

The genetic implications of ecological adaptations in plants

1. INTRODUCTION

During the past decade, great strides have been made in empirical and theoretical plant population ecology. The empirical studies have been highlighted by work on the effect of intraspecific competition on plant size and numbers (HARPER & WHITE 1970, 1974), mortality and fecundity schedules (WHITE & HARPER 1970; HARPER & WHITE 1974; SARUKHAN & HARPER 1973; SARUKHAN 1974; HARPER & WHITE 1970), the spatial dynamics of succession and colonization (YARRANTON & MORRISON 1974), safe site specificity (HARPER 1961, 1965; SHELDON 1974), pollen and seed dispersal (LEVIN & KERSTER 1974), and the dynamics and longevity of the seed pool (ROBERTS 1972; HARRINGTON 1972). Within the realm of theory, special attention has been given to optimizing life history strategies with special regard to seed dormancy (COHEN 1967, 1968), and dispersal (GADGIL 1971; ROFF 1975), reproductive schedules and developmental switching (COHEN 1971, 1976; BRADSHAW 1974; TAYLOR *et al.* 1974; LEVINS 1968; SCHAFFER 1974a, b), and longevity (GADGIL & BOSSERT 1970; GADGIL & SOLBRIG 1972; SCHAFFER & GADGIL 1975; KAWANO 1975).

The descriptions and predictions of life history tactics and responses of plant species adapted to different environments largely have been considered without regard to the genetic consequences which accrue from the adaptations. Some aspects of demographic attributes which have received theoretical genetic treatment are population growth with density-dependent regulation (CHARLESWORTH & GIESEL 1972; CHARLESWORTH 1971, 1973), age-specific selection (ANDERSON 1971; KING & ANDERSON 1971), age-specific fecundity (GIESEL 1974; DEMETRIUS 1975), and migration (JAIN & BRADSHAW 1966; ANTONOVICS 1968; GILLESPIE 1974, 1975, 1976; BULLOCK 1976; NAGYLAKI 1976). With the exception of migration, many of the models employed do not take into account the unique properties of plants, nor do they address many interesting questions relevant to plants.

Our purpose is to discuss some genetic implications of demographic properties of plant populations. Emphasis will be placed upon the genetic consequences of realistic fecundity distributions, reproductive schedules, patterns of differentiated plant subdivisions, and seed-pool characteristics. The cameos which emerge will be painted with broad strokes because of time restrictions and the limited depth to which these problems thus far have been pursued.

2. THE GENETIC CONSEQUENCES OF FECUNDITY DISTRIBUTIONS IN PLANTS

2.1. INTRODUCTORY REMARKS

Recent studies on the population ecology of plants have shown that in natural and experimental populations only a small proportion of the seedling crop survive to reproductive maturity, and that a size hierarchy will be established among the seedlings early in the season which may persist and be magnified as the population matures (WHITE & HARPER 1970; ROSS & HARPER 1972). As a consequence, populations typically are characterized by biomass and fecundity distributions which are L-shaped, wherein a very small proportion of the population may make a substantial and grossly disproportionate contribution per capita to the yield or seed output of the population (KOYAMA & KIRA 1956; RISSER 1969; SARUKHAN 1974; LEVERICH 1977). Indeed, in some populations, the highest fecundity classes may be more frequent than plants of medium fecundity. Conversely, a very large fraction of the population may make only small contributions to yield or seed output. The difference in seed production between large and small plants within a population may differ by several orders of magnitude especially in species with great developmental flexibility. Even the difference between mean seed set and seed set in the most reproductive individuals may be enormous (SALISBURY 1976). The L-shaped performance distribution may arise from competitive interactions between cohorts and the statistical distribution of site quality, as determined in part by the genetic make-up of the population.

The L-shaped fecundity distribution in plant populations is in stark contrast to the poisson distribution which is a cornerstone of population genetic theory (KARLIN & MCGREGOR 1968). What are the genetic consequences of an excess of small plants and an excess of large ones relative to a poisson distribution? Whether we talk of a response to directional selection, decay in variability, or other parameters, it seems likely that the effect would be great. The specific consequences would depend on the importance of the genotype in dictating the observed fecundity hierarchy. We sought answers to the afore-mentioned questions using a simulation model which takes into account micro-environmental hospitality.

2.2. THE MODEL

We began with a population composed of 250 annual plants. They were assumed to compete at the seedling and juvenile stage resulting in the establishment of a size hierarchy which would persist through the remainder of the season. The relative performance of young plants was assumed to be controlled by genetic differences, and genotype-independent factors such as site hospitality. Seedlings were assigned relative fitness values and site hospitality coefficients (based upon a random number between 0.0 and 1.0). The extent to which the genotype contributed to seedling vigor, which we will refer to as

C_{vigor} also was entered into the model so that we might look at different levels of penetrance or plastic response. The vigor of a seedling is established as follows:

$$\text{seedling vigor} = (\text{genotype fitness}) \cdot (C_{\text{vigor}}) + (\text{site hospitality}) \cdot (1 - C_{\text{vigor}})$$

The ultimate performance of the plants was established as seedlings by assigning a potential fecundity value to each in order of the vigor of the seedlings, the most vigorous seedling having the highest fecundity potential. The fecundity upon which seedlings thereby were placed is illustrated in Fig. 1.

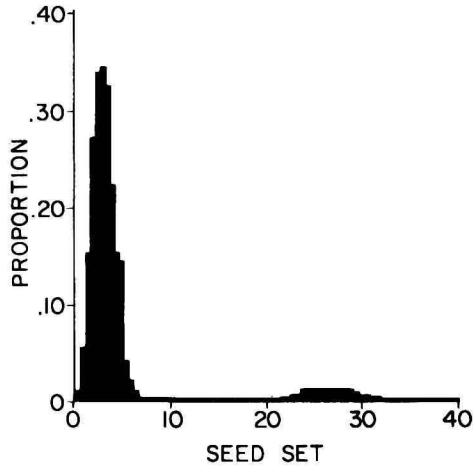


FIG. 1. *The distribution of fecundities under the L-shaped distribution*

This distribution was obtained by superimposing two poisson distributions with different means, λ_1 and λ_2 . We will refer to it as L-shaped, as its shape suggests. For most simulations the mean values chosen were $\lambda_1 = 7.15$ and $\lambda_2 = 35.75$ thus affording a 5 fold difference between the two means and an overall mean of 10. In most simulations 90 per cent of the plants lies within the first distribution. We will contrast a simple poisson distribution with a mean of 10 with our distribution.

The distribution we have chosen to contrast with the standard poisson is not meant to represent a specific study or species. Rather it represents the type of schedule we may expect to find, and contains the essence of the small empirical base in the literature.

2.3. RESULTS

The most important question that arises is how the fecundity distribution affects the rate of response to selection. To examine this, simulations were performed with selection for one allele at a locus, starting with that allele at a frequency of 0.1, and following the population until it reached a frequency of 0.9. The starting point of 0.1 was chosen for the sake of expediency for any lower value would have resulted too often in the chance loss of the favoured allele, or excessively extended response times, both especially in the case of a recessive allele. The minority allele was introduced in the form of homozygous seed.

The effect of an L-shaped fecundity schedule versus a simple poisson on the response to selection is quite striking. If we assume that a recessive homozygote has a relative fitness of 1.0 and that the dominant homozygote and heterozygote have relative fitnesses of 0.75, and that C_{vigor} is .5, the mean sojourn time for a recessive gene from $q = .10$ to $q = .90$ averages about 75 generations for a poisson distribution compared to about 45 generations for an L-shaped one (Fig. 2). The presence of manifestly fecund plants whose success is in part related to a favorable genotype is responsible for the accelerated response to selection. Moreover the response to selection of a recessive gene in the .1 to .9 frequency window, given an L-shaped distribution, is similar to the response features favored of a dominant gene given a poisson distribution. For a dominant gene, the rate of advance also is faster with the L-shaped distribution than with the poisson.

