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Some genetic consequences of skewed fecundity distributions in plants

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Summary. Most plant populations show a "skewed" distribution of fecundity amongst their members, in contrast to the poisson distribution assumed by most population genetical theory. We examine by simulation the consequences of skewed fecundity for plant evolution when combined with sieve selection. In comparison with poisson-based theory, plant populations are likely to show a faster response to selection, especially when the favoured allele is at a low frequency. Selection against a deleterious immigrant allele will also be more effective, reducing its equilibrium frequency in a population. In the special case of heterozygote disadvantage traits will evolve that could not under poisson theory. However, random variation is also higher, giving a 10-plant population an effective population size of about 6.4 under poisson theory. The conclusions are not qualitatively changed by different assumptions on the exact shape of the fecundity distribution, or on heritability, or on reproduction by the smallest plants of the population.

Key words: Skewed distribution fecundity – Selection – Genetic drift – Plant demography

Introduction

Most theory in population genetics is based on the assumption of a poisson distribution of fecundity amongst the individuals of a population. However, higher plant populations typically have an L-shaped or skewed fecundity distribution (Harper 1977).

Skewed fecundity is caused initially by intra-specific competition at the seedling stage (Ford 1975; Rabinowitz 1979). This often results in a hierarchy of a few large plants with many small ones (e.g. Heywood and Levin 1984), which can persist through to the adult population (Watkinson et al. 1983). Koyama and Kira (1956) called it the "dominance hierarchy".

The biomass distribution in a dominance hierarchy typically has a longer tail than the poisson. It is sometimes loosely called log-normal, or leptokurtic, but most usually "skewed". This term is used here since it is now conventional, though Weiner and Solbrig (1984) have pointed out that skewness is an imperfect measure of such a shape. Sometimes the distribution has a very long tail, called by Koyama and Kira (1956) "L-type" (e.g. Koyama and Kira 1956; Gottlieb 1977; Burdon et al. 1983; Dolan 1984; Weiner 1985), or the distribution may even be bimodal (Rabinowitz 1979).

Since fecundity is often correlated with size (Wolfe 1983; Dolan 1984), the distribution of plant fecundity also tends to be skewed (Obeid et al. 1967; Leverich and Levin 1979; Sarukhan 1974; Howell 1981; Zelder et al. 1983; Reynolds 1984; Dolan and Sharitz 1984). This dominance of seed production by a few large plants might be even greater in the presence of predation (van Leeuwen 1983). As a result there is a large number of plants making a very small contribution to the next generation, a smaller number than would be predicted from a poisson distribution making an intermediate contribution, and a larger number than would be expected making very large contribution. Such fecundity distributions have been found in relatively K-selected annuals (Levin and Leverich 1979; Howell 1981) and in perennials (Sarukhan 1974; Jarvinen 1984).

The dominance hierarchy will be genetically important in three ways. Firstly, if the final plant weight, and hence fecundity, is determined largely by competition for light in the early seedling phase, any differences in fitness among seedlings will have a very large selective effect (Wilson 1986). Characters which affect growth rate, reproductive strategy or competitive ability at the adult stage may have little effect when the persistent effects of seedling fitness are so large. The second result is that the difference in fecundity between the most fit plants and the most unfit will be greater than under a poisson distribution, giving the possibility of more effective selection so long as the fecundity differences are genotype-dependent. Thirdly, if there is a considerable environmental effect in the determination of seedling vigour, the effect of selection at any stage will be largely negated.

Obeid et al. (1967); Mather (1969); Levin and Wilson (1978) and ter Borg (1979) all realised that when a plant's fitness is determined by its position in the competitive dominance hierarchy the assumptions normally made in selection theory are invalid, and a different process would operate. Antonovics et al. (1973) termed this process "sieve selection", but did not examine it.

Here, we examine the genetic effects of such sieve selection, operating in a population with a skewed fecundity distribution.

