

THE NATURE OF LIMITS TO NATURAL SELECTION¹

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ABSTRACT

Insufficient genetic variability and the swamping effects of gene flow are inadequate explanations of limits to natural selection. Comparison of evolutionary responses in different populations subjected to similar selective forces, comparison of rare and widespread species, and comparison of marginal and central populations are all neglected research areas that bear on the nature of limits to natural selection. Plant populations provide us with well-defined, operationally viable systems for addressing these comparisons. Several possible constraints on range extension of ecologically marginal populations are considered in detail. Selection on fitness components that are themselves negatively correlated will be ineffective: such negative correlations are to be expected in natural populations. Small size of marginal populations will reduce severely the probability of obtaining appropriate character combinations; it will increase the swamping effects of gene flow; and it may lead to inbreeding depression effects. Gene flow will have different effects depending on whether the genes concerned are effectively neutral, advantageous, or deleterious in the population into which they migrate. Gene flow will spread beneficial genes rapidly, but may retard divergence if density of marginal populations is low and swamping effects are high. Finally a population entering a new habitat is likely to meet new competitors and predators: the coevolutionary responses of the latter may counteract adaptive responses by the species undergoing range extension. All these factors are likely to interact in important ways in marginal populations. The study of limits to natural selection is likely to be a fruitful future research area, and one in which the detailed documentation of the systematist will provide invaluable baseline information.

"The species border is one of the most interesting phenomena of evolution and ecology, yet as a scientific problem it has been almost totally ignored."

"The essential stability of the species border would seem to contradict our belief in the power of natural selection. One would expect the species range to grow by a process of annual accretion like the rings of a tree. That this does not happen is particularly astonishing in the frequent cases where conditions beyond the borderline differ only slightly and in degree from conditions inside the species border."

E. Mayr (1963, Chapter 17)

Population genetics is today in a state of dissatisfaction and ennui. This crisis has come about from what is considered to be one of the most important technological breakthroughs the subject has ever experienced, namely, the use of electrophoresis to study variation at the enzyme level and, by inference, at the level of the gene. The result of this technique has been the discovery of a large amount of genetic variability in natural populations. Yet the cause of such a high level of genetic polymorphism has not been satisfactorily explained. The critical question is not so much can we determine which mechanisms predominate (and

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numerous mechanisms have now been proposed), but can we even distinguish operationally whether selection is acting at all on any particular locus. Given that we can identify genetic variation at a locus, can we pinpoint its phenotypic effect, can we establish its effect on fitness in nature, and, more crucially, can we say the effect is due to that locus and not closely linked genes? Given that the proportional contribution of any individual gene to fitness is likely to be low, these questions become formidable. It is salutary to note that there is still tremendous controversy regarding the mechanisms maintaining some phenotypically overt polymorphisms such as banding color and pattern in the land snail, *Cepaea* (e.g., Greenwood, 1974; Bantock, 1974; Clarke, 1975).

In order to escape from this crisis, either fresh questions need to be asked, or we need to take a fresh approach to old problems. In this paper I want to ask perhaps an obvious yet rarely considered question, namely, what limits natural selection, and pinpoint some approaches to answering it. I say the question is rarely considered, but strictly speaking this is not true, since in fact the question has been frequently asked; yet it has usually had a simple, almost tautological answer, namely, "lack of genetic variability" and the subject has thereby been closed. We now know this answer to be false at least at a superficial level.

Almost every species that has been studied is genetically variable at about 30% of its loci. We know that species which have remained unchanged, as far as we can judge, for millions of years still contain a tremendous amount of variability. The horseshoe crab, *Limulus polyphemus*, has been shown to be polymorphic at 25% of its loci, yet it is a "living fossil" whose close relatives date back 300 million years (Selander et al., 1970). Similarly, *Lycopodium lucidulum*, a clubmoss, has been shown to be polymorphic at 28% of its loci (when summed over all populations), and yet it is considered to be the most primitive living member of the lycopods which had their origin in the Devonian, ca. 400 million years ago (Levin & Crepet, 1973). And studies of rare or vanishing species have shown that these too are genetically variable. For example, the Orang Utan has been declining in abundance over thousands of years and is now a highly restricted species, yet it is one of the most polymorphic primates known (Buettner-Janusch, 1973, personal communication). Babbel & Selander (1974) have shown that the same number of loci were polymorphic in the edaphically restricted *Lupinus sub-carnosus* as in the more widespread *Lupinus texensis*. The number of alleles per locus was greater in the more widespread species, but it was difficult to decide whether this was a cause or effect of its broader geographical range.

Other lines of evidence argue strongly not just for a high level of variation at the enzyme level, but also for a high degree of genetic variation in characteristics at the phenotypic level. The most powerful evidence for this comes from artificial selection experiments. For example, Antonovics (1975) and Lewontin (1974: 89) have collated lists of characters which have responded to artificial selection in *Drosophila melanogaster*: the lists are not exhaustive, yet the number of relatively independent traits that respond to selection is near 50. And Falconer (1960: 343) in summarizing what is known about quantitative variation, stated:

"The genetic variation of metric characters appears from the results of experimental selection to be the product of segregation at some hundreds of loci, or more probably some thousands if the variation of all characters is included. So natural populations probably carry a variety of alleles at a considerable proportion of loci, even perhaps at virtually every locus."

With regard to plant populations it is also clear that ecotypic differentiation is the rule rather than the exception. It is really difficult in a search of the literature to find examples of phenotypically or ecologically distinct populations that do *not* show genetic differentiation. Such cases would be well worth documenting, even though workers in the past may have been reluctant to do so.

If it is indeed insufficient to explain limits to natural selection in terms of overall genetic variation, we must look for alternative approaches. Three approaches seem particularly worthwhile at this time.

1. *Comparison of evolutionary potential.* We can look for contrasting evolutionary responses in different populations (or species) subjected to similar selective forces, and assess reasons for the differences in response. This is difficult because we know relatively few cases of evolutionary change that are sufficiently clear-cut to be amenable to such analysis. One exception is the evolution of metal tolerance in plants: already there are a sufficient number of intriguing observations and initial experiments which suggest that the comparison of evolutionary potential is a tractable approach. Screening seedlings for survival on mine soil can test if nontolerant populations contain genes for metal tolerance (Walley et al., 1974). In this way tolerant genotypes have been found not only in nontolerant populations of species that can colonize metal mines, but also in species that occur in the vicinity of mines but not on them (Gartside & McNeilly, 1974). It is relevant to ask what these genes are doing in the nontolerant populations, why they only seem to be present in some species and not others, and why some species can evolve high degrees of metal tolerance whereas others generally have a lower tolerance and are confined to less toxic regions. For example, *Plantago lanceolata* can evolve tolerance to lead and zinc (Wu & Antonovics, 1975, 1976) yet it seems unable to evolve tolerance to copper (Gartside & McNeilly, 1974); in nature it is rarely found on copper mines. There seems also to be a limit to the level of lead and zinc tolerance which it can evolve since it is only found in areas of low contamination. The grass *Agrostis tenuis*, a species renowned for its ability to evolve tolerance, is not found on certain lead mines in Scotland. Instead the mines are colonized by *Agrostis canina* (Craig, 1970). It is completely unknown why *A. tenuis* is unable to evolve tolerance on these particular mines.

2. *Comparison of highly restricted and widespread species.* It is remarkable, apart from the reference cited earlier (Babbel & Selander, 1974), that in the whole of experimental plant ecology and genetics almost nothing is known about the biology of widespread species as opposed to rare species that were formerly widespread (palaeoendemics). Various factors may contribute to this lack of information, but the primary one is probably the fact that experimental ecology and population genetics has in the past been largely the province of zoologists rather than botanists. If an animal is rare, it is almost by definition difficult to

TABLE 1. Leaf characters of *Plantago cordata*, sampled from three populations along a 3 km stretch of one stream in Davidson County, North Carolina. The means are based on twenty field collected seed families, with five plants per family, and grown in a growth chamber in a completely randomized design.

