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THE EVOLUTION OF REPRODUCTIVE ISOLATION IN CLOSELY ADJACENT PLANT POPULATIONS THROUGH DIFFERENTIAL FLOWERING TIME

P. STAM

Department of Genetics, Agricultural University, Foulkesweg 53, 6703 BM Wageningen, The Netherlands

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SUMMARY

A model is proposed for the non-selective displacement of flowering time in closely adjacent plant populations. Numerical results obtained on a single locus model as well as a polygenic simulation model demonstrate that an environmental difference may trigger genetic divergence of flowering time. This divergence results because there is non-random migration with respect to flowering time, which has effects like those demonstrated by Thoday and Gibson (1970) in an experiment in which selective migration alone gave genetic divergence between habitats with respect to sternopleural bristle number in Drosophila melanogaster.

In view of the results it is suggested that the evolution of reproductive isolation may sometimes start through a selectively neutral process, which can secondarily enhance the adaptation to divergent selection regimes in adjacent plant populations.

1. INTRODUCTION

It is well known from theoretical considerations that gene flow between (sub)populations may retard or prevent local genetic differentiation. The effect of gene flow is to erase both the effects of contrasting selection pressures and patchiness resulting from random drift (Wright, 1943, 1951; Jain and Bradshaw, 1966; Rohlf and Schnell, 1971). In contrast to earlier reports, it is now believed that effective pollen and seed dispersal is rather limited in most plants (Levin and Kerster, 1974). This would enable microgeographic differentiation over distances even less than 50 meters. However, Aston and Bradshaw (1966) and McNeilly and Antonovics (1968) reported substantial gene flow between populations of grasses and yet genetic diversity being maintained over relatively short distances. As indicated by the genotypic differences between adult and seed populations, this must be due to rather strong contrasting selection pressures. Theoretical work of Jain and Bradshaw (1966) also indicates that, in the presence of gene flow, fairly large selection coefficients are required for the maintenance of a steep cline.

In view of the erasing effects of gene flow it is conceivable that the process of local adaptation would benefit from a restriction to gene flow. Local differentiation in flowering time could, among others, be a mechanism preventing effective gene flow. In a series of papers on evolution in closely adjacent plant populations, this isolating mechanism has received a good deal of attention, most probably since it has been observed in conjunction with local adaptation of grasses to high levels of metal concentration in mining areas (McNeilly and Antonovics, 1968).

In the theoretical work on the evolution of reproductive isolation of adjacent or sympatric populations, this evolution is considered a response to some type of contrasting or clinal selection (Crosby, 1970; Caisse and Antonovics, 1978). McNeilly and Antonovics (1968) also interpreted the flowering time difference between metal-tolerant and non-tolerant populations in this sense. The basic idea behind this interpretation is that reproductive isolation evolves because gene flow is inherently disadvantageous (since it leads to less well adapted offspring) and thus any gene which reduces gene flow has an advantage. Notice that this mechanism is essentially the same as the one whereby character displacement in secondarily intergrading species is believed to evolve. It implies that, prior to the evolution of reproductive isolation, a certain level of local adaptation exists.

Crosby (1970) has pointed out that selective forces on isolating genes are second order, because not the carrier of a non-isolating gene but only part of the carrier's offspring is less well adapted. From their work on simulation models both Crosby (1970) and Caisse and Antonovics (1978) concluded that the evolution of reproductive isolation as a response to divergent selection or "hybrid weakness" requires fairly high selection pressures.

The aim of this paper is to draw attention to the possibility that reproductive isolation in plants through different flowering times need not necessarily be a response to divergent selection, but may essentially be non-darwinian if it is triggered by a non-selective environmental difference. The idea is as follows. Suppose a population occupies two adjacent habitats, *A* and *B*. The only difference between *A* and *B* is a slight (environmental) difference in flowering time. We also suppose genetic variation for flowering time. Suppose habitat *A* induces a shift towards earliness and let there be no systematic genetic difference between the *A* and *B* part of the population. Then, even if pollen is transported freely across the boundary between *A* and *B*, gene flow is preferential since pollen from late genotypes in *A* preferentially migrates into *B*. (The dispersal itself is, of course, not preferential, but the effective migration is so). Similarly, genes for earliness in *B* preferentially migrate (through pollen dispersal) into *A*. So the alleles for lateness in habitat *A* preferentially leave *A*, whilst among the inflow from *B* the alleles for earliness are over-represented. The reverse is true for the other habitat. Provided that seed dispersal is limited, this mechanism will lead to a genetic divergence in flowering time between the habitats. Notice that, although migration is automatically preferential, the mechanism involves no selection when the (sub)populations are considered as a single unit. Any shift in frequency of alleles for flowering time in one part of the population is exactly counter-balanced by an opposite shift in the other part. This means that, averaged over the two habitats, the allele frequencies will not change. The alleles are merely sorted out by the mechanism.

