken between populations on the genotypes is probably important populations, especially in a re. It is possible, therefore, that selection in the Park Grass Experiment may

The selection pressures estimated to account for the differences in *A. odoratum* on the Park Grass Experiment (Davies, 1972; Davies and Snaydon, 1973) are also large enough to account for differences between populations at plot b if gene flow is as slight as Griffiths (Snaydon and Davies (unpublished).

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establishing seedlings was not considered here. Coefficients of selection were estimated on the basis of survival and vegetative growth of rooted tillers and plants which failed to establish were replaced 3 weeks after planting. Selection during seedling establishment is probably important and intense. For example, Charles (1961) found large differences between cultivars of grasses in survival during the first year when sown in dense mixtures. Thirdly, no measures were made of possible differences in viable seed set between populations on the various plots. The reproductive capacity of genotypes is probably important in determining the genetic structure of populations, especially in a relatively short lived species such as *A. odoratum*. It is possible, therefore, that selection pressures acting upon the species on the Park Grass Experiment may be even greater than estimated here.

The selection pressures estimated above are large and probably sufficient to account for the differences already observed between populations of *A. odoratum* on the Park Grass Experiment (Snaydon, 1970; Snaydon and Davies, 1972; Davies and Snaydon, 1973a, 1973b, 1974). The selection pressures are also large enough to account for the sharp differences that occur between populations at plot boundaries (Snaydon and Davies, unpublished) if gene flow is as slight as Griffiths (1950), Copeland and Hardin (1970) and Snaydon and Davies (unpublished) indicate.

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