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RAPID POPULATION DIFFERENTIATION IN A MOSAIC ENVIRONMENT

IV. POPULATIONS OF *ANTHOXANTHUM ODORATUM* AT SHARP BOUNDARIES

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SUMMARY

Populations of the grass species *Anthoxanthum odoratum* were collected at intervals across two boundaries between contrasting plots of the Park Grass Experiment, Rothamsted. One boundary (8L/9L) had been in existence for 112 years, and the other (1L/1U) for 60 years. Environmental conditions at both boundaries changed to almost the maximum extent within 0·5 m.

There were significant differences in height, yield, flowering date, and other morphological attributes between populations collected only 0·1 m apart at each boundary, when grown in spaced plant trials. The sharpest differences occurred between populations collected close to the boundary.

The patterns of variation of morphological attributes across one boundary (8L/9L) closely followed the patterns of environmental conditions and vegetation, which were relatively simple. The patterns of variation of morphological attributes across the other boundary (1L/1U) were not simply related to the patterns of environmental conditions or vegetation, which were complex. Reverse clines (Ford, 1971) occurred for several attributes, especially at the 1L/1U boundary.

At both boundaries, the population collected at the boundary flowered 4-6 days earlier than adjacent populations. There appeared to be partial reproductive isolation between these populations and adjacent populations.

Most attributes were highly heritable. Population samples collected *in situ* as seed were closely similar to population samples collected as tillers. The similarities were greatest for populations collected furthest from the boundary.

Comparisons of populations grown from seed and tiller collections indicated that gene flow was greatest 0·2 m downwind of the boundary, but rapidly declines to a small level at 2 m.

1. INTRODUCTION

PREVIOUS investigations (Snaydon, 1970; Snaydon and Davies, 1972; Davies and Snaydon, 1973*a*, *b*, 1974) have shown that morphologically and physiologically distinct populations of *Anthoxanthum odoratum* L. have evolved within the mosaic of contrasting environments of the Park Grass Experiment at Rothamsted, U.K. The populations have evolved within 50 years and over distances of less than 30 m. Each population appears to be morphologically and physiologically adapted to the environmental conditions of its source site. This paper considers population differentiation at the sharp boundaries between adjacent, contrasting environments of the Park Grass Experiment.

The degree of disjunction between populations, at boundaries between contrasting environments, will depend upon the relative magnitude of two opposing forces: (*a*) the contrasting selection pressures in the two environments, which would tend to produce distinct populations on either side of the boundary, and (*b*) genetic recombination within and between populations across the boundary, which would tend to retard the differentiation of distinct populations (Jain and Bradshaw, 1966). The sharpness of the change in selection pressure at the boundary is likely to depend upon: (i) the magnitude of the difference in environmental conditions on the two sides of the boundary, and (ii) the sharpness of the change in environmental conditions at the boundary. The response to those differences in selection pressure is likely to depend on additional factors such as: (i) the amount of genetic variation present, and (ii) the reproductive strategy (Harper, 1967) of the species.

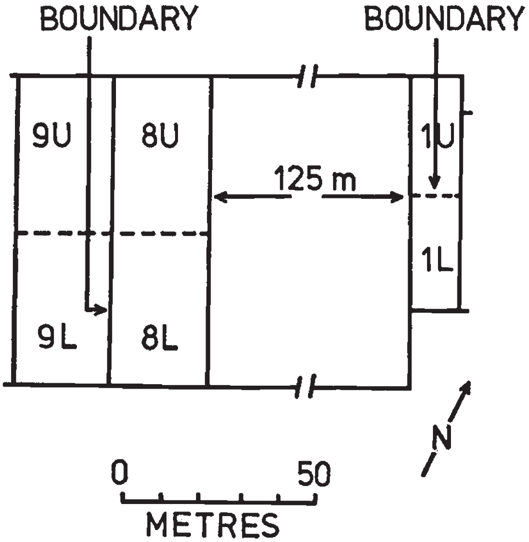

FIG. 1.—Plan of part of the Park Grass Experiment, Rothamsted, showing the location of the two boundaries studied.

The magnitude of genetic recombination, within and between populations across the boundary, is likely to depend upon: (i) the mode of inheritance of the attribute considered; (ii) the breeding system of the population (*e.g.* percentage outcrossing); (iii) the pollination mechanism (wind, insect, etc.); (iv) the seed dispersal mechanism; (v) environmental factors, such as wind speed and direction, which influence pollen or seed dispersal; (vi) the reproductive strategy of the population and especially the relative importance of sexual as opposed to vegetative reproduction; (vii) the relative abundance of the species on each side of the boundary.

There are three major sources of evidence which indicate that population differentiation may occur over relatively short distances. Firstly, the limited evidence from field studies, *e.g.* Creed *et al.* (1959), Aston and Bradshaw (1966), Antonovics and Bradshaw (1970), indicates that population differentiation may occur over distances of less than 10 m, in both plant and animal species. Secondly, evidence from artificial selection in laboratory populations of insects indicates that population differentiation can occur in the face of extensive gene flow, *e.g.* Thoday and Boam (1959), and Streams and Pimental (1961). Thirdly, computer models of population differentiation (*e.g.*

Jain and Bradshaw, 1966) indicate that, at known levels of selection and gene flow, population differentiation might be expected over distances of only a few metres. Most of the available evidence points to the fact that selection pressures in the field may be considerably greater than had previously been suspected (*e.g.* Jain and Bradshaw, 1966, Davies and Snaydon, 1976) and that gene flow in the field may be considerably less than suspected (*e.g.* Griffiths, 1950).

Sharp spatial differences between populations in the field may not always be the result of sympatric or parapatric divergence, in the face of gene flow. Some cases may be the result of allopatric divergence, without gene flow, followed by independent migration and meeting, *e.g.* Heslop-Harrison (1956), Briggs (1962) and Heslop-Harrison (1964).

The present investigation concerns population differentiation where the origin and recent history of the populations are known, and where environmental differences are well defined. Populations of *A. odoratum* have been collected along transects across two boundaries between contrasting environments. The boundary between plots 8L and 9L of the Park Grass Experiment (fig. 1) had been in existence for 112 years, but the boundary between plots 1L and 1U had only been in existence for 60 years. The boundaries also differed in the environmental factors involved, the complexity of vegetational change at the boundary and probably in gene flow across the boundary. Populations collected from the two boundaries were grown in uniform spaced-plant conditions for several years and morphological differences among the populations were observed. We have attempted to interpret these differences in relation to both the pattern of variation in environmental conditions and vegetation across the boundaries (*i.e.* probable selection), and the probable gene flow across the boundaries.