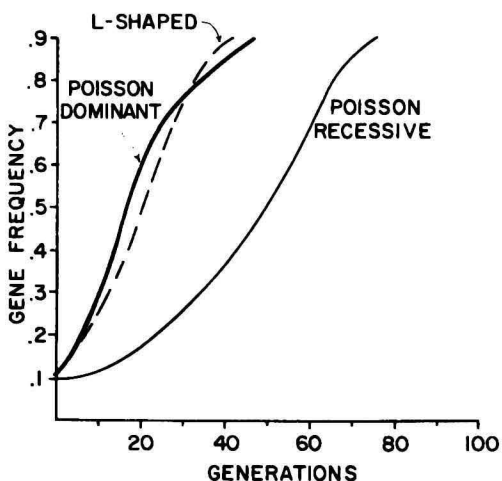


FIG. 2. Rate of response to selection as a function of the fecundity schedule. The "double poisson" refers to the L-shaped schedule. Genotype fitnesses: $W_{AA} = .75$, $W_{Aa} = .75$, $W_{aa} = 1.0$

The rate of evolution with an L-shaped fecundity schedule is a function of the ratio of the mean values of the two distributions comprising the L. In the initial model, the ratio of means was 1:5, and evolution under the L-shaped model was about twice the pace of the poisson. Maintaining an overall mean of 10 seeds as in the first simulation but a lambda ratio of 1:2.5, the sojourn time for a recessive allele was about 1.2 times faster than with a poisson. On the other hand, if the fecundity of the high performing plants is very much greater than the remainder of the population, yielding for example a 1:10 ratio, the rate of response to selection is about 3.2 times greater than with a poisson distribution.

Whereas L-shaped fecundity distribution permits a more rapid response to selection than a poisson, the former also is more likely to foster the extinction of a gene when it is rare and less likely to protect polymorphism when two or more alleles are common. Once again the greater variation in fecundity which accrues from the L-shape is the cause. Consider a population of 10 plants with two alleles in equal frequency, both equally fit, and with an L-shaped fecundity distribution. Based upon 100 runs, the loss of polymorphism occurs in an average of 14.2 generations. In contrast, a similar population with 7 plants and a poisson distribution retains polymorphism for an average of 19.5 generations, and a population with 6 plants retains polymorphism for an average of 13.3 generations. Thus, the decay of variability in populations with "L" fecundity schedules is similar to that in much smaller populations with poisson schedules. With regard to the loss of a rare favored recessive genotype, (relative fitness of AA and Aa = .75) we found that in runs in which $q = .1$, a population size of 250, relative fitnesses of the dominant homozygote and heterozygote of .50, Cvigor is .5, mean ratio 1:5, the recessive allele was lost in 80 per cent of the trials when an l-shaped distribution was used versus 65 per cent when a poisson was used.

Our discussion thus far has been couched in the context of a plant population which is exhibiting a plastic or developmental response to density-stress from conspecifics, other species or the environment as a whole. However, plants may exhibit a mortality response as the environment deteriorates (HARPER & WHITE 1974). The suppressed fraction of the population may fail to produce seed. The effect would be represented by an L-shaped distribution with λ_1 being zero. Since an increase in the ratio between the means of the two distributions comprising "L" results in a more rapid response to selection, removing the less productive plants from the parental pool (assuming size is genotype-dependent) will permit a large variable population to experience much more rapid evolution than a similar population with a poisson fecundity schedule. Note that we are not placing a larger fraction of the population in the high fecundity category; that proportion is assumed to remain constant. If we were simply to increase the proportion of the population in the high fecundity distribution from 10 per cent (as in our initial runs) to higher percentages, the special advantage which accrues to superior genotypes is diluted and the rate of evolution declines.

A mortality response to exigencies of the environment lowers the genetically effective size of the population thus making it more prone to genetic drift. Consider a situation referred to earlier, namely a population of 10 plants whose fecundity distribution is L-shaped, whose lambda ratio is 1:5, and whose 2 alleles were in equal proportions. We estimate that polymorphism would be maintained for an average of 14.2 generations. Eliminating the contribution of plants from the low fecundity distribution, polymorphism will be lost in an average of 3.1 generations. The relationship between rate of gene frequency change in response to a selection model and the decay of genetic variability in a neutral model is not qualitatively altered by a mortality response as opposed to a plastic response. The greater the potential rate of evolution by selection the greater also is the potential for evolution by random drift relative to population genetic theory. Most plants show plastic and mortality responses to density-stress which means that they could respond to selection quite rapidly should variation be present in population, but their populations are not well adapted to protect polymorphism (Fig. 3).

In view of the striking effect of an L-shaped fecundity distribution on the response to selection, it is of interest to determine the effect of this distribution on equilibrium frequencies in a population faced with the immigration of a deleterious gene. This problem was examined with a simulation of a population with 250 plants, poisson and L-shaped fecundity schedules, and immigration rates of 1 per cent, 2 per cent and 4 per cent, a 50 per cent contribution of the genotype to seedling vigor, and a range of selection coefficients. Immigration is in the form of homozygous seed. Dominant and

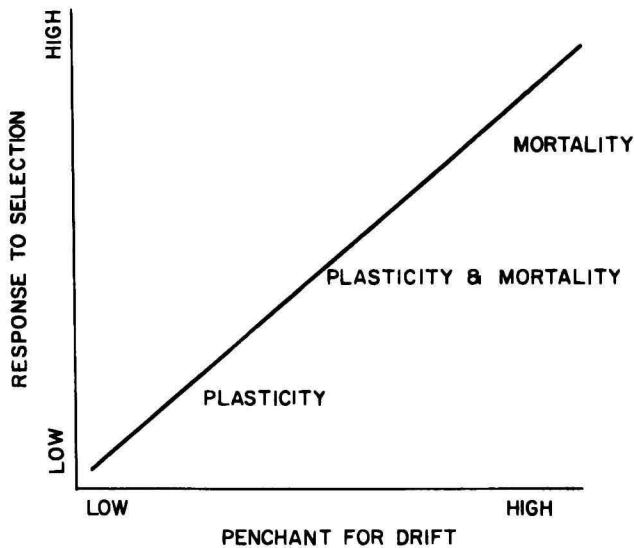


FIG. 3. *The relationship between plastic and mortality responses to stress and the evolutionary potential of populations*

recessive cases were examined. The population is assumed to be monomorphic at the start. The equilibrium frequencies of the alien allele are lower with an L-shaped fecundity distribution than with a poisson. Our estimates of poisson equilibria are in close accord with those obtained by analytical methods. The difference is most extreme when the coefficient of selection against the immigrant is low. For example, consider the case of a dominant gene whose immigration rate is .01 (Fig. 4). When the selective disadvantage is only 1 per cent, the

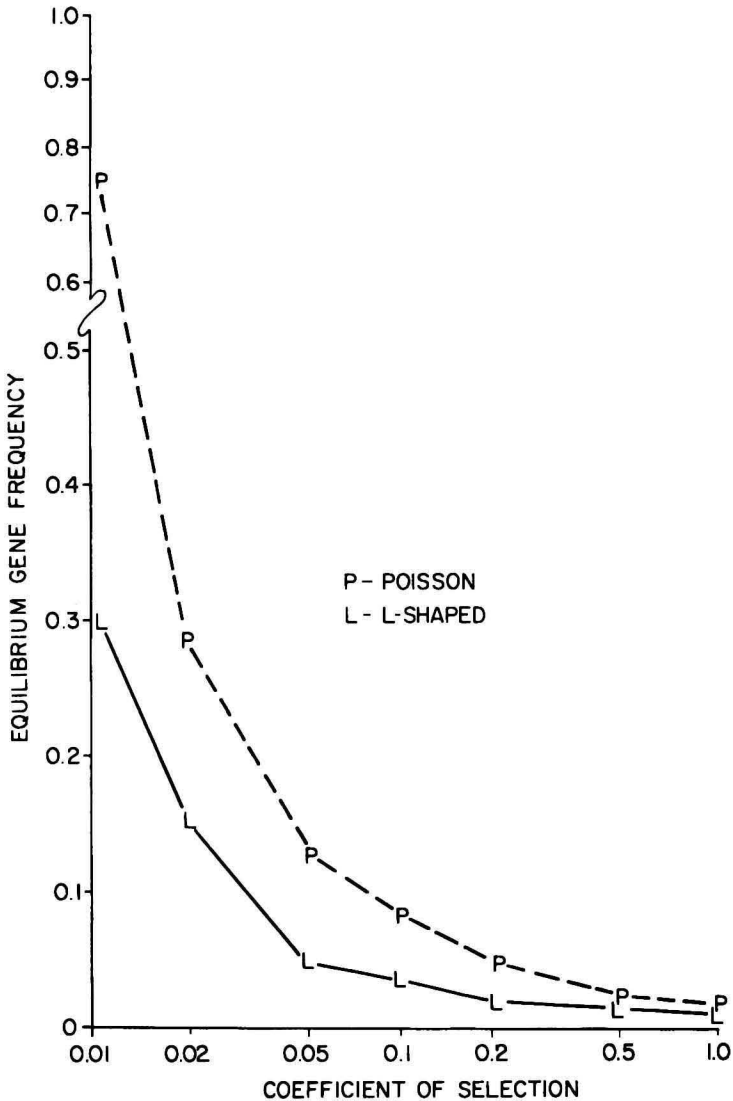


FIG. 4. Gene frequency equilibria for a dominant gene under different levels of selection showing the effect of different fecundity distributions. The term "double poisson" refers to the L-shaped distribution. The immigration rate is 1 per cent. The coefficient of selection against the dominant homozygote and heterozygote are the same

equilibrium level with an L-shaped distribution is only .30 as compared to .75 when a poisson is used. Selection coefficient notwithstanding, the equilibrium alien gene frequency with the poisson is more than twice that with the L. This is generally true for higher levels of immigration. Thus the fecundity schedule may have a profound effect on the impact of deleterious gene flow. When the alien gene is recessive, there is only about a 30 per cent difference at different immigration levels.

