16 The population genetics of mixtures

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Models of competition among species are extended to competition among interbreeding genotypes. Such models show that competitive interactions can maintain genetic polymorphism, that such mixtures may outyield single genotype populations and that equilibrium frequencies are relatively unaffected by the breeding system. Selection for overcompensatory effects among component genotypes should be most effective in highly self-fertilized (or vegetatively propagating) species since new lines with overcompensatory effects are readily preserved, yet are being continuously generated by segregation. The competitive relationships of two species will not be permanent: theoretical studies invariably predict that they will diverge in resource requirements. However, experimental studies indicate that selection for competitive relationships may produce very variable results since competitive ability is a complex trait, and an important fitness component that may be sensitive to inbreeding and have low additive genetic variance. Genetic polymorphism will also be maintained in a heterogeneous environment, but mixtures of genotypes will outyield pure stands in heterogeneous environments only if there is some habitat selection or if competition within the mixture improves adaptation to each microenvironment. There is a great need for empirical data that will document these processes in agronomic and natural populations and establish their practical significance.

Population genetics pertains to mixtures of genotypes. These mixtures have been extensively characterized in terms of their breeding systems, their population size and the selective values of the components. The theoretical paradigms of population genetics, on which development of the science has largely rested, have for obvious reasons of tractability laid emphasis on constant selective values. Yet such values are clearly not constant in nature, but vary with the frequency of the component genotypes (frequency dependent selection), the density of the population as a whole (density dependent selection) and the density and frequency of the population relative to that of other competitors or predators. Wallace (1975) expressed this idea forcefully when he stated that whereas a constant selective value 'is the mathematical geneticists' dream . . . it is the ecologists' nightmare'. The study of populations when their members are in competition with each other and with other species implies, as we shall see, selective values which may vary with density and frequency, and the study of mixtures of genotypes — from the standpoint of competitive interactions — has been a neglected area of population genetics. Only recently have models been developed that allow for consideration of these complex processes; consequently experimental studies have been few, and studies of natural and semi-natural populations have been almost non-existent.

Here I will firstly consider some basic models of competition and their extension to interbreeding populations. I then consider the degree to which competition mediated frequency dependent selection may be responsible for genetic variability and the agronomic counterpart of this question, viz. to what extent mixtures of interbreeding components increase the productivity or yield of the population. Next I will discuss the circumstances under which the competitive performance of a population will change as a result of competition mediated selection. Finally, I explore the consequences of environmental heterogeneity superimposed on competitive differences among genotypes: competitive values will vary in time and space, adding further complexity to the behaviour of mixtures of interbreeding components.

SOME BASIC MODELS OF COMPETITION

Lotka–Volterra Model

Perhaps the most celebrated competition model is that proposed by Lotka (1956) and Volterra (1926; see Scudo 1971 for historical account). This model has been used extensively by theoretical ecologists, particularly in the United States, and has been the foundation for many of our ideas on stability of competitive states, theories of community structure and theories of life-history adaptations. The model is generally expressed in the form of differential equations and cannot therefore be used directly to show output yield in terms of input. However, Pielou (1969, pp. 58–60) gives difference equations that are equivalent to a restricted form of the continuous competition equations of Lotka–Volterra; these take the following form for a three genotype interaction:

$$O_1 = K_1\lambda_1 N_1/\,(K_1 + (\lambda_1\text{-}1)\,(N_1 + \alpha_{12}N_2 + \alpha_{13}N_3))$$
$$O_2 = K_2\lambda_2 N_2/\,(K_2 + (\lambda_2\text{-}1)\,(\alpha_{21}N_1 + N_2 + \alpha_{23}N_3))$$
$$O_3 = K_3\lambda_3 N_3/\,(K_3 + (\lambda_3\text{-}1)\,(\alpha_{31}N_1 + \alpha_{32}N_2 + N_3)),\ \text{where}$$

N and O = input and output numbers of subscripted genotypes respectively

K = carrying capacity (maximum pure stand yield) of populations of subscripted genotypes

$\lambda = e^r$, where r = intrinsic rate of increase of the subscripted genotype growing in pure stand without restriction from other genotypes

α_{ij} = competition coefficient of genotype i with respect to j.