2. Boundary 8L/9L

(i) *Materials and method*

(a) *The site*

The location of the boundary on the Park Grass Experiment is shown in fig. 1. Full details of the fertiliser and liming treatments, and of the effects of these treatments on soil chemical composition, botanical composition and yield of herbage, will be found elsewhere (Brenchley and Warington, 1958; Warren and Johnston, 1964; Thurston, 1969; Snaydon, 1970). Both plots 8L and 9L have received 33 kg P ha^{-1}, 11 kg Mg ha^{-1}, and 16 kg Na ha^{-1} each year since 1856, both plots have also received 2250 kg CaO ha^{-1} once every 4 years since 1903 (table 1). The only difference between the two plots is that plot 9L has received 225 kg K ha^{-1} as potassium sulphate, and 96 kg N ha^{-1} as ammonium sulphate, annually since 1856 whereas 8L has not. This treatment has acidified the soil on plot 9L, so that in 1969 the soil *p*H on 9L was 5·3, compared with 7·0 on plot 8L. It has also increased the herbage yield on 9L, so that the mean annual dry matter yield of herbage between 1920 and 1959, was 5640 kg ha^{-1} on plot 9L but only 2160 kg ha^{-1} on plot 8L (Warren and Johnston, 1964). *A. odoratum* constituted 4·1 per cent of the herbage on plot 9L and 1·4 per cent on plot 8L in 1948 (Brenchley and Warington, 1958).

Differences in soil *p*H, across the boundary between the two plots, occur over a distance of less than 0·5 m (fig. 2A); differences in the height of

TABLE 1

Treatments imposed since 1856 on plots 8L and 9L of the Park Grass Experiment and the resulting effects on the vegetation and soil conditions

Plot	Contrasting treatments*	Common treatments*	Annual herbage yield (kg ha^{-1}) (1920-59)	*A. odoratum* % (1948)	Soil *p*H (1959)	Potassium content† (mg kg^{-1})
8L	225 kg K ha^{-1} yr^{-1} 96 kg N ha^{-1} yr^{-1}	33 kg P ha^{-1} yr^{-1} 11 kg Mg ha^{-1} yr^{-1} 16 kg Na ha^{-1} yr^{-1} 2250 kg Ca ha^{-1} 4 yr^{-1}	2160	1·4	7·0	5
9L	Nil		5640	4·1	5·3	77

* Full details of treatments in text.
† Extracted in water.

vegetation occur over a similar distance (fig. 2B) and closely follow the differences in soil *p*H. The boundary is perpendicular to the prevailing wind direction, so that pollen drift is likely to occur predominantly from 9L to 8L. Little seed is likely to be transmitted across the boundary because of the way the plots are harvested (G. V. Dyke, pers. comm.).

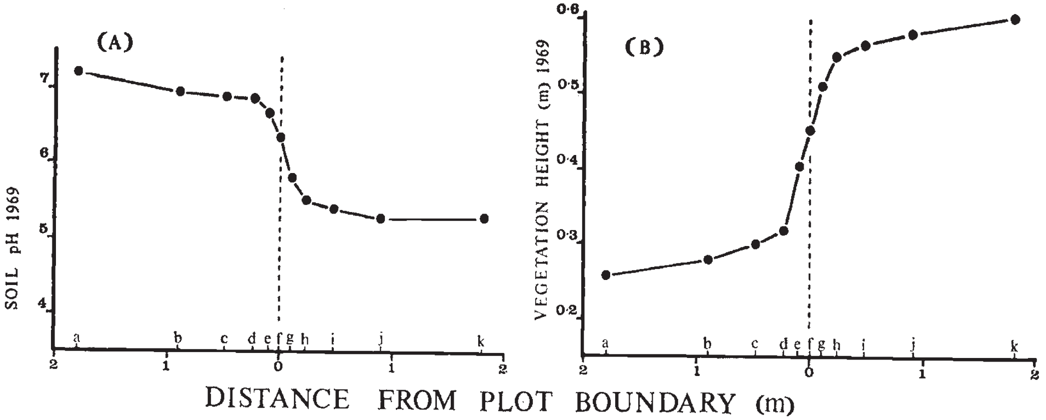

FIG. 2.—The soil *p*H (A) and vegetation height (B) along a transect across the boundary between plots 8L and 9L of the Park Grass Experiment. Soil *p*H was measured in a 1:2·5 suspension in water. The height of the vegetation was measured in June.

(b) *Populations*

Population samples of *A. odoratum* were collected from the 8L/9L boundary in June 1968. Samples were collected from zones of varying width on both sides of the boundary (table 2). The zones ranged from 0·1 m wide at the boundary, where environmental conditions varied over short distances (fig. 2A and B), to 1·2 m wide at each end of the transect, where conditions were more uniform. The zones extended for 35 m along the boundary.

Two tillers were collected from each of 15 randomly located plants in each sampling zone in June 1968. At the same time, seed was collected from each of these plants. Both tillers and seed were planted in " U.C.E.E."

potting compost and grown until May 1969, when rametes, each consisting of two tillers, were removed and planted into a spaced plant trial.

(c) *Experimental methods*

The spaced plant trial was a randomised block design with four replicates. Not all the plants that were collected provided sufficient material of both the tillers collection and seed collection; the number of plants per population in the spaced plant trial therefore varied between four (pop. i) and eleven (pop. e), but was usually eight. Morphological attributes of all the plants in the trial were measured periodically between 1969 and 1972.

TABLE 2

The location of sampling zones, from which population samples of A. odoratum *were collected, at the boundaries between plots 1U and 1L, and 8L and 9L of the Park Grass Experiment, Rothamsted*

Population	Plot	Distance from boundary (m)	Mean distance from boundary (m)
a	1U or 8L	1·20-2·40	1·80
b	1U or 8L	0·60-1·20	0·90
c	1U or 8L	0·30-0·60	0·45
d	1U or 8L	0·15-0·30	0·23
e	1U or 8L	0·05-0·15	0·10
f	Boundary	< 0·05 each side	0
g	1L or 9L	0·05-0·15	0·10
h	1L or 9L	0·15-0·30	0·23
i	1L or 9L	0·30-0·60	0·45
j	1L or 9L	0·60-1·20	0·90
k	1L or 9L	1·20-2·40	1·80

(d) *Statistical analysis*

Analyses of variance were carried out separately for each attribute and each population. The " genotypes within populations " mean square (Harberd, 1957) was used to calculate standard errors (S.E.) for each population. This error term is therefore based on the genetic variation within populations but contains a component due to experimental error.

(ii) *Results*

Comparisons of morphological differences between populations will be considered first for the tiller collection, then for the seed collection, and then the two sets of data will be compared.

