EVOLUTIONARY DIVERGENCE AMONG ADJACENT PLANT POPULATIONS

I. THE EVIDENCE AND ITS THEORETICAL ANALYSIS

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1. INTRODUCTION

Population studies on the pattern of variation in many plant species have revealed the existence of localised races or ecotypes each adapted to the particular environmental conditions of its habitat. The pattern of microgeographical differentiation among such local races is, however, very often complex, as shown by the distribution of gene frequencies or of quantitative characters. In a species with more or less continuous distribution, there may be clines of varying slopes interspersed with rather sharp discontinuities corresponding to changes in the environment. Such a pattern of variation is perhaps best termed a graded patchwork and has been reported in *Agrostis tenuis* (Bradshaw, 1959), *Eschscholtzia californica* (Cook, 1962) and other examples cited by these workers. As shown by Epling and Dobzhansky (1942) in *Linanthus parryae*, as well as by many other workers, the larger geographic subdivisions may give a greater degree of genetic divergence than the smaller microgeographic subdivisions. Therefore, in many reports on the discontinuous patterns of ecotypic variation, a rather small number of widely spaced sampling sites might have been involved, giving an erroneous picture of the true situation (Bradshaw, 1962).

It has been argued frequently that a geographical discontinuity of species distribution is a prerequisite at one stage or another for the occurrence of any marked local differentiation, since any interchange of genes through pollen or seed dispersal is likely to counterbalance the divergent local pressures that might be operating in various neighbourhoods (*e.g.* Dowdeswell and Ford, 1953; Mayr, 1963). The experimental evidence from studies on several plant species (Gregor, 1930 in *Plantago*; Ehrendörfer, 1953 in *Galium*; Bradshaw, 1959 in *Agrostis*; also see Grant, 1963; and Cook, 1962) and certain animal species (Sheppard, 1952 in *Cepaea*; Creed, Ford and McWhirter, 1964 in *Maniola*) suggests that within a continuous range of distribution and under panmixia, the distance separating contrasting populations near the extreme ends of a cline can be as small as 50 to 100 metres, distances over which gene flow can easily occur.

Clearly, the amount and nature of any such differentiation depends on the opposing forces of selection and gene flow, as well as on many other factors. There have been several discussions of this problem (Wright, 1931, 1951; Mather, 1955; Stebbins, 1964). Recently, the work of Thoday and Boam (1959) and Streams and Pimentel (1961) in *Drosophila* has shown clearly that disruptive selection could outweigh the effects of as high as 50 per cent. gene flow between two sub-populations.

However, to our knowledge very little has been done in the past on the study of natural variation in plant species as maintained under joint effects of migration and selection with quantitative data on such factors as rate and form of gene flow, multiplicity of niches, population density, gene frequency distribution, etc. In several recent studies of plant populations, parallel to those initiated by Bradshaw (1959, *et seq.*) in *Agrostis*, data have been gathered on the pattern of variation of tolerance to certain toxic elements and to other analogous ecological factors. We are very grateful to T. S. McNeilly, P. D. Putwain, J. L. Aston and R. W. Snaydon for their kind permission to make use of some of their largely unpublished data in developing a genetic model to simulate these situations (detailed accounts of these situations are in preparation). In the first part of this paper the various examples are briefly described in order to provide some basis for the choice of a model and the numerical values of certain parameters. The genetic model presented in the second part of this paper was used as the first step in studying the joint effects of some of these variables on clinal variation patterns.

2. EXAMPLES

Example 1.—Agrostis tenuis *on Goginan Mine* (*data of A. D. Bradshaw*)

Agrostis tenuis Sibth., Bent or Browntop, is a common perennial grass, occupying a wide variety of habitats in temperate regions. It is wind pollinated and self incompatible. It has been shown to have evolved populations in the neighbourhood of old mine workings possessing tolerance to various heavy metals. Such tolerance does not appear to be able to be induced by conditioning processes, is not lost in cultivation in absence of the metal, and is heritable, (Bradshaw, McNeilly and Gregory, 1965). One such case is the population to be found on the Goginan lead mine near Aberystwyth (Bradshaw, 1960). Since tolerant and non-tolerant populations had been found within a distance of 100 metres, a series of populations were collected along a transect across the mine boundary where the lead contaminated toxic area ended very abruptly and gave way to normal pasture within a few feet. The sharpness of the boundary was indicated by observations on the natural vegetation, and determinations of levels of lead in the soil.

Agrostis tenuis was fairly uniformly scattered along the transect. On the mine the individual plants formed small patches about 1 metre apart, growing in an area otherwise devoid of vegetation because of the toxicity of the soil. In the adjacent pasture the plants were somewhat more frequent, growing in a normal, continuous grassland cover. Although *Agrostis tenuis* is perennial, some deaths and replacement of a certain proportion of the entire population would seem to occur annually in both habitats, particularly on the mine area.

The sampling was by collection of 20 tillers at random over areas 5 metres × 25 metres whose long axis were at right angles to the transect. These were grown on and planted out in a randomised block layout in a garden for 2 years. They were then tested for lead tolerance using the technique of Jowett (1964) using solutions containing 15 p.p.m. lead and ½ gm./litre calcium nitrate. The tolerances of the populations and the distances between them are given in fig. 1.

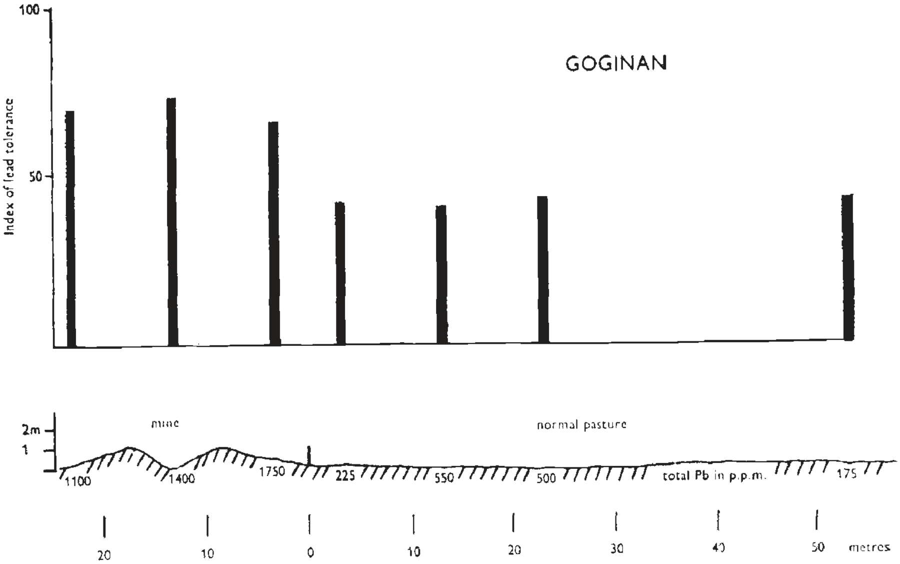


FIG. 1.—*Agrostis tenuis* on Goginan lead mine (tolerance to lead).

FIGS. 1-5.—The patterns of differentiation of populations of a number of plant species across marked ecological boundaries (upper graphs—character concerned: lower graphs—topography of sites).

A very sharp transition over the 20 metres separating the two populations on each side of the boundary can be seen. It is particularly interesting that these two populations have the same levels of tolerance as the populations considerably further away from the boundary. The latter have tolerances typical of fully tolerant and intolerant populations respectively.

Example 2.—Agrostis tenuis *on Drws-y-coed copper mine (data of T.S. McNeilly)*

Agrostis tenuis can also develop natural populations tolerant to copper (Bradshaw, McNeilly and Gregory, 1965). One such population is that found growing on a disused copper mine working at Drws-y-coed, near Rhyd-ddu, North Wales. The contaminated area is small, about 100 m. × 400 m., and is surrounded by a typical upland grassland containing *Agrostis tenuis* and *Festuca ovina*. On the contaminated area *A. tenuis* forms a more or less continuous turf with the exception of site 1 where, similar to Goginan, the plants are scattered, with bare ground in between.

The sampling followed the same pattern as that for Goginan except that the individual areas sampled were closer together and were smaller (3m. × 10 m.); again 20 individuals were taken from each area. The same method of testing was used, but with a solution containing 0·5 p.p.m. copper. The individual genotypes were replicated so that the tolerance of each genotype could be determined; therefore not only the means but also the coefficients of variability of the populations are given in fig. 2.

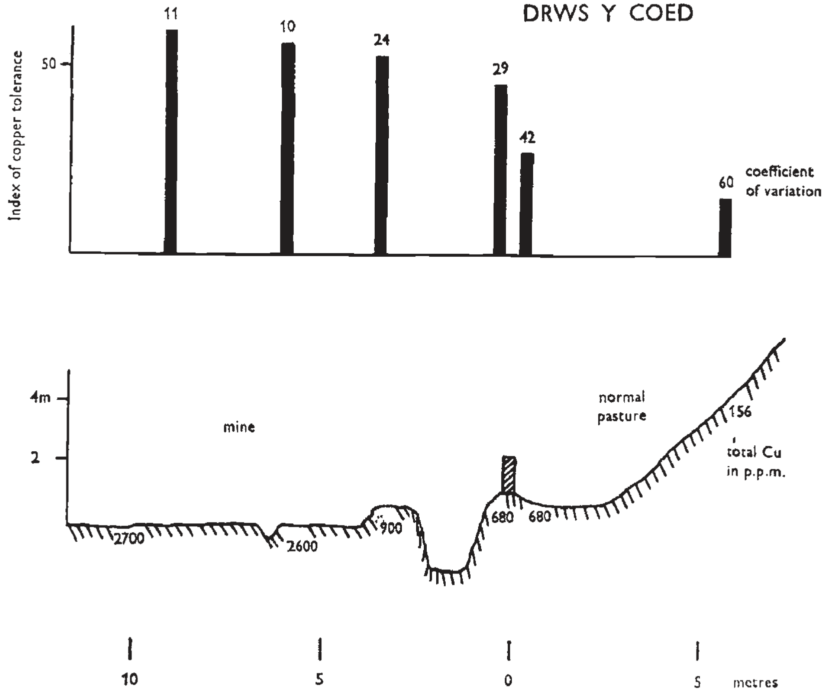


FIG. 2.—*Agrostis tenuis* on Drws-y-Coed copper mine (tolerance to copper).

A very sharp transition over a few metres from fully tolerant to normal intolerant populations is to be seen, similar to that for the previous example. At the same time there is a significantly higher variance in the populations at the ecological transition point.

Example 3.—Anthoxanthum odoratum *on Trelogan zinc mine (data of P.D. Putwain)*

Anthoxanthum odoratum, Sweet Vernal, has been shown to develop marked tolerance to zinc where it grows on the group of calcareous lead and zinc mines in N.E. Wales (Gregory and Bradshaw, 1965). It is a perennial, self incompatible, wind pollinated grass like *Agrostis tenuis*, but differs in being less markedly perennial. On poor habitats where extreme conditions may occur, such as old mine workings, it appears to survive for only two or three years, and replacement from new seedlings can easily be seen. In grassland, it perhaps survives longer.