de Wit Model

The model of competition proposed by de Wit (1960) is based on the crowding of species for the same space. The analytical power of this model has been elaborated by Khan *et al.* (1975; but note that their ratio diagrams are approximated as straight lines and are not curves). The model has provided experimental ecologists and agronomists with an extremely powerful tool for determining and quantifying the nature of competitive effects in operation. It has been used particularly in Europe for analysing the nature of species interactions and how they are influenced by the environment, for analysing the nature of the response to selection for competitive ability and for identifying limiting resources in competitive interactions (Hall 1974). Extending de Wit's treatment of the multispecies case, we get:

$$O_1 = z_1P_1/(z_1 + z_2/k_{12} + z_3/k_{13})$$
$$O_2 = z_2P_2/(z_1/k_{21} + z_2 + z_3/k_{23})$$
$$O_3 = z_3P_3/(z_1/k_{31} + z_2/k_{32} + z_3)$$

where for the subscripted genotypes, P = pure stand yield, z = input proportion, O= output yields, k_{ij} = relative crowding coefficient of genotype i with respect to genotype j.

Schutz–Brim–Usanis Model

Schutz, Brim and Usanis (1968) proposed a model of competition where the reproductive value of a given genotype was changed by the presence of other genotypes, depending directly on their frequency and on the nature of the competitive interaction. The theoretical basis of this model has been generalized and extended by Cockerham and Burrows (1971) to consider many aspects of multiline mixtures. In terms of three components:

$$O_1 = z_1\,(P_1 + z_2\,b_{12} + z_3\,b_{13})$$
$$O_2 = z_2\,(P_2 + z_1\,b_{21} + z_3\,b_{23})$$
$$O_3 = z_3\,(P_3 + z_1\,b_{31} + z_2\,b_{32})$$

where symbols are as in the de Wit model, except b_{ij} = effect of j on the reproductive output of i, under conditions of maximum competition.

Comparison of the Models

These models have yet to stand the test of time both with regard to their generality and their applicability to specific natural situations. The simple, very basic models of Ludwig (1950), outlined in a paper ahead of its time, led him to many conclusions that have been confirmed by recent, more elaborate formulations. However, more complex models of competition, developed particularly in the context of interactions among components in continuous flow culture and incorporating time delay effects, have led to results that are counterintuitive and unpredictable from simpler formulations (Stewart and Levin 1973). There still seems to be tremendous scope for model building in the study of competition, particularly as we learn more about the mechanisms of competition in natural situations.

In all the models outlined above it can be shown that stable coexistence between two genotypes is possible if an individual of one genotype is more inhibited by members of the same genotype than by members of the other genotype. The simplest interpretation of this is that the two components occupy different niches or that they use at least partly different resources. This situation has been termed 'overcompensatory' by Schutz *et al.* (1968) and the process has been given the term 'annidation' by Ludwig (1950). In the models annidation between two components occurs under the following conditions:

Lotka–Volterra: $\alpha_{12} \cdot \alpha_{21} < 1$
de Wit: $k_{12} \cdot k_{21} > 1$
Schutz–Brim–Usanis: $b_{12} + b_{21} > 0$.

In the graphical presentation (Fig. 1) the pure stand yields of the two components are assumed equal and competition equations have been chosen so that in all the models the 'overcompensatory' and 'complementary' effects are the same in the 50:50 mixtures. The choice of competition coefficients and pure stand yields is relatively straightforward in the case of the Schutz–Brim–Usanis model and the de Wit model. In the Lotka–Volterra equation the choice of α_{ij} is dependent on the values of K, λ and N_T; these latter are assigned arbitrarily with the additional constraints that $N_1 + N_2$ remain constant and that values of K and k are the same for both components. The shapes of the curves for the de Wit and Lotka–Volterra