(a) *Tiller collections*

Sharp differences between populations occurred for panicle height (fig. 3A and B) and yield per plant (fig. 3D) at, or close to, the boundary. Populations only 0·1 m apart differed significantly ($P < 0·05$) when compared with the genetic variation within populations. The pattern of differences between populations (fig. 3) followed quite closely the pattern of environmental variation at the boundary (fig. 2), so that there were significant correlations between morphological attributes of populations, grown as spaced plants, and environmental attributes measured on the plots (table 3).

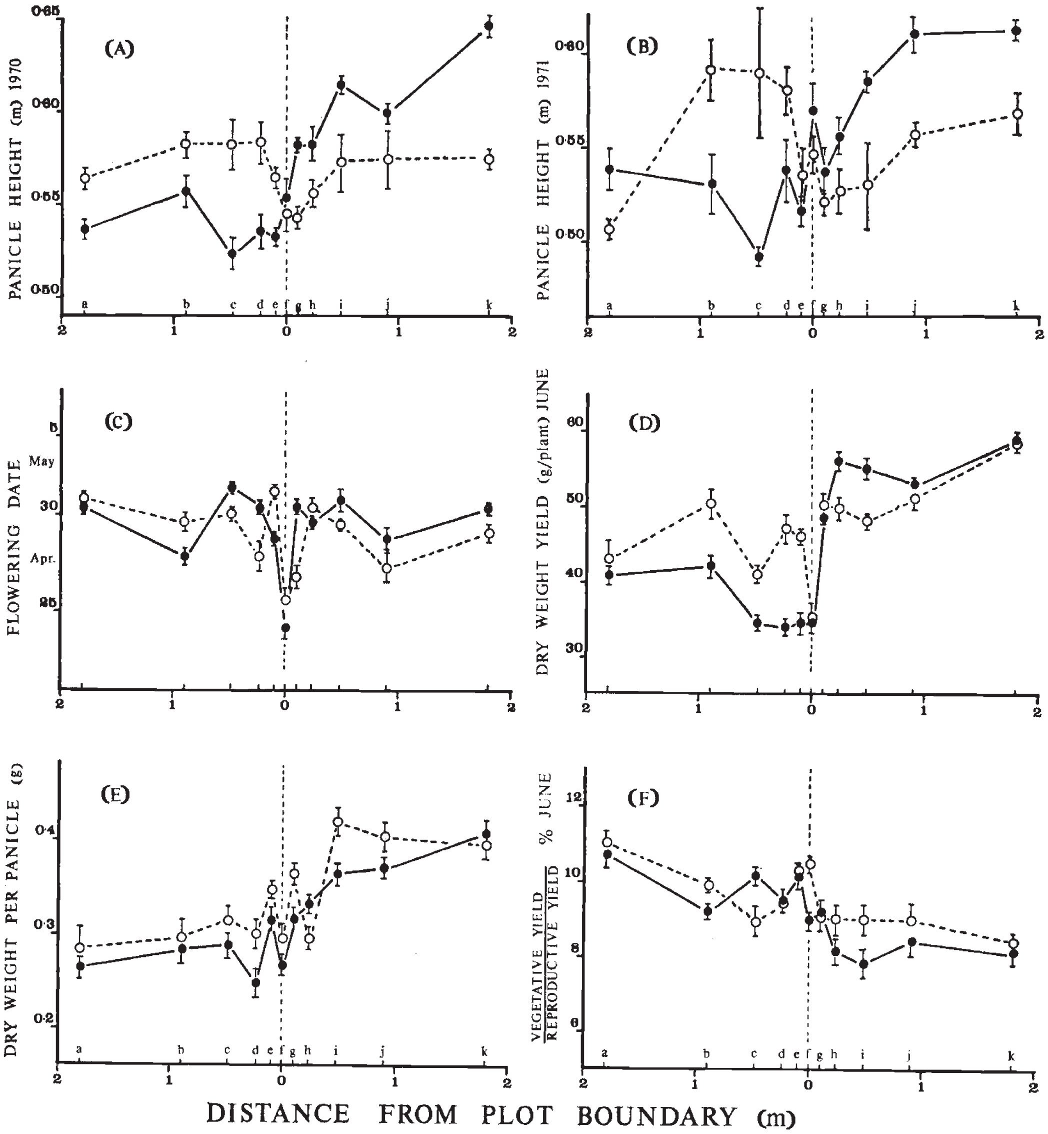

FIG. 3.—Differences between populations of *Anthoxanthum odoratum*, collected at various distances from the boundary between plots 8L and 9L, when grown in a spaced plant trial. (A) panicle height in June 1970; (B) panicle height in June 1971; (C) flowering date; (D) shoot dry weight; (E) dry weight per panicle; (F) ratio

$$\frac{\text{total weight of vegetative tillers} \times 100}{\text{total weight of reproductive tillers}}$$

○----○ populations collected as seed, ●——● populations collected as tillers. The standard errors for each population are based on the " genotypes within population " mean square.

Some morphological attributes, *e.g.* panicle weight (fig. 3E) and the ratio $\frac{\text{vegetative yield}}{\text{reproductive yield}}$ (fig. 3F), exhibited a more of less clinal pattern across the boundary, with few significant differences between adjacent populations, but with significant differences between the ends of the cline.

The pattern of flowering date (fig. 3C) differed from that of all other attributes; there was no significant difference between the populations at each end of the transect, but the boundary population (f) flowered approximately 6 days earlier than contiguous populations on each side.

TABLE 3

Correlations between morphological attributes of populations of A. odoratum, *collected at various distances from the boundary between plots 8L and 9L, and attributes measured in the zones from which they were collected. Figures in bold are for tiller populations, figures in italics are for seed populations*

Environmental attributes measured on plot	Morphological attributes of populations as spaced plants			
	Panicle height	Shoot dry weight	Weight per panicle	Ratio $\frac{\text{Vegetative yield}}{\text{Reproductive yield}}$
Height of vegetation	0·85**	0·78**	0·87**	−0·85**
	−0·31	*0·48*	*0·73*	*−0·56*
Panicle height of *A. odoratum*	0·94**	0·86**	0·89**	−0·86**
	−0·17	*0·59*	*0·78***	*−0·56*

** $P<0{\cdot}01$.

(b) *Seed collections*

Populations grown from seed, collected *in situ*, were generally as strongly differentiated as the tiller populations at the ends of the transect (fig. 3C-F), except for panicle height (fig. 3A and B). The patterns of variation for flowering date (fig. 3C) and panicle weight (fig. 3E) in seed collections were generally similar to those in tiller collections right across the transect. The pattern of variation for plant yield (fig. 3D) and the ratio $\frac{\text{vegetative yield}}{\text{reproductive yield}}$ (fig. 3F) was even more clinal in seed collections than in tiller collections. There was little difference between seed populations in panicle height though tiller populations differed markedly (fig. 3A and B). As a result of these differences between tiller and seed populations, morphological attributes of seed populations were not as closely correlated with environmental attributes as were those of tiller populations (table 3).