Prior to the writing of this paper, Professor Thoday has pointed out to me that the mechanism described above is essentially the same as the one he and his colleagues have used in an experimental set-up for preferential migration with respect to a quantitative character in *Drosophila* (Thoday and Gibson, 1970). The experiment was designed to demonstrate genetic divergence between habitats which themselves induce an environmental difference. A population of *Drosophila melanogaster* was grown in two habitats (20°C and 25°C) known to influence the number of sternopleural

bristles (more bristles at the lower temperature), which is also under genetic control. In each generation, prior to mating, a joint sample of flies from both cultures was divided into a "high" and "low" half, the "low" half being transferred to the "low" environment and the "high" half to the "high" environment. Thus, flies from the "low" environment having a high bristle number (*i.e.*, the "high" genotypes) were forced to migrate to the "high" environment and vice versa. After seven generations a significant genetic difference between the sub populations of the habitats had developed. The genetic variance between habitats had become about three times as large as the average genetic variance within habitats, indicating that the preferential migration scheme had indeed partly sorted out the genes for bristle number.

Since the present paper is written in terms of flowering time and pollen dispersal in plants it deals with a natural way of preferential migration. The mechanism as such is, of course, not restricted to "time of mating" and applies to other forms of mating preference as well. The next section deals with a simple single-locus model, serving as a pilot-study for the more complex simulation model of the section thereafter.

2. Deterministic one locus model

Suppose a population of infinite size occupies two adjacent areas (habitats), *A* and *B*. The habitats induce a difference in flowering time, such that for all genotypes in *A* the onset of flowering is shifted *d* units towards earliness. It is assumed that duration of flowering is equal for all genotypes in both habitats. By setting this duration of flowering equal to unity, time is measured in units of flowering duration. The genetic basis of flowering time is a single locus with 2 alleles, *E* and *e*. Fig. 1 further illustrates the model. For simplicity we assume that pollination is at random within the whole population, such that a plant which is flowering at any given time is equally likely to be pollinated by any other plant in the whole population which is also flowering at that time. We further assume that there is no

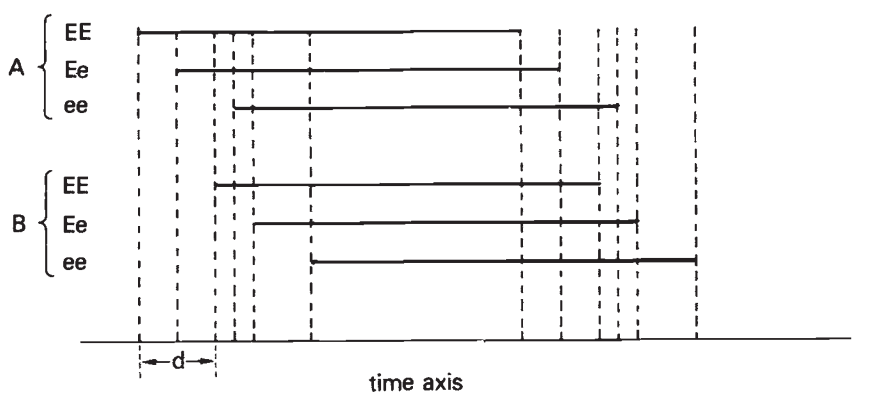

FIG. 1. Flowering periods (horizontal bars) of three genotypes (*EE*, *Ee* and *ee*) in two environments (*A* and *B*). The difference *d* in onset of flowering between *A* and *B* is equal for all genotypes. The vertical dotted lines indicate the distinct intervals into which the total flowering period can be divided. Given the genotype frequencies in both environments, the allele frequencies can be calculated for each of the intervals.

seed dispersal, or, which is equivalent in this case, at least no seed dispersal across the boundary between the habitats. In addition to these simplifying assumptions we assume that fertilization is frequency-independent in the sense that for any genotype the probability of being fertilized at a given moment does not depend on the number of other plants, *i.e.*, potential pollinators, which are flowering at that moment. So we are dealing with a so called "constant fraction" model of assortative mating (cf. Moore, 1979).

In order to study the behavior of the model I have taken the following approach. The total period during which plants are flowering can be divided into a number of non-overlapping intervals, as indicated in fig. 1. Given the genotype distribution in A and B, the allele frequency among the plants which are flowering at that time, can be calculated for each interval. This can be seen as the gene frequency among the pollen which is available during the interval. Denote these allele frequencies by $f_1, \ldots, f_n$ (n intervals). The average allele frequency among the pollen by which a particular genotype is pollinated is then calculated as

$$h_g = \sum_{i=1}^{n} f_1 l_i k(g)_i,$$

where g indicates the genotype in a particular habitat, l_i is the length of interval i, and $k(g)_i$ is an indicator function (1 or 0) for genotype g indicating whether or not g is flowering during interval i.