Population	Leaf Character			
	Number	Blade Length (cm)	Blade Width (cm)	Petiole Length (cm)
Upstream	6.2	19.2	7.3	8.3
Midstream	6.7	20.2	7.9	6.5
Downstream	6.5	15.6	5.9	6.5
Significance of population differences ^a	P = 0.042	P = 0.14	P = 0.048	P = 0.11

^a Multivariate significance of population differences, $P = 0.0008$, taking into account above variables measured at two times.

locate and difficult to study without endangering the species during sampling and experimentation. Plants, however, have tremendous advantages in these respects since they can be precisely and repeatedly located (often data on herbarium sheets is adequate), they can be sampled nondestructively either from seed or from vegetative propagules, and usually they are easily grown in experimental situations. Clearly there is a tremendous potential here for future investigations.

We (Meagher & Antonovics, unpublished) have initiated a study of a rare species of *Plantago* in North Carolina, namely *P. cordata*. This species is rare but fairly widespread west of the Appalachians, but east of the Appalachians has been only recorded from three widely separated localities. One of these localities occurs in Davidson County, North Carolina, where the species is confined to a rocky shallow stream. Seeds were sampled from upstream, midstream and downstream populations, grown in the phytotron and the plants measured for a range of characters. The results (Table 1) show that, even though the species is rare, it still can undergo genetic differentiation between very local populations. This species clearly has the potential for evolutionary change, but it is clearly pertinent to ask what factor is limiting its range extension and what the genetic constraints are with regard to this factor.

3. *Comparison of marginal and central populations.* Marginal populations may be of various kinds. At a geographical level, marginal populations may be found at the periphery of a species range but more or less contiguous with it, or they may be well beyond the general species range and constitute so-called "peripheral isolates." At an ecological level there may be population boundaries at ecotones or a habitat may be marginal in the sense that the population can only maintain itself at an extremely low density. These categories are by no means completely distinct, and their identification depends largely on the level of resolution chosen by the experimenter. For example, all geographically marginal populations and many island populations (particularly where the islands are defined in an ecological rather than physical context) have boundaries that are ecotonal in nature. The nature of the evolutionary process

TABLE 2. Population dynamics of a central (field) and marginal (woodland) population of *Anthoxanthum odoratum* in Durham, North Carolina (after Grant, 1974).

		Central	Marginal
Population density (plants/sq m)		15.8	1.6
Population size (mature individuals)	1972	161	24
	1973	128	29
	1974	99	20
Mortality rate (%)	1972-3	32	77
	1973-4	52	76
Recruitment rate (%)	1972-3	15	76
	1973-4	38	65

going on in these various circumstances are undoubtedly different, and a study of all of them can contribute to our understanding of limits to natural selection.

I want in this paper to concentrate especially on the problem of limits to natural selection in ecologically marginal populations and to consider in some detail the processes that may be acting to limit a species range extension in ecotonal situations. My reason for concentrating on this aspect of the subject is largely the fortuitous result of a long-standing involvement with processes that occur at ecological boundaries. But I hope to demonstrate that some of the processes are much more generally applicable to other evolutionary situations. Intuitively it is easy to understand the problem at ecotones: given that environmental parameters (climatic, edaphic, or biotic) change gradually at a boundary, why are some species unsuccessful in entering into another habitat when there is seemingly no barrier to such invasion? Two hypotheses have usually been put forward to explain such limits. The first we have already considered, namely, lack of genetic variation. The second is that gene flow from the parent population acts to prevent genetic differentiation and hence range extension across the ecological boundary. This hypothesis has been strongly counter-argued by myself (Antonovics, 1968; Dickinson & Antonovics, 1973) as well as other workers (e.g., Jain & Bradshaw, 1966; Ehrlich & Raven, 1969; Endler, 1973). In brief we are left without a satisfactory view on limits to natural selection.

THE NATURE OF ECOLOGICALLY MARGINAL POPULATIONS

Before itemizing and examining in detail each of the constraints that may limit range extension, it is necessary to define the nature of a marginal ecotonal population more explicitly. It is easiest to define a marginal population, as will be done here, in terms of actual density. Any population can be considered marginal if its density falls consistently along an ecological gradient till it becomes effectively zero and the species disappears. However, it would be extremely desirable to consider a marginal population in more explicit demographic terms. It is possible to visualize several regions in an ecotonal situation:

1. A region of density dependent control, where the population is essentially at carrying capacity,

2. A region where mortality is so great that the death rate exceeds the birth rate, but equilibrium is maintained by immigration from adjacent areas of greater density,

3. A region where there is survival but no reproduction, i.e., the population is maintained solely by a balance between immigration and mortality. In this region, by definition, genetic variance in fitness is zero, since fitness is zero.

Perhaps more important than recognizing degrees of mortality may be understanding the nature of the factors which change the population density. What form these factors take depends in part on our view of population regulation. For example, the change may be an increase in the severity of density-independent effects, a change in the number of "safe-sites," or a change in the severity of density dependent effects. The latter may be particularly important in limiting a population since the central population may be already "maximally adapted" (we will return to this concept later) in terms of the density it can sustain and therefore an adjustment to a more severe action of those same factors may be particularly difficult.

This problem is illustrated by the work of Grant (1974), in a study of the grass *Anthoxanthum odoratum*, across a field-woodland ecotone. *Anthoxanthum odoratum* was abundant in the field, but its density declined into an adjacent pine woodland, till beyond about 30 m into the woodland no more plants of *A. odoratum* could be found. There were clear differences in both density and rates of population turnover between central and marginal populations (Table 2); as expected, the turnover in the marginal populations was greater. Nevertheless, population size in this marginal site remained remarkably constant over three years, suggesting some form of density dependent regulation. This regulation must have been acting at a safe site or predator dependent level since individuals were widely spaced ($1.6/\text{m}^2$) with plant-plant interactions very unlikely. However, in the central region it seemed clear from the density of the population that plant-plant interactions were important. In other words, the marginal population did not simply have to adjust to more severe density independent factors, nor to an accentuation of existing density dependent factors, but seemed to be regulated in a completely different way from the central population.

CONSTRAINTS ON RANGE EXTENSION

SELECTION ON SEVERAL CHARACTERS SIMULTANEOUSLY

Fitness is a complex trait made up of many components: when a population migrates to a new habitat, there is frequently simultaneous selection for many traits. For example, mine and pasture populations of *Anthoxanthum odoratum* differ in many characters (see Antonovics & Bradshaw, 1970). Knowing the mean of the traits in the mine populations, and the mean and variance of traits in the pasture population from which the mine population was derived, it is possible to calculate (Van Valen, 1965) the selection pressure on each character that would be needed to effect a shift from pasture to mine traits in one genera-

TABLE 3. Potential intensity of selection on individual characters during colonization on mine soil by a pasture population of *Anthoxanthum odoratum*. Overall selection pressure on morphological traits is very high. (See text for explanation of assumptions on which these calculations are based.)