(c) *Comparison of tiller and seed collections*

The overall differences between tiller and seed collections of each population was estimated by calculating the percentage difference between the collections for each of 11 morphological attributes and then calculating the mean percentage difference (fig. 4).

Seed populations collected further than 0·5 m from the boundary on the 9L side (fig. 4) differed by less than 10 per cent from their parent tiller populations ($P>0{\cdot}05$). The differences between seed and tiller collections increased slightly, but not significantly, towards the boundary, then increased significantly on the 8L side of the boundary. At distances greater than

0·2 m from the boundary, on the 8L side, the differences between seed and tiller collections declined significantly, until at a distance of 1·8 m it was not significantly different from that on the 9L side.

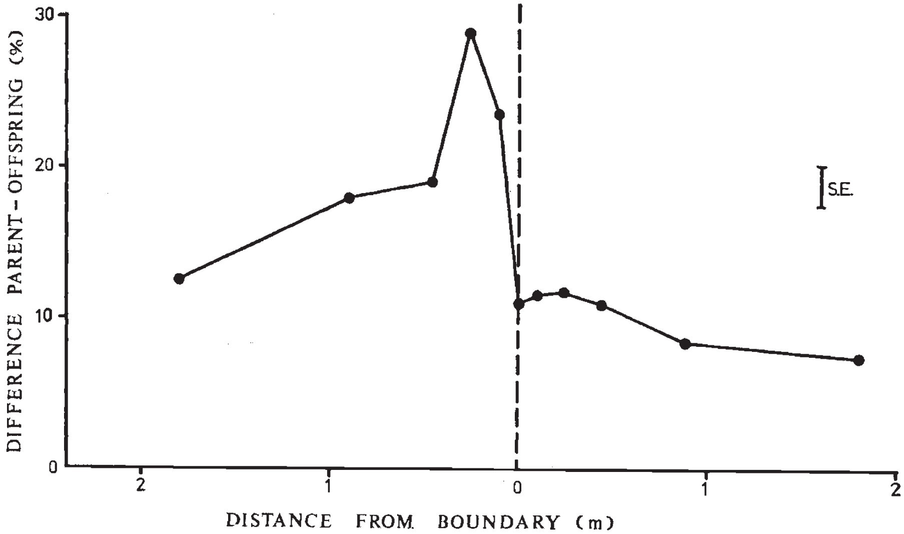

FIG. 4.—The percentage difference between seedling (progeny) populations and tiller (parent) populations collected at various distances from the boundary between plots 8L and 9L. The differences are averaged over 11 attributes and the standard error is based upon the attribute × population interaction mean square.

3. BOUNDARY 1L/1U

(i) *Materials and methods*

(a) *The site*

The whole of plot 1 (fig. 1) has received 48 kg N ha^{-1} year^{-1}, as ammonium sulphate, annually since 1856. The limed part (plot 1L) has received 2250 kg CaO ha^{-1} at 4-year intervals since 1903; the unlimed part (plot 1U) received only a single application (2250 kg CaO ha^{-1}) during the 1880's. The annual yield of herbage on plot 1L is about 40 per cent more than on plot 1U (table 4). *A. odoratum* constituted 0·2 per cent of the herbage yield on plot 1U and 1·4 per cent on plot 1L in 1948 (table 4).

TABLE 4

Treatments imposed on plots 1L and 1U of the Park Grass Experiment and the resulting effect on vegetation and soil conditions

Plot	Contrasting treatments*	Common treatment†	Annual herbage yield (kg ha^{-1}) (1920-59)	*A. odoratum* % (1948)	Soil *p*H (1959)
1L	2250 kg Ca ha^{-1} 4 yr^{-1}	48 kg N ha^{-1} yr^{-1}	2380	1·4	7·2
1U	Nil		1710	0·2	4·0

* Imposed since 1903.
† Imposed since 1856.

Lime applications have been made so carefully that differences in soil *p*H, at the boundary between the two plots, occur over a distance of less than 0·5 m (fig. 5A). The differences in the vegetation at the boundary are complex (fig. 5B); the height of the vegetation is greatest precisely at the boundary and decreases sharply on both sides, presumably because plant growth is normally greatest at soil *p*H 6-6·5 (Russell, 1973).

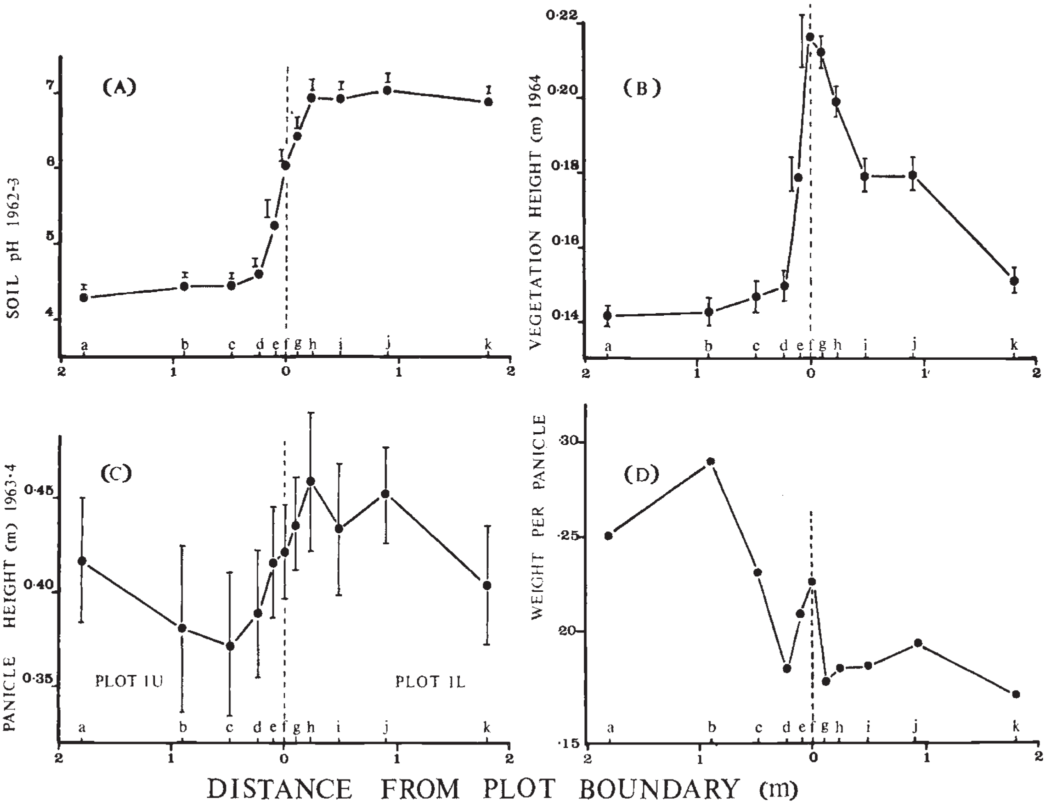

Fig. 5.—The soil *p*H (A), vegetation height (B), panicle height (C) and panicle weight of *A. odoratum* (D) along a transect across the boundary between plots 1L and 1U of the Park Grass Experiment. Soil *p*H was measured in a 1:2·5 suspension in water.