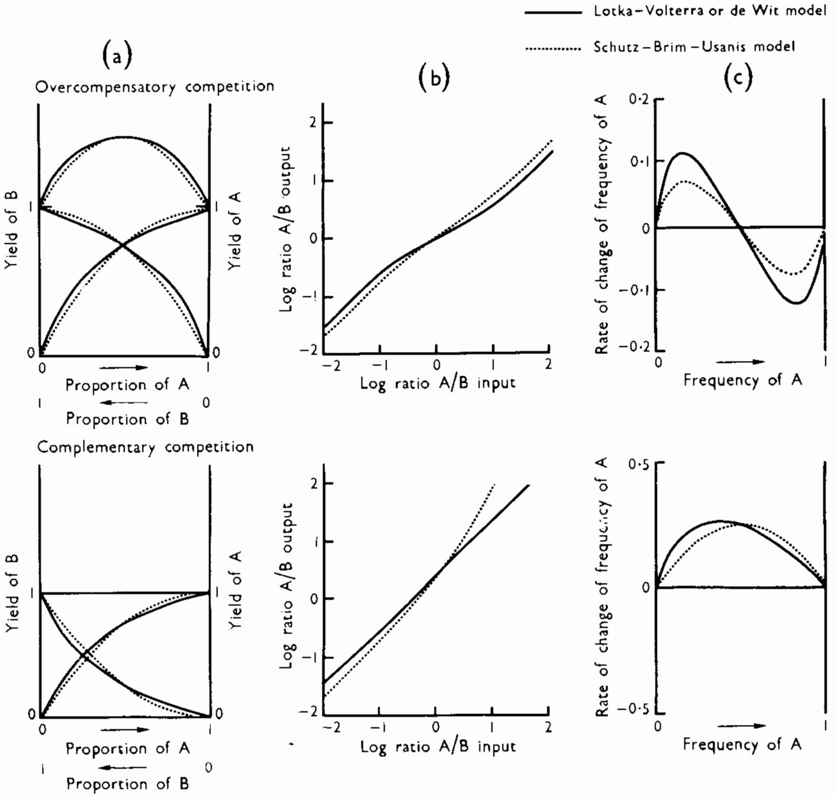

Fig. 1 Comparison of Lotka-Volterra and de Wit competition models (solid line) with Schutz-Brim-Usanis model using (a) replacement series graphs (b) ratio diagrams and (c) graph of rate of change of frequency of a component, with its frequency in mixture. Fig. 1a shows 'overcompensatory competition' where parameters for the computer generated models are: Lotka-Volterra $K_1 = K_2 = 100$, $r_1 = r_2 = 2 \cdot 3026$, $N_1 + N_2 = 100$, $\alpha_{12} = \alpha_{21} = 0 \cdot 259$; de Wit $k_{12} = k_{21} = 3$; Schutz-Brim-Usanis $b_{12} = b_{21} = 1$. Fig. 1b shows 'complementary competition' where parameters for models are: Lotka-Volterra as above except $\alpha_{12} = 0 \cdot 259$, $\alpha_{21} = 3 \cdot 861$; de Wit $k_{12} = 3$, Schutz-Brim-Usanis $b_{12} = 1$, $b_{21} = -1$.

models are coincident in Fig. 1, and are different from the curve for the Schutz–Brim–Usanis model. In the Schutz–Brim–Usanis model the majority component has a relatively greater competitive effect. In the de Wit model the relative reproductive rate (O_1z_2/O_2z_1) of two components that are crowding for the same space (competition is 'complementary') stays constant under all frequencies whereas in the Schutz–Brim–Usanis model the relative reproductive rate depends on the input frequency. In an ecological context, the Schutz–Brim–Usanis model seems more applicable to competition where changes in frequency of a competitor are accompanied by changes in density, or where competition is an active rather than passive process (e.g. exploitative or contest competition rather than scramble competition, as in much animal competition; Nicholson 1954, 1957).

Comparison of the models reveals that while, theoretically, the differences between them are great, these differences are likely to be difficult to detect in practice. *A priori* knowledge of the ecological situation may give a better idea of which model to apply to any situation. The relationship between the de Wit model and that of Lotka–Volterra is complex. The model of Lotka–Volterra simultaneously encompasses the effects of density and frequency, whereas that of de Wit relates only to frequency. These models are also based on different assumptions about resource utilization. However, the two can be reconciled: from yield under a range of pure stand densities of each component and replacement series experiments it is possible to derive both de Wit and Lotka–Volterra parameters (de Wit 1960; Fowler and Antonovics, unpublished data).

EXTENSION OF THE MODELS TO INTERBREEDING MIXTURES

The extension of the competition models to interbreeding mixtures is a relatively straightforward process. The three components are considered to be the genotypes AA, Aa and aa, and the equations describing the relation between input and output frequency describe the process of selection by competition. This is followed by random assortment (with appropriate modifications to simulate different breeding systems) to generate genotype frequencies in the next generation. The resulting equations are then most easily analysed iteratively using computer simulation. I will discuss some results based on the de Wit competition model: my approach has been identical, except for the competition equations, to that of Schutz and Usanis (1969) and the reader is referred to this paper for a summary of the methods involved.

