Frequency-Dependent Selection and Competition: Empirical Approaches

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Frequency-dependent selection and competition: empirical approaches

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When Darwin and Wallace first formulated the theory of evolution by natural selection, they were greatly influenced by the idea that populations tend to increase geometrically and rapidly outgrow the resources available to them. They argued that the ensuing competition among individuals would be a major agent of natural selection. Since their day, competition has become almost synonymous with the idea of natural selection or survival of the fittest. In this paper we examine the relation between competition and selection by using simple competition models, consider the interaction of density and frequency in determining competitive outcome, and review the literature on frequency-dependent competitive interactions among genotypes within populations.

INTRODUCTION

In the plant literature, the most generally accepted model of competitive interactions is that developed by De Wit (1960). Although based on simple theoretical assumptions of species competing for a simplified resource termed 'space', the model has proved to be applicable to many studies in which two species (or genotypes) are grown at a range of frequencies, but at a fixed density (Harper 1977). We can therefore treat the De Wit formulations as summarizing much of the empirically derived data on competition. In two-component (i.e. two-species or two-genotype) mixtures the outcome of competition can be described by

$$O_1 = z_1 P_1/(z_1 + z_2/k_{12}) \qquad (1)$$

and

$$O_2 = z_2 P_2/(z_1/k_{21} + z_2), \qquad (2)$$

where O is the output yield, P is the pure stand yield, z is the frequency of the component and k is the crowding coefficient, with the subscripts referring to each of the two components in the mixture. If the two components compete for space such that any gain in space by one component results in a corresponding loss of space by the other, then

$$k_{12} \cdot k_{21}, = 1. \qquad (3)$$

Under these conditions, we can now calculate the relative fitness of the two components (or De Wit's measure of relative reproductive rate) as

$$(O_1/z_1)/(O_2/z_2) = k_{12} \cdot (P_1/P_2). \qquad (4)$$

The result is a constant which is a compound of the relative performance of the two components in pure stand (i.e. relative fitness without competition), and their relative ability to crowd for space. Natural selection under this mode of competition is not frequency dependent, and we can predict that the component with the highest relative fitness will displace

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the other. This is clearly what Darwin (1858, p. 92) had in mind when he wrote 'for instance, if several varieties of wheat be sown together, and the mixed seed be resown, some of the varieties which best suit the soil or climate, or are naturally the most fertile, will beat the others and so yield more seed, and will consequently in a few years supplant the other varieties.'

However, rather different, frequency-dependent results are obtained if the two components do not compete for the same space. If they mutually inhibit each other such that the level of resources available to the mixture is less than when each is presently singly, then

$$k_{12} \cdot k_{21} < 1 \tag{5}$$

and the outcome is positively frequency dependent, i.e. fitness increases with an increasing frequency in the mixture. However, if the two components use resources that are to any degree different, then

$$k_{12} \cdot k_{21} > 1, \tag{6}$$

and the outcome is negatively frequency dependent, i.e. fitness decreases with an increasing frequency in the mixture. This kind of relation will have the effect of stabilizing the mixture, producing intermediate equilibrium frequencies of the two components. The finding that negative frequency-dependence results from differing resource use is well known and quite general for nearly all classes of competition models, whether they describe competition processes by competition coefficients (Lotka 1956; Schutz *et al.* 1968; Cockerham & Burrows 1971) or use models based on explicit formulations of resource use (Levin & Stewart 1973; Tilman 1972).

Although these models predict frequency dependence, they do not necessarily predict a stable coexistence of the two components. This depends on the performances in pure stands, and on how the frequency dependence varies with population density. Moreover, because the De Wit (1960) model assumes that the total density of the mixture remains constant, it is useful when the sowing density is reset to the same value in each generation (as in many agricultural crops), but does not apply to natural populations where the density may change over successive generations (Inouye & Schaffer 1981).