The prevailing wind direction is parallel to the boundary, so pollen drift across this boundary should be less than that at the 8L/9L boundary. However, there is probably considerable transmission of seed in both directions across the boundary, because of the way the plots are harvested (G. V. Dyke, pers. comm.).

(b) *Populations*

Population samples of *A. odoratum* were collected from the boundary between plots 1L and 1U in May 1962, and again in June 1963. A similar sampling procedure was used to that described for the 8L/9L boundary (table 2). The total length of each sampling zone was 11 m.

Two tillers were collected from each of 15 randomly located plants within each of the 11 zones. In 1963 the panicle height of each of the sampled plants was measured at the time of sampling. The sample plants, collected in 1962 and 1963, were grown in John Innes potting compost for 6 months and 4 months respectively before being used for experimental purposes.

(c) *Experimental methods*

Two-tiller rametes were removed from five random genotypes of each of the populations from the first collection and planted in boxes of calcareous and acid soil during November 1962. A double split-plot layout with six replicates was used; soils constituted the first split and populations the second. Dry matter yield was measured in February 1963; the results are expressed as yield on acid soil relative to that on calcareous soil (fig. 6F).

Two-tiller rametes from 10 random genotypes of each of the populations from the second collection were planted into a spaced plant trial in October 1963. A randomised block design with three replicates was used. Measurements of various attributes were made during 1964 (fig. 6A-E).

(ii) *Results*

Contiguous populations collected only 0·1 m apart at the boundary of plots 1U and 1L were morphologically different, when grown in uniform conditions (fig. 6). All attributes showed a major discontinuity at the boundary, or within 0·25 m of it. For most characters, there were no significant differences between populations further than 0·5 m from the boundary on each side. Some characters, *e.g.* dry weight yield, rust score, and response to soils (fig. 6B, D, E and F), showed the " reverse cline " pattern previously observed at boundaries between insect populations (Ford, 1971, p. 83); populations close to the boundary, on each side, were more dissimilar than those at the ends of the transect.

The actual pattern of variation between populations varied from attribute to attribute. The simplest pattern was for flowering date (fig. 6C), where only one population (g) differed significantly from others; it flowered 4 days earlier than contiguous populations. This pattern was similar to that at boundary 8L/9L (fig. 3C).

The patterns of variation for panicle height (fig. 6A) and panicle weight (fig. 6D) were similar to each other and were somewhat like that for rust score (fig. 6E), though the peak was slightly displaced. The pattern of these three attributes was similar to that of the height of the vegetation on the plots (fig. 5B), though again the peaks were not coincident. The pattern of variation for panicle height (fig. 6A) was also quite similar to that for panicle height on the plots (fig. 5C) though none of the latter differences was significant. In contrast, the pattern of panicle weight (fig. 6D) was totally unlike that on the plots (fig. 5D).

The patterns of variation in plant yield (fig. 6B) and response to contrasting soils (fig. 6F) were similar to each other, but unlike the patterns for other attributes or environmental variables. These two attributes showed the most marked " reverse cline " effect.

The complex patterns of morphological variation (fig. 6) were either not closely similar to those of environmental variation (fig. 5), or were laterally displaced, as a result there were no significant correlations between morphological attributes and environmental variables such as occurred at the 8L/9L