Clearly, a vast array of pure stand yields and competition coefficients could be chosen to describe the relationships between three genotypes. For simplicity I have chosen competition coefficients such that when pure stand yields are equal the 50:50 mixtures between AA and aa yield 25% more than the pure stands. Within this context, in one case AA contributes more than aa to the overall yield; in the other case they contribute equally. Throughout, the heterozygote is considered as intermediate (no dominance with regard to competitive relationships). Given these competitive relationships I have varied the pure stand yields of AA and aa, keeping the yield of the heterozygote intermediate, and studied under what range of pure stand yields gene frequency equilibrium is maintained (Fig. 2a), under what range the yield of the equilibrium population outyields that of the highest yielding single genotype (Fig. 2b), and the nature of the departures at

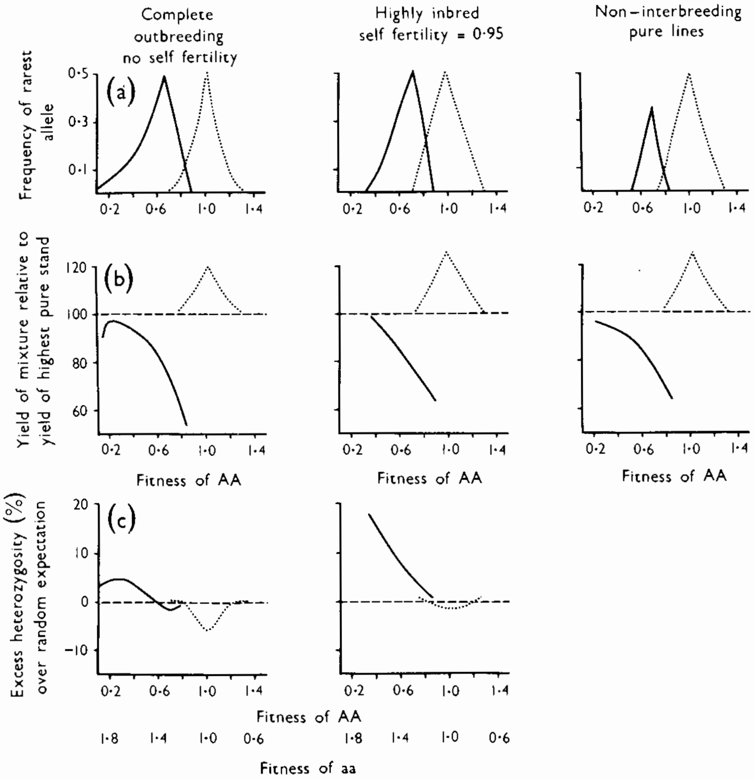

Fig. 2 Results of selection by competition (de Wit) model under 3 breeding systems. Dotted lines show a symmetrical competition model ($k_{12}=k_{21}$ = 1·286, $k_{13}=k_{31}$ = 1·667, $k_{23}=k_{32}$ = 1·286), and solid lines show a competition model where components contribute differentially to the mixture (k_{12}=2·2, k_{21} = 0·778, k_{13} = 7, k_{31} = 0·6, k_{23} = 2·2, k_{32} = 0·778). (N.B. 1 = AA, 2 = Aa, 3 = aa). In both cases the k values were chosen so that a 50:50 mixture of 2 homozygotes (components 1 and 3) of equal pure stand reproductive output would have an output of 25% more than that of the pure stands. The heterozygote (component 2) is assumed intermediate with regard to its competitive behaviour. The pure stand fitness (reproductive output) of the heterozygote is an assumed one, and fitness of the homozygotes are varied as shown on the abscissa. Fig. 2a shows pure stand fitnesses that result in genetic polymorphism: ordinate shows frequency of rarest allele. Fig. 2b shows reproductive output of mixture at equilibrium relative to that of highest yielding homozygote. Fig. 2c shows excess or deficiency of heterozygotes at equilibrium cf. Hardy Weinberg expectations.

equilibrium from Hardy-Weinberg genotype frequency expectations (Fig. 2c). These results confirm that annidation effects can maintain contrasting genotypes in an interbreeding population. It is also noteworthy that the degree of self-fertility of the population has relatively little effect on the conditions for equilibrium: the forces described here act almost as effectively in highly inbred as highly outbred species. Similar results were obtained by Schutz and Usanis (1969) with their competition model. The conditions under which mixtures outyield pure stands are also not over-influenced by the breeding system. In both the inbreeding and non-interbreeding cases the range of conditions over which the mixture outyields the pure stands is somewhat greater than in the interbreeding case. It is assumed that the strongest overcompensatory effects are among the homozygotes; the generation of heterozygotes by random mating therefore weakens these effects and lowers the productivity of the population.