In this way six h-values (three genotypes in each habitat) are calculated. The next step is to calculate the seed offspring distribution for each genotype in both habitats, using the corresponding h-values. It is not difficult to write down the set of recurrence equations connecting genotype frequencies in successive generations. In the following the gene frequencies in habitats A and B are denoted by P_A and P_B, respectively.

I have not pursued a detailed mathematical analysis of the model, but confined myself to numerical iteration of the recurrence relations. The following results, most of which are rather obvious, emerged.

(a) The joint gene frequency, $P_A + P_B$, remains constant over generations. The trajectory in the $P_A - P_B$ plane is a straight line: $P_A + P_B = \text{constant}$.
(b) Starting with identical (non-trivial) genotype distributions in A and B, the gene frequencies, P_A and P_B, will diverge.
(c) Divergence of gene frequencies continues until a stable equilibrium $(\hat{P}_A, \hat{P}_B)$ is reached. If A is the "early" habitat and P_A and P_B denote the frequencies of the early allele (E), then $\hat{P}_A > \hat{P}_B$. It is easy to see that, as long as there is overlap in flowering time between the earliest genotype in the "early" habitat and the latest genotype in the "late" habitat, divergence will not lead to fixation of alleles in either habitat.
(d) The equilibrium values depend on
    (a) the value of $P_A + P_B$,
    (b) the environmental difference in flowering time, and
    (c) the differences between the genotypes within a habitat.
(e) For a given value of $P_A + P_B$, the genetic difference between the habitats at equilibrium, $|\hat{P}_A - \hat{P}_B|$, increases as the environmental difference increases.

(f) For a given environmental difference, the genetic difference at equilibrium, $|\hat{P}_A - \hat{P}_B|$ increases with increasing difference between genotypes within a habitat.

A sample of numerical results, illustrating several of these points is given in fig. 2.

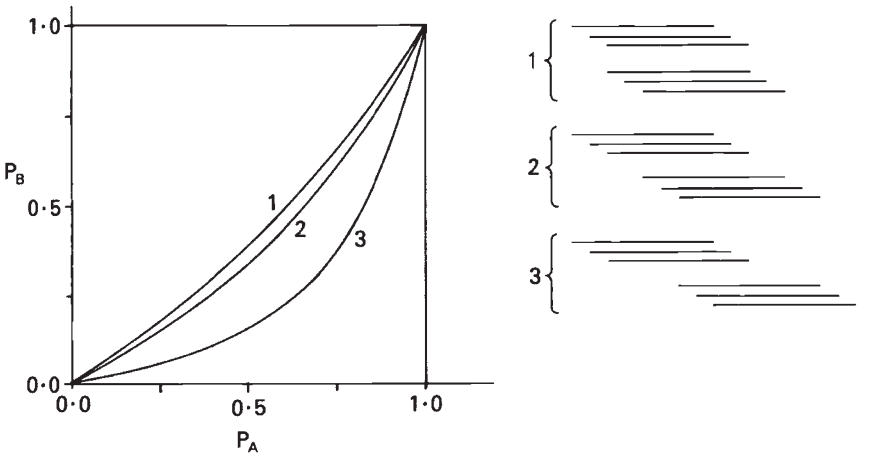

FIG. 2. Equilibria $(\hat{P}_A, \hat{P}_B)$ for the deterministic one locus model. For a given value of $P_A + P_B$ the equilibrium point is the intersection of the given curve and the line $P_A + P_B$ = constant. The numbering corresponds to the flowering periods indicated at the right (cf. fig. 1). Numbers 1, 2 and 3 represent an increasing environmental difference between habitats *A* and *B*.

The above results confirm the idea outlined in the previous section, *i.e.*, genetic divergence can be triggered by an environmental difference between adjacent habitats. The model of this section is, in several respects, an oversimplification. Though seed dispersal is in general much less than pollen dispersal, the assumptions (no seed dispersal and "random" pollination) are unrealistic. In the next section a simulation model is described which accommodates a more natural way of pollen and seed dispersal and in which, in contrast to the single locus model, flowering time is under polygenic control.

3. Simulation model

There are, of course, several ways to model gene flow through pollen and seed dispersal between subpopulations occupying adjacent habitats. One approach is to consider a number of infinitely large populations along a transect running across the boundary between the habitats. Migration of male gametes (pollen) and zygotes (seeds) between subpopulations should then be simulated according to an appropriate scheme. However, since effective pollen migration depends on the genotypic constitution of each subpopulation with respect to flowering time (a polygenic character), such a deterministic approach would either necessitate the manipulation of a high number of variables, or numerical integration of the flowering time distribution in each subpopulation in order to determine the overlap and

the amount of pollen exchange. For these reasons, though the stochastic aspects of the model are not of primary interest, I have taken the approach of a stochastic simulation, also used by Crosby (1970).