Methods

We simulated a plant population with a finite number of plants, usually 250. These plants were assumed to compete at the seedling stage, resulting in variation in adult plant size, reflected in both the amount of pollen and the number of ovules produced – their fecundity. We examined various distributions of fecundity. All simulations dealt with a single locus with two alleles.

Seedling vigour was assumed to determine the position of a plant in the dominance hierarchy and hence in the fecundity distribution, and to be controlled by both genotype and environment. The genotypic component is called "seedling genotypic value" (Y_S). Since these values had only relative significance they were represented by a number between 0.0 and 1.0, 1.0 being the most fit. It is convenient to define the difference between two genotypic values (Y_S) as the genotypic advantage, A_S.

The environmental effects on plant size (plasticity) were represented by a value E, a random number in the range 0.0–1.0, 0.0 representing the most unfavourable microenvironment and 1.0 representing the most favourable microenvironment. The relative importance of genotype and environment in the dominance hierarchy is very unclear from the literature. We represented the importance of genotype by a factor (normally 0.5) equivalent to a broad-sense heritability, h:

$$\text{Seedling vigour} = Y_S h + E(1.0 - h)$$

There are too few reports of the distribution of fecundity amongst the members of a plant population to know which is the most common shape. A distribution with a marked tail was therefore used to provide a contrast to a normal or poisson one. This was obtained by superimposing two poisson distributions with different means, Lambda$_1$ and Lambda$_2$. A certain proportion, p, of the fecundities followed the first poisson distribution, and a certain proportion, 1-p, the second. For most simulations the values were chosen as Lambda$_1$ = 7.15, Lambda$_2$ = 35.75, $p = 0.9$, giving a five-fold difference between the two means, and an overall mean of 10 (see Levin and Wilson 1978, for further details of such a distribution). Although the double distribution was used only as a means of producing a long tail, it would be possible to think of the two as representing the suppressed and dominant plants in the population. A poisson distribution with a mean of 10 was used as control.

A random number generator, drawing values from the fecundity distribution being considered, was used to produce a set of fecundities for the population. These fecundity values were allocated to the plants in the order of their seedling vigour [as determined by genotypic value (Y_S), environmental effects (E) and h in the formula above] the highest fecundity going to the plant with the highest seedling vigour, etc.

Given the genotype of each plant, and the fecundity allocated to it above, the population frequencies of the alleles in the pollen and ovules could be calculated. Hardy-Weinberg formulae were then used to calculate the proportions of genotypes amongst the zygotes, assuming random mating. Thus the assumption was made that, whatever the size of the adult population, the number of pollen grains and of ovules was far greater, and could be ignored as a source of variation.

There were two possibilities at this point. For investigation of genetic drift there was special interest in random processes in a population of a particular size; the genotype of each seedling of the next generation was therefore chosen at random from the zygote frequencies. In other cases the exact size of the population was not of interest, so to reduce one source of variation the genotypes of the seedlings were chosen in proportion to the genotypic frequencies of the zygotes, with a random choice only to resolve fractional numbers.

Rate of response to selection

The most important question that arises is how the fecundity distribution affects the rate of response to selection. To examine this, simulations were performed for selection with a genotypic advantage, A_S of 0.25 (influencing seedling vigour as described above). The favoured allele started with a frequency of 0.01, and was followed until it reached a frequency of 0.9. The starting point of 0.01 might be reached by immigration, the most likely source of a new allele. Any lower value would have resulted too often in loss of the favoured allele by random drift, or in excessively extended selection response times, both especially in the case of a recessive allele. The immigrant allele was introduced as homozygous seed.

A skewed fecundity distribution was compared to a poisson fecundity distribution, and the favoured allele was considered in the dominant and recessive form. The rates of response to selection are expressed as the change in gene frequency per generation for those cases when the allele was not lost.