These results, therefore confirm that mixtures of genotypes that utilize different resources can not only coexist but can also outyield pure stands: the breeding system will only influence the particular circumstances under which this is true. It is important in this context to state a generally ignored maxim, viz. that factors which maintain different species in a mixture or a community can also be effective in maintaining genotypes in an interbreeding population. The precise conditions for equilibrium will be different in the two situations since in the case of interbreeding populations the processes of random reassortment, various degrees of dominance and linkage or gene interaction effects will complicate the situation.

Up to now we have phrased the competition models in terms of input and output numbers (or frequencies) of particular genotypes. In any evolutionary model with non-overlapping generations, if we assume equal offspring quality, reproductive output in terms of number of offspring will be equivalent to fitness. With overlapping generations and with different classes of propagules (inbred, outbred, vegetative) the situation is obviously more complex. It will also be more complex in an agricultural context since reproductive output will only approximate agronomic yield in some situations (e.g. seed crops); more frequently, the connection between the two will be less direct, and more precise models would have to take this into account. With these qualifications, it is interesting to note that even under the simple assumptions of these models, equilibrium frequencies of these mixtures may not coincide with frequencies that maximize total reproductive output and, by implication, agronomic yield. This is illustrated in Fig. 3. In such instances, reproductive output can only be maximized by regenerating the appropriate frequency artificially each generation. Conditions both for stability and for maximization of total reproductive output are given by Schutz *et al.* (1968) and Cockerham and Burrows (1971) for both two and three component non-interbreeding mixtures. For more than three components or interbreeding mixtures the solutions are complex and Cockerham and Burrows (1971) suggest they be obtained in particular instances by direct computer simulation.

A further deficiency in all these models is that competition coefficients are expressed in terms of pairwise interactions among the components. It is remarkable how few studies have actually tested the importance of higher order interactions, i.e. whether the nature and degree of competition between two particular components is affected by the presence of a third component. The few competition experiments that have been done with more than two components have sometimes supported the idea that higher order competition effects, while present, are much less important than the pairwise interactions themselves (e.g. in plants, Bornkamm 1963; Haizel 1969; in *Paramecium*, Vandermeer 1969), whereas in other experiments (Wilbur 1972; Neill 1974) higher order interactions

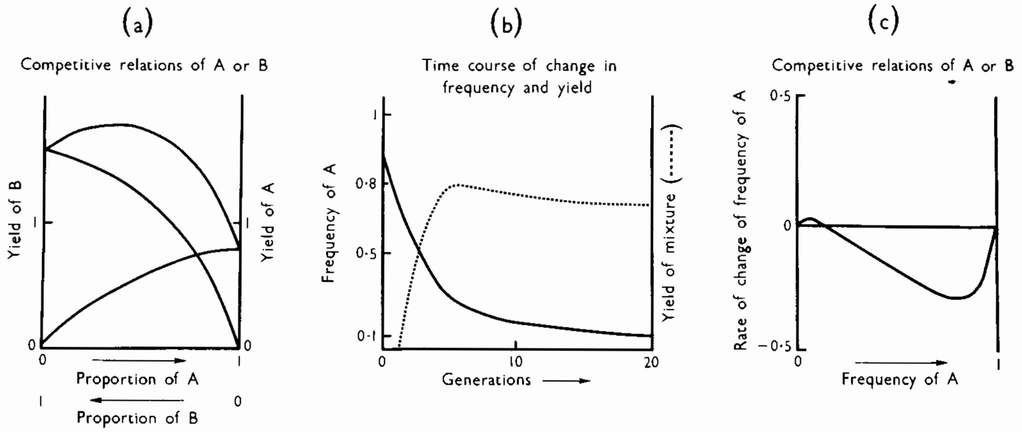

Fig. 3 Example of a situation where the equilibrium frequency of a mixture does not correspond with maximum reproductive output of the mixture, based on de Wit's model assuming 2 non-interbreeding lines with pure stand yields, $P_1 = 0{\cdot}8$, $P_2 = 1{\cdot}6$ and competition coefficients $k_{12} = 3{\cdot}0$, $k_{21} = 2{\cdot}25$; (a) replacement series graph (b) time course of change of frequency of components and reproductive output of mixture (c) frequency diagram.

have been demonstrably important. If one is to consider the applicability of these models to multiline interbreeding mixtures it is imperative to obtain further experimental generalization about the importance of higher order interactions: as Neill (1974) has suggested, perhaps more explicit models based on resource utilization and growth may provide better descriptors of community dynamics.