The population to be simulated consisted of a finite number of plants growing in a narrow strip which runs (perpendicularly) across the boundary between the habitats, such that equal numbers of plants were growing in either habitat. In each generation one site of the two-dimensional array was available for one plant, and all sites were occupied. Thus plant density was constant over generations. Flowering time was determined by the genotype at a number (which could be varied from 1 to 36) of independently segregating loci, each with two alleles with equal additive effects. Both the difference between the extreme homozygotes and the environmental difference between the habitats were expressed in units of flowering duration. To assure the presence of substantial genetic variance, the initial gene frequency at each locus was sampled from a rectangular distribution between 0·4 and 0·6. In the starting population individual genotypes were sampled from these binomial distributions. The following attributes were recorded per plant:

—the site of growing (*i.e.*, the indices in the two-dimensional array)
—genotype, genotypic value and flowering time
—number of seed offspring and growing sites of these seeds.

Reproduction, seed and pollen dispersal were dealt with in the following way. First, for each site to be occupied in the future generation, the seed parent's growing site was sampled, using a negative exponential seed dispersal curve. At this stage the number of seed offspring per parent was recorded. Next, for all adults having non-zero seed offspring, its set of offspring was generated. The sampling of the male parent was as follows. At a random moment during the flowering of the female parent a flowering male parent was sampled, again using a negative exponential curve for pollen dispersal. By means of the usual bit-by-bit techniques, gametes from both parents were generated and were pairwise stored in the zygotic array. After completion of reproduction the adult population was replaced by the zygotes. At pre-defined intervals average flowering times of groups of plant along the transect were collected for output. In order to avoid excessive non-successful sampling (as would occur if, for example, an early seed parent happened to be surrounded by late neighbours), some minor refinements were incorporated in the above scheme. In addition, in the program an environmental gradient of variable steepness between the habitats instead of a sharp boundary could be defined. In most runs a strip of 4 by 100 plants (200 plants in either habitat) were simulated.

Fig. 3 summarizes a typical result. Notice that the values of the pollen and seed dispersal parameters ($\lambda_p = 0{\cdot}005$ and $\lambda_S = 1{\cdot}0$) amount virtually to "random pollination" over the whole population on the one hand, and no seed dispersal on the other hand; so in this respect these values more or less correspond to the deterministic model of the previous section. From fig. 3 we see that the population behaves, as was to be expected, similarly as in the deterministic model, *i.e.*, flowering times diverge genetically between the habitats with a steep cline near the boundary.

The influence of the rate of pollen dispersion is shown in fig. 4. Less pollen dispersal retards the divergence. This is obvious, because if no fertilization across the boundary could take place to start with, no change