In general the rate of response to selection is much greater with the skewed distribution for both recessive and dominant alleles (Fig. 1). There was the expected slow response when the favoured allele is rare, a fast response in the frequency range 0.3 to 0.7, and then a slower response again as fixation is approached. As would be expected, if the favoured allele is recessive (Fig. 1a), the response to selection at first is very slow. A skewed fecundity distribution shortens this lag considerably, since the homozygote is able to produce many offspring when it does appear. Conversely, when the favoured allele is dominant (Fig. 1b) the initial response to selection is very fast, but the last stages of fixation are extremely slow. Under these conditions the result of skewed fecundity distribution is little different from the poisson. Sieve selection operating on a skewed fecundity distribution selects effectively for a rare fit genotype because the few plants at the top of the dominance hierarchy make a very disproportionate

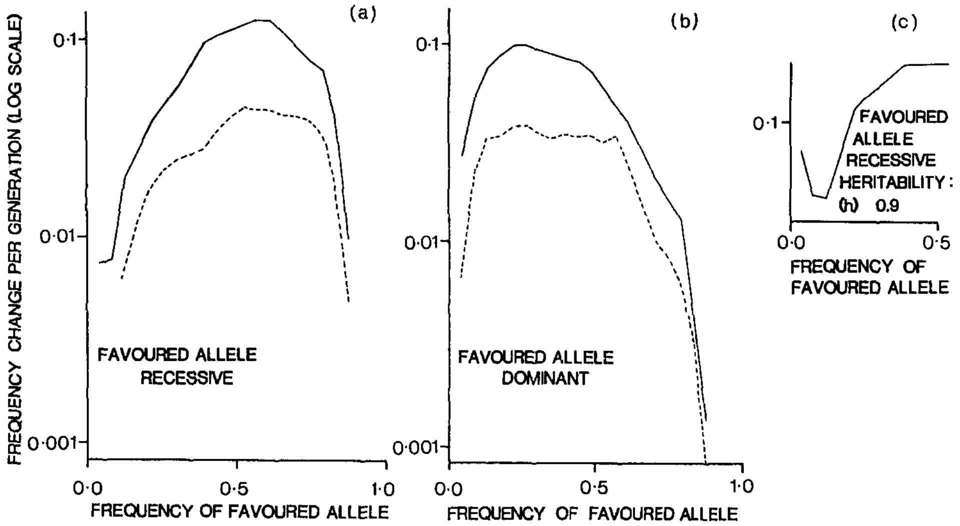

Fig. 1. The effect of fecundity distribution on the rate of response to selection, with A_s 0.25, and the initially-rare favoured allele either dominant or recessive. All curves are the mean of six simulation. - - - - - = poisson fecundity, ——— = skewed fecundity

Table 1. The fate of a rare favoured allele in a population of 250 plants, out of 100 runs for each of various genetic conditions, all with a genotypic advantage in sieve selection of 0.25

Dominance of favoured allele	Fecundity distribution	Percentage of runs in which the favoured allele was lost
Dominant	poisson	0
	skewed	0
Recessive	poisson	84
	skewed	65

contribution to the next generation, but it is not particularly efficient in selection against a rare unfit genotype.

One apparently anomalous feature of the graphs is a shoulder at very low frequencies with the favoured allele recessive and skewed fecundity. With a higher value of h (Fig. 1 c) this became an upturn, representing a faster response at very low frequencies than at slightly higher ones. This is due to effects in the first generation. The favoured allele was introduced as homozygous seeds which could germinate, reach the top of the dominance hierarchy, and with skewed fecundity produce a large number of ovules and pollen gains. This enabled the recessive allele to make considerable gains in frequency in the first generation, before most genes were sheltered by heterozygous combination. In confirmation, a simulation with the allele introduced at the same frequency but in Hardy-Weinberg ratios, showed no such effect. However, the effect seems a realistic result of sieve selection with skewed fecundity, in that homozygous seed is a likely form of immigration into a population. Such effects are not allowed for in conventional formulae.