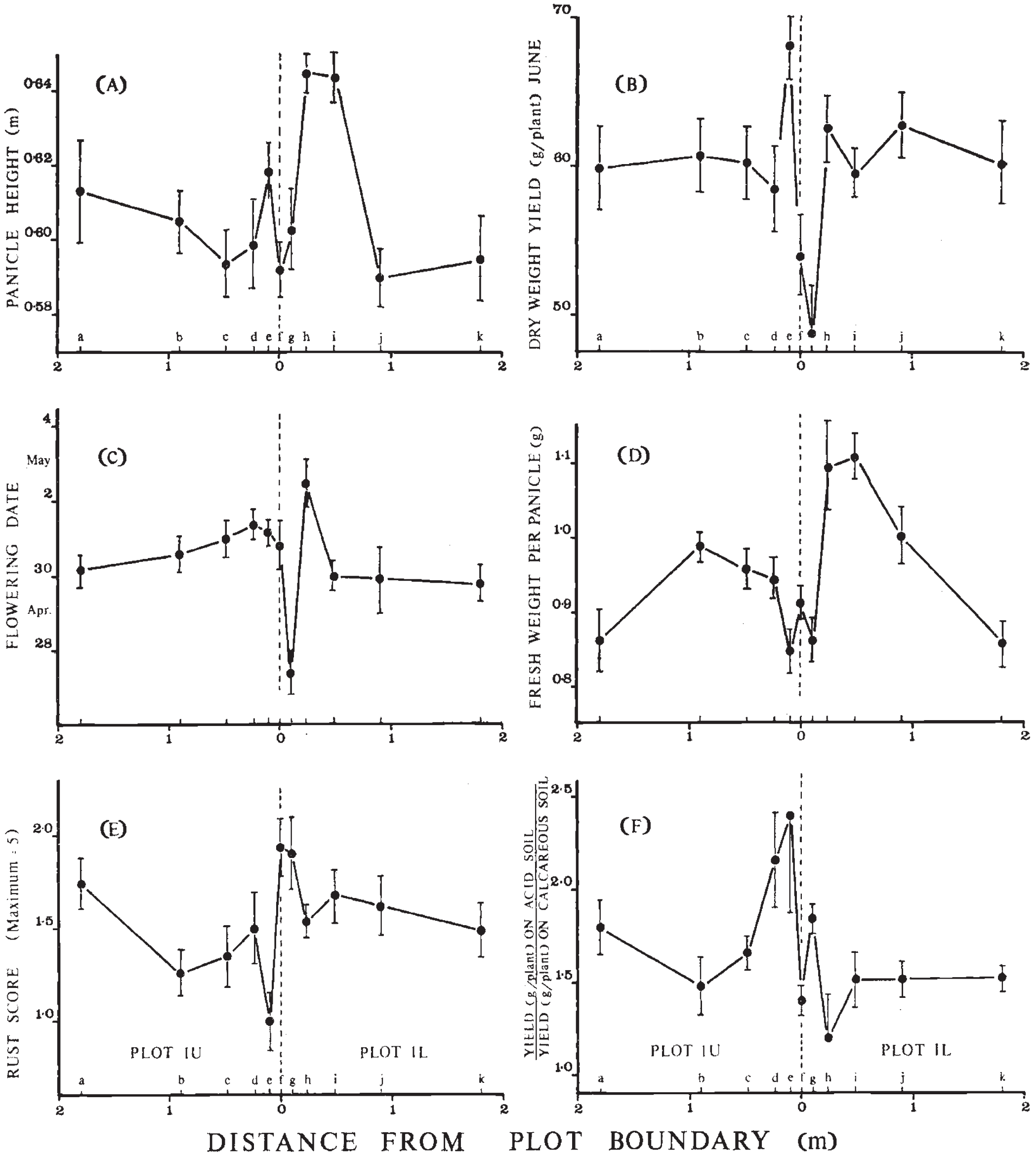

Fig. 6.—Differences between populations of *Anthoxanthum odoratum* collected at various distances from the boundary between plots 1U and 1L of the Park Grass Experiment, Rothamsted, when grown in a spaced plant trial (A-E) or in boxes (F). (A) Panicle height (June); (B) total shoot weight (June); (C) flowering date (April-May); (D) weight per panicle (June); (E) rust score (August); (F) relative yield on acid and calcareous soils (November-February). The individual S.E.'s for each population are based on the " genotypes within population " mean square.

boundary (table 3). The panicle height of genotypes within each population, when grown the spaced plant trial, could be compared with that of the same plants measured *in situ* on the plots at collection. In the boundary population, and in the populations at the 1U end of the transect, genotypes performed similarly in the trial and *in situ* (fig. 7). Other populations showed no such correlation.

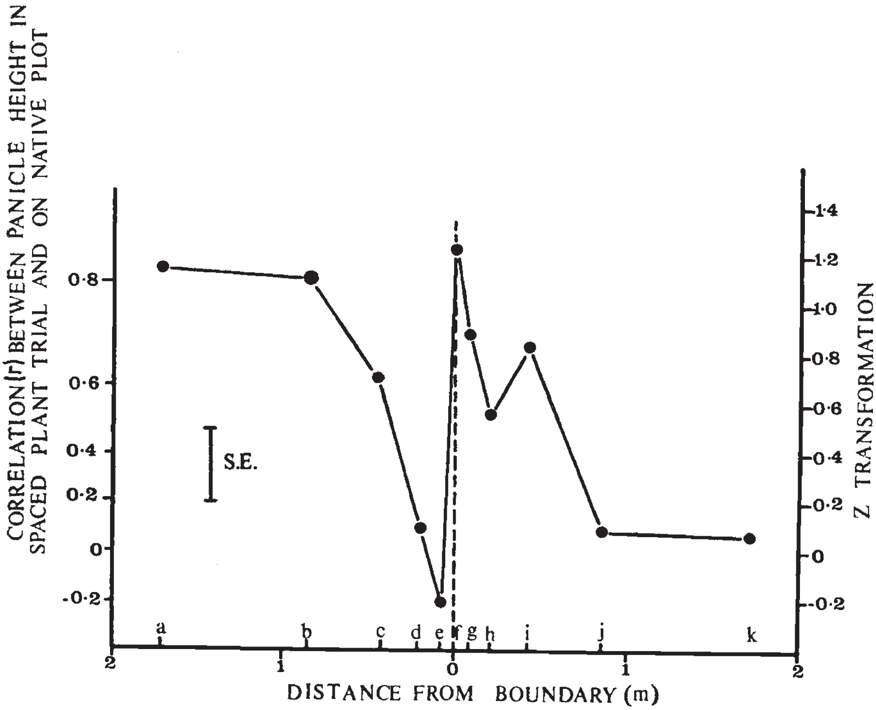

FIG. 7.—The correlation between the panicle height of *A. odoratum* plants when collected at various distances from the boundary between plots 1U and 1L, and the panicle height of the same plants when grown in a spaced plant trial. Both *r* values and *z* transformations are indicated on the vertical axis.

4. DISCUSSION

(i) *Boundary 8L/9L*

(a) *Spatial differences*

Populations only 0·1 m apart differed significantly in a number of attributes. These sharp differences are surprising since the sampled zone at the boundary, where differences were sharpest, was 0·1 × 35 m. The differences are unlikely to be due to duplication of a restricted number of genotypes (Harberd, 1961), since the length of sampling zones was between 30 and 350 times greater than the width of the zone. If only a few genotypes occurred, then they must have spread vegetatively along the narrow zones. This is unlikely because *A. odoratum* has a tufted habit and a half-life of only 2 years (Antonovics, 1972; Davies and Snaydon, 1976). If vegetative spread did occur along the narrow zones, it would imply intense selection in the vegetative phase. For similar reasons, it seems unlikely that the sharp differences are due to the survival and vegetative spread of highly adapted individuals from an original population, or to random differences between founder plants.

The differences between populations do not appear to be due to somatic differences (Breese *et al.*, 1965; Hayward and Breese, 1966, 1968), since they were generally transmitted by seed (fig. 3C-F), except perhaps for differences in panicle height (fig. 5A and B). Similarly, the differences are unlikely to be due to carry-over of phenotypic modification from the field, since they were usually seed transmitted and were maintained through two tiller generations and 3 years in spaced plant trials (*e.g.* fig. 3A and B).

The pattern of morphological variation at the boundaries is unlikely to be due to migration of genotypes towards the boundary, following allopatric divergence of populations on the adjacent plots (Heslop-Harrison, 1956; Briggs, 1962), since there is little vegetative spread of plants, plants are relatively short lived (see above), and crossing will tend to occur between zones (see below). It seems more likely that the pattern of morphological variation at the boundaries is a dynamic one, determined by the continuing interaction of selection, recombination and gene flow. The sharp differences between populations at the boundaries imply intense selection pressures and/or limited gene flow between populations.

(b) *Gene flow*

The comparison of differences between parent (tiller) populations and progeny (seed) populations (fig. 4) indicated that gene flow was greatest 0·2 m downwind from the boundary. This pattern was most apparent for plant height and weight (fig. 3A, B and D) but was also apparent for other attributes (*e.g.* fig. 3C and E).