Character	Pasture		Mine		Standard Deviations of Change From Pasture to Mine	Selection Pressure
	$\bar{x}$	s.d.	$\bar{x}$	s.d.		
Index of tolerance (%)	8.8	10.56	75.4	23.81	6.31	ca. 0.9999
Self-fertility (log # seeds)	0.051	0.12	0.156	0.19	0.88	0.55
Flowering time (days after 9/5/1966)	21.3	5.22	17.3	4.39	0.77	0.48
Height (cm)	53.4	10.35	39.6	5.41	1.33	0.70
Flag leaf length (mm)	32.8	8.06	25.4	5.04	0.92	0.57
Number of inflorescences	79.2	36.3	52.6	32.83	0.73	0.46
Overall selection pressure on traits other than tolerance (assuming traits act independently and effect on fitness is multiplicative) =						0.9837

tion (see Table 3). This calculation is grossly over-simplified since it assumes, among other things, that we are measuring additive genetic variance, and I therefore use it only for the sake of illustration. If we assume that each character contributes multiplicatively to fitness, and that the characters are independent, then we can calculate the selection pressure which would be needed to effect a simultaneous shift in all characters, from the product of the individual fitness (Table 3). We can see that although the selection pressure on each morphological trait individually is moderate, a very large selection pressure would be needed to change all the traits simultaneously. The inverse of this value is equivalent to the probability of finding a typical mine genotype in the pasture population. If we include metal tolerance in the calculations, the probability that the pasture population will produce a perfectly adapted mine genotype becomes extremely low. From these considerations we are left with an intriguing dilemma: the lower the probability that an appropriate variant ("mine genotype") can be produced, the greater will be the selection pressure tending to preserve it.

The studies of Grant (1974) mentioned previously provide us with a more realistic view. He sampled *Anthoxanthum* adults as single tillers from three sites across a field-woodland ecotone; he termed the populations at these sites the central population (in the field), the ecotonal population (at the woodland margin itself), and the marginal population (in the woodland). These single tillers were multiplied up in the greenhouse and reciprocal transplants carried out between the field, ecotonal and woodland sites. The transplants were placed into

TABLE 4. Survivorship, seed output per survivor, and relative fitnesses of central (field) and marginal (woodland) populations of *Anthoxanthum odoratum* transplanted reciprocally as adult tillers into the central and marginal habitats.

Habitat		Population	
		Central	Marginal
Central (Field)	Survivorship =	79%	53%
	Seed number =	197	74
	Relative fitness =	1	0.25
Marginal (Woodland)	Survivorship =	36%	86%
	Seed number =	59	62
	Relative fitness =	0.14	0.34

pots sunk in the ground, and the pots contained soil of the site into which the transplants were made so as to simulate field conditions closely, yet insure a reasonable survivorship. The results showed that there were genetic differences between the marginal population and the central population for many traits, and each population did best in its own habitat in terms of the fitness components, seed set and survivorship (Table 4). The ecotonal population was generally intermediate in character to the central and marginal and is not included in Table 4 nor in most of the subsequent discussion.

This kind of experiment permits an interesting sequence of comparisons which serve to illustrate the complexity of changes that occur when a population moves into a new habitat (Fig. 1). A comparison of the central population in the central habitat with the central population in the marginal habitat represents the phenotypic response of the central population to the new habitat immediately after migration. (Clearly adult tillers cannot migrate, but this experiment could be readily carried out with seed progeny.) If we now compare the central population in the marginal habitat with marginal population grown in the marginal habitat, then this represents the genotypic or evolutionary response of the central population following migration into the new habitat. Finally, it is possible to compare the marginal population in the marginal habitat with the marginal population in the central habitat. This tells us if there are characters which appear to be the same in the marginal and central populations (when both are grown in the marginal habitat) yet which have undergone genetic change in the marginal habitat: these characters would probably not remain the same when returned to the central habitat. Figure 1 includes all the characters that showed significant differences in at least one of the above comparisons. Firstly, there is a change in many characters. Secondly, the central population can seemingly adapt phenotypically as far as several traits are concerned, but this phenotypic change becomes genetically fixed, presumably because the phenotypic plasticity involves some cost (either energetic or as a result of phenotypic correlations reducing fitness). Thirdly, phenotypic response is usually in the same direction as genetic response. A system of reciprocal transplants done under field conditions, and

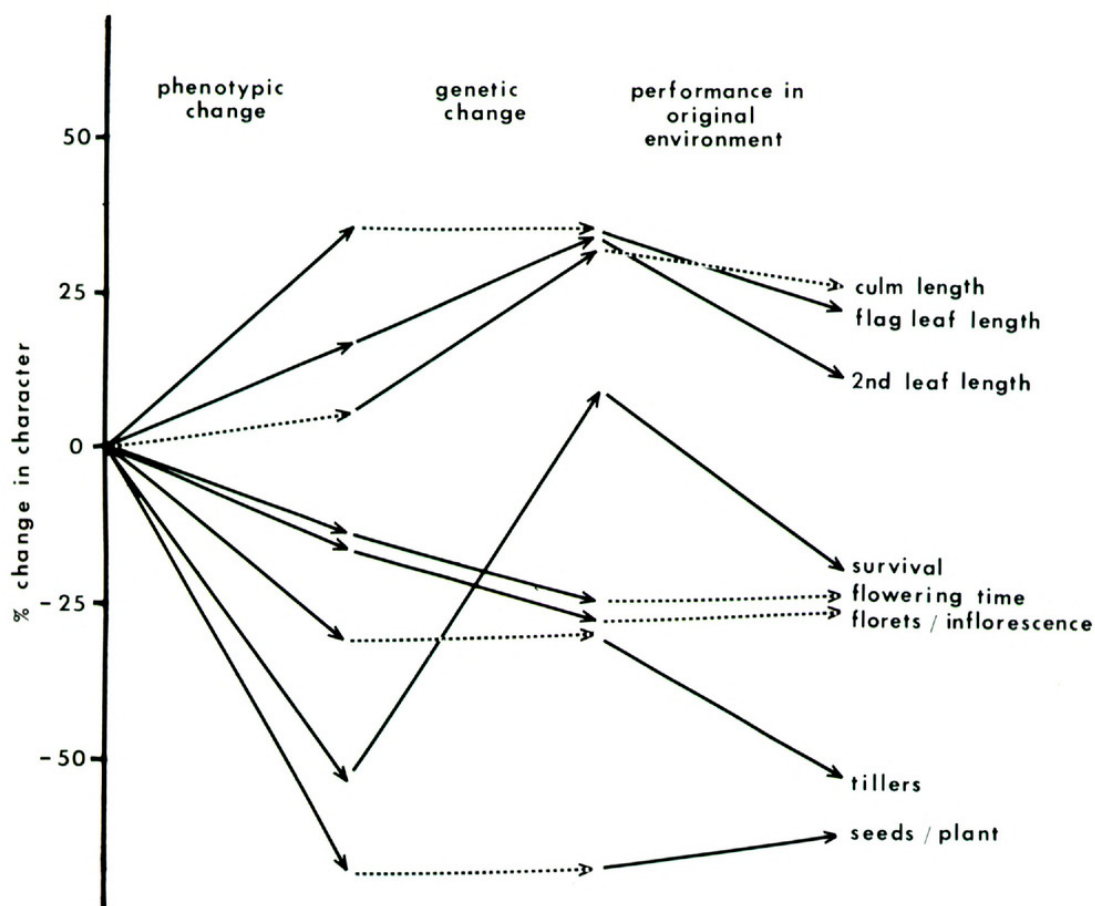


FIGURE 1. Diagram showing the phenotypic and genetic changes in a range of characters when a central (field) population of *Anthoxanthum* migrates into a marginal (woodland) habitat. The changes are expressed as percentages of the measure of the character in the central population in the field habitat; solid lines represent statistically significant ($P < 0.05$) changes. The data is calculated from the transplant experiments of Grant (1974). Phenotypic change is represented by a comparison of the central population in the field with the same population in the woodland; genotypic change is calculated by a comparison of the central population in the woodland with the marginal population in the woodland; and performance in the original environment represents the comparison of the marginal population in the woodland with the same population in the field.

using rigorous experimental design, can therefore provide us with a large amount of information about selection processes, how they interact with phenotypic responses, and how different characters interact in selection responses. When combined with realistic fitness estimates based on survivorship and fecundity, and extended to seedling-adult comparisons to estimate on-going selection pressures, this simple and in fact rather old-fashioned genecological approach can become very powerful.