A series of populations were collected over a sharp boundary between the mine workings at Trelogan, Flintshire and a normal pasture. The mine workings are covered by a variety of species. There is, however, a considerable quantity of bare ground. The adjoining pasture is a typical low grade lowland pasture, fairly heavily grazed, with only a small amount of *Anthoxanthum*.

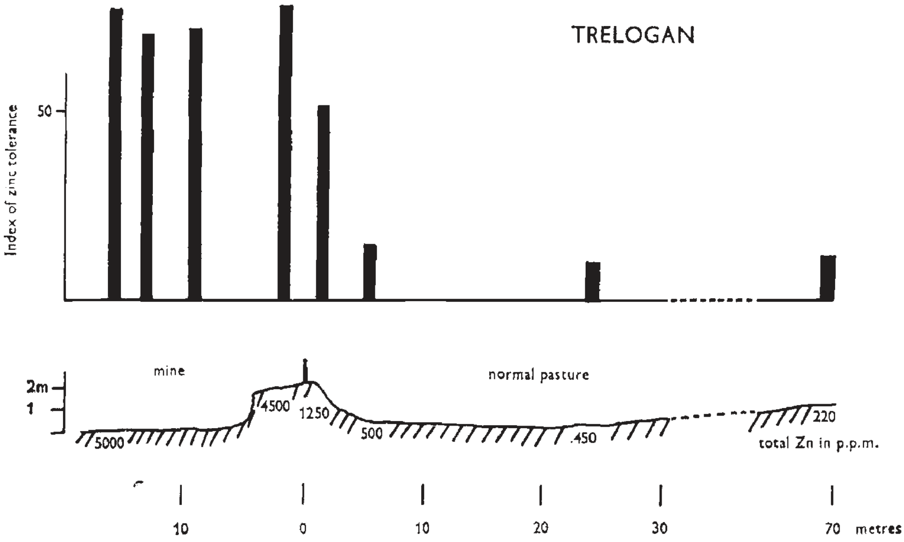


FIG. 3.—*Anthoxanthum odoratum* on Trelogan zinc mine (tolerance to zinc).

The sampling followed the pattern as in the previous case, but about 30 tillers were taken at random from each area, and these were grown on for 3 months in ordinary soil in a greenhouse. Tillers were then taken at random from this material and tested in the same manner as previously, using solutions containing 15 p.p.m. zinc. The mean tolerance levels of various samples are given in fig. 3.

A pattern of differentiation similar to that demonstrated previously can again be seen. The populations at each end of the transect show the maximal extremes of tolerance and intolerance.

Example 4.—Agrostis stolonifera *on sea cliffs at Abraham's Bosom (data of J. L. Aston)*

Agrostis stolonifera, Creeping Bent, is closely related to *Agrostis tenuis* and is similarly perennial and self incompatible, but differs in being markedly more stoloniferous. It is found occurring commonly in a variety of fertile permanent pastures, where its stolons ramify through the vegetation. It occurs also growing in crevices and pockets of earth on exposed, bare sea cliffs. The populations in such situations have a very different morphology; the plants are tufted, and the stolons are much shorter due to a reduction in internode length. This character is retained in cultivation, is heritable, and appears to be an adaptation to exposure to wind (Aston, 1962).

Populations were sampled along a transect which went from an exposed cliff into protected pastures (fig. 4). All the populations at the cliff foot and up to the cliff top edge suffer severe wind exposure; the rest do not. *A. stolonifera* is very abundant as tufts or patches over the area on the bare cliff or in the pasture (about 4 plants per sq. metre). The sample areas were the same as in the other investigations with *Agrostis*. Twenty plants were taken from each site. These were put into trial under garden conditions and the mean stolon length of the populations determined (fig. 4).

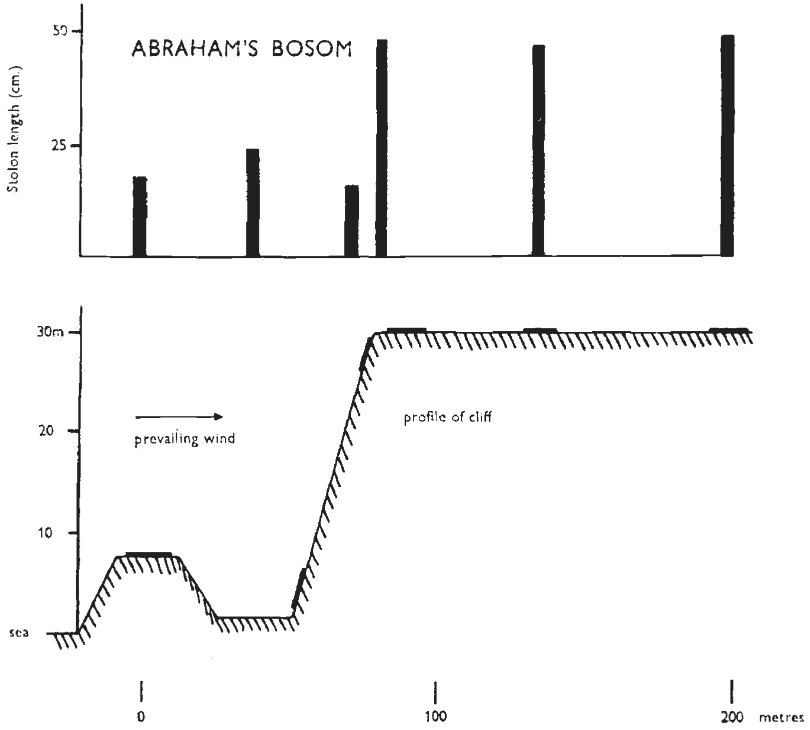


FIG. 4.—*Agrostis stolonifera* on sea cliffs at Abraham's Bosom (stolon length).

A very marked transition between the exposed and protected parts of the transect is to be seen. As in the first example the transition appears complete even in the populations most closely adjacent to the boundary.

Example 5.—Anthoxanthum odoratum *on the Park Grass plots at Rothamsted (data of R. W. Snaydon)*

Anthoxanthum odoratum is a common component of many lowland pastures in the British Isles. It occurs in most plots of the Park Grass Experiment at Rothamsted. These plots were established in 1856 by Lawes and Gilbert to investigate the effect of continuous application of fertilisers to an otherwise uniform area of meadowland. In 1903 additional lime treatments were applied across the existing plots and have been continued to the present day. The various fertiliser and liming treatments have greatly altered the species composition and general growth of the vegetation on the plots, which have a mean size of 20 m. × 35 m. (Brenchley, 1958).

Population samples of *A. odoratum* collected from a number of contrasting plots have been shown to differ significantly in a large number of morphological and physiological attributes correlated with environmental conditions existing on the mature plots (Snaydon, 1963). The boundary between contrasting plots is extremely clear cut, environmental changes being complete over distances of less than 50 cm. Therefore, investigation has been made of population differentiation across the abrupt boundary between limed and unlimed sub-plots of plot 1 which has received 43 lb./acre/annum of *N* as ammonium sulphate. Population samples of *A. odoratum* tillers were collected at random within sample strips running across the entire width of the plots and parallel to the boundary; the sample strips varied in size from 5 cm. × 12 m. at the boundary to 120 cm. × 12 m. at the two ends of the transect. The density of *A. odoratum* plants was approximately twenty times greater on the limed than on the unlimed plot. Sampled tillers were grown on for 4 months then broken down to individual tillers and planted into both acid and calcareous soil and grown for 5 months in greenhouse conditions. The mean dry weights per plant at the end of this period are given in fig. 5.

It will be seen that there is a very marked transition in the average plant size along the transect. However, the point at which the change occurs does not coincide with the point of ecological change despite the precision of the latter. The coefficient of variability between genotypes within populations shows considerable increase in this transitional zone.

Parameters of gene flow and selection

In each of these five cases, the general ecological picture has been given. It remains to give what information on gene flow and selection is available.

At present it is unfortunate that no critical observations on gene flow in any of the examples have been made. These are being obtained. However, preliminary observations where the characteristics of seed produced *in situ* has been compared with the characteristic of the adult population suggests a considerable gene flow (about 25 per cent.) from the cliff into the pasture populations in *Agrostis stolonifera* at Abraham's

Bosom (example 4), but because of the prevailing wind none in the reverse direction (Aston, 1962). Similar observations in *Agrostis tenuis* at the Drws-y-Coed mine (example 2), suggest less gene flow even over short distances (T. S. McNeilly, unpublished).

In order to get an estimate of rates and pattern of gene flow in plants we must therefore refer to the elegant work of Bateman (1947) and of Griffiths (1950). It is interesting in this and other work with a variety of species, both insect and wind pollinated, the general pattern of gene flow over distance varies little. For the present the results reported by Griffiths for ryegrass, *Lolium perenne*, a wind pollinated self incompatible plant, are adequate. The layout adopted in his experiments of several rows of spaced tester plants leading away from a contaminating larger block, approaches most nearly the situation in nature. However, it is clear that many factors can alter the amount of gene flow and these results serve only as an indication. One set of Griffiths' results is given in fig. 6. They show very high gene flow over short distances but a very rapid fall off, so that at distances of 30 ft. the amount of gene flow is of the order of 5 per cent.

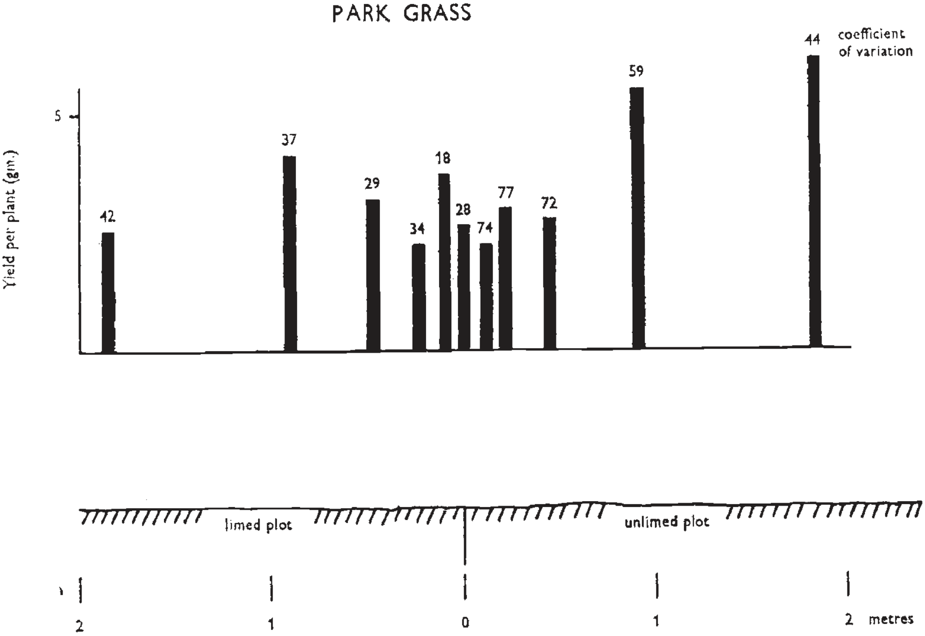


FIG. 5.—*Anthoxanthum odoratum* on Park Grass plot 1 at Rothamsted (dry weight).