Some of the differences between seed and tiller populations, *e.g.* panicle height in populations b, c and d (fig. 3A, B and D) might be attributed to hybrid vigour in offspring from wide crosses. This does not invalidate the conclusion that gene flow between plots is mainly limited to populations less than 1 m from the boundary, since populations more than 1 m from the boundary should also express hybrid vigour, if cross-pollination occurred.

The apparent absence of gene flow into the boundary population (population f, fig. 4) is at first surprising, particularly since the population was collected from a zone only 0·1 m wide but 35 m long. The population was significantly differentiated from upwind populations for most attributes (fig. 3A-E), and ought therefore to be susceptible to change by gene flow. The answer may lie in the fact that this population flowers 6 days earlier (fig. 3C), and completes the flowering process more rapidly (Snaydon, 1973) than adjacent populations. It may therefore be, in part, reproductively isolated from surrounding populations and therefore less subject to gene flow.

(c) *Selection pressure*

The close correlation between various morphological attributes in the trial and the height of the vegetation in the zone from which they were collected (table 3) may be regarded as evidence of intense selection pressure, provided the differences between populations are genetically determined and not due to phenotypic modification (see above).

A. odoratum is a short-lived perennial, dependent upon seed establishment for its continued occurrence, therefore intense selection must act on those populations (*e.g.* c, d and e) where gene flow was greatest and where offspring differed significantly from parents (figs. 3 and 4). Reciprocal transplant experiments carried out on several plots of the Park Grass Experiments (Davies and Snaydon, 1976) indicate the magnitude of this selection. In those experiments, selection coefficients between 0·15 and 0·65 were measured on established plants; we have no measure of the selection pressures acting upon seedlings.

(ii) *Boundary 1L/1U*

Populations at the 1L/1U boundary (fig. 6), like those at the 8L/9L boundary (fig. 3), differed even if collected only 0·1 m apart. However, the patterns of variation at the 1L/1U boundary were very different from those at the 8L/9L boundary. Whereas the patterns at the 8L/9L boundary (fig. 3) were relatively simple and generally followed the pattern of environmental conditions, the patterns at the 1L/1U boundary (fig. 6) varied between attributes, were generally more complex, and were only very loosely related to the pattern of environmental conditions (fig. 5). This is not altogether surprising in view of the complex effects of environmental conditions on the vegetation (fig. 5B) and on *A. odoratum in situ* (fig. 5C and D).

One attribute, flowering date, showed a remarkably similar pattern at both boundaries (figs. 3C and 5C). The possible importance of this variation in flowering date on reproductive isolation has already been considered.

The pattern of variation of panicle height (fig. 6A) and panicle weight (fig. 6D) in the spaced plant trial was fairly similar to that of vegetation height on the source sites (fig. 5B) but slightly displaced. We conclude that the pattern is largely determined by selection, but that it has been shifted laterally, by asymmetrical gene flow, in the way described by Endler (1973). Little pollen drift is likely across the boundary, but there is likely to be considerable seed dispersal because of harvesting methods (G. V. Dyke, pers. comm.). Seed dispersal will produce double the gene flow of pollen drift, since the genomes of both parents are dispersed.

There was considerable variation in panicle height between genotypes within populations when measured *in situ* (fig. 5C), but less variation when grown as spaced plants (fig. 6A). It would seem that much of the variation *in situ* was due to phenotypic variation, and therefore it is not surprising that there was generally little correlation between panicle height of genotypes *in situ* and in the trial (fig. 7). This lack of correlation again points to the probable unimportance of carry-over of phenotypic modification.

Marked " reverse cline " patterns (Ford, 1971) were apparent for dry weight yield (fig. 6B) and response to contrasting soils (fig. 6F). This pattern has been previously observed at boundaries between insect populations (Ford, 1971; Handford, 1973) and snail populations (Bailey, 1956). Ford (1971) has suggested that the phenomenon may occur because " selection is eliminating to a disproportionate degree the less precisely adapted intermediates between (populations) ", and that the subsequent development of reproductive isolation may enhance the distinction. This hypothesis fails to explain the phenomenon. Elimination of hybrids or intermediates will not, of itself, cause greater differences between the adjacent populations. However, competition between the two populations in the zone of overlap could lead to greater niche specificity and therefore to greater differences. This would only be detected if the two subpopulations could be separately identified, otherwise the measured values would be means of the two subpopulations and therefore intermediate. In addition, the subpopulations would only remain discrete if reproductive isolation occurred. In the situation studied here, the subpopulations could not be separately identified, even if they existed, and there is no evidence of reproductive isolation between most populations (R. W. Snaydon unpublished). These hypotheses therefore fail to explain the phenomenon. Other hypotheses, such as greater genetic diversity and hybrid vigour in boundary populations, caused by greater gene flow, also fail to fully explain the phenomenon.

(iii) *General considerations*

Previous studies (Aston and Bradshaw, 1966; McNeilly, 1968; Watson, 1969; Antonovics and Bradshaw, 1970) have shown that morphological differences can occur between plant populations only a few metres apart. The results presented here indicate that significant differences can occur over distances of only 0·1 m, provided the environmental conditions change sufficiently sharply.

The steepness of the cline seemed to be determined more by the steepness of the change in environmental conditions, than by the effects of gene flow. Gene flow mainly occurred over distances of less than 1 m (fig. 6), and even within this range its effects seemed to be largely negated by subsequent selection (fig. 3). This occurs in a species which should be subject to considerable gene flow, since it is relatively short-lived and is wind pollinated.

The steepness of the cline across the boundaries was different for the various plant attributes. For example, dry weight yield at boundary 8L/9L (fig. 3D) changed sharply close to the border, but weight per panicle (fig. 3E) changed clinally. This presumably reflects differences in selection pressure, and perhaps mode of inheritance, since gene flow should be similar for both attributes.

The steepness of the cline would also depend on the duration and stability of the selection pressures involved. The treatments at the 8L/9L boundary had been imposed annually for 112 years, but those at the 1L/1U boundary had been imposed for only 60 years and then only at 4-year intervals. Conditions at the 1L/1U boundary may therefore be less stable; this may in part account for the generally greater genetic variation within populations (cf. figs. 3 and 6) and the less distinct differences between populations.

The fertiliser and liming treatments imposed on the Park Grass Experiment probably produce sharper and more stable differences between environments than normally occur in the wild, but these plots are also prone to environmental fluctuations that may modify selection and gene flow. Year to year variations in climate affect the relative density of *A. odoratum* (Brenchley and Warington, 1958; E. D. Williams, pers. comm.), and the yield and height of vegetation (E. D. Williams and J. Thurston, unpublished data); they are therefore likely to influence selection pressures within each plot. The management regime of two cuts per year will also cause fluctuations in the selection pressures within each year. Fluctuations in climate also affect the relative flowering date and seed production on adjacent plots (E. D. Williams, pers. comm.), as well as the magnitude and direction of pollen drift; these fluctuations probably cause differences in gene flow from year to year.