The effect of simultaneous selection on several characters will depend on how these characters are correlated with each other genetically, and how they are correlated with regard to their effects on overall fitness. There are two fundamental, but often poorly appreciated, tenets of quantitative population genetics which arise from considering the effects of directional selection on a quantitative

trait. The first is that there will be a rapid reduction in the additive genetic variance of the character undergoing selection. This is sometimes translated into the "law" that the greater the contribution of a character to fitness, the less will be the genetic variance in that character. This generalization requires the assumption that there is only directional selection operating: under various forms of balancing selection there can be considerable genetic variation in an adaptive trait. The second tenet is that there will be rapid selection for (and hence rapid fixation of) genes that contribute to characters having a strong positive genetic correlation with regard to their effect on fitness. Genetic correlation results either from pleiotropic gene action or from linkage disequilibrium. The relationship between selection for two traits simultaneously and their response to selection can be stated (after Falconer, 1960) as follows:

$$\begin{aligned} R_x &= S_x h_x (h_x + r_{xy} h_y) \\ R_y &= S_y h_y (h_y + r_{xy} h_x) \end{aligned}$$

where x, y = two traits under selection (expressed as standardized scores, i.e., with mean = 0, standard deviation = 1); R = response to selection (change in mean of selected group); S = selection differential (mean of group selected); h^2 = heritability (additive genetic variance/phenotypic variance); r_{xy} = genetic correlation of x and y . In other words, even though each trait individually may show genetic variance, if they are negatively correlated ($r_{xy} < 0$), they will show a reduced selection response. If the negative correlation is -1 , then clearly there will be no response to selection by either character. This is illustrated diagrammatically in Fig. 2.

As a result of these two tenets, we would expect a natural (as well as an experimental) population undergoing selection to show a reduced genetic variance for fitness traits, and a negative correlation among components contributing to fitness since genes or gene combinations contributing positively to several fitness components will be rapidly fixed in all members of the population (see Falconer, 1960: 328 for discussion). A negative correlation among fitness traits is often evidenced in plant populations. Intuitively we might think that larger plants live longer and have more fruits per inflorescence, and more or bigger seeds. However, if we look at field-collected plants, negative correlations between the fitness components are often evident (Table 5). Such negative correlations are well known to plant and animal breeders (Adams, 1967; Grafius, 1961; Grafius & Thomas, 1971) but have been infrequently studied in natural populations.

When a population enters a new habitat, the nature of the character correlations may change in very crucial ways. If the character that is advantageous in the new habitat is not negatively correlated with any of the other characters influencing fitness (i.e., there is a new correlation among the fitness components), then evolutionary response may be rapid and relatively easy. For example, in those plants that are successful in colonizing mine soils we might predict that the property of tolerance is relatively independent of other characters. Indeed, Antonovics & Bradshaw (1970) found that tolerance in *Anthoxanthum odoratum* was not correlated with any of the traits they measured when considered on a within-population basis. On the other hand, evolutionary re-

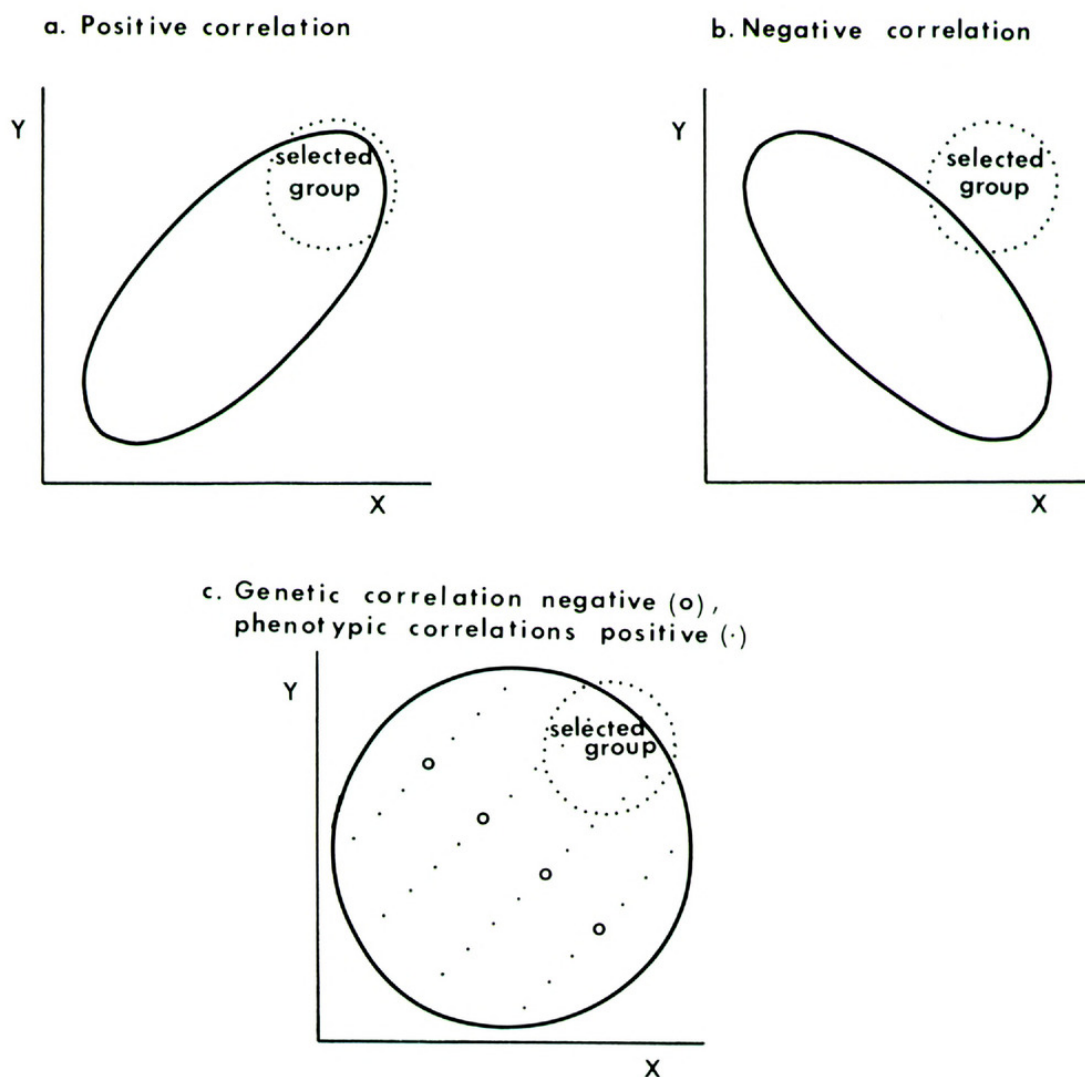


FIGURE 2. Schematic diagrams showing the effect of genetic and phenotypic correlations between two characters x and y on the response to selection. The solid ellipse or circle represents a frequency isocline of a bivariate normal distribution.—a. There is a positive genetic correlation between the characters with regard to their effects on fitness. Selection for one character reinforces selection for the other; the selected group is large and response to selection rapid.—b. There is a negative genetic correlation between the characters with regard to their effects on fitness. Selection for increased fitness in one character is counteracted by correspondingly lowered fitness in the other character. The probability of obtaining individuals which have a high expression for both characters is low; the selected group is small, and response to the same criteria of selection as in diagram a is slow.—c. Phenotypic correlations may mask the effects of genetic correlations, giving apparently a larger selected group but still a slow selection response. (For further discussion, see text.)

sponse to the new habitat may be difficult if in that habitat characters are favored which have a strongly negative effect on other fitness components, i.e., if the existing "correlation structure" of fitness components is maintained. For example, *A. odoratum* may successfully colonize a woodland by increasing its photosynthetic efficiency, by increasing its energy contribution to reproduction (and not competition as in the field), or by changing leaf area. There is evi-

TABLE 5. Phenotypic correlations among fitness components of individuals of a central (field) and marginal (woodland) population of *Anthoxanthum odoratum*. Correlations are based on twenty individuals from each population measured in the field under natural conditions. Flowering time refers to date of flowering, i.e., a positive correlation with the numerical traits indicates that later flowering individuals had more of that trait. (Correlations expressed as %, where values greater than 44 or less than -44 are significant, $P = 0.05$.)