3. GENETIC IMPLICATIONS OF DIVERSE REPRODUCTIVE SCHEDULES

The reproductive schedules of plants are extremely diverse. Some plants flower the first year of their life and then die, others flower periodically after a pre-reproductive period of two to several years, and others only flower once after achieving considerable age (HARPER & WHITE 1974). Correlatively, the generation times of different species may vary by at least an order of magnitude. Most theoretical and experimental population geneticists have been concerned with the rate of response to selection per generation, and as such have ignored the genetic implications of diverse reproductive schedules in terms of a chronological time table. Only plant breeders have addressed the matter of progress per unit time, but their interests have centered on annual and short-lived perennials (FALCONER 1960). Molecular geneticists have suggested that the rate of evolution is independent of generation time (NEI 1975). Regardless of the validity of their arguments, they have not considered characters which are only intermittently exposed to selection, namely, juvenile or reproductive characters. Surely the rate of evolution of juvenile and floral characters per unit time in an annual could be different than from a century plant assuming equivalent selection pressures.

We have constructed a series of life histories depicted in Fig. 5. Assuming a population of infinite size and an initial frequency of .2, semidominance (relative fitness: AA = 1.0, Aa = .75, aa = .50), a L-shaped fecundity distribution and a 50 per cent environmental impact on seedling vigor (C_{vigor}), we determined the mean number of years for a gene to move from $p = .2$ to .8 as a function of absolute time. The relationship between these variables is shown in Fig. 6. The correlation mean between generation time and rate of response is .98. Changing the selection coefficients alters the slope but not the compelling relationship between generation time and response to selection.

Having emphasized directional selection, consider next the implications of different reproductive tactics in perennials when long-term selection is cyclic or random. Long-lived populations with delayed reproduction would be poorly equipped to respond to a change in selection regime, and thus would be more likely to retain genetic polymorphism than would short-lived populations which reach reproductive maturity in one or a few years. The genetic structure of long-lived populations would be tuned to their long-term environmental

LIFE HISTORY	MEAN REPRODUCTIVE AGE	YEARS 0.2 → 0.8
●	1	4.7
● ● ● ●	2.5	11.2
○ ○ ○ ●	4	18.6
○ ● ○ ●	3	13.9
● ● ● ● ● ● ● ●	4.5	20.3
○ ○ ○ ○ ● ● ● ●	6.5	27.6

● FLOWERING ○ NON FLOWERING

FIG. 5. *The effect of different life histories on rates of change in gene frequency*

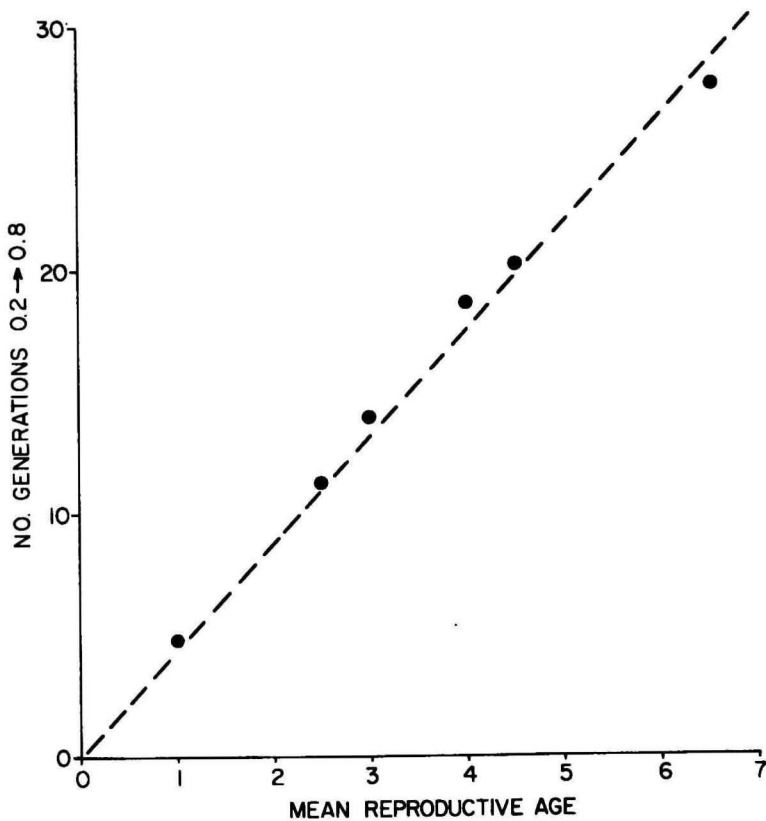


FIG. 6. *The relationship between rate of evolution and mean reproductive age*

experience, whereas the genetic structure of short-lived populations would reflect recent experiences which may have had a pronounced impact upon their genetic structure.

Thus far the potential to respond to selection has been within the context of 100 per cent sexual reproduction. However, hundreds of species are facultative apomicts capable of reproducing in part by agamospermy, or by stolons or rhizomes. Agamospermy is more common in fugitive species, whereas vegetative reproduction is more common in late successional or climax species (GUSTAFFSON 1946; VAN DER PIJL 1969; SALISBURY 1976; MYGREN 1954). Apomixis is important in a discussion of generation related phenomena, since this mode of reproduction effectively extends the age of plants and thus their generation time. Agamospermy and vegetative expansion have the same effect, although the spatial pattern of the individual in time will be much more diffuse in the case of the former. Thus species which are facultative apomicts should respond more slowly to selection than those which are strictly sexual. Moreover, we expect apomixis to reduce the response to selection because it reduces the effective population size and thus the amount of additive genetic variance in individual fitness (FISCHER 1930).

4. GENETIC IMPLICATIONS OF SEED POOL DYNAMICS

Thus far rates of evolution have been considered with regard to life history features of perennial plants. Annuals also should be considered since they too have age-structured populations by virtue of their seed pools. The annual habit in plants is accompanied by specialized physiological mechanisms which permit seeds to remain dormant in the soil for a few years to decades (MAYER & POLJAKOFF-MAYBER 1975; ROBERTS 1972; KOLLER 1969). The nearly universal imposition of germination regulating mechanisms prevents the reproductive potential of a population from being gambled except when the probability of survival is maximal. The longevity of seeds tends to be a positive function of environmental unpredictability and is correlated with other adaptations to cope with unpredictability. The seeds of desert ephemerals and fugitive species are relatively long-lived (50 to 100 years) whereas the seeds of mid-successional annuals in mesic habitats often are short-lived (10-20 years) (TOOLE & BROWN 1946; KIVALAAN & BANDURSKI 1973; HARRINGTON 1972). The buried seed population has a constant death risk (HARPER & WHITE 1974).

The seed bank is based upon contributions made over several years, during which time selection may have favored alternate alleles at a particular locus related to temperate tolerance, pubescence, etc. The seed pool therefore provides the population with a memory of its recent history and is tuned to the general experience of the population over several years rather than just the past 1 or 2. A seedling crop is drawn from this potentially diverse seed pool.

The optimal germination tactics for a seed pool have been studied by COHEN (1966, 1967, 1968). The question now is not what is best for a population in terms of its persistence, but what are some genetic consequences of different seed pool histories. What constraints do seed pools impose on evolution at a single locus unrelated to dormancy? A. TEMPLETON (unpublished) has considered the effects of directional and disruptive selection in time taking into account the impact of the environment on population size. I will summarize some of his findings which are based upon analytical solutions.

By virtue of its history, the seed pool retards the rate of evolution when fitness is constant, balancing or directional selection notwithstanding. There is a simple linear relationship between the change in gene frequency per year and the average number of years a seed has spent in the seed pool prior to germination. Consider a case of directional selection in a population of annuals. If the mean time that plants spent in the seed pool prior to germination were 10 years, then the number of years required for selection to alter the frequency of a gene from one value to another would be 10 times greater than if there were no seed pool. If the average time in the seed pool were 3 years, then the rate of evolution would be 3 times lower than if there were no seed pool. Consider a case of balancing selection at a single locus where the heterozygote was favored and both homozygotes had relative fitness of .99. The number of years required to move a gene from one frequency to the equilibrium value (.5) also would be a simple function of time plants spent in the seed pool (Fig. 7).