We should also mention the semantic distinction that is sometimes made between frequency-dependent selection and frequency-dependent competition (De Benedictis 1977). The former implies that the relative fitness of two components varies with their frequency, whereas the latter implies that the effect per head of one component on the absolute fitness of the other varies with frequency. In the latter case the absolute fitness of the target species varies as a linear function of the frequency of the competitor (i.e. the partial derivative of the competition function is a constant). The term 'frequency dependence' has also been used in situations where the absolute fitness of the target species is a linear function of its frequency (Khalifa & Qualset 1974; Early & Qualset 1971; Phung & Rathjen 1977); however, this is to be expected in any situation where the two components differ in their competitive performance, even if they do so reciprocally (i.e. even if they share the same resources such that $k_{12} \cdot k_{21} = 1$, but $k_{12} \neq k_{21}$). Decreasing the frequency of the stronger competitor will result in an increased absolute yield of that competitor, because now it will be surrounded by a greater number of weaker competitors. Therefore, it is important to distinguish clearly between frequency-dependent selection, frequency dependence of the competitive effect and the effect of frequency on absolute fitness. These distinctions are now always made when the term 'frequency dependence' is used.

The above formulation of the De Wit (1960) model could apply to two non-interbreeding species or to two allelic variants in a haploid population. The extension of the model to interbreeding diploid genotypes is relatively straightforward (Antonovics 1978), and for the one locus, two allele case, the following recursion equations describing fitnesses of the genotypes can be obtained:

$$O_1 = z_1 P_1/(z_1 + z_2/k_{12} + z_3/k_{13}), \tag{7}$$

$$O_2 = z_2 P_2/(z_1/k_{21} + z_2 + z_3/k_{23}) \tag{8}$$

and

$$O_3 = z_3 P_3/(z_1/k_{31} + z_2/k_{32} + z_3), \tag{9}$$

where the symbols are as before, but subscripted with regard to three components. The results of these models are interesting in two ways (Antonovics 1978). First, the competitive outcomes and equilibrium conditions are not highly dependent on the breeding system when competitive coefficients are determined by single loci with additive effects: interbreeding probably only makes a large difference when there is overdominance in competitive performance or when many loci determine the competitive outcome. Second, if the two homozygotes use somewhat different resources, but the heterozygote is intermediate, then there can be (depending on yields in pure stands, and on the values of the competition coefficients) a reduced overall fitness of the heterozygote and a net deficiency of heterozygotes over Hardy–Weinberg expectation (Antonovics 1978). Other models that have considered interbreeding genotypes have obtained a similar result (Christiansen & Loeschcke 1980; Wilson & Turelli 1986; Asmussen 1983). The implication of this result is that it opens up the possibility of selection for loci that increase the amount of assortative mating within such mixtures, and hence the development of reproductive isolation without any physical separation of either the component genotypes or of the resources (Udovic 1980). The possibility of such an extreme form of sympatric speciation was raised nearly 40 years ago (Ludwig 1950) and has recently been explored in relation to an explicit resource-use model by Seger (1985).

A major and frequently noted difficulty with the De Wit formulation is that it only considers the outcome of competition when the mixture is held at a constant density (Inouye & Schaffer 1981). Similarly, the demonstration of negative frequency dependence, although it may predict the coexistence of two components in a mixture at a particular density, may not do so when the population is allowed to vary both in frequency and density (Nunney 1983). In a natural population, frequency and density will vary simultaneously, and the stability properties of mixtures will be functions of both. To understand these properties it is essential to develop models and experiments where the fitness of a component in a mixture is measured as a function of the absolute numbers of the two components, rather than just their relative frequencies.

There are two difficulties in doing this. The first is purely empirical and relates to the fact that to study a wide range of densities and frequencies requires, by definition, a large number of treatments, and hence a very large experiment. Second, although certain models such as that put forward by De Wit have proved empirically useful in experiments where only frequency is varied (replacement series experiments), no such generally acceptable model is available for the case where density and frequency vary simultaneously. Such models will have the general form

$$N_1(t+1) = \lambda_1 N_1(t) \cdot F(N_1(t) \cdot N_2(t)) \tag{10}$$

and

$$N_2(t+1) = \lambda_2 N_2(t) \cdot F(N_1(t) \cdot N_2(t)), \tag{11}$$

where F are general competition functions, λ represents the numbers of progeny (seeds) produced per single individual in the absence of any inter- or intraspecific competition, N is the number of individuals at time (t) or $(t+1)$, and subscripts represent the two components.