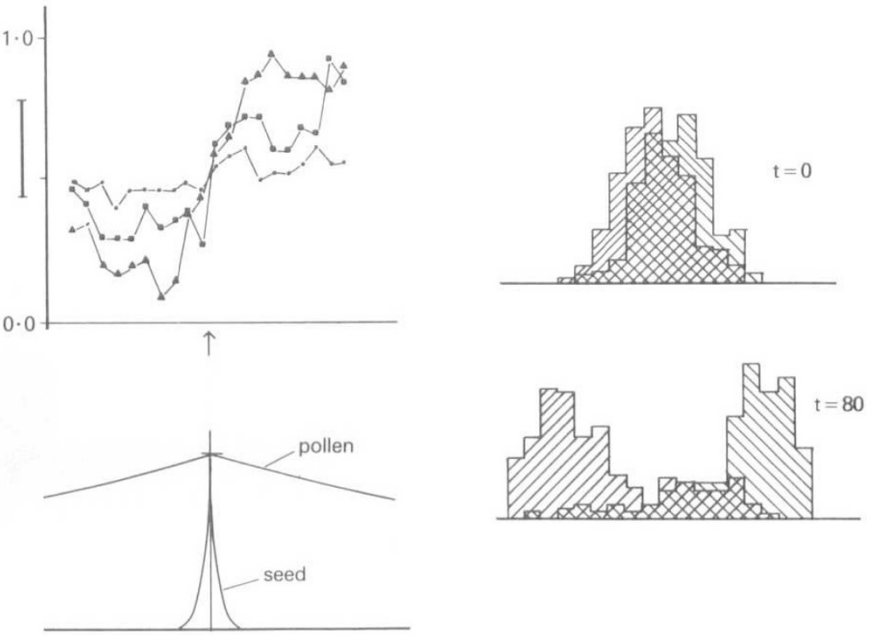

FIG. 3. Result of a simulation run with 8 flowering time loci. (a). Upper part: flowering times (scaled to (0, 1)) of groups of 20 plants along a transect running across the boundary (indicated by the arrow) between two adjacent habitats: ●—●: generation 0, ■—■: generation 20; ▲—▲: generation 40. Left of the arrow is the early habitat. The vertical bar on the left indicates the length of the flowering period on the same scale. (a). Lower part: pollen (p) and seed (s) dispersal curves pollen: $y = e^{-0{\cdot}005x}$; seed: $y = e^{-x}$. Horizontal scale same as upper part of diagram. (b). Distributions of flowering time in early (////) and late (\\\\) habitat at generations 0 and 40.

would occur whatsoever. Conversely, a decrease of seed dispersal has the opposite effect, as illustrated by fig. 5. Since gene flow through seed dispersal is independent of flowering time, an increase of seed dispersal will, because of its erasing effect, retard differentiation between the habitats.

In a few additional runs the environmental difference between the habitats was absent. In these runs it was observed that after some 20 generations the population developed alternating clusters of early and late genotypes. Obviously, this patchiness was generated by slight genotypic differences due to sampling. The decay of patchiness of this kind is severely retarded by preferential mating, that is the tendency to mate within a patch. Once such a clear-cut pattern existed, it might last for more than 20 generations, eventually being substituted by a different one, or, in case of smaller population sizes, lost due to fixation. Thus, random genetic drift, in combination with a preferential mating mechanism, may generate fairly stable local differentiation, involving no selection pressure.

In order to study the possible influence of the preferential migration mechanism on the rate of adaptation to locally contrasting selection regimes, the simulation program was adapted to incorporate natural selection at a second set of (independently segregating) loci. In addition to the environmental difference in flowering time, a selective difference between the

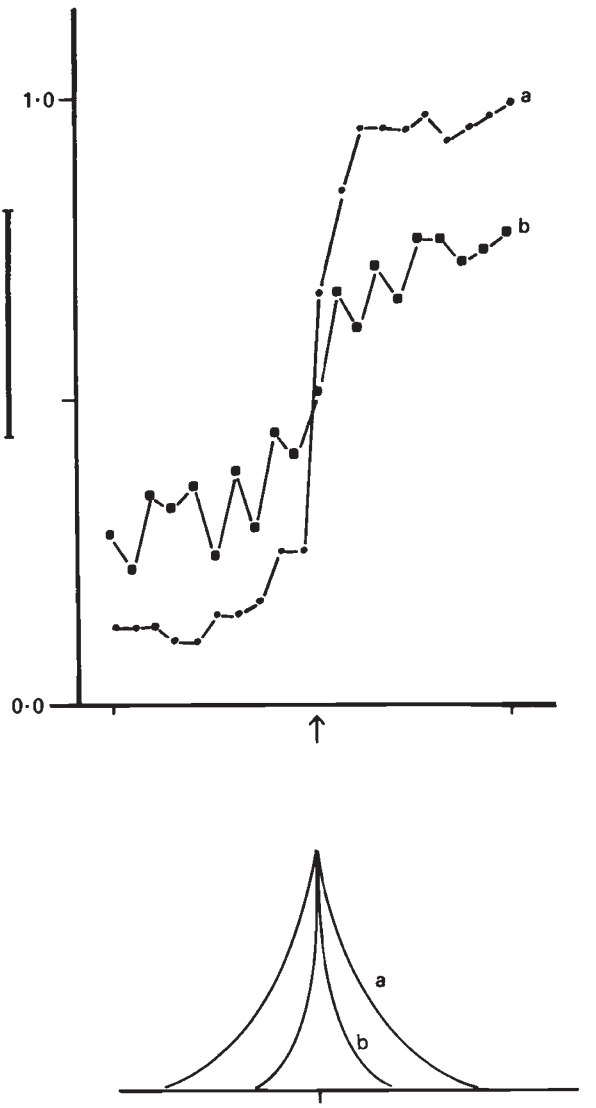

FIG. 4. Effect of a change in pollen dispersal ($y = e^{-\lambda x}$) on the outcome simulations at generation 80. (a) $\lambda = 0{\cdot}01$; (b) $\lambda = 0{\cdot}05$. Lower part: relative pollen abundance on the same horizontal scale for these λ-values. Other parameters and further legend the same as in fig. 3.

habitats was included. This selective difference could be defined as an environmental gradient of given steepness.