The extent to which the seed pool retards the response to selection not only is dependent upon the age structure of the seed pool, but also is dependent upon the growth rate of the population. The discussion thus far assumed that population size is constant. Should populations pass through a period of growth, the seed pool would be weighted in favor of recent seeds since they would be increasingly abundant and constitute a higher proportion of the pool than if the population was not expanding. The mean age of the seeds in the pool would decline. On the other hand, if populations were contracting, the seed yield per year would also contract so that the pool would be weighted in favor of the older seeds relative to what would be the case with a stable population size. The mean age of seeds in the pool would increase. Accordingly, the rate of evolution will be faster in expanding populations with seed pools than in stable populations. Correlatively the rate of evolution will be slower in contracting populations than in stable ones.

The seed pool allows the existence of a covariance between fitness and absolute seed production during years in which the environment is hospitable and plants generally are large. The genotype favored in that environment will produce more seeds and thus have a greater impact on the seed pool than an alternate genotype favored in years when conditions for survival are marginal. With a seed pool not only the relative fitness is important but the absolute

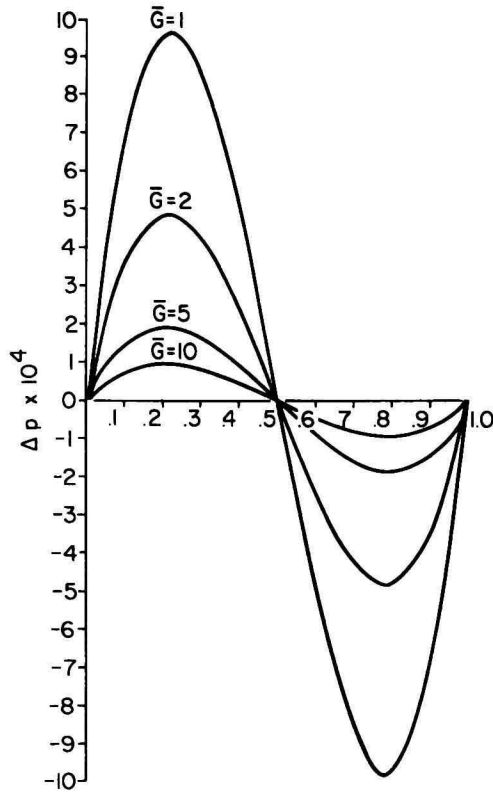


FIG. 7. Rate of change in gene frequency toward an equilibrium value of .5 as a function of mean numbers of years seeds spend in the soil prior to germination. The plants are assumed to be annuals

performance of the best genotype in year 1 vs. the best in year 2. Differential contribution of seeds to the seed pool both within and between years, but especially the latter, may have the same consequences as directional selection. Let us assume that in good years the relative fitness of 3 genotypes are $AA = 1.00$, $Aa = 0.75$, and $aa = 0.50$. Let us also assume that in marginal years the fitnesses are $AA = 0.50$, $Aa = 0.75$, and $aa = 1.00$. Population size is constant. In the good years the seed production of the favored homozygote (AA) is 100, whereas in the marginal years the seed production of the favored homozygote (aa) is only 50. If the environment alternates between good and marginal years in a regular cyclic fashion the A gene eventually will be fixed even though environments and relative fitnesses are symmetrical. Random fluctuations in the environment will have the same effect. Accordingly selection will favor genes that do the best when the environment is most hospitable. The greater the mean age of seeds in the pool the more pronounced is the filtering effect of selection in a fluctuating environment.

5. THE EFFECT OF PATCH SIZE AND SHAPE ON MIGRATION-SELECTION EQUILIBRIA

5.1. INTRODUCTORY REMARKS

There has been much interest in the joint action of migration and selection on the level of genetic variability in subdivided populations occupying spatially heterogeneous environments. Two and multi-niche models have been constructed which relate to organisms in general (CHRISTENSEN 1975; KARLIN 1976; FLEMING 1975; GILLESPIE 1974, 1975, 1976; HEDRICK *et al.* 1976) or plants specifically (JAIN & BRADSHAW 1966; ANTONOVICS 1968; NAGYLAKI 1976; LEVIN & KERSTER 1975; GLEAVES 1973). Unfortunately, most treatments make assumptions about the mating system, the spatial distribution of patch types, and dispersal distributions which are contrary to what one actually finds in plant populations. Plant populations are not panmictic, incoming genes are not randomly distributed throughout a population, and environmental patches are two-dimensional arrays with specific dimensions.

Using computer simulation, we chose to answer the following questions: What are the equilibrium gene frequencies in subpopulations adapted to different environments when patch size and shape are variables? To what extent do the equilibria differ with different gene dispersal schedules?

5.2. THE MODEL

The model involved a population of 4096 plants occupying a site with patch type A and B in equal proportions. Only a single locus with two alleles (A and a) was considered possible. The relative fitnesses of genotypes in patch A are AA = 1.0, Aa = 0.75, aa = 0.50. The relative fitnesses of genotypes on patch B are AA = 0.50, Aa = 0.75, aa = 1.0. The size and shape of patches varies as prescribed with at least 4 plants per patch. The plants were assumed to occupy a 64 x 64 grid of uniformly spaced safe sites. Every plant was one map unit from its nearest neighbors.

The initial population is composed of AA plants in the A patches and aa plants in the B patches. Patches alternate in space in a checkerboard fashion. The breeding structure of the population was defined by the dispersal of pollen. Dispersal followed random, leptokurtic, or nearest-neighbor patterns. No seed dispersal is assumed. Seeds occupy the same site as the seed parent. The stepping stone schedule involves the movement of seeds to one of the four or eight nearest sites at the cardinal compass points. For the leptokurtic schedule, pollen dispersal distances assumed the distribution shown in Fig. 8. The direction of broadcast was designated by a random number generator. Each plant produced 18 pollen grains, a number sufficient to insure that each plant almost certainly would receive 1 pollen grain. Pollen falling outside the grid was lost. Plants were assumed to be self-incompatible. The number of ovules per plant is assumed to be very large so that the number of seed produced is equivalent to the pollen receipt.

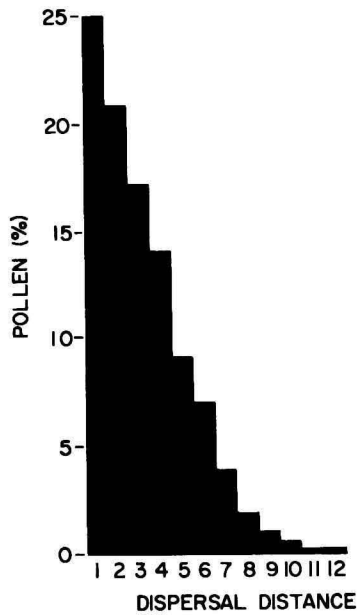


FIG. 8. *Distribution of pollen dispersal distances under the leptokurtic pollen schedule*

Competitive selection occurs when more than one seed is deposited per site. The surviving seed genotype is a function of frequency of the genotypes and the relative fitness of each. The frequency of the genotypes after selection is calculated. Each genotype then is assigned a region on a scale from 0 to 1 equivalent to its frequency. The genotype of the surviving seed is determined by the genotype domain into which a randomly drawn number between 0 and 1 falls.

Since the model was of a finite population, there were considerable edge effects. For the examination of most of the results, therefore, the grid was divided into a center and an edge. This enables the center results to be generalized to the center of any sized population, and also gives an indication of the magnitude of the edge effects. The boundary between the edge and center and the edge was placed at a patch boundary, such that the areas of the center and the edge were as similar as possible. In the case of 32 x 32 patches, the boundary had to run through the middle of the patches, but this introduces no bias. In those cases where the patch arrangement was at random, the random process was constrained to ensure equal representation of both patch types both in the center and round the edge.