To overcome some of the experimental difficulties involved in replicating a large number of frequencies and densities, we have explored the use of 'hexagonal fan designs' (Antonovics & Fowler 1985) in competition experiments between *Linum grandiflorum* and *Salvia splendens*. In these designs relative frequency is varied along the arcs of the fan design, so that each individual is surrounded in turn by 0–6 neighbours of its own type, and correspondingly 6–0 neighbours of the alternate type (see Boffey & Veevers (1977) for a description of these lattice designs). Density is varied along the radii of the fan by increasing the spacing by a constant multiplier. In one fan we thereby achieved a combination of seven frequencies and thirteen densities. These combinations of treatments presuppose that all the plant–plant interactions are based on nearest-neighbour effects. By running control experiments at particular frequencies or particular densities, we found that although there was evidence for effects beyond those of the immediate neighbours, the magnitude of these effects was small and did not invalidate the qualitative pattern of results. These results showed an interaction of frequency and density in their effects on the fitness of *Salvia* and *Linum*, confirming that studies of frequency-dependent behaviour at one density would give an inadequate description of the two-component dynamics of the system (Antonovics & Fowler 1985). To investigate these dynamics, we have employed a number of functions to describe interspecific competition (see table 1). Functions 1–3 are exponential polynomials of increasing degree, and are related to the Ricker formula that has proved successful in models of fish populations (Ricker 1954; Levin & Goodyear 1980) and insect populations (Hassell & Comins 1976; Bellows & Hassell 1984). Function 4 is based on the reciprocal yield law for intraspecific density effects. Functions 5 and 6 have been recently advocated as providing good fit to data derived from nearest-neighbour studies in random mixtures (Pecala & Silander 1987) or from experiments where species have been

Table 1. Two species competition: functions fitted to experimental data and used for the prediction of dynamical outcomes

Model 1. Ricker
$F_S = \exp(a_1 S + a_2 L)$
$F_L = \exp(b_1 S + b_2 L)$
Model 2. 2nd order Ricker
$F_S = \exp(a_1 S + a_2 L + a_3 S^2 + a_4 L^2 + a_5 SL)$
$F_L = \exp(b_1 S + b_2 L + b_3 S^2 + b_4 L^2 + b_5 SL)$
Model 3. 3rd order Ricker
$F_S = \exp(\text{`as above'} + a_6 S^3 + a_7 L^3 + a_8 SL^2 + a_9 S^2 L)$
$F_L = \exp(\text{`as above'} + b_b S^3 + b_7 L^3 + b_8 SL^2 + b_9 S^2 L)$
Model 4. Thinning law
$F_S = [1 + a_1(S + a_2 L)^a]^{-1}$
$F_L = [1 + b_1(L + b_2 S)^b]^{-1}$
Model 5. Law & Watkinson
$F_S = [1 + S^a + L^a]^{-1}$
$F_L = [1 + S^b + L^b]^{-1}$
Model 6. Pacala
$F_S = [1 + a_1 S + a_2 L + a_3 SL]^{-1}$
$F_L = [1 + b_1 S + b_2 L + b_3 SL]^{-1}$

grown under a range of densities and frequencies as separate combinations of treatments (Law & Watkinson 1987). The functions were chosen because of their potential 'curve fitting properties', and they do not explicitly derive from mechanisms of competitive interactions among plants. We estimated the seed production of *Salvia* by using a regression of flower number of the mass of floral parts, and making the assumption that this labiate plant produces four seeds per flower. For *Linum* we counted the numbers of flowers, and assumed there were ten seeds per capsule. The dependent variable was then calculated as the number of seeds produced per seed sown (absolute fitness). A log transformation allowed a fit to a multiple linear regression for competition functions 1–3; nonlinear regressions were fitted to the other models by using a Levenberg–Marquardt gradient search algorithm.