Parameters of selection can only be obtained with great difficulty, since selection in natural conditions very often involves competitive interactions occurring over many years. However, material of all the examples has been grown under a variety of conditions and from them coefficients of selection have been estimated (table 1). In each case the selective value of the adapted type in its habitat is assumed to be 1, and only the coefficient of selection against the fully unadapted type, *i.e.* the type adapted to the opposite habitat, is given. Since the conditions under which the determinations were made were not natural, in most cases did not involve conditions of competition, and are based on the vegetative growth of the plants, the values given can only be used as a guide; they are almost certainly under-estimates. But in most perennial grasses selection mainly occurs in the vegetative phase and the reproductive capacity of the plants tends to be directly determined by the vegetative growth. It is clear that coefficients of selection against unadapted types may often be very high, particularly on the mine habitats.

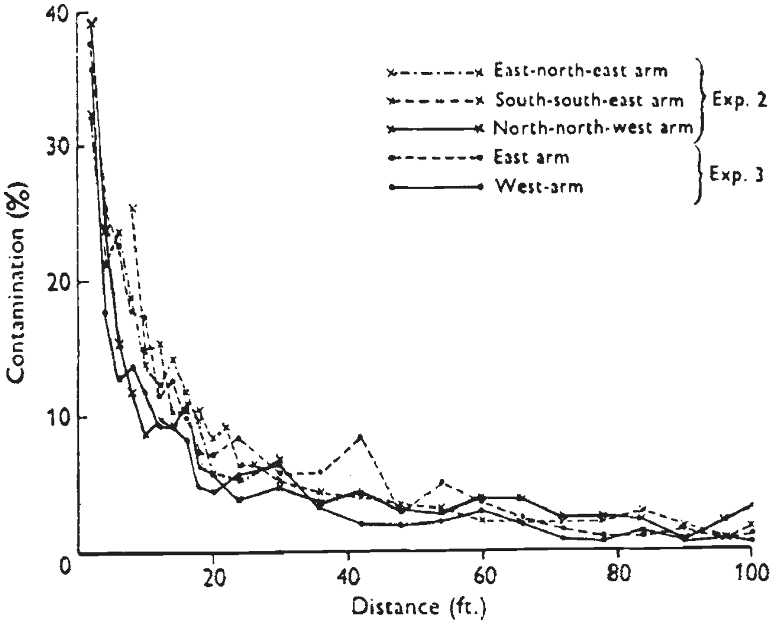


FIG. 6.—Effect of isolation distance on the relative decrease in contamination (*i.e.* pollen dispersal) in *Lolium perenne* (Griffiths, 1950).

3. CONCLUSIONS FROM EXPERIMENTAL DATA

The five examples illustrate two-environment situations and divergence across a boundary. They show clearly that distances as low as 1 or 2 metres are sufficient to permit populations of certain species occupying contrasting habitats to become very distinct from each other; indeed in none of the examples quoted are distances of more than 20 ft. involved.

Although gene flow by pollen migration over short distances may be quite high, the amount falls off very markedly with distance. Wind direction, aggregation of plants and other factors may affect this

TABLE 1

Estimates of coefficients of selection against unadapted types in the two habitats of each example (see text)

Example	Species	Habitats and coefficients of selective against unadapted types	Source of evidence
1	*Agrostis tenuis*	Mine, 0·95 : pasture, 0·4	Growth of spaced plants on two soils (A.D.B.)
2	*A. tenuis*	Mine, 0·95 : pasture, 0·05	Growth of plants under spaced and competitive conditions on two soils (T.S.McN.)
3	*Anthoxanthum odoratum*	Mine, 0·99 : pasture, 0·3	Growth of plants under spaced and competitive conditions on two soils (P.D.P.)
4	*Agrostis stolonifera*	Cliff, 0·8 : pasture, 0·5	Growth of spaced plants under exposed cliff and garden conditions (J.L.A.)
5	*Anthoxanthum odoratum*	Unlimed, 0·09 : limed, 0·27	Estimated from three competition experiments carried out under greenhouse conditions: under field conditions higher values seem likely (R.W.S.)

pattern, as shown by Bateman and Griffiths. The abnormally high amount of gene flow reported in *Agrostis stolonifera* at Abraham's Bosom is probably due to the very specific prevailing west wind in this site. Gene flow can also be caused by seed migration. The effect per propagule will be twice that for pollen. However, all the species, although they have small seeds, have no particular adaptations to dispersal by wind or other means, and the seed are born in inflorescences very close to the ground. It seems unlikely that in the present examples gene flow by seed is important in comparison with that by pollen.

The estimates of coefficients of selection are in many cases very high. In other cases they are low: but in no case are they as low as those often used in the past in calculations of the effects of selection. Indeed no coefficient is estimated to be less than 5 per cent.

From the balance of the values for selection with those for gene flow it would appear very possible for differential selection on two sides of an ecological boundary to hold populations, only a very short distance apart, different from each other. Thus from the values of Griffiths (1950) gene flow of over 15 ft. is about 10 per cent. Many of the coefficients of selection could overcome such gene flow.

However gene flow over a continuous series of populations (the situation in nature) is not the same as that between two single populations. The effects of unequal population size causing more gene flow in one direction than the other, suggested by example 5 and earlier by Blair (1947), are likely to be complex. The degree of perenniality of the species may also be important. Selection is also not operating on individuals of extreme type, representative of the contrasting populations, but on the results of hybridisation between the populations: the degree of dominance will be important. It therefore seems necessary to examine the process of evolution in adjacent populations in a more precise manner, before any further appraisal can be made of the five cases already described.

4. SIMULATION OF JOINT EFFECTS OF MIGRATION AND SELECTION

(i) *Previous work*

The effects of migration in relation to random processes of differentiation has been studied by Wright (1931, 1943). He considered two different models of migration, namely, (1) the so-called " island " model in which a population might be subdivided into several panmictic units that receive a certain proportion of migrants drawn at random from the entire population and (2) the " isolation-by-distance " model in which a more or less continuously distributed species has interbreeding limited to small distances due to the short range dispersal of gametes or zygotes following a normal curve thus resulting in some isolation among the remote populations. As noted by Wright himself (1943), the island model is rather unlikely to be exactly realised in nature whereas the isolation-by-distance model is realistic and more likely to be interesting. Although his treatment was primarily concerned with the effect of isolation-by-distance on the amount of nonadaptive random differentiation among various effective neighbourhoods, he remarked that " diversity in degree and direction of selection among localities is of course a wholly different matter and may bring about great differentiation if not overbalanced by migration ". Kimura and Weiss (1964) have studied the problem of random differentiation under a stepping stone model of migration where migration occurs only between adjacent colonies. The island model represents an extreme form of long range dispersal in contrast to the short range nature of Kimura's model. Clearly, the average *rate* of migration as well as the *range* in terms of mean distance are important in relation to the extent of adaptive, or nonadaptive differentiation.

The effects of migration in relation to divergent selection pressures have been studied by several models. Levene (1953) analysed a multiple environment situation but with complete random mating among the members of all neighbourhoods (sub-populations occupying different environments). On the other hand, Haldane (1948) and Fisher (1950) have studied clinal variation as maintained under opposing forces of selection and gene flow with a normal distribution, for a simple character involving complete dominance or no dominance. Fisher's model assumes selection intensity to be a function of distance from an intermediate region of no selection. Under the weak selection considered by Haldane, the slope of the cline measuring the amount of divergence was consequently low.

However, the examples of clinal variation presented in the previous sections suggest fairly potent selection pressures to be involved. Moreover, as shown by the work of Bateman (1947), Griffiths (1950), Colwell (1951) and others, the leptokurtic distribution of pollen seems to be the most likely form of gene flow in these examples as well as more generally. Therefore, the present study was undertaken to simulate a wide variety of model situations, with particular emphasis on leptokurtic distribution of gene flow, to examine the quantiative inter-relations between the parameters of selection and gene flow. In addition, the degree of dominance, unequal rates of dispersal and generation intervals are considered. The comparison that can be made between the leptokurtic and normal curves is of particular significance in view of their differences in the lower and extreme ranges of dispersal.

(ii) *The genetic model*

(1) The species is assumed to be continuously distributed along a linear habitat (the width of distribution area is relatively smaller than the length) with nearly uniform density, or with unequal density, in two environments (in the latter case only gene flow and not selection is density-dependent). (2) The range of the effective breeding unit is relatively small so that isolation-by-distance results in partially isolated neighbourhoods (sub-populations). (3) A sharp boundary line between two environments (toxic *vs.* non-toxic, limed *vs.* nonlimed, etc.) is assumed by taking an arbitrary number of sub-populations, five in each environment, corresponding to the equispaced sampling sites used for determining the gene frequency distribution: so a continuous distribution takes the form of a histogram. (4) The tolerance to zinc, copper, or response to liming, etc., is assumed to be governed for the sake of simplicity, by one or more non-interacting loci with either additivity or complete dominance: the number of loci involved makes no difference to the outcome. (5) Selection is assumed to favour differently two different alleles (say A_i or a_i) at each of these loci in the two contrasting environments. Where dominance is considered the dominant allele is assumed to be favoured in environment *I*: preliminary evidence (Jowett, 1959, Wilkins 1960, Broker 1963) suggests that metal tolerance may be dominant. (6) Gene flow occurs only through pollen: a smaller component due to seed dispersal is ignored here. The proportion of gene flow in reciprocal directions may be the same or different depending on the density of plant stand. (7) From the evidence already reviewed, the average rate of replacement annually

(equivalent to taking the extent of perenniality or duration of a generation) may be the same or different for the two environments. (8) Finally, the effective size of each sub-population is assumed to be infinitely large so that random differentiation is absent. This might not be a serious restriction on the model in view of rather strong selective forces involved. In view of the purpose of the investigation it was considered a valid simplification.

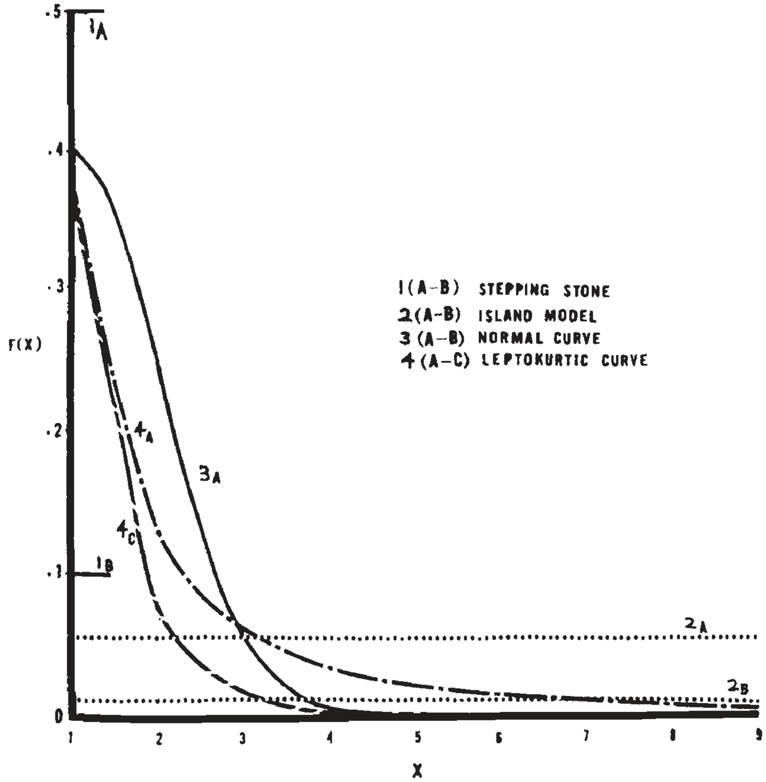


FIG. 7.—Modes of pollen dispersal as given by $f(x)$, a function of distance (x).