	SEED #	TILLER #	INFLORESCENCE #	SPIKELETS / INFLO	SEEDS / INFLO	FLOWERING TIME	
SEED #		89	53	32	-61	51	CENTRAL POPULATION
TILLER #	63		93	35	40	-76	
INFLORESCENCE #	32	77		71	46	-94	
SPIKELETS / INFLO	35	-43	23		29	-27	
SEEDS / INFLO	29	-40	-27	-2		-40	
FLOWERING TIME	52	-83	-91	-23	55		
	MARGINAL POPULATION						

dence (Grant, 1974) that marginal woodland populations indeed have a higher chlorophyll *b*/chlorophyll *a* ratio and are therefore more shade tolerant, devote more energy to reproduction, and have larger flag leaves. Yet these characters are clearly in conflict with other attributes since survivorship of woodland plants is low, and their reproductive output is only somewhat greater than that of field plants transplanted into the woodland (Fig. 1).

Numerous aspects of selection in natural populations still need to be studied:

1. How does selection on several individual traits contribute to overall fitness? Does it contribute additively, multiplicatively, or in some more complex fashion to overall fitness? How does it depend on the correlation among the characters?
2. How can we define fitness in demographic terms? Concepts of reproductive value, quality of seed (inbred/outbred), and degree of relatedness of competitors are all important and deserving of study in plant populations.

TABLE 6. Number of correlations that are significant at $P < 0.001$ or in parentheses, $P < 0.01$, among nine characters measured on the 10th leaf of four different varieties of climbing beans, *Phaseolus vulgaris*, grown under three temperatures. Characters are petiole length, length of petiole of terminal leaflet, length and width of two lateral leaflets, and length and width of left and right halves of the terminal leaflet. Each correlation is based on twelve plants; a total of thirty-six correlations are possible for each variety at each temperature. Mexican A and B are two wild varieties from Mexico.

Variety	Temperature (Day/Night)		
	26°/23°C	23°/20°C	20°/17°C
Kentucky Wonder	34 (2)	33 (3)	4 (3)
Half Runner	1 (3)	9 (8)	8 (9)
Mexican A	15 (6)	1 (1)	1 (13)
Mexican B	1 (4)	2 (2)	7 (5)

3. How do widespread versus restricted species differ with regard to the degree of correlation among fitness components? It is well known (see also Adams, 1967) that levels of correlation between characters differ between strains, and are also influenced by the environment (Table 6). Do more restricted species show a greater interdependence of their characters? If so, how has this come about? Does specialization (strong directional selection towards a particular optimum) lead to stronger character interdependence?

4. What is the relationship between directional selection for fitness traits and stabilizing selection (or some other forms of balancing selection) on component traits?

5. How does the relationship between genetic and phenotypic correlation between characters influence selection on these characters? It is often clear that an individual may show positively correlated phenotypic responses (e.g., get larger in many traits as a result of being grown in a favorable environment), yet show negatively correlated genetic responses (e.g., selection for larger leaves generally results in a slower rate of leaf production; Edwards & Cooper, 1963; Edwards, 1967).

6. What are the consequences of gene flow between populations differing in direction and magnitude of character correlations?

7. What is the relationship between within-species correlations and between-species correlations? Does taxonomic diversification occur more frequently along within-species correlation axes, and is it rarer to have taxonomic diversification in an opposite direction? There is evidence in many plant and animal groups that between-species correlations may be either in the same or opposite direction as within-species correlations (Fig. 3).

The problems inherent in assessing the relative fitness of different genotypes and in measuring heritability and genetic correlations are formidable. But it seems that understanding the variance-covariance structure of fitness traits is essential if we are to get away from a simplified view of genetic variation in natural populations. *Anthoxanthum odoratum* in pastures, woodlands, and on mines is genetically variable for numerous quantitative traits: the im-

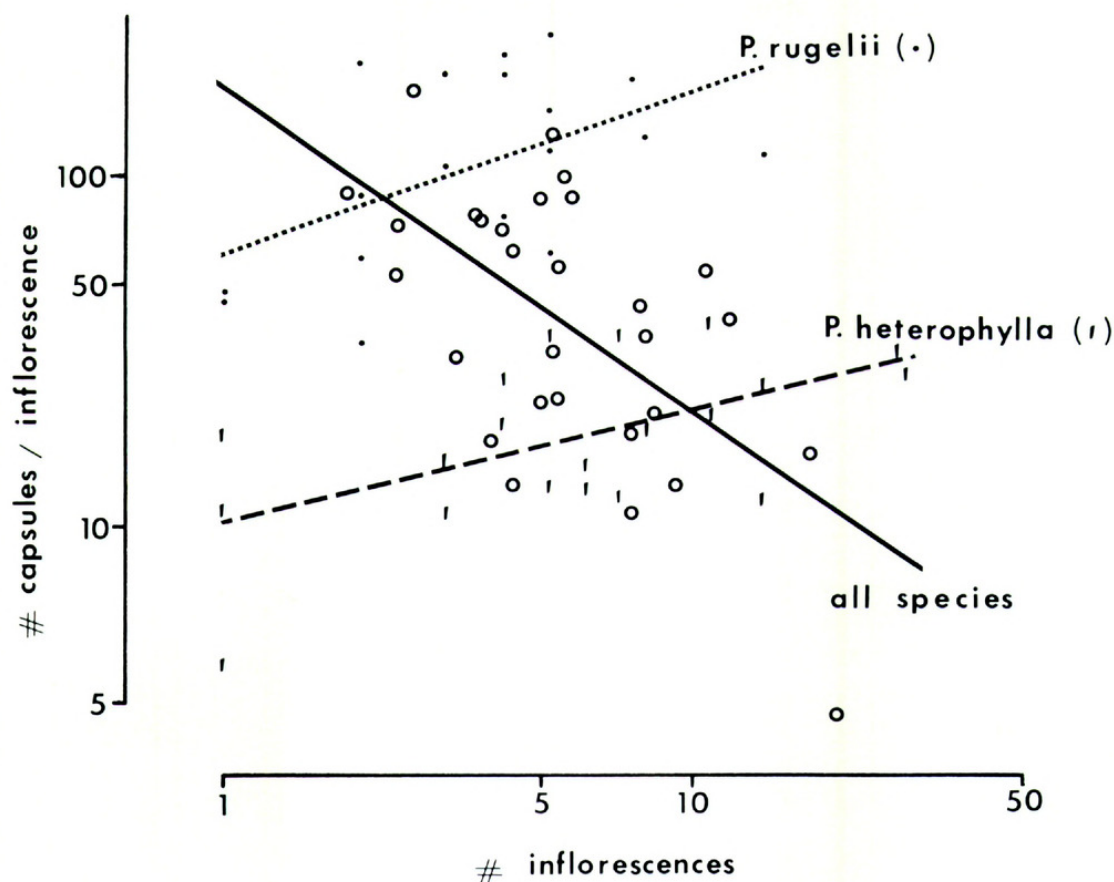


FIGURE 3. Graph showing the between-species correlation for a pair of characters (number of inflorescences and number of capsules per inflorescence) in the genus *Plantago*, and the within-species correlations for two particular species. The between-species correlation was highly significant ($P < .01$). Of the within-species correlations, 27 were positive (11 significantly so, $P < 0.05$) and only 6 were negative (none significantly so). Each within-species correlation and each value for a species mean (circles) is based on approximately twenty well-preserved herbarium specimens from a wide range of localities (data from R. Primack, unpublished).