In most cases the models explained a large proportion of the variance in the data, except for function 6, and perhaps function 5. Although all the other models gave excellent fits and were relatively indistinguishable in the proportion of variance explained, they generated remarkably different zero growth isoclines and correspondingly gave contrasting predictions about the outcomes of competition (figure 1 and table 2). The outcomes also depended on whether we used log transformed or untransformed data (figure 2).

Although we are continuing to explore the exact reasons for the highly diverse predictions, we can already conclude from these data that no clear consensus can yet be reached about which competition function best describes empirical data. For instance, our data clearly did not

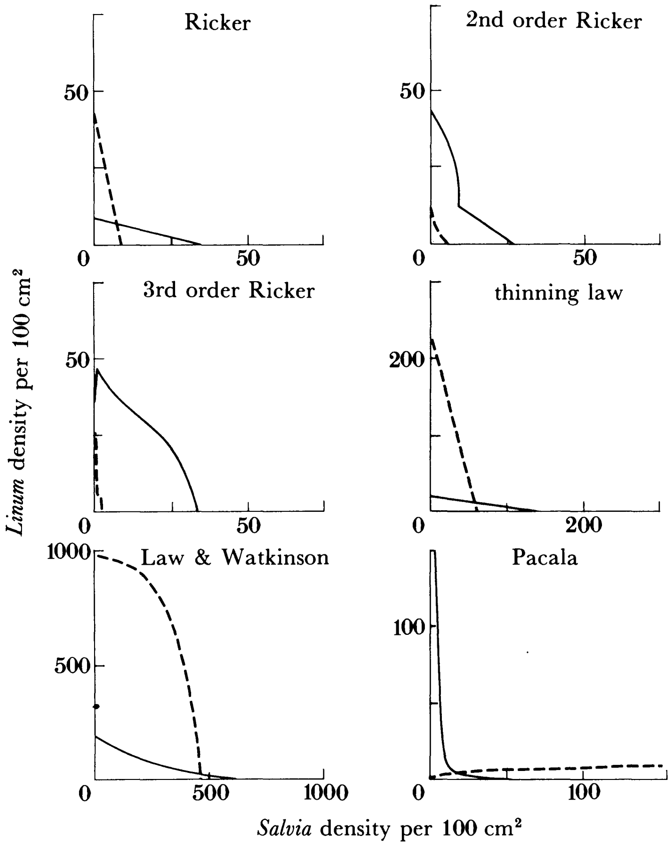

FIGURE 1. Zero-growth isoclines associated with the models, described in table 1, that best fit the log-transformed data. Broken and solid lines indicate zero growth for *Salvia* and *Linum* respectively.