1. Stepping stone: $f(x) = (A)\ 0{\cdot}50, \quad (B)\ 0{\cdot}10$ for $x = 1$ only
2. Island: $f(x) = (A)\ 0{\cdot}50, \quad (B)\ 0{\cdot}10$
3. Normal curves: $f(x) = (A)\ e^{-x^2}, \quad (B)\ \frac{1}{2}e^{-x^2}$
4. Leptokurtic curves: $f(x) = (A)\ \frac{e^{-\sqrt{x}}}{x}, \quad (B)\ \frac{1/2e^{-\sqrt{x}}}{x}, \quad (C)\ \frac{e^{-x}}{x}$.

Several different modes of pollen dispersal can be studied by the choice of a distribution function, $f(x)$, where x denotes in units the distance among the sub-populations along a linear habitat. Fig. 7 shows graphically the different choices of $f(x)$ that give island model, stepping stone model, normal and leptokurtic curves. The scale for measuring the linear distance in x units can be suitably chosen to simulate the probable dispersion range for any specific population (*cf.* Bateman, Griffiths). Let p_j, q_j represent the allelic frequencies of A and a in jth population ($j = 1 \ldots i \ldots k$). and p_{mj}, q_{mj} be the corresponding frequencies in the pollen pool soon after dispersal. Given any function $f(x)$ which may be treated as a discontinuous function to give a histogram for a finitely small number of sub-populations, the values of q_{mj} for the nth generation after dispersal can be determined with, say, $f(x) = \exp(-cx)/x$, by the relation

$$q_{mj}^{(n)} = q_j^{(n)} + \sum_k^i \left[\frac{e^{-c/k-i/}}{/k-i/} \left(q_k^{(n)} - q_i^{(n)}\right) \right] \qquad \ldots\ldots(1)$$

where $k \neq i$ and / / indicates absolute value,

and change in q_j through pollen dispersal,

$$q_j^{(n)} = \tfrac{1}{2}\left(q_{mj}^{(n)} - q_j^{(n)}\right).$$

If t_1 and t_2 are generation intervals, and selection operates in the following form:

Genotype at *i*th locus

Environment	*AA*	*Aa*	*aa*
1	1	$1-h_1s_1$	$1-s_1$
2	$1-s_2$	$1-h_2s_2$	1

where s_1, s_2 are selection coefficients and h_1, h_2 are measures of dominance, the gene frequencies q_j in $(n+1)$th generation are given by the relations: for environment 1, $j = 1$ to 5

$$q_j^{(n+1)} = \frac{1}{t_1}\left[\frac{\frac{1}{2}(1-h_1s_1)A - s_1B(1-h_1)}{1-s_1B-h_1s_1(A-2B)}\right] + \left(1 - \frac{1}{t_1}\right) \left[\frac{q_j^{(n)}(1-s_1q_j^{(n)}) - h_1s_1q_j^{(n)}(1-q_j^{(n)})}{1-s_1q_j^{(n)2} - 2h_1s_1q_j^{(n)}(1-q_j^{(n)})}\right] \qquad \ldots\ldots(2)$$

for environment 2, $j = 6$ to 10

$$q_j^{(n+1)} = \frac{1}{t_2}\left[\frac{\frac{1}{2}(1-h_2s_2)A + h_2s_2B}{1+s_2(1-A+B)-h_2s_2(A-2B)}\right] + \left(1 - \frac{1}{t_2}\right) \left[\frac{q_j^{(n)} - h_2s_2q_j^{(n)}(1-q_j^{(n)})}{1-s_2(1-q_j^{(n)})^2 - 2h_2s_2q_j^{(n)}(1-q_j^{(n)})}\right] \qquad \ldots\ldots(3)$$

where $A = q_j^{(n)} + q_{mj}^{(n)}$ and $B = (q_j^{(n)})(q_{mj}^{(n)})$.
Thus, using relations (1)—(3) the distribution of gene frequencies q_j can be determined during the successive generations and finally at equilibrium as given by $\Delta q_j = 0$. With several loci which are more or less similar and noninteracting, the above expressions can be summed over all loci to give total change in mean, variance or other statistics. Unequal rates of dispersal are also easily introduced in the model by taking different functions $f(x)$ in two directions. With these several variables in the model, to obtain literal solutions is apparently much

too involved and therefore, it was necessary to find particular solutions for gene frequency distribution by simulation on an electronic computer (IBM 7040) to a wide range of numerically specified situations.

(iii) *Numerical results from simulation*

Populations initially at gene frequencies $q_j = 0{\cdot}95$ or $0{\cdot}999$ (for all ten sub-populations) were allowed to change under migration and selection for a large number of generations until a stable equilibrium was reached. The stability of the equilibria is ensured by the counteracting forces of selection and gene flow. These initial gene frequencies were chosen on the assumption that genes governing tolerance are in fact rare in these natural populations (for which there is evidence: Bradshaw, McNeilly and Gregory 1965 and unpublished) and thus, rates of initial increase in their frequency could also be studied. Since the equilibrium solutions are in this case independent of initial frequencies, any other initial values of q_j would not change the results of our model.

TABLE 2

Mean amount and range of pollen dispersal

Model		$\bar{m}$	$\bar{x}$
Stepping stone:	1A	0·0110	1
	1B	0·0022	1
Island model:*	2A	0·0556	5
	2B	0·0111	5
Normal curve:	3A	0·0236	1·52
	3B	0·0118	1·52
Leptokurtic curve:	4A	0·0221	1·55
	4B	0·0111	1·55
	4C	0·0130	1·28

$\bar{m} = \frac{\Sigma x f(x)}{\Sigma x}$ = mean dispersal per unit distance (x 1-9)

$\bar{x} = \frac{\Sigma x f(x)}{\Sigma f(x)}$ = mean weighted distance for pollen flow (x 1-9)

* Under island model, distance x is disregarded.

The choice of values for the various parameters has been essentially based on our findings from examples described above, but includes other generalised cases. The modes of pollen dispersal as given by $f(x)$ are compared in table 2 for their mean amount and distance of dispersal as determined by the quantities $\bar{m}$ and $\bar{x}$ respectively.

$$\bar{m} = \frac{\sum_j x f(x)}{\sum_j x} \quad \text{and} \quad \bar{x} = \frac{\sum_j x f(x)}{\sum_j f(x)}.$$

Thus, it is to be noted that for nearly the same average amount ($\bar{m}$) in the case of models 1A vs. 2B or 3A vs. 4A, the ranges are different. To measure the relative amount of differentiation among various sub-populations, the variance σ_q^2 and an index

$$E = \sqrt{\frac{\sigma_q^2}{q(1-q)}}$$

(where σ_q^2 is adjusted for gene frequency) used by Wright (1943) were computed. Values of E as high or higher than 0·5 indicate significant amounts of this differentiation. This use of E under a model involving selection is not exactly as that under Wright's models for random differentiation but serves as an approximate index of divergence. The mean of q_j's, $\bar{q}$, was also calculated. This is of value if the populations are considered to be sub-populations of a large population subject to disruptive selection due to local permanent variations in habitat, since it indicates the equilibrium point of the overall population.

For various combinations of parametric values, the values of $\bar{q}$, σ_q^2 and E are given in table 3 for stepping-stone and island models and in table 4 for the normal and leptokurtic forms of pollen dispersal. In some cases involving relatively weak selection (*viz.* $s_1 = 0{\cdot}25$, $s_2 = 0{\cdot}10$) the population reached either only an approximate equilibrium, indicated by very slow change in q_j, or did not attain equilibrium even after 250 generations. In general, there are several interesting points to note from these results:

(1) The variance, σ_q^2 and the values of E are, as expected, large or small respectively with low or relatively high rates of gene flow, or short versus long range dispersal. The effect of different rates of dispersal on σ_q^2 is proportionately larger under island model than the stepping stone model. Moreover, given nearly the same value of $\bar{m}$ (amount of gene flow), the range as measured relatively by $\bar{x}$ has conspicuous effects on the amount of differentiation. Obviously, the intensity of selection in the two environments further influences the pattern of gene frequency distribution. It is significant to note that even with as high gene flow as occurring with 50 per cent. or more pollen replacement through dispersal (1A, 3A, 4A) and rather moderate selection, the values of E are quite high, indicating some differentiation; and in fact marked differentiation occurs with all other lower rates of migration even with a leptokurtic pattern of gene flow. As emphasised repeatedly, the effects of selection and migration are in delicate balance at such high intensities of both pressures.

(2) Unequal selection coefficients result in even more complex relationships with different forms and amounts of pollen dispersal. This can yield higher or lower degrees of differentiation depending essentially on the relative intensities of selection and migration.

(3) With equal selection coefficients and same generation time ($s_1 = s_2$, $t_1 = t_2$), the equilibrium gene frequencies are 0·5 under all

TABLE 3

Values of $\bar{q}$, σ_q^2 *and* E ($R = 1$, $h_1 = h_2 = 0{\cdot}5$) *under different models of pollen dispersal and different selective values*

Selective values		Generation time	1A			1B			2A			2B		
s_1	s_2	$t_1{:}t_2$	$\bar{q}$	σ_q^2	*E*	$\bar{q}$	σ_q^2	*E*	$\bar{q}$	σ_q^2	*E*	$\bar{q}$	σ_q^2	*E*
0·95	0·50	1:1	0·464	0·217	0·933	0·491	0·259	1·018	0·368	0·084	0·601	0·474	0·221	0·941
		1:5	0·511	0·244	0·987	0·500	0·269	1·037	0·533	0·171	0·830	0·507	0·253	1·006
0·75	0·25	1:1	0·419	0·180	0·859	0·476	0·243	0·987	0·130	0·0084	0·274	0·419	0·180	0·859
		1:5	0·505	0·228	0·954	0·502	0·263	1·026	0·517	0·120	0·694	0·504	0·234	0·968
0·25	0·10	1:1	0·379†	0·107	0·675	0·457	0·207	0·914	0	0	0	0·335†	0·012	0·521
		1:5	0·544†	0·173	0·836	0·514	0·238	0·976	0·727*	0·017	0·290	0·544	0·152	0·784
0·25	0·25	1:1	0·500	0·160	0·801	0·500	0·231	0·961	0·501	0·016	0·255	0·517	0·129	0·719
		1:5	0·586	0·180	0·862	0·526	0·244	0·989	0·890	0·007	0·264	0·577	0·170	0·834

* Not at equilibrium.
† Near equilibrium.