In some cases the rare favoured allele was lost from the population by drift (Table 1). This occurred only when the favoured allele was recessive, and occurred less often under skewed fecundity than under poisson fecundity. This is due to the possibility of a few homozygotes of the favoured allele producing many offspring, and raising the allelic frequency above the threshold.

All these effects seem biologically real, and mean that evolution in many plant species will exceed the rates previously calculated.

The relative effectiveness of seedling and adult selection

Although rank in the seedling dominance hierarchy often has a persistent effect (Watkinson et al. 1983), fecundity is affected also by differences in growth, competitive ability and reproductive strategy in the adult plant. This sometimes results in a less skewed distribution for fecundity than for biomass (e.g. Obeid et al. 1967; Sarukhan 1974; Zelder et al. 1983). Since the processes that operate are different, relative fitnesses at the two stages may differ (Clegg et al. 1978).

We investigated the effect of counterbalancing adult selection for an allele by determining intermediate fecundities in the way outlined above (from Y_s, E and h) to represent seedling selection, then multiplying the intermediate fecundities by a conventional fitness expressed as selection coefficient (s_a) to represent adult selection, giving the final fecundity. The value of A_s was fixed, and the value of s_a (for the opposite allele) was varied until the allelic frequencies remained at 0.5 : 0.5 from generation to generation.

From theory, sieve selection operating on a poisson fecundity distribution of mean 10.0, A_s of 1.0, half dominance and h at 0.5, is as effective as conventional selection with s_a of 0.5. This is so in our simulations (Table 2), validating our model. The relative effectiveness of sieve and conventional selection also depends on the type of dominance, but either complete dominance or complete recessiveness for the favoured allele give greater effectiveness for sieve selection than does half dominance (Table 2). With skewed fecundity, sieve selection is 1.56 times as effective. This is not due to the different variance of the skewed distribuion, for a poisson distribution with the same variance as the skewed one used (83.83) is ineffective (Table 2). We conclude that the effectiveness of sieve selection depends on the shape rather than the variance of the fecundity distribution.

Selection and immigration

The balance between immigration and selection in the case of a deleterious immigrant allele has often been discussed, e.g. Wright (1969). Formulae have been presented, based as usual on the assumption of a poisson distribution of fecundity. With a more skewed distribution, the selection process would be expected to be generally more efficient, and therefore the equilibrium levels of the immigrant alleles in the population lower.

This was examined in a simulation of a population with immigration at the rates of 1%, 2% and 4% of each generation's seed pool; poisson or skewed fecundity; various selective disadvantages and with either dominance or recessiveness for the imigrant allele.

Immigration and selection were followed until equilibrium was reached. When the forces of selection and immigration are closely balanced there is a zone of allele frequency in which the change in allele frequency is imperceptibly slow. Therefore, simulations were run starting at both high and low frequencies.

Formulae are available (Wright 1942) for the equilibrium frequency of the allele in the poisson case. These formulae are in terms of s_a, but the conversion to A_s in the poisson case is known (see above). Such theoretical values gave good agreement with our poisson results.

Skewed fecundity had a large effect, varying from a decrease of about 20% in the equilibrium frequency to one of 90%, the difference generally greater when the frequency of the immigrant allele was high and in the dominant case. Under these conditions the native allele will be a rare favoured recessive, and as remarked above these are the conditions under which sieve selection with a skewed fecundity distribution is most effective.

Random drift

The phenomenon of random drift in allelic frequencies in finite populations has been widely recognised, both in theory and in the field, and its significance for evolution has often been pointed out. However, all theory, both analytical and simulational, has been based on a poisson model, either an assumption that next-generation offspring are contributed at random from the parents, or with an additional poisson assuption that plants differ at random in their numbers of flowers (Karlin and McGregor 1968).