portant question is not how much variation there is, but how that variation is constrained. The fact that variation is in some sense constrained has been long appreciated in the notion of coadapted gene complexes (Dobzhansky, 1951). The concept has been in large measure philosophical if not simply "felicitous" (Mayr, 1963: 272), being based on observations that crosses between similar phenotypes from different populations may result in hybrid breakdown, that the expression of a gene is dependent on its genetic background, and that different inversion karyotypes become adjusted to each other in experimental populations. It has had little operationality in that it has been impossible to measure or quantify "degree of coadaptation." Recently there has been an increasing interest in quantifying "coadaptation" at the gene level and a search for nonrandom gene association along chromosomes. Taxonomists (Sokal & Sneath, 1963) and palaeontologists (Olson & Miller, 1958) have approached their subjects from a multivariate context, and it seems that defining "coadaptation" at the phenotypic and genotypic level will require that natural selection be looked at from a similar standpoint.

TABLE 7. Effect of different character correlations among fitness components on selection in a finite population. For explanation, see text and Grant (1974).

Correlation Matrix					Generations to Max. Fitness	Number of Extinctions
1	+0.6	0			4.6	1
	1	0				
		1				
1	-0.6	0			15.3	17
	1	0				
		1				
1	-0.2	-0.2			28.1	7
	1	-0.2				
		1				
1	-0.2	-0.2	-0.2	-0.2	16.1	5
	1	0	0	0		
		1	0	0		
			1	0		
				1		

SMALL POPULATION SIZE

Frequently marginal populations are either physically small (peripheral isolates) or show a reduction in density (ecotonal populations). This can have several consequences:

1. Given that selection acts on many characters and that adaptation may be required in many characters simultaneously, there may be a real problem, if the population is small, of obtaining genotypes with the appropriate combination of characters. Grant (1974) developed a stochastic model of selection on a multivariate character. The results showed that in a population of 50 individuals extinctions could readily result if selection demanded new combinations of characters that were themselves negatively correlated (Table 7). Several small negative correlations could have as serious an effect as a few large negative correlations, a rather disheartening conclusion in view of the sample sizes needed to detect small correlations as being statistically significant. (For example a correlation between two traits of 0.2 would require a sample size of the order of 100 to be deemed significant: for the estimation of genetic correlations far larger sizes would be needed.)
2. Gene flow into a peripheral isolate would be largely dependent on its degree of isolation. In an ecotonal population, however, a lower density of marginal individuals would increase the swamping effect of gene flow (this is discussed later).
3. In a population that is small there will be a high probability of mating between relatives and a possibility of severe inbreeding depression effects. In a population subject to strong selection these inbreeding depression effects may be more severe (Latter & Robertson, 1972). This is well illustrated in the work of Ford (1973). In competition experiments between wild type and Bar eye mutant *Drosophila*, he maintained lines where Bar was permitted to interbreed

with wild type, and lines where interbreeding was not permitted. In the interbreeding lines the competitive ability of Bar increased over controls. In the non-interbreeding lines, where the improvement of competitive ability of Bar might have been expected, there was actually a decline. This was interpreted as being due to inbreeding plus strong selection due to competition with the wild type: when the separated wild type and Bar lines were crossed there was an immediate increase in the competitive ability of Bar (see Fig. 4). Precisely why populations should show inbreeding depression for fitness traits is not clear to me and, even given the extended arguments of the 1950's, I feel it has never been satisfactorily explained. Perhaps consideration of genetic variation in natural populations may throw light on this dilemma, since much of the earlier experimental work was agronomically oriented. Above all, inbreeding depression, whatever its precise mechanism (dominance of favored genes, overdominance, "relational balance," or variance in regulatory genes) must have an evolutionary explanation, and it must in some way be related to the forces that mold fitness components.

GENE FLOW

The role of gene flow in natural populations remains an enigma. Several years ago it was considered to be a cohesive force in evolution, and was central to the concept of a species and how speciation occurs. Demonstration that selection could overcome the swamping effect of gene flow opened up the controversy of whether sympatric divergence and sympatric speciation was possible, and, as a corollary, whether it was common. Subsequent emphasis on the limited extent (Ehrlich & Raven, 1969; Levin & Kerster, 1974) and limited effectiveness (Endler, 1973) of gene flow raised an issue very disturbing to taxonomists: why, given the limited extent of gene flow, were species still relatively uniform? It is pertinent therefore to ask what role gene flow plays in limiting natural selection.

It seems to have been underemphasized that gene flow will have drastically different effects depending on whether the genes concerned are effectively neutral, advantageous, or mildly deleterious in the population into which they migrate. If the genes are neutral, their spread, particularly if the population structure is viscous (as in many plants, see Levin & Kerster, 1974), will be very slow. If the genes are advantageous, they will not only spread in the local population but will migrate and spread into other populations. This process can be very effective and very rapid. For example, if we assume that dispersal follows a leptokurtic distribution of the form, $y = x^{-k}$, where x is the distance and k is some constant, it is possible to estimate at what distance from the source the migration rate will be equivalent to the mutation rate. Taking the function $y = x^{-1.5}$, where x is in meters, and a migration rate of 10^{-5} as equivalent to a mutation rate, then we find that even if the population into which the new allele is migrating is over 2 km (2,154.4 m) away, the migration rate will still be greater than the mutation rate. The dispersal function chosen is rather conservative, giving a dispersal of 3% of the source at about 10 m—a figure typical of many grasses. The process of spread of favorable genes across the geographical range of a species