TABLE 4

Values of $\bar{q}$, σ_q^2 *and* E (R = *1*) *under different models of pollen dispersal, different selective values and different levels of dominance*

Selective values		Dominance	Generation time	Normal curve						Leptokurtic curve								
				3A			3B			4A			4B			4C		
s_1	s_2	h_1 h_2	t_1:t_2	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E
0·95	0·50	0·5, 0·5	1:1	0·423	0·154	0·794	0·455	0·198	0·893	0·406	0·129	0·802	0·449	0·184	0·744	0·454	0·199	0·803
			1:5	0·522	0·208	0·913	0·512	0·236	0·972	0·526	0·196	0·887	0·514	0·231	0·962	0·513	0·235	0·970
		0, 1·0	1:1	0·555	0·144	0·763	0·555	0·178	0·849	0·562	0·126	0·715	0·564	0·165	0·716	0·552	0·179	0·851
			1:5	0·605	0·163	0·825	0·580	0·191	0·886	0·617	0·150	0·797	0·590	0·180	0·863	0·580	0·192	0·888
0·75	0·25	0·5, 0·5	1:1	0·318	0·083	0·619	0·392	0·145	0·780	0·264	0·050	0·507	0·369	0·119	0·715	0·393	0·148	0·620
			1:5	0·510	0·177	0·841	0·506	0·214	0·925	0·512	0·156	0·790	0·507	0·204	0·903	0·506	0·214	0·925
		0, 1·0	1:1	0·486	0·983	0·627	0·516	0·144	0·761	0·460	0·069	0·527	0·517	0·124	0·705	0·513	0·147	0·767
			1:5	0·606	0·142	0·770	0·584	0·174	0·847	0·619	0·126	0·731	0·594	0·162	0·820	0·583	0·175	0·848
0·25	0·10	0·5, 0·5	1:1	0·185*	0·012	0·287	0·316†	0·057	0·516	0·104*	0·003	0·170	0·255*	0·029	0·394	0·324†	0·062	0·534
			1:5	0·602†	0·081	0·583	0·560†	0·138	0·745	0·637†	0·052	0·473	0·576	0·110	0·670	0·559†	0·141	0·756
		0, 1·0	1:1	0·374*	0·185	0·282	0·495	0·070	0·529	0·234*	0·003	0·120	0·457†	0·042	0·411	0·498	0·074	0·545
			1:5	0·690	0·069	0·569	0·649	0·108	0·689	0·715	0·050	0·496	0·667	0·090	0·636	0·647	0·111	0·697
0·75	0·75	0·5, 0·5	1:1	0·500	0·172	0·829	0·500	0·210	0·916	0·500	0·152	0·780	0·500	0·199	0·892	0·500	0·210	0·916
			1:5	0·561	0·192	0·894	0·533	0·230	0·961	0·570	0·183	0·864	0·537	0·224	0·948	0·535	0·229	0·959
		0, 1·0	1:1	0·616	0·145	0·782	0·590	0·177	0·856	0·630	0·130	0·748	0·601	0·165	0·830	0·589	0·178	0·857
			1:5	0·634	0·150	0·804	0·598	0·181	0·868	0·648	0·137	0·774	0·609	0·170	0·844	0·599	0·182	0·870
0·25	0·25	0·5, 0·5	1:1	0·500	0·068	0·522	0·500	0·121	0·695	0·500	0·042	0·412	0·500	0·092	0·607	0·500	0·125	0·708
			1:5	0·694	0·082	0·621	0·614	0·145	0·782	0·751	0·048	0·508	0·638	0·120	0·720	0·613	0·149	0·792
		0, 1·0	1:1	0·641	0·065	0·530	0·619	0·103	0·662	0·654	0·045	0·445	0·633	0·083	0·599	0·616	0·106	0·671
			1:5	0·737	0·070	0·602	0·678	0·112	0·715	0·766	0·052	0·540	0·696	0·095	0·672	0·677	0·114	0·721

* Not at equilibrium.
† Near equilibrium.

models of migration. Any inequality, $t_1 \neq t_2$, tends to yield differential effective rates of replacement through migration and influences equilibrium gene frequencies accordingly. Thus, in our model q_j at equilibrium, as well as σ_q^2 and E, are always higher with unequal generation times. The distribution of q_j becomes asymmetrical in the two environments despite apparent symmetry of selection and migration parameters.

(4) Likewise, the degree of dominance has a significant influence on gene frequencies under such interacting forces. Higher dominance in general yielded a higher value of $\bar{q}$ and a lower index of differentiation.

(iv) *Pattern of divergence*

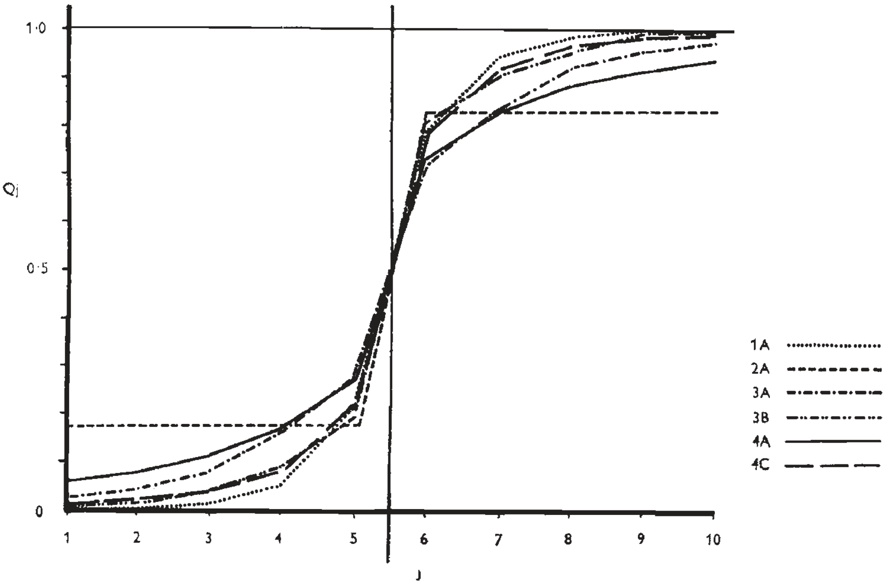
The actual distribution of gene frequencies over the entire linear habitat gives clines of varying slopes. These are shown for two equal selection intensities (fig. 8) and two unequal intensities (fig. 9), with equal versus unequal generation times. In general the slopes of the clines give the same relations between selection and migration as already described. It is of particular interest to note that under $t_1 \neq t_2$, the amount of differentiation is higher than with $t_1 = t_2$ and the clines under different migration models are closer to each other. Model 4A has slightly lower slope than 3A but even with weak selection it gives some degree of differentiation. Under the island model, 2A, the value of q_j is the same for all five sub-populations within each environment and allows relatively less differentiation. Another characteristic which can be related to the slope of these clines is the magnitude of difference between q_1 and q_{10}. This is usually high even for models 3A and 4A that represent rather heavy amounts of gene flow.

(v) *Population loads due to migration*

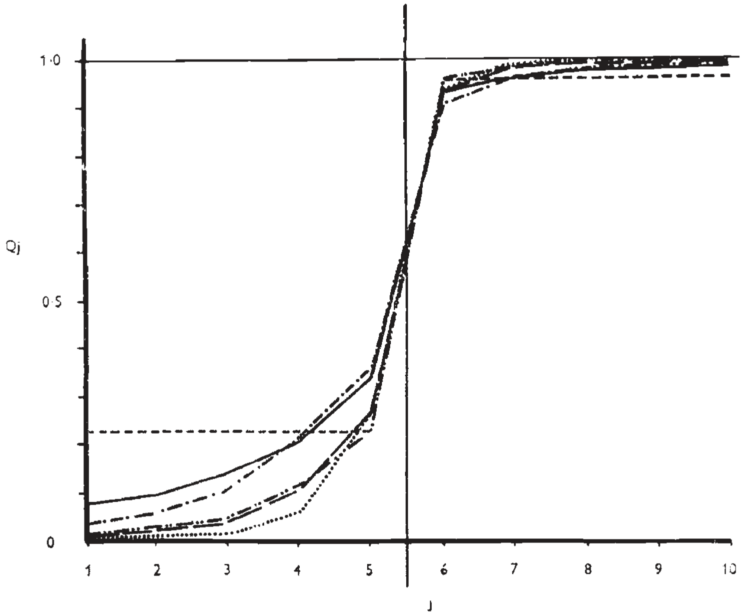
In view of stable equilibria with allelic frequencies (p_j, q_j) not at zero or unity, and migration of the less favoured alleles in both directions, the population incurs a loss in fitness which may be called migrational load. If $\bar{W}_1$ and $\bar{W}_2$ are the relative average fitnesses of populations within the two environments respectively, a quantity

$$L_m = 1 - \tfrac{1}{2}(\bar{W}_1 + \bar{W}_2)$$

measures this load, where $\bar{W}$'s are the sum of genotypic frequencies weighted by the corresponding selective values ($\bar{W} = \Sigma f_i w_i$, where f_i are genotypic frequencies and w_i are relative selective values). Table 5 gives the value of L_m obtained for several different examples. As expected, the migrational load is a function of both the amount or average rate and range of dispersal so that its highest values are obtained under model 2A and lowest with 1B. Complete dominance and unequal generation times have some tendency to lower the load due to migration by influencing the effective intensities of selection and gene flow respectively.