However, a realistic model would be one where the second process followed a skewed distribution, rather than a poisson one. For this case the formulae are inappropriate (Wright 1969). It would be expected that because the skewed distribution gives more variation in the number of offspring per parent, it would increase the rate of genetic drift.

To test this point, 250 simulations were run with a ten-plant population. Parallel runs were made with a poisson fecundity distribution, with various population sizes.

Skewed fecundity speeds up the rate of loss of genetic variability considerably (Fig. 3), giving fixation within considerably fewer generations. The time to fixation in a 10-plant population with skewed fecundity is intermediate between that for populations of six plants and seven plants with poisson fecundity. We can therefore say that the effective population size (Wright 1931) is 6.4 plants (or 6.9 using geometric means).

Mortality and plasticity

In other simulations it has been assumed that most of the less successful plants produce a small number of flowers. In fact, plant survivorship is usually of a logarithmically decreasing type, Deevey Type II (e.g. Mack and Pyke 1984; Young 1984; Klemow and Raynal 1985) or even Deevey Type III (e.g. Sarukhan and Harper 1973; Sharitz and McCormick 1973; Meagher and Antonovics 1982), so that very few of the initial population survive even until germination, and far fewer reach maturity. Some of this mortality is density-dependent, and therefore caused by competition, so-called "self thinning" (Harper and White 1974); in this process the smaller plants of the population die (Ford 1975). Moreover, in many populations the smaller surviving plants produce no flowers at all (e.g. Sarukhan and Harper 1973; Sarukhan 1974; Leverich and Levin 1979; Jarvinen 1984), sometimes because small plants do not have sufficient energy to mature one fruit (Chaplin and Walker 1982). Zero fecundity has the same effect genetically as death.

If the less successful members of a population die, the effect can be represented by a skewed distribution with Lambda$_1$ being zero. This could accentuate the effectiveness of sieve selection.

Simulations bear out this prediction. The maximum rate of response to selection, measured as in Figs. 1 and 2, is 0.332 per generation. This is not only higher than