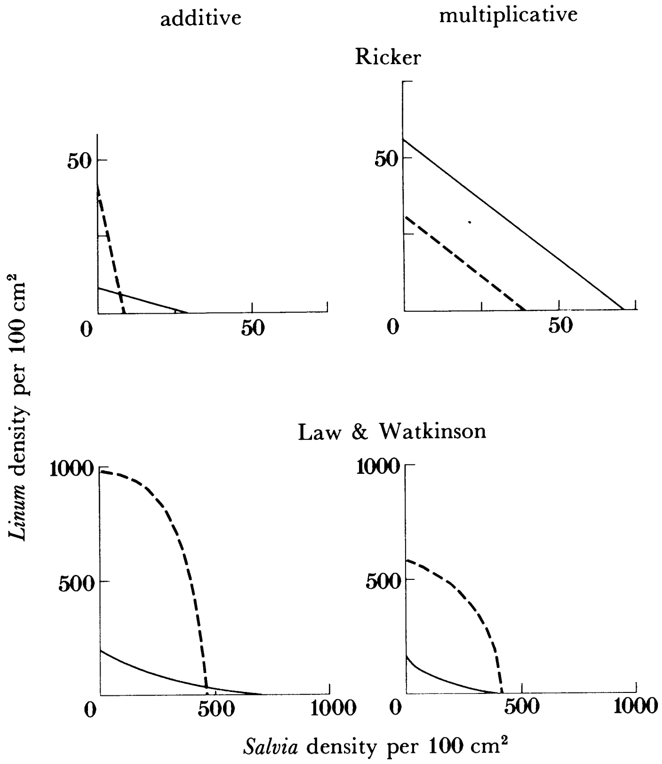

FIGURE 2. Zero-growth isoclines for two models fitted with and without log-transformations. Broken and solid lines indicate zero growth for *Salvia* and *Linum* respectively.

TABLE 2. SUMMARY OF THE REGRESSION ANALYSES AND INTERPRETATIONS OF THE DYNAMICAL OUTCOMES BASED ON ISOCLINES

(The decimal numbers are the r^2 values for the models, averaged over values for *Salvia* and *Linum*. Associated with each model is the predicted outcome of competition, the winning species being designated when one replaces the other. ('Nonsense' indicates that one of the species is predicted to grow to infinity, an impossible outcome.))

	Ricker	2nd order Ricker	3rd order Ricker	Thinning	Law & Watkinson	Pacala
Additive error	coexistence 0.73	*Linum* 0.82	*Linum* 0.76	coexistence 0.86	coexistence 0.36	nonsense 0.14
Multiplicative error	*Linum* 0.71	*Salvia* 0.86	*Linum* 0.89	coexistence 0.96	*Salvia* 0.61	coexistence 0.46

fit models that Law & Watkinson (1987) found satisfactory for two sanddune plants. Nor did our data fit the functional forms that Pacala & Silander (1987) have used to develop a sophisticated theory of population regulation based on neighbour interactions. And even when we consider just our own experiment, it is not clear whether further experiments need to be done around the regions of the isoclines, so that they can be defined more explicitly. To reach some generalizations about how the dynamics of two components can be predicted, it will be necessary to do many more detailed experimental analyses of particular cases. Such experiments, we suspect, would have to be two-stage endeavours, the first being to identify the general positions of the isoclines, and the second stage being to do more detailed experiments around these critical densities and frequencies. Given the potential for a wide diversity of mechanisms for interspecific (and perhaps intergenotypic) interactions, completely general models may not be forthcoming.

All the competition functions that we have used imply frequency dependence in the relative performance of *Linum* and *Salvia*, when considered on an arithmetic scale. On a logarithmic scale, competition function 1 does not admit the possibility of frequency-dependence, whereas functions 2 and 3 imply frequency dependence if there are significant non-zero coefficients associated with the interaction terms. Whether or not functions 4 or 5 imply frequency dependence on a log scale is best judged by plotting the curves for particular suites of coefficients. When we use our best-fit coefficients, these functions suggest marked frequency dependence for the *Salvia–Linum* interaction.

One does not, however, need a model to detect frequency dependence; straightforward plots of a species' fitness as a function of its frequency and density are illuminating. Both *Salvia* and *Linum* show dramatic variation in both absolute and relative fitness as their frequencies change at any fixed density but the effects of frequency tend to be less at high densities (figure 3). For reasons we do not understand, our data from the *Salvia* and *Linum* competition experiments revealed a consistent trend for the lowest fitnesses to occur at intermediate frequencies; this result requires further examination.