Single gene effects could, theoretically, be responsible for overcompensatory interactions but direct evidence for such effects is lacking. The phenomena of frequency dependent effects in mixtures (Harding *et al.* 1966; Kojima and Yarborough 1967) and of persistence of mutants at low frequencies in populations (for review see Jones and Barker 1966) are consistent with the idea of annidation due to single locus effects. It would seem difficult for specific genotypes differing by many genes to coexist in the same population since interbreeding among them would result in intermediates; however, genotypes could be preserved by way of linked blocks of polygenes or by a switch gene mechanism. Linked gene complexes may be important: studies on chromosomal inversion types have demonstrated that chromosomally polymorphic populations outyield monomorphic ones (this phenomenon has been termed 'facilitation': Beardmore *et al.* 1960; Dobzhansky and Pavlovsky 1961; Beardmore 1963) and that different inversion types may show frequency dependent interactions (Tobari and Kojima 1967). Switch-genes determining large differences between morphs are well known in species showing mimetic polymorphism (Ford 1964) and switch mechanisms responsible for sex determination may also determine sexual dimorphism of ecological significance. Evidence for the latter phenomena comes from competition experiments among members of the two sexes (Putwain and Harper 1972) and from different ecological ranges of the two sexes (e.g. Selander 1966; Levin 1974). The genetic basis of annidation is clearly diverse and complex; correspondingly, it would be interesting to extend the models discussed here to the two locus case to take into account the effects of linkage and gene interaction.

From a purely practical standpoint, mixtures of lines that are largely self-fertilized would seem to optimize conditions for selecting and maintaining overcompensatory effects. The following conditions could be expected:

(i) Genetic variability would be preserved.
(ii) New lines would be continuously generated at a low rate by recombination or segregation.
(iii) New beneficial lines would be preserved since, with strong inbreeding, gene combinations would tend to break down slowly.

Significantly, perhaps, the best recorded instances of overcompensatory effects were detected among barley genotypes selected from a composite cross that had been maintained for 18 generations, and which therefore had a history of mutual selection (Allard and Adams 1968, 1969). Although there was only 1% outcrossing, genotypes showing mutual annidation effects were generated and preserved by selection.

THE PERSISTENCE OF NEW MUTATIONS BY ANNIDATION

We can approach competitive interactions among genotypes from another viewpoint. Consider the situation where a new allele arises that permits its bearer to use some unique resource. Even if the new genotype has a lower pure stand reproductive output it may be maintained in the population and can result in an overall greater reproductive output of the population. Ludwig (1950) termed such mutations 'ecomutations' and the process 'annidation'. He considered annidation equally as important in evolution as mutation, drift, selection and non-random mating in determining change of gene frequencies. Any new mutation will be characterized by a certain pure stand yield, and by competition coefficients relating it to other genotypes in the population. These determine if the mutation is preserved or eliminated by selection. For example, using the de Wit model we can describe the relationship between the pure stand disadvantage of a new mutant, the uniqueness of resource utilization that it determines (as defined by the relative crowding coefficients of the genotypes) and the equilibrium gene frequency and total reproductive output or overall fitness of the population (Fig. 4)

MacArthur and Levins (1967) and May (1973) extend such discussion to consider the probability of invasion of a two species mixture by a third species. Their considerations could be applied, with qualifications, to a population of interbreeding genotypes into which there is recruitment of new genotypes by migration or mutation. From their model, it is possible to plot values of K, for given values of α, that permit a genotype to invade either to one side of the resource utilization spectrum of a single component or to invade between two components (Fig. 5). Since an increase in pure stand yield is likely to occur at the expense of competitive ability and vice versa (the Montgomery effect), the class of mutants affecting K and α are likely to be negatively correlated with a probability distribution as in Fig. 5. It can be seen that, in terms of relative frequency of different mutant types, most will be displaced, some will invade to one side of the resource utilization spectrum (thereby extending range of resources used) and coexist, and only a very small portion will invade in the middle of preexisting types (thereby intensifying the use of resources). New mutations are, therefore, more likely to extend the range of