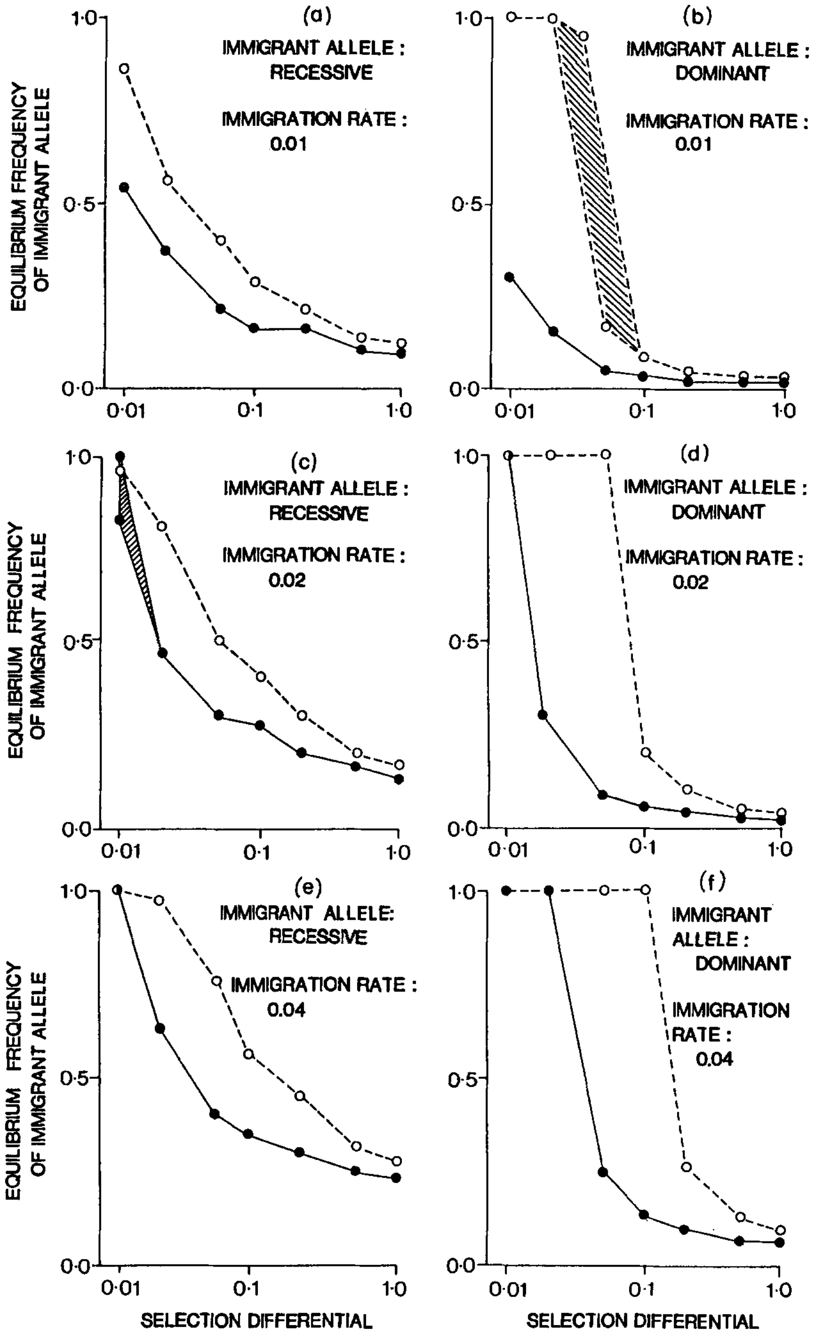

Fig. 2. The equilibrium frequency of an allele with immigration into a population, and selection against it. o---o = poisson fecundity; ●——● = skewed fecundity. Shading represents areas of uncertainly

Table 2. The adult selection coefficient (s_a) required to balance a particular seedling sieve selection coefficient (A_s), under various conditions

Fecundity distribution	Mean	s_a	Dominance of favoured state		A_s required to balance
			Seedling fitness	Adult fitness	
Poisson	10	1.0	half	half	0.500
Poisson	10	1.0	dominant	recessive	0.450
Poisson	10	1.0	recessive	dominant	0.390
Poisson	83.8	1.0	recessive	dominant	0.200
Skewed	10	1.0	recessive	dominant	0.780

the maximum for a poisson distribution at 0.046, but also considerably higher than with our standard skewed distribution at 0.125.

With the 10-plant random drift model (cf. Fig. 3), polymorphism is retained in the population for a mean time of only 2.90 generations (SE of mean = ±0.07), compared to 15.0 generations for our standard skewed distribution.

Heterozygote disadvantage

Fisher (1930) discussed the situation of a rare allele which produces a fitness advantage in the homozygous state, but with a heterozygote less fit than either homozygote. He concluded that such a trait was very unlikely to evolve with conventional selection.

We investigated whether skewed fecundity would affect his conclusion, using genotypic values of 1.0 and 0.75 for the homozygotes and 0.5 for the heterozygote, starting with vaious frequencies and following the population until one allele or the other was fixed. The high cost of simulation to fixation allowed only 10 runs, but though this is too few to give precise fixation probabilities it is clear (Fig. 4) that there is a big difference between the situation Fisher envisaged with poisson fecundity, and that with skewed fecundity.

Model parameters

The comparisons above used one particular skewed distribution for fecundity, as specified in Methods. The choice of these parameters was essentially arbitrary because of the paucity of information on the distribution of fecundity in plants. It is almost certain that any real population will not have this exact distribution, and it is very likely that different species and different populations will have different distributions of fecundity. It is therefore necessary to consider the effect of variation in the parameters.