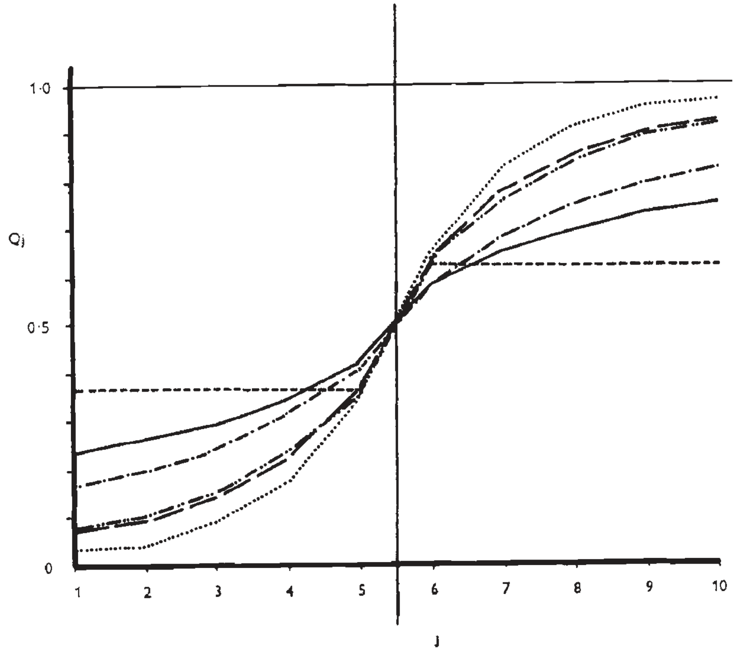


(*a*) $s_1 = s_2 = 0{\cdot}75$; $t_1 = t_2 = 1$

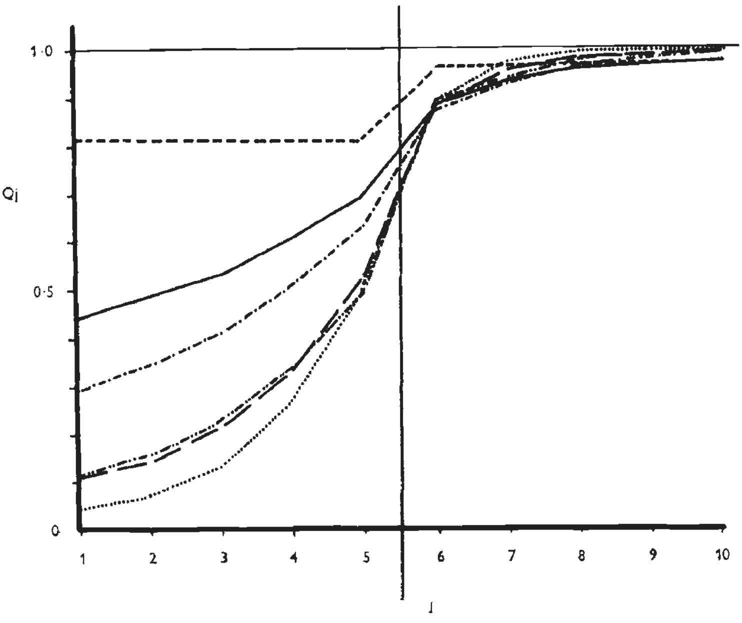


(*b*) $s_1 = s_2 = 0{\cdot}75$; $t_1 = 1$, $t_2 = 5$

Fig. 8.—Distribution curves of allelic frequencies (Qj) at equilibrium with $R = 1$ and symmetrical selection

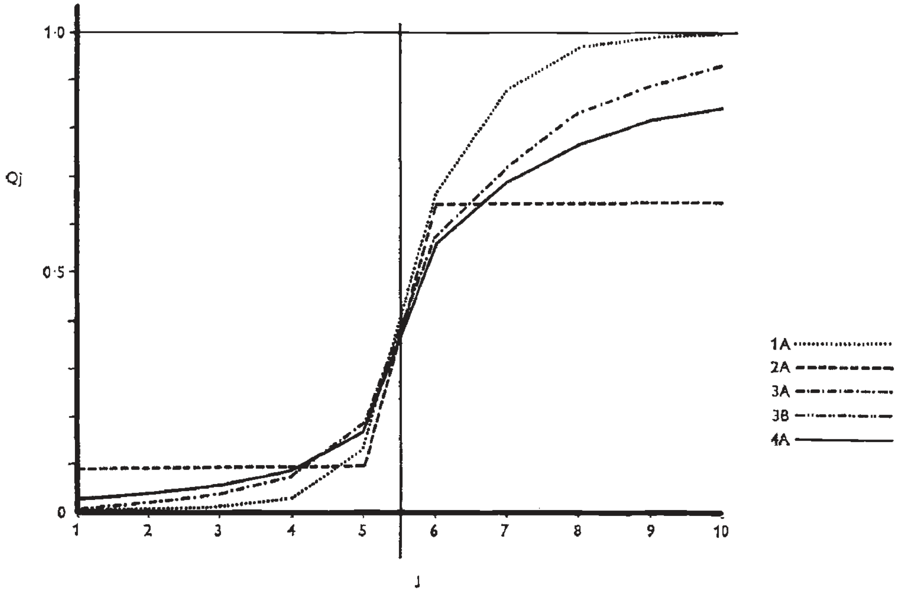


(*c*) $s_1 = s_2 = 0{\cdot}25$; $t_1 = t_2 = 1$

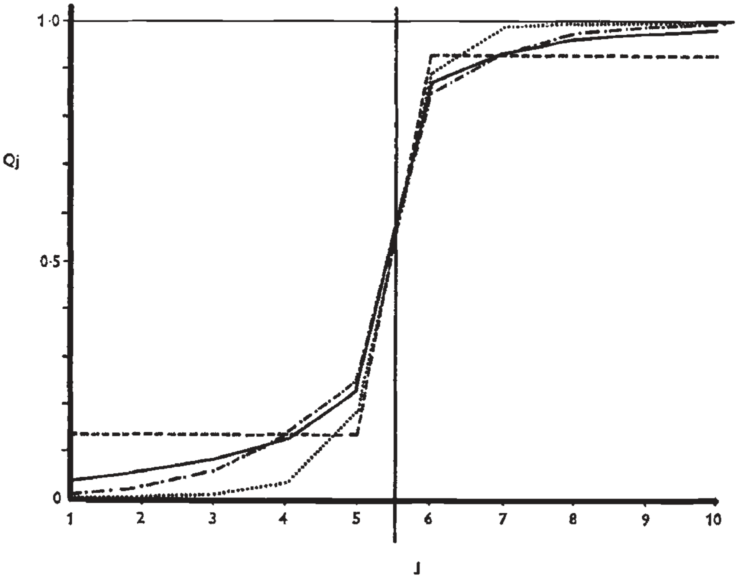


(*d*) $s_1 = s_2 = 0{\cdot}25$; $t_1 = 1$, $t_2 = 5$

FIG. 8.—*Continued*

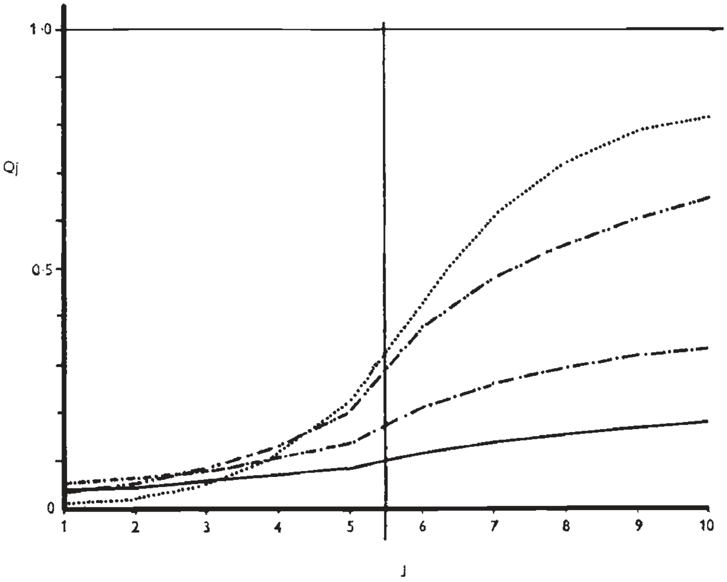


(*a*) $s_1 = 0{\cdot}95$, $s_2 = 0{\cdot}50$; $t_1 = t_2 = 1$

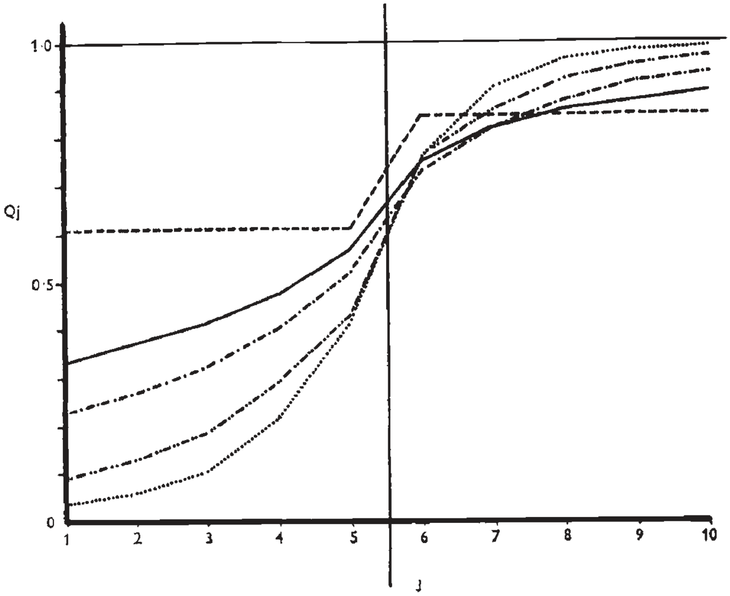


(*b*) $s_1 = 0{\cdot}95$, $s_2 = 0{\cdot}50$; $t_1 = 1$, $t_2 = 5$

FIG. 9.—Distribution curves of allelic frequencies (Qj) at equilibrium (cases $a+b$), or after 250 generations (cases $c+d$) with $R = 1$ and asymmetrical selection



(*c*) $s_1 = 0{\cdot}25$, $s_2 = 0{\cdot}10$; $t_1 = t_2 = 1$



(*d*) $s_1 = 0{\cdot}25$, $s_2 = 0{\cdot}10$; $t_1 = 1$, $t_2 = 5$

FIG. 9.—*Continued.*

TABLE 5

Migrational load (L_m) *under different models of pollen dispersal and different selective values*

Model of pollen dispersal	Dominance h	Selective values		Generation time t_1, t_2	$\bar{W}_1$	$\bar{W}_2$	L_m
		s_1	s_2				
1A	0·5	0·75	0·75	1:1	0·936	0·935	0·064
	0·5	0·25	0·25	1:1	0·962	0·962	0·038
	0·5	0·95	0·50	1:1	0·944	0·934	0·061
	0·5	0·95	0·50	1:5	0·923	0·970	0·054
	0·5	0·25	0·10	1:1	0·975	0·965	0·030
	0·5	0·25	0·10	1:5	0·954	0·990	0·028
1B	0·5	0·25	0·10	1:1	0·989	0·989	0·012
	0·5	0·25	0·10	1:5	0·984	0·996	0·010
2A	0·5	0·75	0·75	1:1	0·798	0·798	0·202
	0·5	0·25	0·25	1:1	0·897	0·897	0·103
	0·5	0·95	0·50	1:1	0·839	0·784	0·188
	0·5	0·95	0·50	1:5	0·763	0·908	0·165
	0·5	0·25	0·10	1:1	1·00	0·90	0·050
	0·5	0·25	0·10	1:5	0·840*	0·982*	0·089
2B	0·5	0·25	0·10	1:1	0·978†	0·946†	0·038
	0·5	0·25	0·10	1:5	0·951	0·989	0·030
3A	0·5	0·75	0·75	1:1	0·870	0·870	0·131
	0·5	0·25	0·25	1:1	0·926	0·926	0·074
	0·5	0·95	0·50	1:1	0·889	0·865	0·123
	0·5	0·95	0·50	1:5	0·840	0·938	0·111
	1·0	0·95	0·50	1:1	0·928	0·869	0·102
	1·0	0·95	0·50	1:5	0·906	0·920	0·087
	1·0	0·25	0·10	1:1	0·982	0·923	0·048
	1·0	0·25	0·10	1:5	0·939	0·981	0·040
4A	0·5	0·75	0·75	1:1	0·846	0·846	0·154
	0·5	0·25	0·25	1:1	0·914	0·914	0·086
	0·5	0·95	0·50	1:1	0·871	0·838	0·146
	0·5	0·95	0·50	1:5	0·817	0·929	0·127
	1·0	0·95	0·50	1:1	0·915	0·848	0·118
	1·0	0·95	0·50	1:5	0·894	0·909	0·099
	1·0	0·25	0·10	1:1	0·990*	0·907	0·052
	1·0	0·25	0·10	1:5	0·924	0·978	0·049

* Not at equilibrium.
† Near equilibrium.