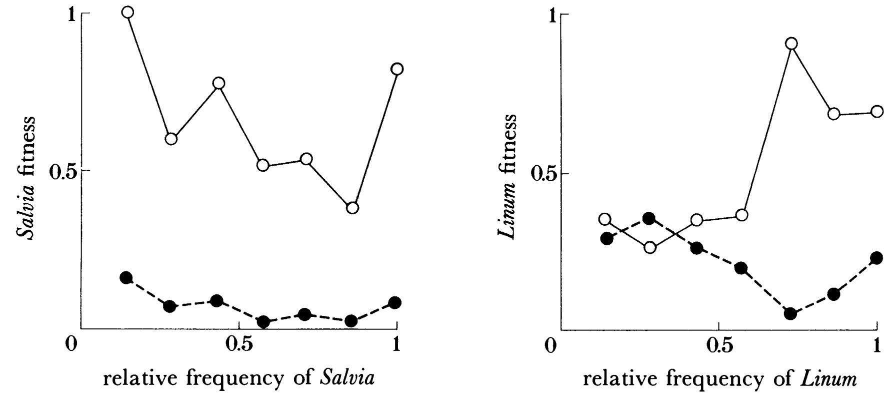

FIGURE 3. Relation between the seed numbers (fitnesses) of *Salvia* and *Linum* and their frequency in the mixture, at low (1.5 per 100 cm^2) and high 25.2 per 100 cm^2) density. Each value is based on four replicates, and fitnesses are scaled to maximum seed output. Open circles, low density; filled circles, high density.

As far as we know, there have been no studies that have investigated the frequency–density-response surfaces for different genotypes sampled from the same population. It seems unlikely that for genotypes the patterns would be so extreme. In this study we deliberately chose *Linum* and *Salvia*, not only because of their short life-cycles, but also because of their contrasting morphologies. *Salvia* is a spreading plant with large leaves, whereas *Linum* is tall, terminally branched with small narrow leaves. Differences among genotypes within populations are likely to be much subtler than this. Although such ornate experiments have not been done with genotypes, a substantial number of studies have directly or indirectly examined frequency-dependent interactions among genotypes within the same species. In the next section we review this work.

FREQUENCY-DEPENDENT INTERACTIONS AMONG GENOTYPES

The demonstration of frequency-dependent interactions among genotypes sampled from within a species is difficult for two reasons. First, it is necessary to obtain replicates of particular genotypes. Where the genotypes represent polymorphisms at single loci, appropriate crossing schemes can be used to isolate the requisite genotypes. However, where the genotypes represent individuals whose competitive interactions are determined as quantitative traits, then individuals can either be cloned, or one has to resort to the use of inbred lines or contrasting sub-populations. One could look for effects among the progeny from particular crosses by using the approaches of standard quantitative genetics, but this appears not to have been done. Second, it is obviously necessary to do experiments at a range of frequencies. However, when many genotypes are to be examined with regard to their mutual interactions, this creates an enormous number of treatments. Several workers have therefore resorted to the demonstration of 'overyielding', as an indirect test of resource partitioning and hence of negative frequency dependence (see, for example, Allard & Adams 1969).

TABLE 3. SUMMARY OF DEMONSTRATIONS OF FREQUENCY-DEPENDENT SELECTION IN EXPERIMENTAL STUDIES WITH SPECIES OF *DROSOPHILA*

Character	References
	Drosophila melanogaster
white vs wild-type	Lewontin (1955)
sepia vs wild-type	Anxolabéhère (1971)
chromosome IV variants	Bungaard & Christiansen (1972)
coevolved lines, *dumpy vs* wild-type	Seaton & Antonovics (1967); Antonovics (1978)
chromosome inversions	Tobari & Kojima (1967); Kojima & Tobari (1969)
chromosome inversions	Nassar *et al.* (1973)
esterase-6 alleles	Kojima & Huang (1972); Huang *et al.* (1971); Yarborough & Kojima (1967); Morgan (1976)
alcohol dehydrogenase alleles	Kojima & Tobari (1969); Downes & Thoday (1983); Morgan (1976)
leucine aminopeptidase alleles	Nassar (1979)
phosphoglucomutase alleles	Snyder & Ayala (1979); Carfagua *et al.* (1980)
	Drosophila pseudoobscura
overyielding of variable *vs* uniform populations	Tosic & Ayala (1980)
overyielding in chromosomally uniform *vs* variable populations	Dobzhansky & Pavlovsky (1961); Beardmore (1963)
malate dehydrogenase alleles	Tosic & Ayala (1981)
	Drosophila buskii
mixtures of various mutants	Lewontin & Matsuo (1963)