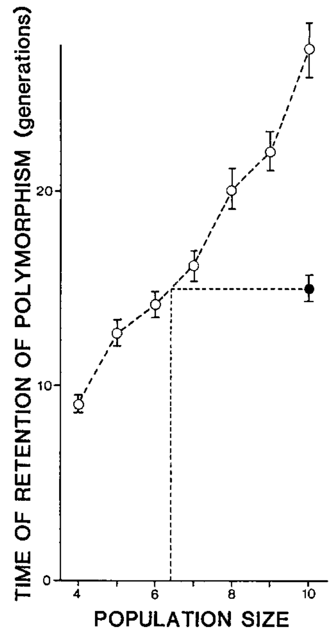

Fig. 3. The mean time for which selectively neutral polymorphism is retained in a small population, starting with two alleles equally frequent, with poisson or skewed fecundity. The standard error of the mean is indicated by a bar

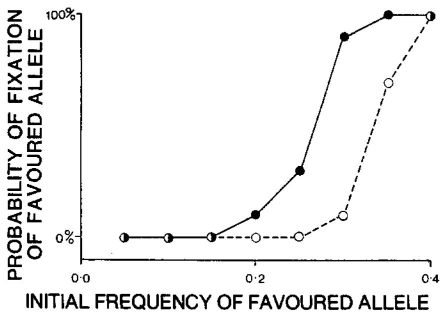

Fig. 4. The probability of fixation of a favoured allele with heterozygote disadvantage. Relative fitnesses were 1.0, 0.5 and 0.75. ○---○ = poisson fecundity; ●—● = skewed fecundity

For investigation, the situation of selection for an initially uncommon allele was chosen. This is a system examined above, and represents the most important effect of the skewed distribution – that the rates of response to selection will generally be faster. The rate of response was averaged over the frequency range 0.2 to 0.8. Six values for p were examined, and for each three values of Lambda$_1$ and Lambda$_2$, with the ratio Lambda$_1$: Lambda$_2$ 1 : 2,5 1 : 5 or 1 : 10. Results showed that the difference between a skewed and a poisson distribution is not peculiar to the values of p, Lambda$_1$, and Lambda$_2$ chosen; all skewed distributions resulted in a quicker response to selection than with a poisson one. However, the exact form of the skewed distribution affected the outcome. Rates of response to selection varied from 1.22 times the value with poisson to 3.20 times the value. Increasing the relative difference between Lambda$_1$, and Lambda$_2$ led, at all values of p, to a faster response to selection. Increasing p from 0.225 to 0.75 resulted in quicker selection, at all values of Lambda$_1$ and Lambda$_2$, but increasing it further to 0.975 reduced the rate of response.

The simulations so far reported assumed a genotypic contribution to the position of a plant in the dominance hierarchy, h, of 0.5. Since it is currently very unclear what value of h normally obtains in nature, we ran some simulations with other values, to check that our results were not critically dependent on the value used. The rate of response to selection with a higher h was somewhat greater, as would be expected, but the difference between poisson and skewed fecundity remained. The difference in the probability of loss of a recessive favoured allele was greater: a 32% chance with poisson fecundity and no losses in 100 simulations with skewed. The selection coefficient of "adult" selection required to balance is not markedly affected by h. An h value of 1.0 in place of 0.5 increased the balancing s_a from 0.50 to 0.55, an h of 0.25 reduced it to 0.31. A higher h increased the ability of a skewed fecundity to overcome heterozygote disadvantage. We conclude that the directions of our results are not critically dependent on the value of h that we chose.

Conclusions

The results show very considerable differences between the poisson distribution and a skewed distribution. Whilst the exact distribution used probably never occurs, distributions like it certainly do. This has considerable consequence for plant evolution. It means that plants can evolve, and genetic frequencies can drift, at a considerably greater rate than the usual formulae would indicate.