The pattern of morphological variation at the two boundaries is apparently determined by selection, gene flow and by dynamic interactions between these two factors. Selection can directly affect gene flow, through its effect on reproductive isolation, *e.g.* in the case of flowering date (figs. 3C and 6C). Selection may also indirectly affect gene flow, by its affect on the relative density, genetic composition, reproductive strategy and longevity of *A. odoratum* in the various zones. Conversely, gene flow may influence selection through its affects on the genetic structure of populations. More information is needed on the genetic and ecological processes involved in selection, gene flow and their interactions.

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5. REFERENCES

ANTONOVICS, J. 1972. Population dynamics of the grass *Anthoxanthum odoratum* on a zinc mine. *J. Ecol.*, *60*, 351-365.

ANTONOVICS, J., AND BRADSHAW, A. D. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity*, *25*, 349-362.

ASTON, J. L., AND BRADSHAW, A. D. 1966. Evolution in closely adjacent plant populations. II. *Agrostis stolonifera* in maritime habitats. *Heredity*, *21*, 649-664.

BAILEY, D. W. 1956. Re-examination of the diversity in *Partula taeniata*. *Evolution*, *10*, 360-366.

BREESE, E. L., HAYWARD, M. D., AND THOMAS, A. C. 1965. Somatic selection in perennial ryegrass. *Heredity*, *20*, 367-379.

BRENCHLEY, W. E., AND WARINGTON, K. 1958. *The Park Grass Plots at Rothamsted, 1856-1949.* Rothamsted Exptl. Sta., Rothamsted.

BRIGGS, B. G. 1962. Interspecific hybridization in the *Ranunculus lappaceus* group. *Evolution*, *16*, 372-390.

CREED, E. R., DOWDESWELL, W. H., FORD, E. B., AND MCWHIRTER, K. G. 1959. Evolutionary studies on *Maniola jurtina*. The English mainland, 1956-57. *Heredity*, *13*, 363-391.

DAVIES, M. S., AND SNAYDON, R. W. 1973*a*. Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment, Rothamsted. I. Response to calcium. *J. appl. Ecol.*, *10*, 33-45.

DAVIES, M. S., AND SNAYDON, R. W. 1973*b*. Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment, Rothamsted. II. Response to aluminium. *J. appl. Ecol.*, *10*, 47-55.

DAVIES, M. S., AND SNAYDON, R. W. 1974. Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment, Rothamsted. III. Response to phosphate. *J. appl. Ecol.*, *11*, 669-707.

DAVIES, M. S., AND SNAYDON, R. W. 1976. Rapid population differentiation in a mosaic environment. III. Coefficients of selection. *Heredity*, *36*, 59-66.

ENDLER, J. A. 1973. Gene flow and population differentiation. *Science*, *179*, 243-250.

FORD, E. B. 1971. *Ecological Genetics*, 3rd edition. Methuen & Co., London.

GRIFFITHS, D. J. 1950. The liability of seed crops of perennial ryegrass (*Lolium perenne*) to contamination by wind borne pollen. *J. agric. Sci., Camb.*, *40*, 19-38.

HANDFORD, P. T. 1973. Patterns of variation in a number of genetic systems in *Maniola jurtina*: the boundary region. *Proc. R. Soc. Lond. B*, *183*, 265-284.

HARBERD, D. J. 1957. The within population variance in genecological trials. *New Phytol.*, *56*, 269-280.

HARBERD, D. J. 1961. Observations on population structure and longevity in *Festuca rubra*. *New Phytol.*, *60*, 184-206.

HARPER, J. L. 1967. A Darwinian approach to plant ecology. *J. Appl. Ecol.*, *4*, 267-290.

HAYWARD, M. D., AND BREESE, E. L. 1966. The genetic organisation of natural populations of *Lolium perenne*. I. Seed and seedling characters. *Heredity*, *21*, 287-304.

HAYWARD, M. D., AND BREESE, E. L. 1968. The genetic organisation of natural populations of *Lolium perenne*. III. Productivity. *Heredity*, *23*, 357-368.

HESLOP-HARRISON, J. 1956. Some observations on *Dactylorchis incarnata* L. *Proc. Linn. Soc. Lond. Session*, *166*, 51-83.

HESLOP-HARRISON, J. 1964. Forty years of genecology. *Adv. Ecol. Res.*, *2*, 159-247.

JAIN. S. K., AND BRADSHAW, A. D. 1966. Evolutionary divergence among adjacent plant populations. 1. The evidence and its theoretical analysis. *Heredity*, *21*, 407-441.

MCNEILLY, T. 1968. Evolution in closely adjacent plant populations. III. *Agrostis tenuis* on a small copper mine. *Heredity*, *23*, 99-108.

RUSSELL, E. W., 1973. *Soil Conditions and Plant Growth*, 10th edition. Longman, London.

SNAYDON, R. W. 1970. Rapid population differentiation in a mosaic environment. I. The response of *Anthoxanthum odoratum* populations to soils. *Evolution*, *24*, 257-269.

SNAYDON, R. W. 1973. Ecological factors, genetic variation and speciation in plants. In *Taxonomy and Ecology*, ed. V. H. Heywood, pp. 1-29. Academic Press, London.

SNAYDON, R. W., AND DAVIES, M. S. 1972. Rapid population differentiation in a mosaic environment. II. Morphological variation in *Anthoxanthum odoratum*. *Evolution*, *26*, 390-405.

STREAMS, F. A., AND PIMENTAL, D. 1961. Effects of immigration on the evolution of populations. *Am. Nat.*, *95*, 201-210.

THODAY, J. M., AND BOAM, T. B. 1959. Effects of disruptive selection. II. Polymorphism and divergence without isolation. *Heredity*, *13*, 205-218.

THURSTON, J. M. 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland. In *Ecological Aspects of the Mineral Nutrition of Plants*, ed. I. H. Rorison, pp. 3-10. Blackwell Scientific Publications, Oxford.

WARREN, R. G., AND JOHNSTON, A. E. 1964. The Park Grass Experiment. *Rep. Rothamsted Exp. Sta.*, 1963, 240-262.

WATSON, P. J. 1969. Evolution in closely adjacent plant populations. VI. An entomophilous species, *Potentilla erecta*, in two contrasting habitats. *Heredity*, *24*, 407-422.