Perhaps for these reasons the majority of studies on frequency-dependent selection have been done by using species of *Drosophila* (table 3). The studies are impressive in demonstrating the action of frequency-dependent selection on a wide range of traits, from chromosome inversions to specific laboratory mutants, and to a number of naturally occurring electrophoretic variants. These interactions appear to be best explained by competitive processes. Negative results have sometimes been reported (Barnes 1983; Dolan & Robertson 1975), but unfortunately it is not at all clear whether frequency-dependent selection as a result of competition is as commonplace as suggested by the studies mentioned above, or whether negative results simply fail to be reported. Frequency-dependent selection has also been detected in *Tribolium* (Sokal & Huber

1963; Sokal & Karten 1964), houseflies and blowflies (Bhalla & Sokal 1964; Taylor & Sokal 1973; McKenzie *et al.* 1986), and *E. coli* (Smouse & Kosuda 1977; Kosuda 1981). Again there are only a few reports of negative results (Brookfield 1981).

In plants, the majority of studies on frequency-dependent selection have been done by using mixtures of lines of crop plants. Such studies have usually asked the question whether mixtures outyield the average of the two pure stands, or of the best pure stand; these are questions of obvious interest to the agronomist. The inference of frequency dependence is therefore necessarily indirect. Evidence for 'overyielding' of mixtures has not been readily forthcoming (Shorter & Frey 1979; Khalifa & Qualset 1974; Early & Qualset 1971) or where it has been observed it has been clearly due to large differences in the growth forms and maturity times of the varieties chosen for study (e.g. flax *vs* linseed; Khan *et al.* 1975). The clearest evidence for overyielding has been obtained using inbred lines extracted from mixtures maintained for a large number of generations (Allard & Adams 1969; Adams & Allard 1969). Lines showed evidence of overyielding up to 30%, whereas among mixtures of randomly chosen varieties overyielding was much less. This suggested that variation among lines was being maintained by frequency-dependent selection. Shorter & Frey (1979) also found greater overyielding (up to 17%) among lines taken from a composite cross mixture of oats than among regular varietal mixtures, but the effects were weaker than those found by Allard and Adams. Other studies have demonstrated frequency-dependent effects by growing mixtures over a wide range of frequencies. Thus Phung & Rathjen (1976) and Harding *et al.* (1966) showed a frequency-dependent advantage of hybrid forms when they were grown in mixtures with the parental lines: often the advantages were considerably more pronounced at very low frequencies. Other studies (including those of Phung & Rathjen (1976) and Khalifa & Qualset (1974)) show that the absolute yield of lines sown into a background variety at a range of frequencies varies with the frequency. However, this can be ascribed to changes in the frequencies of components differing in their competitive abilities, and does not necessarily imply frequency-dependence of the relative yields (i.e. frequency-dependent selection).

Evidence from natural populations is extremely scant. Putwain & Harper (1972) showed frequency-dependent competition among the two sexes of *Rumex acetosella*, suggesting they differed in their resource use or phenology. Otherwise very few studies have been done using genotypes derived from natural populations, either in experimental gardens or, more critically, in the field. We did such experiments by using clonally sampled replicates of *Anthoxanthum odoratum*, growing in a long-established mown field as part of a long-term study on the adaptive significance of sexual reproduction (Antonovics & Ellstrand 1984). The results showed large and consistent frequency-dependent effects, with the minority components having substantial advantages in fitness, ranging from 1:0.66 to 1:0.46 depending on the experiment. Seedlings surrounded by genetically unrelated individuals performed better than seedlings surrounded by their siblings (Schmitt & Antonovics 1986). However, there was very little evidence that the individuals in these experiments were interacting competitively; very few density effects could be detected at the spacings used in the designs. We therefore interpreted our results as being more likely to be due to the effects of pathogens than to competition. Experiments done with arrays of genetically uniform *vs* genetically variable progeny did not show an advantage to variable arrays at higher density, suggesting that resource partitioning among genotypes was not important (Antonovics & Ellstrand 1985).