The simulations involving heterozygote disadvantage show that there are some circumstances in which traits can evolve in real plant populations, when poisson-based theory suggests they cannot. There are two mechanisms involved in general and in this particular case. Firstly, the advantage possessed by the few fittest plants is greater with a skewed distribution. It is therefore easier for the advantage of highly-fit immigrant homozygotes to outweigh the disadvantage of the heterozygous condition. Secondly, the greater random variance associated with the skewed distribution can enable a popoulation, starting with a marginally low frequency of the immigrant allele, to reach by chance the critical frequency above which the advantage of the immigrant homozygote outweighs the disadvantage of the heterozygote.

Our results have implications also for the cost of selection controversy. The processes discussed here do not depend on mortality, so the argument that a certain number of deaths are necessary for gene substitution is not relevant. It is true that it is necessary in this mechanism for many plants to achieve far less than their maximal development, but this is a universal feature of plant populations. Moreover such suppression of potential is often due to competition (Clements et al. 1929), and competition will be strongest between members of the same species, since they are occupying almost exactly the same niche. Therefore, to some extent, selection such as that envisaged here is based on the existing distribution of fecundity among the members of a population, rather than any loss of opportunity by the population.

The importance of sieve selection depends on the extent to which mortality and position in the size hierarchy are genetically determined. In the only direct investigation, Gottlieb (1977) found no genetic differences between plants at the small and large extremes of the dominance hierarchy; similarly, Linhart et al. (1981) found no allozymic differences between four age classes. On the other hand, Clegg and Allard (1973); Burdon et al. (1983); Antonovics (1978) and Bazzaz et al. (1982) found changes in gene or genotype frequencies between the seedling and adult stages, and Schaal and Levin (1976) showed differences in heterozygosity and genetic variance between plants of apparently different age. In most of these studies it is unclear whether the mortality that caused the change in genetic frequency was true self-thinning, i.e. density-dependent mortality caused by competition. In some cases the change in genetic frequency could be interpreted as adaptive. For example, the changes that Bazzaz et al. (1982) found depended on the soil nutrient level, and those of Antonovics (1978) involved different responses to cutting. The question is still open.

Other workers have attempted to determine the genotypic contribution to position in the dominance hierarchy by estimating the proportion of the variance in plant size that could not be accounted for by environmental effects. Knight (1983) could account for only 3.8% by using emergence date alone, and 20% by using emergence date with the space available to each plant and size and distance of neighbours. It would be very rash to conclude that the remaining 80% of the variation is genetic, but some may be. Howell (1981) found no significant effect of seed size, and an effect of emergence date accounting for only 10% of the variation in fecundity. Perhaps some of the remainder was genetic. Hartgerink and Bazzaz (1984) showed that substrate heterogeneity increased the variance in seedling height. They concluded that genetic differences would be "overridden" by environmental variation. They also showed that up to 50% of variation in final biomass could be explained by seedling size, though that leaves open the question whether seedling size was genetic or plastic.

Clearly there is within-population genetic variation in growth characteristics. Solbrig (1981) showed the presence of additive genetic variation for germination and morphology, though not for growth, but genetic differences certainly occur within populations in growth characteristics such as photosynthetic rate (Rapson and Wilson 1987), leaf emergence (Eagles and Othman 1978), RGR (Burdon and Harper 1980; Antlfinger et al. 1985) and competitive ability (Solbrig and Simpson 1974). Since growth rates determine size, and size is related to fecundity (Wolfe 1983; Dolan 1984) and survival (Maruta 1983), it must be possible for sieve selection to operate on such differences.

There is thus much indirect evidence for the possibility of sieve selection, but no direct evidence. However, if sieve selection were operative, its very efficiency ought to make it hard to find, since the weaker competitors would already have been eliminated and an evolutionary plateau/genostasis reached (Bradshaw 1984). Such selection would occur only in or after speciation, when a population was colonising an ecologically different habitat for which different adaptations were required, or when the environment changed.

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