To fix ideas, one could think of a gradient of metal concentration in the soil and a set of gene loci determining metal tolerance. For convenience I will discuss the model in these terms, although it applies to any other environmental gradient and corresponding genes as well. Gene action at the tolerance loci was assumed to be additive over loci. An optimum model was chosen to relate an individual's fitness to (a) its number of tolerance

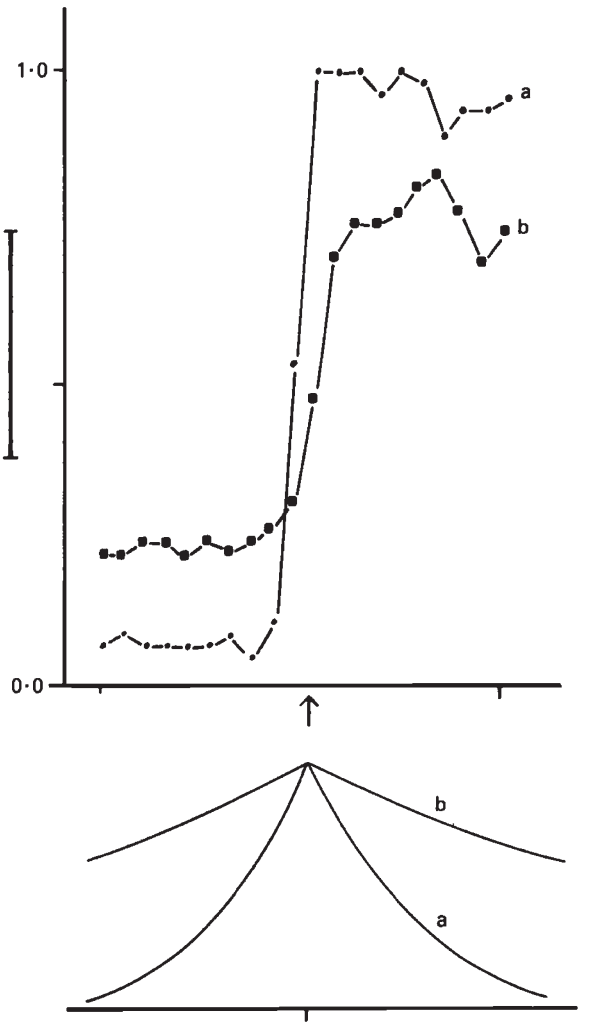

FIG. 5. Effect of a change in seed dispersal ($y = e^{-\alpha x}$). (a) $\alpha = 0{\cdot}50$; (b) $\alpha = 0{\cdot}10$. Lower part: relative seed abundance on the same horizontal scale. Other parameters and further legend the same as in fig. 3.

genes, and (b) the metal concentration at its site of growing. For a given site along the gradient the optimum fraction of tolerance genes (scaled to the interval (0, 1)) equals the metal concentration (also scaled to the interval (0, 1)) at that site. Fitness was assumed to decrease linearly with the difference between metal concentration and optimum tolerance level. In this way clinal selection for a polygenic character was accommodated for. Parents were, apart from the rules for pollen and seed dispersal, sampled with probabilities weighted by their fitness. Simulations started with a population almost completely adapted to one of either habitats (*e.g.*, a tolerance level of 0·02). Two simulations were run for comparison. In the first one, no genetic variation existed for flowering time, nor was there an environmental flowering time difference. The second run was, apart from