5.3. RESULTS

Consider first the proportion of pollen entering a patch whose source was from the other patch type. We will refer to this pollen as alien pollen. The alien

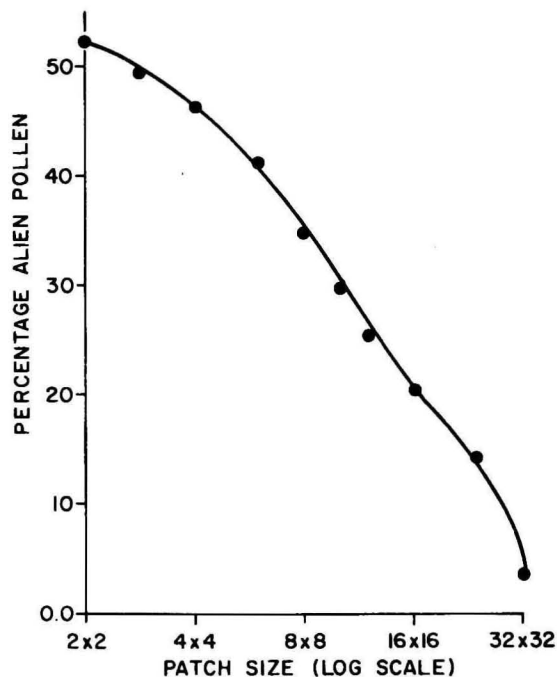


FIG. 9. *The relationship between patch size and the percentage pollen received from the alternate patch type*

pollen influx is a function of patch size, large patches receiving less of it than small ones (Fig. 9). The proportion of alien pollen decreased from about 50 per cent with 3 x 3 patches to only 5 per cent with 32 x 32 patches. Note that for the latter a boundary of several rows was omitted. The overall pattern would not change appreciably were the entire grid treated. If we shift from a checkerboard to a random distribution of patches (frequency of A patches still = B patches) the level of alien pollen receipt declines for each patch size.

The influx of alien pollen also is affected by the patch shape. Given subpopulations of 64 plants, the proportion of alien pollen varies from 55 per cent for 1 x 64 patches to 26 per cent for 8 x 8 patches. Regardless of patch size or shape, the levels of alien pollen receipt is a curvilinear function of the amount of contact between opposite patch types (Fig. 10).

The mean frequency of the maladapted gene in each patch type is a function of patch size. Equilibrium frequencies range from .38 for 2 x 2 patches arranged in a checkerboard fashion to 0.11 for 32 x 32 patches. Moving to a random patch distribution results in lower equilibria values. Equilibrium gene frequencies also are greatly influenced by patch shape. With a patch size of 64 plants, equilibrium frequencies of the maladapted gene vary from .16 with 8 x 8 patches to 0.25 with 4 x 16 patches to 0.34 with 2 x 32 patches and 0.38 with 1 x 64 patches. These values are based upon checkerboard patch patterns (Fig. 11).

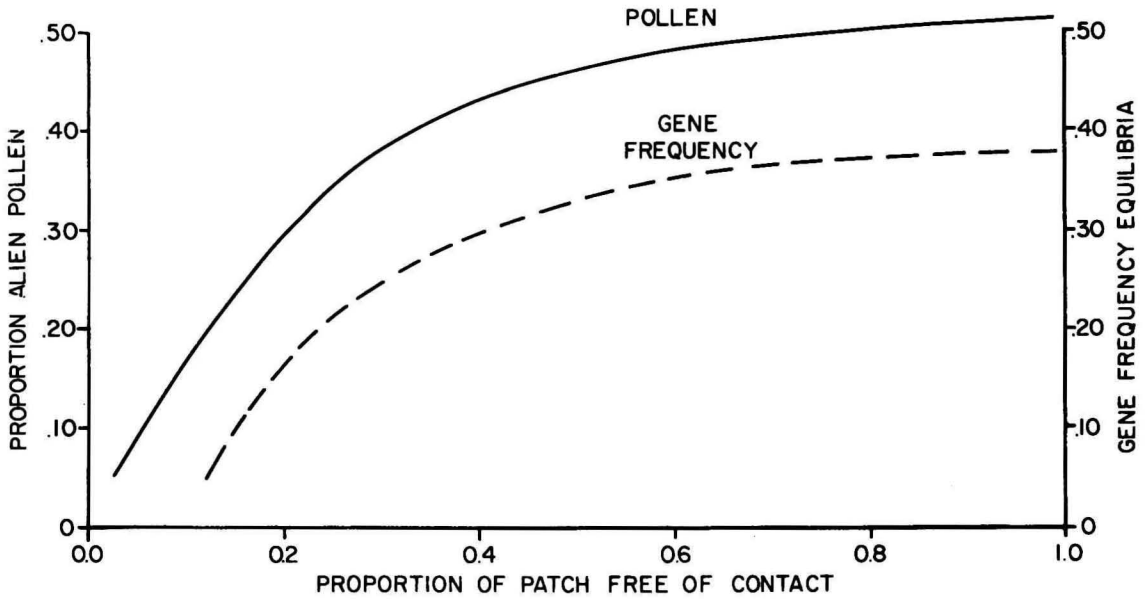


FIG. 10. Alien pollen influx and gene frequency equilibria as functions of level of patch contact

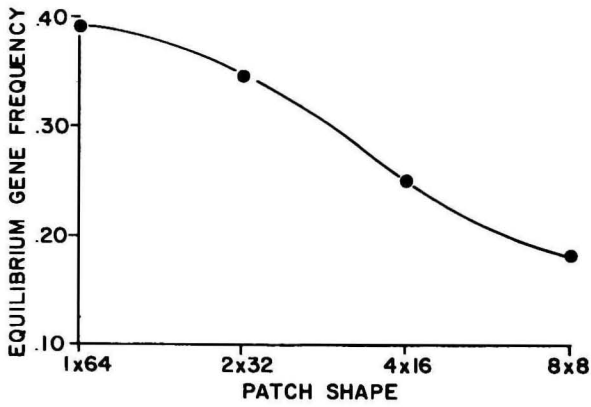


FIG. 11. Equilibrium gene frequency as a function of patch shape

At equilibrium the maladapted gene is distributed in a non-random fashion within patches. This is most evident where patch size is large (Fig. 12). This gene tends to be higher in frequency near the edge of the patch than near the interior and in patches larger than 8x8 rarely reaches the center. This pattern results from narrow pollen dispersal between and within patches. The former dictates the initial deposition sites, and the latter the penetration rate. Once in a patch an alien gene will move over short distances which are random with regard to direction. This provides ample opportunity for its selective elimination beyond the area of continual immigration.

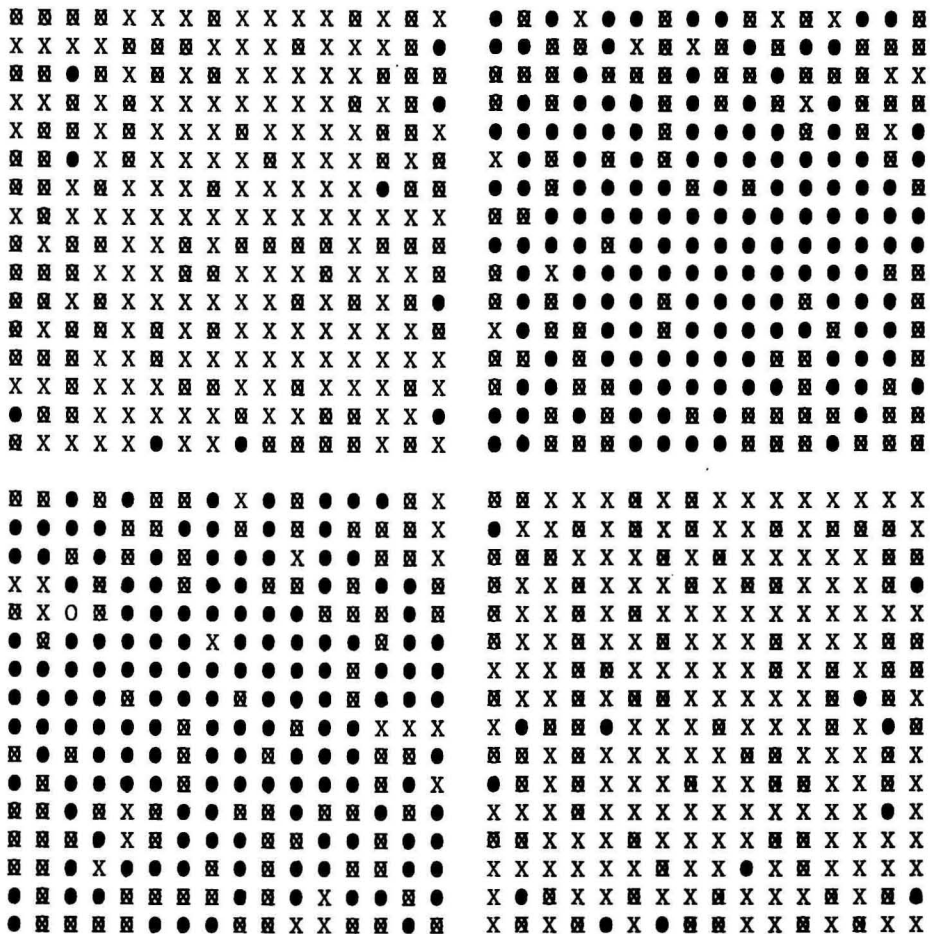


FIG. 12. The distribution of genotypes within patches

Thus far equilibrium frequencies have been considered within the context of a given leptokurtic dispersal schedule. It is of interest to determine the consequences of various schedules including that assumed in most population genetic models. We will compare the equilibrium levels of maladapted genes under the following pollen dispersal schedules: (a) random, (b) leptokurtic with a mean distance of 2.5 and S.D. of 2.8 units as used previously, (c) leptokurtic with a mean distance of 1.25 and S.D. of 1.4 units, (d) leptokurtic with a mean of 5.2 and S.D. of 5.6 units, (e) 4 nearest-neighbors, (f) 8 nearest-neighbors. The leptokurtic distributions have the same kurtosis. The nearest-neighbor distributions provide for equal dispersal of pollen for each of the nearest-neighbors in question.