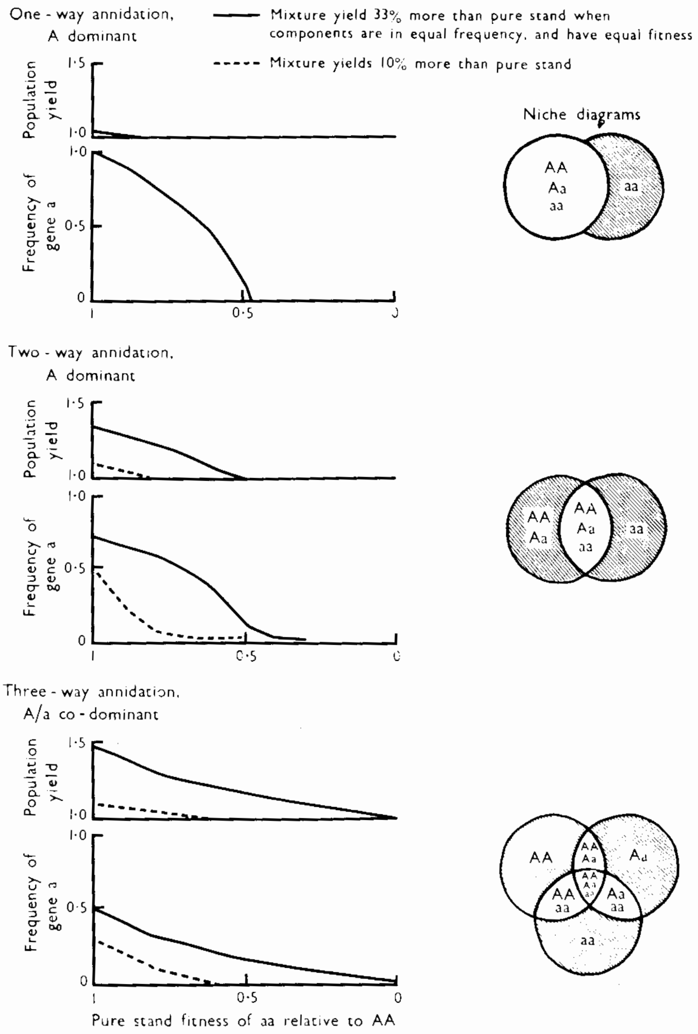

Fig. 4 Gene frequency and population reproductive output at equilibrium, when the gene a, of lowered pure stand fitness but determining different annidation relationships, is introduced into a random breeding population. Simulation based on the de Wit model, with the following parameters — 1 way annidation: 33% increase in mixture $k_{12}=k_{21}=k_{13}=k_{23}=1$, $k_{31}=k_{32}=5$; 2 way annidation: 33% increased output of mixture, $k_{12}=k_{21}=1$, $k_{13}=k_{31}=k_{23}=k_{32}=2$, 10% increased output of mixture, $k_{12}=k_{21}=1$, $k_{13}=k_{31}=k_{23}=k_{32}=1\cdot222$; 3 way annidation: 33% increased output of mixture $k_{ij}=1\cdot6$; 10% increased output of mixture $k_{ij}=1\cdot158$. Pure stand fitness of aa relative to AA shown on abscissa; heterozygote assumed intermediate. Venn diagrams schematize the different types of annidation in terms of niche space overlaps, where shaded areas represent unshared resources and unshaded areas represent shared resources.