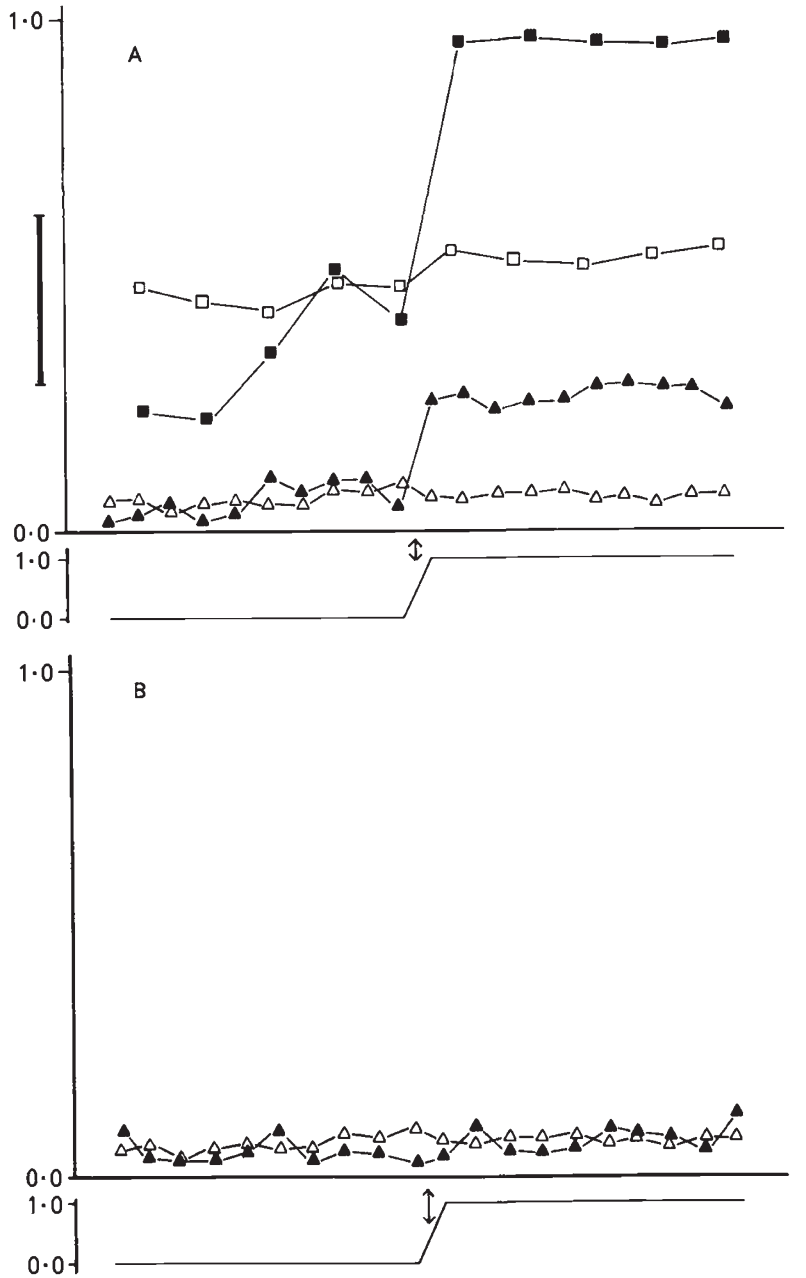

FIG. 6. The effect of the presence of both genetic variation in flowering time and an environmental difference on the selective response to contrasting selective forces in adjacent habitats. The upper part shows average flowering times at generation 0 (□—□) and 50 (■—■) and level of metal-tolerance at generations 0 (△—△) and 50 (▲—▲), both scaled to (0, 1).

The lower part shows the environmental gradient (*e.g.*, metal concentration) along the transect.

Further legend same as in fig. 3. The least well adapted genotypes (*i.e.*, the completely tolerant in the non-metal area and the non-tolerant in the metal area) both have relative fitness 0·2.

A: initial variation for flowering time.

B: no initial genetic variation for flowering time

For further details see text.

the selection gradient, similar to the non-selective ones, described earlier. The results, as illustrated by fig. 6 were strikingly different. In the run with no variation for flowering time, adaptation to the alternative adjacent habitat was almost completely inhibited by the inflow of "unadapted" pollen; by generation 50 the tolerance level had not increased. In the second run however, the subpopulations of the two habitats started to diverge with respect to flowering time, and once a certain degree of reproductive isolation was established, adaptation to the environment of the adjacent habitat started to evolve rather quickly.

The results of the simulations can be summarized as follows.

(a) The proposed mechanism for genetic divergence in time of mating, induced by an environmental difference between closely adjacent habitats, is likely to work under certain circumstances. Conditions for this non-selective divergence are the initial presence of substantial genetic variation, and, of course, little or no overlap in flowering periods between the extreme early and late genotypes. An additional condition is that little gene flow through seed dispersal occurs between the habitats.
(b) Since the mechanism automatically gives rise to a certain degree of reproductive isolation, it is likely to enhance microgeographical differentiation.
(c) Although contrasting selective forces may favour the evolution of reproductive isolation, the proposed mechanism itself is essentially non-selective. Moreover, random drift may generate a long lasting patchiness with respect to flowering time in plant populations.

It is interesting to know under which conditions (in terms of contrasting selection forces, amount of gene flow, and amount of genetic variation in flowering time) an environmental difference will enhance local adaptation. With the approach of the present paper however, the computing time needed for such an analysis would be prohibitive. The aim of this paper is merely to demonstrate the mechanism.

4. Discussion

Theoretical work on the evolution of reproductive isolation has treated this evolution as a response to some form of contrasting or clinal selection pressures (Maynard Smith, 1966; Antonovics, 1968*b*; Caisse and Antonovics, 1978). Also the inference from field data was to regard the phenomenon as a selective response to, or, at least an, evolution occurring simultaneous with local adaptation (Antonovics, 1968; McNeilly and Antonovics, 1968; McCauley, 1979; Mulroy, 1980). According to this view, the evolution of reproductive isolation is due to the same mechanism as the one whereby secondary intergrading species will tend to develop reproductive character displacement. Studying the simultaneous behaviour of allele frequencies at a selected locus and an "isolating" locus, Caisse and Antonovics (1978) had to assume a slight initial difference between habitats with respect to the isolating allele frequencies. As Maynard Smith (1966) has pointed out, this is necessary for further reproductive isolation to evolve under the given circumstances. The present paper shows that without selection, reproductive isolation may also evolve in the presence

of a small non-genetic initial difference. Thoday and Gibson (1970) demonstrated this mechanism to be effective in an experimental set up with forced preferential migration between two habitats based on phenotypic values of a quantitative character, not naturally associated with mating preference.