CONCLUSIONS

Models of competition that incorporate non-reciprocal resource utilization predict frequency-dependent selection. When components use alternative resources, frequency-dependent selection will be in the direction of preserving both components in the mixture, although the actual outcome will also depend on the performance in a pure stand as well as on the shape of the two-species response surface (i.e. density and frequency). The study of frequency-dependent selection resulting from competition among individuals in experimental and natural populations is difficult because the experiments need to be done over a range of frequencies and densities, something that entails large experiments and extensive replication of individual genotypes. The latter may only be possible in organisms that are genetically tractable or that can be clonally replicated. The use of hexagonal fan designs, followed by more precise experiments centred on the equilibrium regions, provides a useful approach that minimizes the size of experiments. The extension of experimental approaches to natural populations is a major challenge. Natural populations are spatially substructured, such that the effects of frequency and density may be highly localized in space and time, especially in plants. Such substructuring may drastically affect theoretical predictions. This has been forcefully argued by Price & Waser (1982) and again in this symposium, where it has been pointed out that positive (destabilizing) frequency-dependent selection, if it occurs in different directions in different habitats or in association with different genotypes, may generate a 'biotic' multiple-niche that actually preserves a polymorphism globally. Moreover in nature, genotypes will not only interact intraspecifically, but will interact with genetically diverse heterospecifics. Heterospecific genotype–genotype interactions can be very diverse in natural populations (Clay & Kelley 1987) and we are a long way from understanding how intra- and interspecific frequency dependence combine to generate patterns of diversity in species and genotypes. There is a serious need for empirical information about genetic variation in competitive performance at a community level.

The interest in frequency-dependent selection mediated by competition has, to a large extent, arisen out of the idea that it (with other forms of frequency-dependence), may be an important force in maintaining genetic polymorphisms. The pervasive evidence for frequency-dependent effects in experimental populations of *Drosophila*, argues very strongly in favour of this idea. Two ingredients make the evidence less convincing. First, the demonstration of frequency-dependence may be necessary, but it is not a sufficient condition for stability: we need to know the precise density-frequency dynamics to predict a stable polymorphism. Second, there is very little evidence from natural populations. Our evidence for strong frequency-dependent effects in *Anthoxanthum* supports the ideas that these effects are mediated not through resource partitioning but by pathogens. Nevertheless, the effects themselves are strong enough to provide a force to explain the maintenance of sexual reproduction in natural populations. Clearly, many more empirical data are needed, even those of the simplest kind. Indeed, if the level of frequency-dependence that we have found is quite general, it should be detectable by quite simple field experiments. The dissection of these effects into causes due to predators, pathogens or competition will require more sophisticated experiments, and perhaps only once this is achieved will the kind of ornate hexagonal fan designs described here be necessary to understand the dynamics of particular phenotypic and genotypic classes.

Finally, it is by no means clear whether frequency-dependent effects mediated by the use of alternative resources can ever be a basis for speciation. Certainly one might expect the evolution of some assortative mating (Udovic 1980), but whether this would proceed to substantial reproductive isolation is not clear. If the use of alternative resources depends on developing complex traits, then this may provide a continuing force for further isolation. It would be very interesting to have some formal theories relevant to these points.

Frequency-dependent selection is almost by definition a dynamic process: the effects of selection depend on the composition of the population, not on the 'intrinsic' properties of particular genotypes grown in isolation. It is therefore difficult to study and to characterize. Nevertheless, there is abundant evidence that it occurs as a result of competition. Although the experiments that have been used to study it are more sophisticated than those needed to establish fixed fitness difference, they have still been limited in the range of densities and frequencies used, they have been rarely done in the context of the natural environment, and their interpretation has been too often based on a theory that is convenient rather than proven in its assumptions. The subject remains a rich area for future investigation.

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