(vi) *Effect of unequal gene flow*

Perhaps in all the examples described in the first section of this paper there are significant differences in the density of plant distribution within the two environments, (*e.g.* example 5). As pointed out by Bateman, the quantity of available pollen can have a direct proportional effect on the rate of dispersal. Table 6 gives the values of $\bar{q}$, σ_q^2 and E for several models of migration under unequal rates of dispersal where R measures the ratio $\left(\frac{r_1}{r_2}\right)$ between two rates:

$$\text{environment 1} \underset{r_2}{\overset{r_1}{\rightleftharpoons}} \text{environment 2}$$

TABLE 6

Values of $\bar{q}$, σ_q^2 *and* E *with inequal rates of pollen dispersal between two environments and different selective values*

Selective values		$R = r_1/r_2$	Models of pollen dispersal														
			3A			3B			4A			4B			4C		
s_1	s_2		$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E	$\bar{q}$	σ_q^2	E
0·75	0·75	1	0·500	0·172	0·829	0·500	0·210	0·916	0·500	0·152	0·780	0·500	0·199	0·892	0·500	0·210	0·916
		2	0·337	0·110	0·701	0·391	0·131	0·742	0·369	0·111	0·689	0·327	0·100	0·676	0·359	0·125	0·736
		10	0·141	0·214	0·421	0·137	0·020	0·413	0·151	0·024	0·430	0·137	0·020	0·413	0·148	0·024	0·434
0·50	0·50	2	0·203	0·037	0·481	0·302	0·675	0·566	0·258	0·045	0·484	0·181	0·028	0·437	0·244	0·054	0·543
		10	Allele *A* fixed														
0·25	0·25	2	Allele *A* fixed														
		10	Allele *A* fixed														

It can be seen that (1) only strong selection maintained both alleles in the population against the swamping effect of larger gene flow rates from environment 1 to environment 2, and (2) the amount of differentiation as well as $\bar{q}$ again depend on the specific combination of the values assigned to various parameters. Fig. 10 shows the form of $f(q)$ under model 4A: that for 3A is very similar. The curves are asymmetrical and close to each other in environment 1 due to the relatively larger coefficients of migration for the favoured allele A, but more different in environment 2. Thus, asymmetry in both selection and gene flow can result in much more complex patterns of gene frequency distribution.

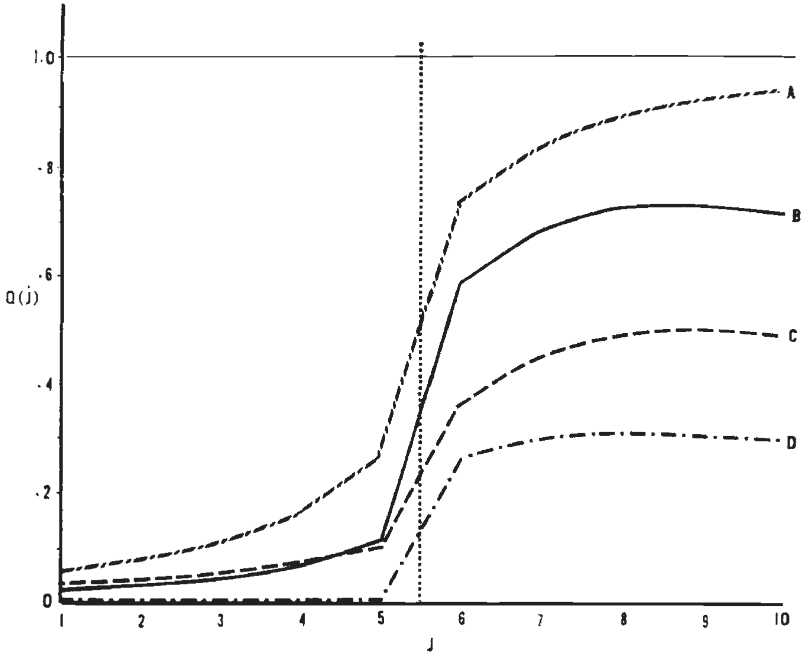


FIG. 10.—Distribution curves of allelic frequencies (qj) at equilibrium with unequal dispersal ($R \neq 1$) for dispersal model 4A

$A-R = 1$; $s_1 = s_2 = 0{\cdot}75$
$B-R = 2$; $s_1 = s_2 = 0{\cdot}75$
$C-R = 2$; $s_1 = s_2 = 0{\cdot}50$
$D-R = 10$; $s_1 = s_2 = 0{\cdot}75$

(vii) *Agreement between simulation and observed examples*

The results from simulation of two-environment situations seem to be in general agreement with the observed examples as illustrated in figs. 1-5, especially where the most likely models of gene flow, such as 4A are taken. If pollen distribution similar to that reported by Griffiths is assumed, one unit of x is equal to 12 ft. Good agreement is found for examples 1, 3 and 4, where the levels of selection are sufficiently high to result in the very sharp differentiation found. However, in examples 2 and 5 the differentiation is sharper than would be suggested theoretically. Either selection coefficients must be higher than estimated or gene flow is restricted in ways not appreciated at the moment. There is some evidence of reduced gene flow at Drws-y-coed. These two cases need further investigation.

The further observation of rather large phenotypic variance for characters under investigation, *e.g.* in examples 2 and 5, in the region near the boundary also seems to be in agreement with the expected variances based on intermediate values of q. The total genetic variance, $\sigma_G^2 = 2pq[\alpha + h(q-p)]^2 + [2pqh]^2$, (where p, q are the allelic frequencies of A, a and α, h, $-\alpha$ are the phenotypic values of AA, Aa and aa respectively) is expected to be large in this region.

(viii) *Rate of increase of allele for tolerance*

Starting with a very low frequency of allele $A(p_j)$, say 0·0001 or 0·05, it is seen from fig. 11 that for model 4A under relatively strong selection pressures the allele A for tolerance increased to a frequency approaching its final equilibrium value within the first 5-20 generations.

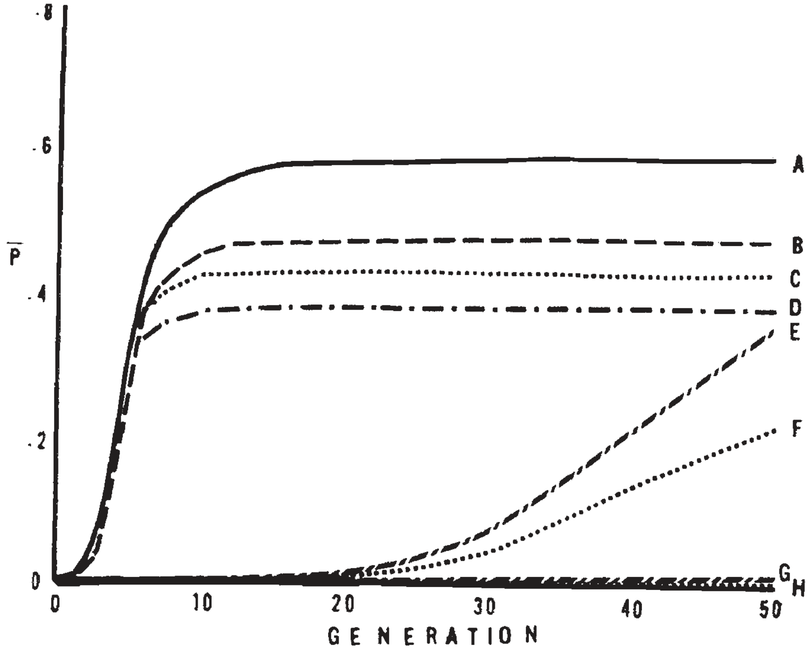


FIG. 11.—Rates of initial increase of allele A under dispersal model 4A

A—$s_1 = 0·95$, $s_2 = 0·50$; no dominance; $t_1 = t_2 = 1$
B—$s_1 = 0·95$, $s_2 = 0·50$; no dominance; $t_1 = 1$, $t_2 = 5$
C—$s_1 = 0·95$, $s_2 = 0·50$; complete dominance; $t_1 = t_2 = 1$
D—$s_1 = 0·95$, $s_2 = 0·50$; complete dominance; $t_1 = 1$, $t_2 = 5$
E—$s_1 = 0·25$, $s_2 = 0·10$; complete dominance; $t_1 = t_2 = 1$
F—$s_1 = 0·25$, $s_2 = 0·10$; complete dominance; $t_1 = 1$, $t_2 = 5$
G—$s_1 = 0·25$, $s_2 = 0·10$; no dominance; $t_1 = t_2 = 1$
H—$s_1 = 0·25$, $s_2 = 0·10$; no dominance; $t_1 = 1$, $t_2 = 5$

TABLE 7

Values of q_5, $\bar{q}$ *and* σ_q^2 *with differential selection acting on one sub-population only under different models of pollen dispersal and different selective values*

($s_1 = s_5$; $s_2 = s_j$, $j \neq 5$; $t_1 = t_2 = 1$)

Selective values*		Degree of dominance h_1, h_2	Models of pollen dispersal														
			1A			2A			3A			4A			4C		
s_5	s_j		q_5	$\bar{q}$	σ_q^2	q_5	$\bar{q}$	σ_q^2	q_5	$\bar{q}$	σ_q^2	q_5	$\bar{q}$	σ_q^2	q_5	$\bar{q}$	σ_q^2
0·95	0·50	0·5, 0·5	0·316	0·834	0·045	0·248	0·856	0·046	0·613	0·916	0·012	0·538	0·905	0·018	0·395	0·888	0·033
		0, 1·0	0·444	0·901	0·030	0·375	0·915	0·036	0·563	0·911	0·016	0·525	0·910	0·019	0·453	0·906	0·028
0·75	0·50	0·5, 0·5	0·489	0·879	0·025	0·375	0·881	0·032	1·0	1·0	0	0·826	0·966	0·002	0·609	0·930	0·014
		0, 1·0	0·551	0·922	0·020	0·449	0·925	0·028	0·739	0·949	0·006	0·670	0·939	0·009	0·560	0·926	0·018
0·75	0·75	0·5, 0·5	0·561	0·913	0·018	0·390	0·903	0·033	0·891	0·974	0·001	0·788	0·953	0·004	0·582	0·917	0·017
		0, 1·0	0·593	0·942	0·016	0·453	0·935	0·029	0·795	0·968	0·004	0·703	0·957	0·008	0·587	0·943	0·016
0·25	0·25	0·5, 0·5	1·0	1·0	0	1·0	1·0	0	1·0	1·0	0	1·0	1·0	0	1·0	1·0	0
		0, 1·0	1·0	1·0	0	1·0	1·0	0	1·0	1·0	0	1·0	1·0	0	1·0	1·0	0

*	Environment I (Only sub-pop. No. 5)	Environment II (All other sub-pop.)
AA	1	$1-s_2$
Aa	$1-hs_1$	$1-hs_2$
aa	$1-s_1$	1

This is true for other models although the rate of initial increase is much slower under models 1B and 2B especially with weak selection. Complete dominance and unequal generation times tend to give slightly lower value of $\bar{q}$ at equilibrium but rates of approach to equilibrium are quite high. Thus, a newly arising favourable gene with such a distinct selective advantage could easily be increased in a population largely irrespective of the form of migration over a very few generations.