The results of this paper are in agreement with Lande's (1981, 1982) results for quantitative models of sexual selection. In these models the co-evolution of a female character, y (determining mating preference) and a secondary sexual character (z) in males is considered. Mating preference, $\psi(z, y)$ is defined as the relative preference of females with phenotype y to mate with males with phenotype z. In these terms differential flowering time amounts to unimodal mating preference of the form

$$\psi(z, y) = \max(0, 1 - |z - y|),$$

which is not qualitatively different from

$$\psi(z, y) = \exp\left(-\frac{1}{2}\frac{(z-y)^2}{v^2}\right),$$

used by Lande. It is not difficult to see that, in a homogeneous population where y and z are identically distributed (as in the case when both y and z refer to flowering time), this will not lead to a runaway process (cf. Lande, 1981). When, on the other hand, the distribution of z and y varies geographically, as is the case with an environment-induced shift of the means, Lande's (1982) model predicts amplification of the phenotypic difference, much the same as the present paper describes.

The model of this paper demonstrates the possibility of non-selective reproductive isolation. The question remains whether this situation is likely to be met in nature. It could be argued that an environmental difference which causes a shift in flowering time will most probably also affect selection coefficients at a number of other loci. Or, handling the argument the other way round, one may expect the plants of a population colonizing a new habitat to which they are not yet adapted, to have to cope with physiological stress. The latter often induces a shift in flowering time. The data on flowering times in *Agrostis tenuis* growing on adjacent mine and non-mine soils, presented by McNeilly and Antonovics (1968), indicate that the difference between the populations is indeed both genetic and environmental. This suggests that local adaptedness and reproductive isolation are evolving simultaneously. As pointed out earlier, once they get started, the two kinds of divergence will enhance one another. It should be emphasized however that local differentiation may be drastically retarded as long as effective pollen flow dilutes the adaptive characters (cf. Antonovics, 1968*b*). One might say that under these circumstances the non-darwinian evolution of reproductive isolation is necessary to enable further darwinian evolution.

The results of this paper might suggest that microgeographical differentiation in conjunction with divergent flowering times must be a widespread phenomenon. Several reasons exist why this need not be the general case. First, a major feature of the model is that flowering periods of the extreme early and late genotypes do not overlap. Although plant breeders' experience confirms the presence of genetic variation for flowering time in many populations of cultivated crops, it is hard to imagine that for

species with flowering periods of over 4 to 6 weeks a difference in onset of flowering between extreme genotypes could cover such a long period. A plant's physiology may set natural limits to time of flowering without seriously affecting its fitness.

Closely associated with the foregoing is the possibility that flowering time is a canalized character. The latter may be the case in insect pollinated species in which a minority of odd flowering (*i.e.*, extreme early and late) plants are at a disadvantage, because the pollen vector's behaviour is adjusted to the majority of the population (cf. Levin, 1972). Studying a so-called "mass action" one locus model of assortative mating (implying this minority disadvantage), Moore (1979) concluded that the presence of genetic variation with respect to assortative mating must be regarded unlikely, because, neglecting mutation, the equilibria of the model are unstable. With polygenic inheritance of flowering time, normalizing selection and/or canalization will reduce the (observable) genetic variation. However, though canalization may mask genetic variation in an established population, one could imagine canalization to break down when the population colonizes a new, harsh environment, thus releasing the hitherto hidden genetic variation and enabling assortative mating.

Thirdly, divergent flowering time is not the only isolating mechanism one can think of. Evolution of self-fertility in small marginal populations of an otherwise self-sterile species is an alternative way to reduce the erasing effect of pollen dispersal (Antonovics, 1968*a*). Needless to say that in a discontinuously distributed population spatial isolation can prevent gene flow.

Moore (1979) has pointed out that flowering time genes will only respond to intermediate contrasting selection pressures when there is no determination of fitness associated with the time of mating (*i.e.*, in the constant fraction model). He therefore deems "inferences based on the assumption that variation for assortative mating genes (if there is any) will respond to selection favouring reproductive isolation . . . suspect" (loc. cit). In view of the present paper Moore's statement can only be a stimulus to investigate whether minority disadvantage associated with flowering time really is a widespread phenomenon in plants.

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