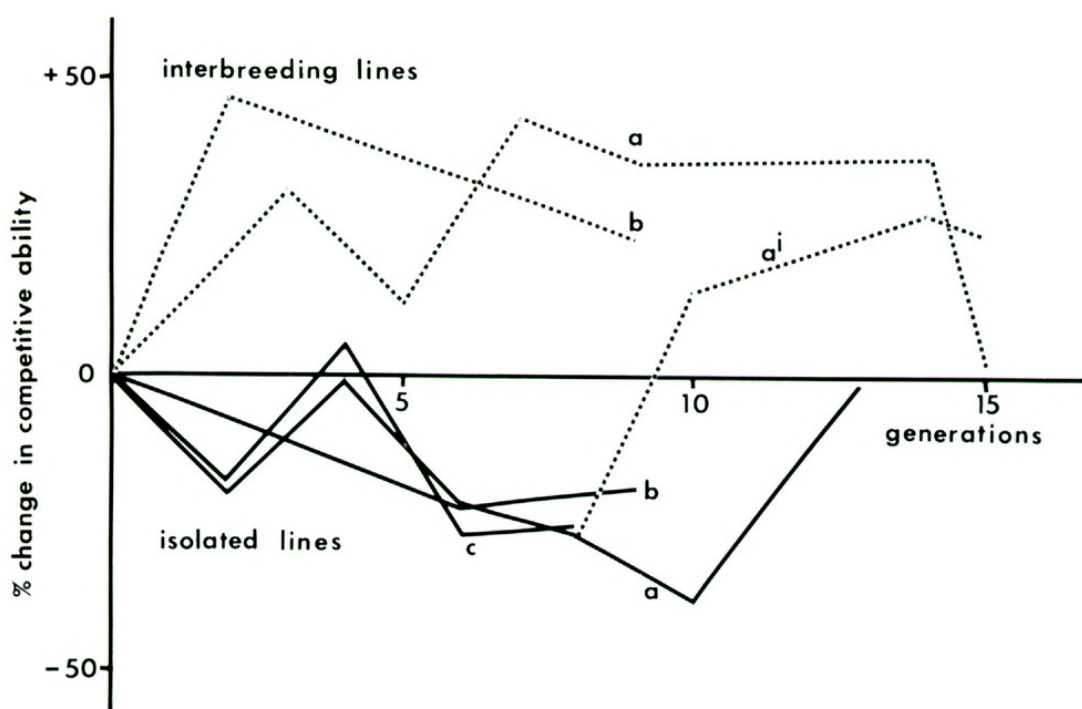


FIGURE 4. Change in competitive ability of Bar strains of *Drosophila melanogaster* tested in competition against control wild type *D. melanogaster*, following experience for a certain number of generations in isolated and interbreeding mixtures with wild type strains. The different lines refer to different experiments. Lines *a* and *c* were started from general laboratory stocks of Bar and wild type. Line *b* was started from a Kaduna strain into which Bar gene had been introduced and maintained polymorphic for 30 generations by J. Endler. In the isolated lines only within-type matings were allowed. In the interbreeding lines random mating was allowed and an equal number of wild type or Bar homozygous female parents was used to continue the next generation: heterozygous Bar parents were discarded. In each generation of both, the isolated lines and interbreeding lines were started using 10 females of each type. In *a*, a rotating mating scheme was used where half the flies from a given replicate were included with another replicate and so on. In *b*, there were four independent replicates. In *c*, there were ten independent replicates. (Data from Ford, 1972.)

has been considered more rigorously by Fisher (1937), Moran (1962) and Cavalli-Sforza et al. (1971: 485). They show that the rate of spread of a favorable gene will be approximated by the equation

$$v = \sigma\sqrt{2s}$$

where v = velocity of a point at which gene frequency has a prescribed value; σ = standard deviation of the dispersal distribution assuming the latter is normal; s = selective advantage of the favored allele. Given a mean dispersal distance of 10 m, a selective advantage of 0.1, we get a velocity of spread equivalent to 4.47 m per generation. It can be seen from the equation that the rate of spread is directly proportional to the dispersal distance. In a population that disperses 50 m on average, the rate of spread will be 20.1 m per generation. These rates of spread are calculated on the basis of a normal dispersal function; with a leptokurtic pattern, they would undoubtedly be greater. Gene flow of favorable genes can therefore occur relatively rapidly, and genes that are beneficial to many

populations of a species will be readily disseminated throughout that species range.

In an ecotonal situation, where population density declines, the levels of gene flow may be very different from that expected from a study of dispersal patterns. One can readily simulate the effects of density on gene flow using a highly iterative computer model. The model assumes the individuals are in a rectangular grid and that the central population has a high density of individuals, whereas the density in the marginal population declines as some function of distance away from the central population. At any point in this grid, one can estimate the amount of pollen received from the central population and the amount from the marginal population, assuming dispersal from each individual follows a particular function describing dispersal from a point source. In the results described here, this function is assumed to be $y = x^{-1.5}$, where y is amount of dispersal and x is distance in meters. This function closely approximates dispersal distances for many wind-dispersed herbaceous plants (for review see Raynor & Ogden, 1965). The ratio of central/total pollen received is a measure of gene flow from the central population into itself or into the marginal population. The results show that gene flow into the marginal population will be very high if the density of the individuals in the marginal population declines rapidly. Given a very rapid decline in density, we can get situations where gene flow actually increases with distance and is greater at the periphery than near the boundary of the central and marginal population (Fig. 5). Applying this model to the populations studied by Grant (1974) we find that, whereas dispersal from the central habitat falls off rapidly into the ecotonal and marginal areas, gene flow is actually greater in the marginal population than in the ecotonal. The swamping effects of gene flow can therefore be very real and substantial (e.g., Antonovics, 1968).

Gene flow might be expected to have interesting interactions with selection for character complexes. If there is selection for multiple traits, then the selection pressures in the marginal habitat are likely to be severe. Given that a substantial fraction of the variants in the marginal population is adapted to the new habitat with regard to many of their traits, this selection is likely to overcome the effects of gene flow. However, it may be that the gene flow prevents adaptation with regard to many traits simultaneously: this idea has frequently been expressed in the idea that gene flow results in "a relentless destruction of suitable new gene complexes" (Mayr, 1963: 524). The result will depend not simply on the intensity of gene flow or on the intensity of selection; it will also depend on the variance-covariance structure of the component characters in the two populations. The impact of gene flow on such complexes is in need of study and documentation in model systems as well as in natural populations.

COEVOLUTIONARY RESISTANCE

A population entering a new habitat will meet new competitors and new predators: adaptation to these will be different from adaptation to abiotic conditions since coevolutionary responses of competitors, predators, and parasites may counteract adaptive responses on the part of the species undergoing range extension. Character displacement has been well known (Brown & Wilson, 1956)