The effect of the six dispersal schedules on equilibrium frequencies in populations with different patch sizes is shown in Fig. 13. The equilibria

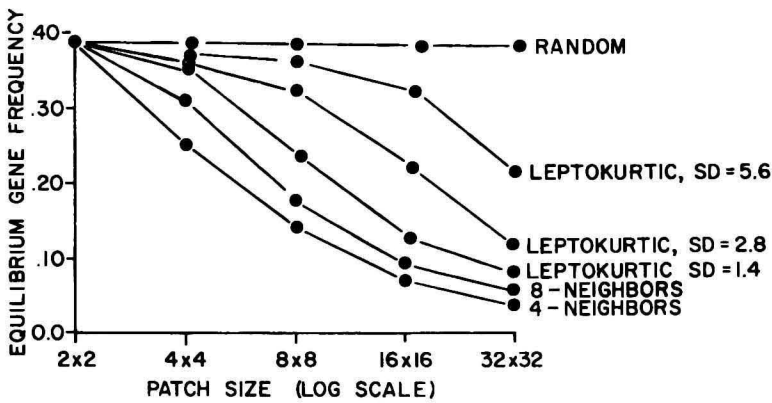


FIG. 13. *Equilibrium gene frequencies in patches of different sizes as a function of pollen dispersal schedule*

vary widely especially in populations with large patch size. With random mating, the maladapted gene frequency averages 0.38, patch size notwithstanding. If we consider the 32 x 32 patch population, the frequency of the maladapted gene equilibrates at about 0.04 with pollen dispersal to the 4 nearest-neighbors, and at 0.07 with pollen dispersal to the eight nearest-neighbors. With narrow, moderate and broad leptokurtic dispersal, frequencies are 0.08, 0.11, and 0.21, respectively. The more restricted is pollen flow, the lower the equilibrium value. Correlatively, the more restricted is pollen flow the more highly adapted are subpopulations to their respective environments.

Self-fertilization is a method for insulating plants from the flow of deleterious genes from other populations. Thus we would expect selfing to result in lower equilibrium levels for the maladapted genes in our models.

Consider the consequences of 50 per cent selfing and 50 per cent outcrossing relative to our standard leptokurtic (2.5 mean) schedule. Surprisingly 50 per cent selfing only had a moderate effect on equilibrium frequencies, regardless of patch size (Fig. 14). However, predominantly self-pollinating populations contain a lower level of the maladapted gene than those discussed thus far.

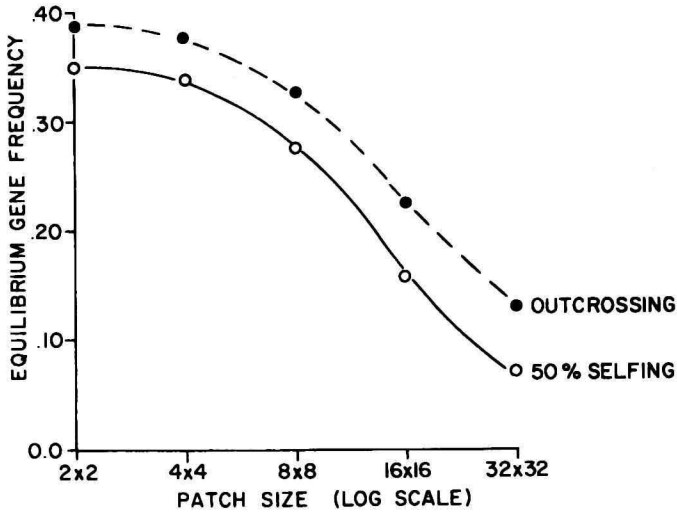


FIG. 14. *The effect of 50 per cent self-fertilization on equilibrium gene frequencies in different patch sizes*

For example, in a population with 90 per cent selfing and patch size of 8 x 8, the equilibrium gene frequency is 0.18 versus 0.27 with 50 per cent selfing, and 0.35 with obligate outbreeding.

In view of the effect of different dispersal schedules and selfing on equilibrium gene frequencies, it is of interest to determine the time to equilibrium. With panmixia we would expect subpopulations to reach equilibria in one generation. With our standard leptokurtic distribution, equilibria are reached in an average of 12 generations when patches are 8 x 8 or larger. For populations with 2 x 2 patches equilibria are achieved in an average of 5 generations and with 4 x 4 patches in an average of 7 generations. Selfing significantly retards the time to equilibrium. Consider a population with 8 x 8 patches. The time to equilibrium with 50 per cent selfing averages about 17 generations; with 90 per cent selfing the average is about 30 generations (Fig. 15).

Thus far we have considered patches to be contiguous. However, it is possible that distinctive patches may be separated by small uninhabitable areas.

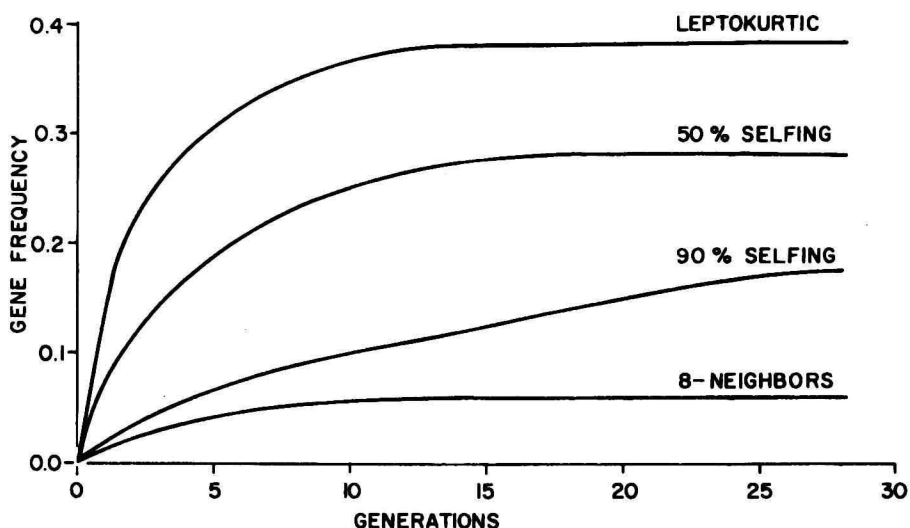


FIG. 15. The approach to equilibrium as a function of mating scheme in a population with 8 x 8 patches

We explored the effect of habitat discontinuity by introducing a 2-position (unit) gap between patches. As one might anticipate, habitat discontinuity and restricted gene flow (in the form of our standard leptokurtic schedule) confers an excellent opportunity for interpatch differentiation. In populations where patch size is large, the frequency of the maladapted gene may be nearly 50 per cent of that in the absence of the gap (Fig. 16). The impact of the gap is even larger with

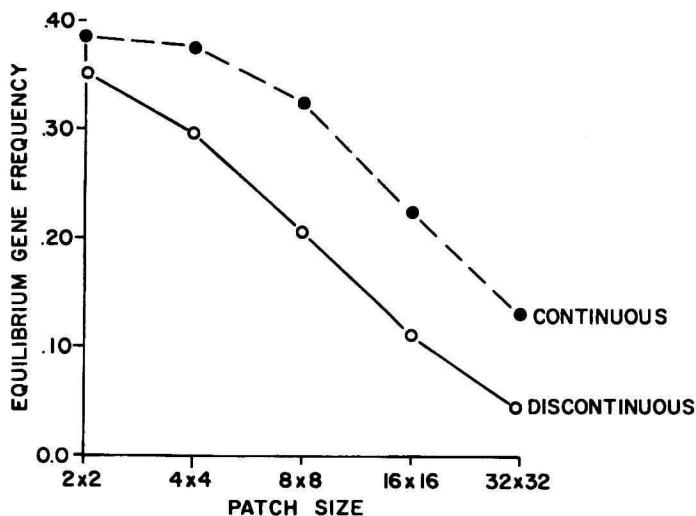


FIG. 16. The effect of discontinuity between patches on equilibrium gene frequencies

more restricted dispersal schedules since the size of the gap is proportionally greater relative to the dispersal limits. With nearest-neighbor dispersal, the gap cannot be crossed and subpopulations remain monomorphic.