(ix) *Some variations in environment arrangement*

The linear arrangement of sub-populations belonging to the different environments might be varied such that only a small central area might differ in selection rather than two wide regions. A further set of calculations has therefore been made in which it has been assumed that selection favours allele *A* only in a centrally located sub-population (No. 5) and allele *a* elsewhere, with selection coefficients s_1 and s_2. Table 7 gives $\bar{q}$ for the entire population and for q_5, together with σ_q^2 under four different sets of selective values. It is significant to note that moderately strong selection pressures *can* maintain a certain degree of local differentiation even within such a single small central area in face of continuum of species dispersion and gene flow at levels such as we have already considered.

5. DISCUSSION

The important conclusion from the above results is that selection can cause very localised patterns of microgeographical variation despite migration through pollen dispersal. But the situation in nature is likely to be very complex, depending on various ecological and genetic factors. Any one factor may be important under one set of conditions and not under another. Thus the different effects of various modes of gene dispersion can be large or small depending on a combination of all other variables, of which the magnitude and persistence of selection pressures are most important. Under a model of divergent or disruptive selection, as shown by Mather (1955), the quantitative rather than qualitative statements about these interacting forces leads to a more appropriate evaluation. For instance, while occasional long range dispersal may have significant effects in establishment of new colonies (Baker, 1951), quantitatively speaking its importance in opposing local differentiation would depend on the values of parameters involved, as we have shown. In fact, under real situations in nature these processes are likely to be far more complex than visualised in our model.

There are several factors that can influence the population structure and the magnitude of selection and migration pressures. The integration of the gene pool and epistatic control of adaptive traits tend to lower the net effect of selection; while a non-homogeneous species distribution, inbreeding arising from assortative mating, and initial failure of immigrants, or alien genes, to adjust in the receptor genetic background, etc., would tend to reduce the effective rate of gene flow (Mayr, 1963; Grant, 1963). In a well-studied example of microgeographic variation in *Linanthus parryae*, Epling, Lewis and Ball (1960) have recently shown that such factors as maintenance of large effective population size through storage of seed in soil, yearly and local fluctuations in systematic pressures, density-dependent selective forces and dispersal of pollen and seed by beetles and wind respectively results in a very complicated picture. Seasonal fluctuations in selective values such as those observed by Allard and Workman (1963) further indicate the complexity of population dynamics.

In general we believe that the problem of local differentiation should be reviewed from at least two new perspectives, namely, (1) that selection pressures in closely adjacent micro-environments even only a few feet apart can differ greatly and (2) that gene dispersion is likely to be of leptokurtic form resulting in isolation-by-distance rather than stepping-stone or island model situations. The actual and potential gene flow may accordingly be quite different in any given ecological and genetic situation (Epling, 1947). The migrational load may be quite high. Yet the fecundity of most species is sufficiently high that such loads are unimportant. This is certainly true in the examples studied and is supported by Barber (1964).

In view of the recent evidence for conditioning processes in plants (Durrant, 1962; Hill 1965), it is tempting to believe, in the absence of theoretical evidence, that the very localised differentiation described can occur only because the species concerned have the ability to develop the relevant characters by processes of conditioning in the vegetative phase. As has already been discussed, there is as yet no evidence of this for the characters concerned: but conditioning cannot be precluded and is being investigated. However, the theoretical evidence makes it clear that we have no need to seek an explanation of localised differentiation by such means: normal processes of selection can readily achieve it.

The problem of the evolution of this type of local differentiation is directly related to the evolution of the larger taxonomic unit, the race, or subspecies. A distinction is often made between (*a*) the intrapopulational polymorphism in sympatric forms and (*b*) the divergence among allopatric populations arising under geographical isolation. This has led to polemics about the so called theory of sympatric speciation. Several authors have discussed this problem with numerous examples (Grant, 1963; Mayr, 1963 for references) so that various arguments put forth in support or against the sympatric speciation need not be repeated here. However, several points can be emphasised.

Firstly, as Stebbins (1964) pointed out recently, the degree of spatial isolation needed during the initial stages of any such barrier must vary greatly from one group to another and genetic changes tending to suppress gene exchange between differentiating groups are as important as the mere chance events of geographical isolation. Experimental evidence suggests that reproductive barriers between and within species, disfavouring the wasteful hybridisation can develop as a result of natural selection (Dobzhansky, 1958; Knight, Robertson and Waddington, 1956; and see Spiess, 1962). Secondly, it is necessary to resolve whether such hybridisation occurs only during secondary intergradation (Mayr, 1963), or is in fact a primary stage in speciation. Huxley (1942) clearly emphasised the need of distinguishing the results of ecogeographical divergence followed by migration, from those of ecoclimatic divergence *in situ*. The examples that have been described in this paper are certainly cases of divergence *in situ*. Thirdly, it might be temping to attribute differences in plant and animal examples rather generally to their mode of life and reproduction. Huxley (1942), for instance, concluded that " the multiple-ecotype species-structure of higher plants is to be contrasted with the regional differentiation typical of higher animals . . . the difference is doubtless due to the random methods of fertilisation and distribution in plants ". While in a generalised consideration this is true, in a detailed analysis the quantitative nature of the sympatry versus allopatry in the species, or in other words the juxtaposition of different populations and the degree of gene flow between them is more significant, and some situations in plants may be found very similar to some in animals.

There is a great confusion over the use of the terms sympatric and allopatric, and it is this that has perhaps contributed most to the arguments about sympatric speciation. The examples we have described illustrate the confusion. If we take the present usage of the terms, based on criteria of interbreeding, such as by Mayr (1963, p. 23) then all the cases are sympatric. But if we take the original definition, based on geographical criteria, of Poulton (1903), they are allopatric. Because of this confusion which is permanently engrained in the literature, it is better to resolve it by describing such situations as *parapatric* (Smith, 1965), implying that a form of *allopatry* exists in which although the populations are geographically separate yet they are in sufficient proximity for some interchange of genes to occur.

Whatever definitions are used, complications in terminology need not blind us to the fact that populations of plants closely adjacent can diverge very remarkably even if there is only a small degree of geographic isolation. The same appears to be true in many animals, notably *Cepaea nemoralis* (Sheppard, 1952). If allowance is made for the scale of dispersal it may also be found in species with high levels of dispersal. Thus Barber and Jackson (1957) found marked clines in *Eucalyptus* despite dispersal of pollen over considerable distances by birds. Ford (1964, p. 43) and Barber and Jackson (1957) emphasise that although it was once considered that complete isolation is necessary for race formation, it is now clear that the selection pressures which normally maintain and adjust the characters of wild populations are powerful enough for differentiation to occur between geographically contiguous populations.

This is perhaps what has occurred in many cases in which sympatric speciation seems to have occurred, *e.g.* the apple and walnut Codling Moths in California. Detailed analysis may reveal parapatric differentiation, with differential selection supported by geographical restriction of gene flow, and make such cases more easily understood. Such a viewpoint is supported by Mayr (1963, Chap. 15). Thus Ford (1964, Chap. 5) and Creed, Ford and McWhirter (1964) have discussed examples of evolutionary differentiation in *Maniola jurtina* which they term sympatric. But in their general pattern and in their details these examples are very similar to the general pattern in *Agrostis tenuis* (Bradshaw, 1959) and to the detailed patterns reported here. The case of *Pinus monticola* (Squillace and Bingham, 1958), quoted by Grant (1963) as being sympatric speciation, is similar. However, it must not be forgotten that divergence under true sympatric situations is possible under certain conditions (Thoday and Boam, 1959).

Finally, it is important to realise that the process of local differentiation and its various controlling forces have evolutionary significance not only in connection with formation of subspecies or species but also in the adaptive improvement within the whole taxonomic entity. The capacity to evolve locally adapted populations may increase considerably the total area and number of habitats the species can occupy. Wright (1951) suggests that the problem of localised differentiation leading to incipient speciation may be of secondary importance to considerations of maintenance of variation and improvement in fitness of the species as a whole. It is significant that the ability of a species to form a graded patchwork of adaptation matches very well the pattern of environmental variation found in nature.

More studies in ecological genetics should be carried out in order to understand the genetic basis of evolutionary divergence under a wide variety of species-environment strategies. The relationship between modes of reproduction and the variables of ecologic opportunity can be understood only when comparative studies on a variety of species have been made. *A priori*, such relationships can only have developed under the influence of natural selection. Inbreeding species, for instance, have generally been contrasted with outbreeders in their potential for race and species formation (Baker, 1951; Grant, 1963). However, the recent work of Imam and Allard (1965) in *Avena fatua* suggests that any such distinction is likely to be more a matter of degree than in kind. At the same time it would appear that the ability of outbreeding species to form localised populations in the manner we have described is little different from that suggested for inbreeders. The strategy evolved by species in relation to their environments are many and complex. The full significance of each can only be appreciated by detailed analysis. It is one aspect of such strategies which has been considered in this paper. It is to be hoped that further experimental work and theoretical analysis will be forthcoming in the future to help our understanding of natural variation and evolution.

6. SUMMARY

1. The results of several studies on variation patterns in various grass species were briefly reviewed to show that very steep clines can be maintained due to rather strong selective forces in face of gene flow through pollen dispersal under random mating and within short distances.

2. These studies provide a general framework, in terms of various ecological and genetic parameters involved, for developing a model involving two environments with disruptive selection favouring different alleles in them. In order to analyse the joint effects of selection and migration of various forms including the isolation-by-distance model, a simulation method was used to obtain numerical solutions to a wide range of specified situations.

3. In general, selection as strong as observed in the actual examples maintains local differentiation under gene flow even as high as given by 50 to 60 per cent. pollen " contamination " at any site. Both mean rate and range of dispersal have significance in the study of migration pressures.

4. The degree of dominance involved in the genetic system governing the character and inequality of generation interval have significant influence on the amount of local divergence. Unequal rates of gene flow in reciprocal directions are able to maintain polymorphism only with very strong selection whereas under weak selection gene flow results in fixation of the allele " dispersed " more heavily. Therefore interrelationships between the opposing forces of selection and migration tend to become very complex when all such variables are considered jointly.

5. The term sympatric has been used to include such cases of differentiation of adjacent populations. This usage is misleading, since on geographical criteria such cases are allopatric. They are therefore described as *parapatric*. It seems likely that many reported cases of supposed sympatric differentiation are in fact parapatric.

6. It was concluded that only quantitative studies on the interplay of selection, migration and other such forces allows a fair evaluation of their relative influence on the patterns of evolutionary changes. The present work emphasises the need of considering the leptokurtic form of gene dispersal under an isolation-by-distance model conjointly with moderate to strong selective forces. Under this set of conditions, despite any intuitive conclusions to the contrary, it is clear that marked differentiation can occur.

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