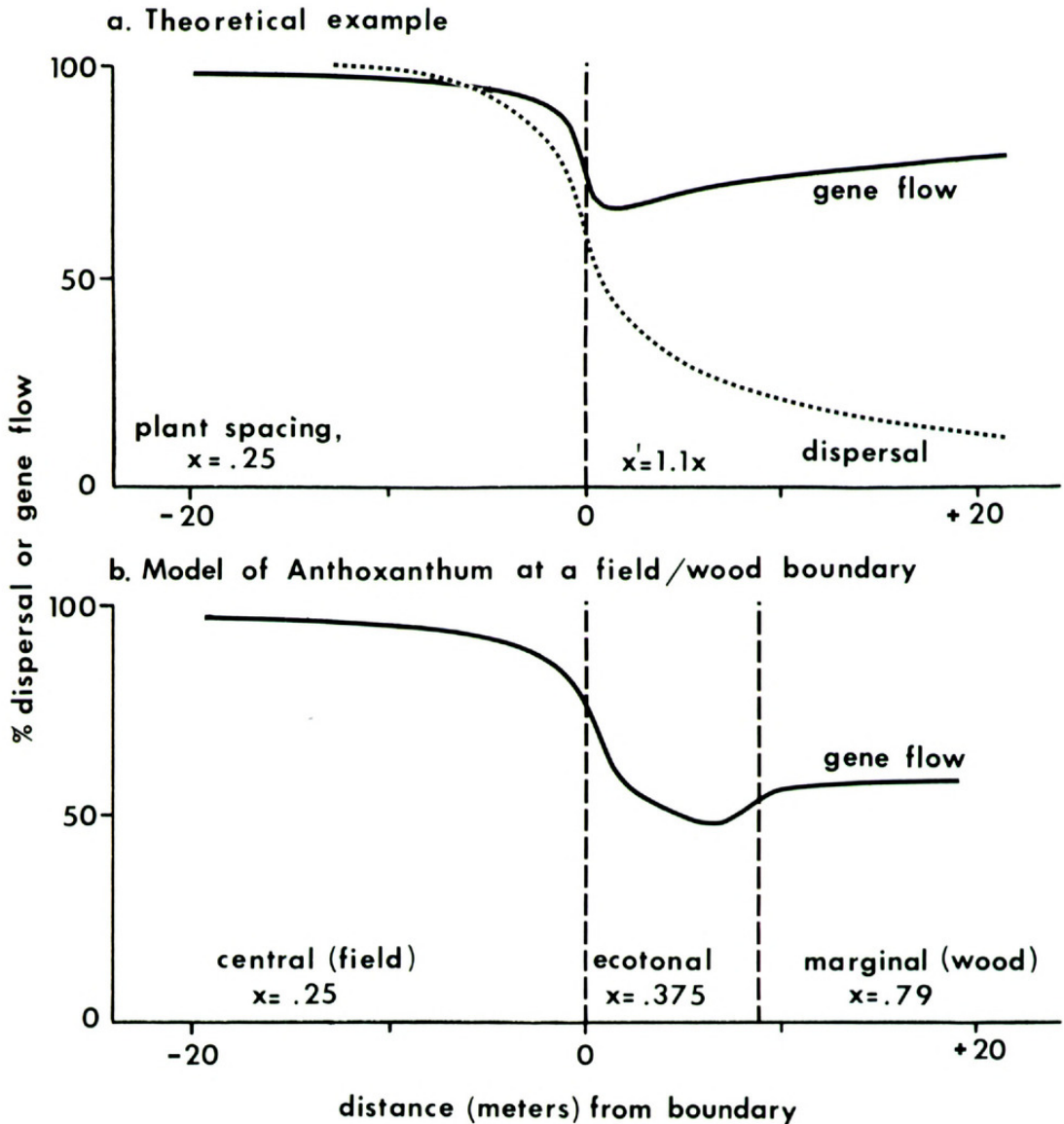


FIGURE 5. Graphs showing the effect of density on gene flow, when population density decreases at increasing distances from a habitat boundary. Data is based on a computer simulation explained in the text. It assumes a point-source dispersal function of $y = x^{-1.5}$ where x is in meters. Plants are assumed to be spaced in a rectangular grid, separated by different distances, x .—a. Theoretical model assuming that on the left-hand side of the boundary, the plants are at a density of $16/\text{m}^2$, and that to the right-hand side their spacing increases (density decreases) by the iterative relation $x' = 1.1x$, i.e., the plant-plant spacing between any two rows or columns is 1.1 times that of the spacing between the previous rows or columns. Dispersal from the central (left-hand) population is measured as the number of propagules, say, pollen arriving at any one point expressed as a percentage of the maximum amount of pollen produced. Gene flow is measured as the amount of pollen from the central population expressed as a percentage of the amount of pollen from the central plus that from the marginal population.—b. Model based on actual data obtained from *Anthoxanthum odoratum* at a field/wood boundary (see Grant, 1974, and text for discussion). The plant-plant spacings (x) closely approximate field observed densities of 15.8, 7.1, and 1.6 plants/ m^2 for the central, ecotonal, and marginal populations. Otherwise the assumptions of the model are as above.

and the subject of much discussion among zoologists: as pointed out by Grant (1972), character displacement may take many forms and is essentially any evolutionary change that results from competitive interactions among species. Nevertheless, it is remarkable that apart from the evolution of *Camelina* in flax fields (quoted in Stebbins, 1950: 123) and instances of reproductive character displacement (Grant, 1966; Levin & Kerster, 1967; McNeilly & Antonovics, 1968) there have been virtually no studies of evolutionary changes in plant-plant competitive relationships. There are probably several reasons for this. Systematists tend to study characters that are relatively invariant with regard to ecology. Adaptive characters in plants are frequently physiological and difficult to study without special techniques. There is also often no way of telling whether minor changes in a character are due to phenotypic or genetic effects: in animals it can often be assumed with a fair degree of confidence that morphometric changes have a genetic basis. And it is not till recently that competition experiments have been refined to the point where they can be used to define population interrelationships in general ways (De Wit, 1960; Khan et al., 1975; Hall, 1974) without recourse to detailed analysis of the mechanistic aspects of competition.

We therefore must turn to experimental evidence with regard to evolutionary response to competition. The results of several recent experimental studies in this area are summarized in Table 8. They show that evolutionary responses to competitors can occur readily, but that the extent and nature of the response is very variable. By inference such changes should occur in natural populations and may be most readily detectable in ecotonal situations where community composition is changing rapidly. Their importance in limiting range extension may be considerable, particularly in view of the frequent observations that species distributions are severely limited by competition. This has long been realized with regard to water-logging (Lieth, 1960), the calcicole-culcifuge problem (Rorison, 1960; Gigon, 1971), salt tolerance (Barbour, 1970) and metal tolerance (Cook et al., 1972). It is therefore all the more surprising that the evolutionary dynamics of these competitive relationships have never been studied.

CONCLUSION

The study of the nature of limits to natural selection has taken impetus from the realization that previous explanations were based on concepts which are erroneous (such as the unifying effect of gene flow) or essentially tautological (such as statements about genetic variance or coadaptation). The comparative ecological genetics of rare and widespread species, or of ecotonal populations, is an area that has been severely neglected creating a serious gap in our evolutionary thinking.

The present paper has indicated several factors which may all act interactively and to different degrees in limiting populations. It has been my intention not to come up with a coherent explanation of selection limits but above all to point to approaches and kinds of information that are needed to approach an understanding of this important evolutionary enigma. Many of the advances will occur

TABLE 8. Summary of a number of studies on selection for competitive ability in experimental populations (after Chen, 1973).

Author	Species	No. of Generations or Time	Evidence For			Changes in Associated Characters
			Genetic Changes in Competitive Ability	In-creased Niche Diver-gence	In-creased Yield of Mixtures	
Moore (1952)	<i>Drosophila simulans</i> & <i>D. melanogaster</i>	500 days	Good evidence	— ^a	—	—
Lewontin (1955)	<i>D. melanogaster</i>		Good evidence	—	Yes	—
Chen (1973)	<i>D. melanogaster</i>	1	Good evidence	Yes	Yes	—
Seaton & Antonovics (1967)	<i>D. melanogaster</i>	4	Good evidence	Yes	Yes	Yes
Futuyma (1970)	<i>D. melanogaster</i>	10	Some lines increased others decreased	—	—	—
Bryant & Turner (1972)	<i>Musca domestica</i>	5	Good evidence	Yes	Yes	Yes
Ayala (1969)	<i>D. serrata</i> & <i>D. nebulosa</i>	31 weeks	Good evidence	Yes	—	—
Ford (1972)	<i>D. melanogaster</i>	15	Often negative	Slight	No	Yes

^a Means no evidence obtained.

through an increasingly demographic view of fitness and adaptation, a multivariate view of selection and adaptation, an appreciation of the nature of gene flow and inbreeding depression, and through a study of coevolutionary phenomena.

The elegance of one locus deterministic models seems to have constrained our thinking, not simply with regard to variation at the gene level, but also with regard to selection at the character level. There are, for example, no *a priori* criteria for determining how selection on different characters acts with regard to fitness, and similar problems exist in modelling multi-locus systems. It seems trite but it is unfortunately necessary to say that we need to understand selection before we can understand variation.

Since this is a symposium primarily for plant systematists, it is appropriate to end by pointing out that they have a very important role to play in backgrounding the studies outlined here. We are largely dependent on systematists for identifying rare species, identifying species ranges, and for establishing their historical status plus evolutionary affinities. We are largely dependent on systematists for accurate herbarium records and location of field sites. We are largely dependent on systematists for information on basic ecology and biology of the species concerned and their cohabitants. I hope this paper has served the dual function of perhaps interesting the systematist in that frightening, highly mathematical subject

of population genetics and the population geneticist in that highly specialized, "someone's-got-to-do-it" subject of plant systematics. Both disciplines may be less dull as a result of such interaction.

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