In summary, the level of polymorphism within subpopulations occupying heterogeneous environments is a complex function of patch size, shape, spatial distribution of patch types, and gene dispersal schedule. Simply to note that an environment is heterogeneous and that gene flow is restricted fails to provide a meaningful insight into gene frequency heterogeneity between subpopulations, the correlation between patch type and gene frequencies, or the extent to which the adaptedness of populations is reduced by a selection-migration equilibrium. We need to know about the organization and size of patch types if we wish to appreciate the potential and actual level of differentiation which may ensue in the face of gene flow.

6. CONCLUSIONS

In 1972 BRADSHAW wrote an essay on some evolutionary consequences of being a plant. He emphasized the implications of the strength and diversity of selection which operate on closely adjacent populations, the restriction of gene flow between neighboring populations, the correlation of habitats between parents and offspring, the flexibility of the breeding system, and the nature and organization of genetic variation within species. He concluded that "to understand what is actually happening in plant species, we need to assume very different premises from many of those exercising the minds of many population geneticists". As we have attempted to convey in this presentation, we vigorously endorse this position. Moreover, we urge the exploration of the evolutionary implications of demographic features which typically have resided in the domain of ecologists. Fecundity schedules, reproductive schedules, seed pool properties and the pattern of differentiated population subdivisions all are variables which have manifest genetic consequences, which in turn may free or restrict the evolutionary potential of populations. Moreover, the aforementioned demographic properties either have not been considered by population geneticists or their actual expression is contrary to many assumptions used in genetic models. The theory and illustrations presented here only represent a small sample of the kinds of problems that we need to address if we hope to understand what is actually happening in plant species, why it is happening, and what it means.

7. REFERENCES

- ANDERSON, W.W., 1971 - Genetic equilibrium and population growth under density-regulated selection. *Am. Nat.*, 105, 489-498.
- ANTONOVICS, J., 1968 - Evolution in closely adjacent populations. VI. Manifold effects of gene flow. *Heredity, London*, 23, 507-524.

- BRADSHAW, A.D., 1972 - Some evolutionary consequences of being a plant. *Evol. Biol.*, 5, 25-47.
- BRADSHAW, A.D., 1974 - Environment and phenotypic plasticity. *Brookhaven Symp. Biol.*, 25, 75-94.
- BULLOCK, S.H., 1976 - Consequences of limited seed dispersal within a simulated annual population. *Oecologia*, 24, 247-257.
- CHARLESWORTH, B., 1971 - Selection in density-regulated populations. *Ecology*, 52, 469-475.
- CHARLESWORTH, B., 1973 - Selection in populations with overlapping generations. V. Natural selection and life histories. *Am. Nat.*, 107, 303-311.
- CHARLESWORTH, B. & J.T. GIESEL, 1972 - Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. *Am. Nat.*, 106, 388-401.
- CHRISTIANSEN, F.B., 1975 - Hard and soft selection in a subdivided population. *Am. Nat.*, 109, 11-16.
- COHEN, D., 1966 - Optimizing reproduction in a randomly varying environment. *J. theoret. Biol.*, 12, 119-129.
- COHEN, D., 1967 - Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *J. theoret. Biol.*, 16, 1-14.
- COHEN, D., 1968 - A general model of optimal reproduction in a randomly varying environment. *J. Ecol.*, 56, 219-228.
- COHEN, D., 1971 - Maximizing final yield when growth is limited by time or by limiting resources. *J. theoret. Biol.*, 229-307.
- COHEN, O., 1976 - The optimal timing of reproduction. *Am. Nat.*, 110, 801-807.
- DEMETRIUS, L., 1975 - Reproductive strategies and natural selection. *Am. Nat.*, 109, 243-249.
- FALCONER, D.S., 1960 - *Introduction to quantitative genetics*. Oliver & Boyd, London.
- FISHER, R.A.; 1930 - *The genetical theory of natural selection*. Clarendon Press, Oxford.
- FLEMING, W.H., 1975 - A selection migration model in population genetics. *J. math. Biol.*, 2, 219-233.
- GADGIL, M., 1971 - Dispersal: population consequences and evolution. *Ecology*, 52, 253-261.
- GADGIL, M. & W. BOSSERT, 1970 - Life history consequences of natural selection. *Am. Nat.*, 104, 1-24.
- GADGIL, M. & O.T. SOLBRIG, 1972 - The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *Am. Nat.*, 106, 14-31.
- GIESEL, J.R., 1974 - Fitness and polymorphism for net fecundity distribution in iteroparous populations. *Am. Nat.*, 108, 321-331.
- GILLESPIE, J.H., 1974 - Polymorphism in patchy environments. *Am. nat.*, 108, 145-151.
- GILLESPIE, J.H., 1975 - The role of migration in the genetic structure of populations in temporally and spatially varying environments. I. Conditions for polymorphism. *Am. Nat.*, 109, 127-135.
- GILLESPIE, J.H., 1976 - The role of migration in the genetic structure of populations in temporally and spatially varying environments. II. Island models. *Theoret. pop. Biol.*, 10, 227-238.
- GLEAVES, J.T., 1973 - Gene flow mediated by wind borne pollen. *Heredity*, London, 31, 355-366.
- GUSTAFFSON, A., 1946 - Apomixis in higher plants. *Acta Univ. lund*, 39, 1-370.
- HARPER, J.L. & J. WHITE, 1970 - The dynamics of plant populations. *Prov. Adv. Study Inst. Dynamics Numbers Popul.*, (Oosterbeek, 1970), 41-63.
- HARPER, J.L. & J. WHITE, 1974 - The demography of plants. *A. Rev. Ecol. Syst.*, 5, 419-463.
- HARRINGTON, J.F., 1972 - Seed storage and longevity. In: T.T. KOZLOWSKI (Editor), *Seed biology*, Vol. 3, Academic Press, New York, p. 145-245.
- HEDRICK, P.W., GINEVAN, M.E. & E.P. EWING, 1976 - Genetic polymorphism in heterogeneous environments. *A. Rev. Syst.*, 7, 1-32.
- JAIN, S.K. & A.D. BRADSHAW, 1966 - Evolutionary divergence among adjacent plant populations. I. Evidence and its theoretical analysis. *Heredity*, London, 21, 407-441.

- KARLIN, S., 1976 - Population subdivision and selection-migration interaction. In: A. KARLIN & E. NEVO (Editors), *Proc. Int. Conf. Pop. Genet. Ecol.*, Academic Press, New York.
- KARLIN, S. & J. MCGREGOR, 1968 - The role of the poisson progeny distribution in population genetic models. *Math. Bio Sci.*, 2, 11-17.
- KAWANO, S., 1975 - The productive and reproductive biology of flowering plants. II. The concept of life history strategy in plants. *J. Coll. Liberal Arts, Toyama Univ.*, 8, 51-86.
- KING, C.E. & W.W. ANDERSON, 1971 - Age-specific selection. II. The interaction between r and K during population growth. *Am. Nat.*, 105, 137-156.
- KIVALAAN, A. & R.S. BANDURSKI, 1973 - The ninety-year period for Dr. Beals seed viability experiment. *Amer. J. Bot.*, 60, 140-145.
- KOLLER, D., 1969 - The physiology of dormancy and survival of plants in desert environments. *Symp. Soc. Expt. Biol.*, 23, 449-469.
- KOYAMA, H. & T. KIRA, 1956 - Intraspecific competition among higher plants. VIII. Frequency distribution of individual weight as affected by the interaction between plants. *J. Inst. Polytech. Osaka cy. Univ. (D)*, 7, 73-94.
- LEVERICH, J., 1977 - Demographic studies of a population of *Phlox drummondii*. Ph. D. Thesis. University of Texas, Austin.
- LEVIN, D.A. & H.W. KERSTER, 1974 - Gene flow in seed plants. *Evol. Biol.*, 7, 139-220.
- LEVIN, D.A. & H.W. KERSTER, 1975 - The effect of gene dispersal on the dynamics of gene substitution in plants. *Heredity, London*, 35, 317-336.
- LEVINS, R., 1968 - *Evolution in changing environments*. Princeton Univ. Press, Princeton.
- MAYER, A.M. & A. POLJAKOFF-MAYBER, 1975 - *The germination of seeds*. Pergamon Press, London.
- NAGYLAKI, T., 1976 - Dispersion-selection balance in localized plant populations. *Heredity, London*, 37, 59-67.
- NEI, M., 1975 - *Molecular population genetics and evolution*. North Holland, Amsterdam.
- NYGREN, A., 1954 - Apomixis in angiosperms. II. *Bot. Rev.*, 20, 577-649.
- PIJL, L. VAN DER, 1969 - *Principles of dispersal in higher plants*. Springer-Verlag, New York.
- RISSER, P.G., 1969 - Competitive relationships among herbaceous grassland species. *Bot. Rev.*, 35, 251-284.
- ROBERTS, E.H., 1972 - *Viability of seeds*. Chapman & Hall, London.
- ROFF, D.A., 1975 - Population stability and the evolution of dispersal in a heterogeneous environment. *Oecologia*, 19, 217-237.
- ROSS, M.D. & J.L. HARPER, 1972 - Occupation of biological space during seedling establishment. *J. Ecol.*, 60, 77-88.
- SALISBURY, E.J., 1942 - *The reproductive capacity of plants*. Bell & Sons, London.
- SALISBURY, E., 1976 - A note on shade tolerance and vegetative propagation of woodland species. *Proc. R. Soc. B.*, 192, 257-258.
- SARUKHAN, J., 1974 - Studies on plant demography. *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. II. Reproductive strategies and seed population dynamics. *J. Ecol.*, 62, 151-177.
- SARUKHAN, J. & J.L. HARPER, 1973 - Studies on plant demography. *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. I. Population flux and survivorship. *J. Ecol.*, 61, 675-716.
- SCHAFFER, W.M., 1974a - The evolution of optimal reproductive strategies: the effect of age structure. *Ecology*, 55, 291-303.
- SCHAFFER, W.M., 1974b - Optimal reproductive effort in fluctuating environments. *Am. Nat.*, 108, 783-790.
- SCHAFFER, W.M. & M.D. GADGIL, 1975 - Selection for optimal life histories in plants. In: M. CODY & J. DIAMOND (Editors), *Ecology and evolution of communities*, Harvard Univ. Press, Cambridge, p. 142-157.
- SHELDON, J.C., 1974 - The behavior of seeds in soil. III. The influence of seed morphology and the behavior of seedlings on the establishment of plants from surface-lying seeds. *J. Ecol.*, 62, 47-66.
- TAYLOR, H.M., GOURBY, R.S., LAWRENCE, C.E. & R.S. KAPLAN, 1974 - Natural selection of life history attributes: an analytical approach. *Theoret. pop. Biol.*, 5, 104-122.

- TOOLE, E.H. & E. BROWN, 1946 - Final results of the Duvel buried seed experiment. *J. agric. Res.*, 72, 201-210.
- WHITE, J. & J.L. HARPER, 1970 - Correlated changes in plant size and numbers in plant populations. *J. Ecol.*, 58, 467-485.
- YARRANTON, G.A. & R.G. MORRISON, 1974 - Spatial dynamics of a primary succession: nucleation. *J. Ecol.*, 62, 417-428.

8. DISCUSSION

WATKINSON (Norwich): I accept what you said about seed dormancy and the unpredictability of the environment, but if one is going to make meaningful comparisons between environments and between species in different environments, how would you suggest that one quantifies the predictability of the environment, because I see that this is a major stumbling block preventing the empirical workers in the field from getting much further in this area.

LEVIN: I don't think I am in a position to tell you how to quantify the environment. What I am trying to do is simply show that seed pools have an effect, have a genetic effect, and that it makes a difference in genetic currency in terms of the kinds of seed-pool dynamics you have. Now, exactly how one wants to describe environmental predictability or demonstrate it or study it, is something which is really beyond an answer from me. I don't think I really want to respond to that.

HARPER (Bangor): Due to technical difficulties this question was very badly recorded and cannot be reproduced in detail. Professor Harper asked why a double poisson was used to imitate the L-shaped curve. His second question concerned the relationship between the genetic and non-genetic components in the fecundity frequency distribution.

LEVIN: In response to your last comment: we simply were interested in looking at a combination of genotype and environmental effects and we just chose 50 per cent for heuristic purposes just to include some environment and some genetic effects. We gave equal weight to both, since in many cases we do not know what the causal factors are. I certainly agree that it will be more interesting to use real values than the ones we have chosen just because they relate to the nature of the problem, and the same answer holds for our L-shaped fecundity distribution. It was simply, let us say, for heuristic purposes, that we chose that particular distribution. JOHN WILSON can express exactly why he wanted to use a double poisson to generate the L, although we did want a little hump out on the tail of the L. We wanted a little bit of a hump for those special plants out at the end rather than just having a flat L, and the fact that you suggested that we understated the case and that the difference would be even greater, makes me feel very fine, because what I am trying to do is just show that plants are different from the simple theory that has been applied to them. What we really have to know is what plants are doing, in order to fully appreciate plant evolution and ecology and the

interface between them.

ANONYMOUS (1): Don't you think that the main effect of the seed bank is to diminish the genetic drift because it increases the size of the population first and also avoids selection for one part of it?

LEVIN: The seed pool acts as a buffering device. You may have environmental fluctuations up and down, but the seed pool will tend to stabilize the populations within a gene frequency range and reduce the probability of genetic drift. So when we look at populations of annual plants and we see populations going from 10,000 to 100, this is not an adequate picture of the true population dynamics in a sense that if seeds are live plants, the populations size may be very constant. The number of individuals that are reproducing in any given year fluctuates considerably, but the actual population size is maintained and the seed pool does act as a buffer but also acts as a drag, because it provides a memory. I think that after a bad year the seed pool will be more important, and in Texas in some of our annuals we have good years and bad years where in the bad year maybe only 10 per cent of the plants were there, compared to what we saw the year before, in which case the next year, if you draw at random from the seed pool, the older seeds will make a relatively larger contribution. So I am not sure that you need catastrophic events. I think you can have good and bad years, where there is always a seed pool that remains intact. I think you can draw from the past in the sense that, like migration seed pools from the past provide heterogeneity as well as all those things that migration would do to maintain genetic polymorphism. But it does retard the response to selection as does migration.

BELL (Bangor): Following up the point that Professor HARPER made on the importance of distance between neighbours, did you take into account in your grid systems, that if you are considering four neighbours and then considering eight neighbours that actually different distances are involved?

LEVIN: Well, the distances were determined in advance, and the distance is reflected in the mating systems, so to speak. If you are crossing with plants that are very close to you, you could be crossing with a brother and a sister, since we are dealing with annuals. So the spatial pattern affects the breeding system, which affects the outcome, as I showed you. So in a sense distance was considered. I mean it is built in, but not in the way that you are suggesting. But it is reflected in the nature of the output, whether we are looking at four nearest neighbours or eight nearest neighbours or whatever. You get different values, and this is due to differences in the restriction of the movement of pollen.

BELL: But the subtle difference that four of the eight are further away than the other four does not make any difference?

LEVIN: I cannot say it does not make any difference. I have to think about exactly what we might expect to find, other than what I have just said that the farther away the pollen is moving the more open the breeding system is and

the less likely you are to be mating with relatives. In terms of the plastic response to competition as a function of distance, we could not build that into our model, since we had decided that there should be some simple pattern of safe sites; therefore, there is no way we could get a distance effect, an interference effect over space. We have considered it, but I am not sure how you could bring that in. If you had empty spaces you could do that, but with all spaces filled, I am not sure you could handle it.

ANONYMOUS (2): Did you say that in the cyclic environment your model predicts that the genotypes that perform better in good years are favoured?

LEVIN: Yes, if you simply go back and forth from a good year to a bad year and if you had different genotypes favoured in the two years. If in the good year the best genotype produces 100 seeds and if in a bad year the best genotype only produces 50 seeds, you have differential contribution to the seed pool between years; and by going back and forth, back and forth, you gradually weight the seed pool by the population in terms of the genotypes that do best in the favourable years. So even though you might have a cyclical environmental pattern with a seed pool, the result is the same as directional selection; you end up fixing the genes or the genotype that does best in the best environment.

ANONYMOUS (2): What happened when you had several bad years in succession, what happens in the population?

LEVIN: The seed production would be lower; you would have your seed pool to draw upon in the event of good years, but if you had several bad years you would simply have a lower contribution of seeds in those years weighted in terms of the relative fitness of the three genotypes in those year. I am not sure I am answering your question.

ANONYMOUS (2): It seems to me that the frequency in the seed pool of seeds produced from genotypes that are better performers in good years would be higher. Is that right?

LEVIN: Yes. One good year could greatly outweigh several bad years, according to my model, if the good ones were producing fewer seeds in good years. If the best genotype in poor years was producing few seeds relative to the best genotype in good years, you might have several bad years and one good year and that would compensate for it, or even more than compensate.