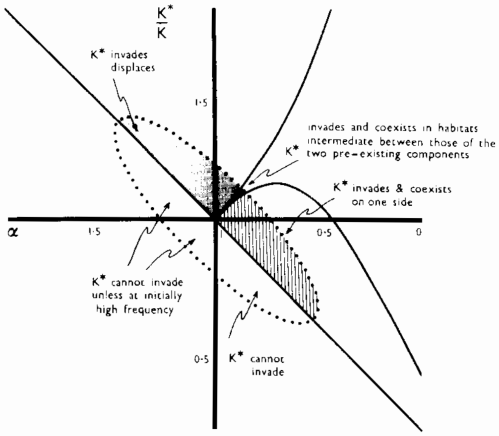

Fig. 5 Diagram showing the relationship between the carrying capacity (maximum pure stand yield) of a new genotype (K*) relative to that of other genotypes (K), its competition coefficient relative to other genotypes (α), its likelihood of arising by mutation and its probability (represented by size of shaded regions) of establishing in a population given that one or two genotypes are already present. Dotted ellipse shows probability distribution of values of K*/K and α in a genotype on the assumption that K* and α are negatively correlated. When one genotype is already present α must be less than K*/K to invade and use a different resource. When two genotypes are already present and coexisting, then values between curves show regions of K*/K and α where a new mutant would invade and use resources intermediate between those used by the genotypes already there. Decreasing α values indicate greater annidation effects.

resource utilization and less likely to result in more efficient utilization of existing resources.

Again, we only have circumstantial evidence for such processes. Ayala (1968) showed that populations of *Drosophila*, maintained for many generations, slowly increased their productivity, more so in irradiated populations. These results do not distinguish increased efficiency of resource utilization from increased breadth of resource utilization; it is likely that both types of evolutionary change were occurring in these populations. Ecologists have frequently inquired into what determines the species diversity of communities. Clearly, such a discussion deserves extension to the intra-specific level, since interbreeding is often not an essential component to many models of genetic diversity. We can consider diversity of a community to be partitioned into a number of components, so that the overall phenotypic diversity is a compound of between species diversity, between genotypes within species and between phenotypes (plasticity) within genotypes. From an agronomic viewpoint, equivalent yields could be obtained from different magnitudes of these components. But natural populations have been insufficiently studied to provide guidelines as to what particular contribution each component should make in any given situation.

EVOLUTION OF COMPETITIVE RELATIONSHIPS

If we establish a mixture of two or more non-interbreeding populations that are genetically variable, their relationships may change for two reasons:
(a) Each population may adapt separately to the extant environment as a result of differential fitness among the individuals; this effect may be intensified by intrapopulation competition.
(b) Alternatively, the populations may adapt to each other or coevolve. Competition will impose selection pressures and eliminate individuals whose fitness is lowered by competition. The response to this pressure will depend on the parameters that determine the response of any population to selection (genetic variability, correlated responses, population size and the intensity of selection) and also on the nature of the competitive interaction.

The relative roles of (a) and (b) will, in part, be a function of frequency. At low frequency, selection will be mostly interspecific, whereas at a high frequency mostly intra-specific selection will operate. One can visualize a system of negative frequency-dependent adaptation to competition which would lead to a cyclical system maintaining both species in the population: such a situation has been demonstrated experimentally in flies (Pimentel *et al.* 1965; Pimentel 1968). There are, however, no known equivalent examples from natural or agricultural populations.

The intensity of selection will depend, in part, on the difference between the pure stand reproductive output of the population and the reproductive output of the population at that same density only in the presence of a competitor. Quantifying the competitive relationship among two species using replacement series experiments alone tells us nothing about the selection pressures acting on the components: it is necessary to know the pure stand yields at corresponding densities (Seaton and Antonovics 1967).

Several approaches have been used to study, theoretically, the effects of selection by competition on competitive relationships (MacArthur and Levins 1964, 1967; Levin 1971; Bulmer 1974; Crozier 1974; Lawlor and Maynard Smith 1976). Analogous changes are expected in more conventional models of selection: modifiers will be selected that improve the performance of a gene against which selection is acting (O'Donald 1968, 1969). The conclusion of theoretical studies is that populations will tend to diverge in their ecological requirements so that they increasingly use different resources, with the accompanying consequences of increased stability (Lawlor and Maynard Smith 1976) and reproductive output of the mixture. MacArthur and Levins (1967) suggested that the results would depend on the presence of a third species: if it is a particularly strong competitor it may cause the two species under consideration to converge, rather than diverge, in their requirements. Lawlor and Maynard Smith (1976) point out that such convergence is the result of the two species adapting to a common extraneous influence (the third species); nevertheless, the basic expectation of competition among species is still divergence.

The rate of divergence will depend on the initial difference between the competitors. There will be a degree of difference between the components at which selection for divergence will be maximized. Little or no difference will give slow response to selection — at least initially — and, obviously, if the initial difference is large, the pressures will be weak for still further divergence.

Experimental studies on changes in competitive performance as a result of competition are noteworthy for the variability of the results. Frequently, competitive performance does change in the theoretically expected direction of increased

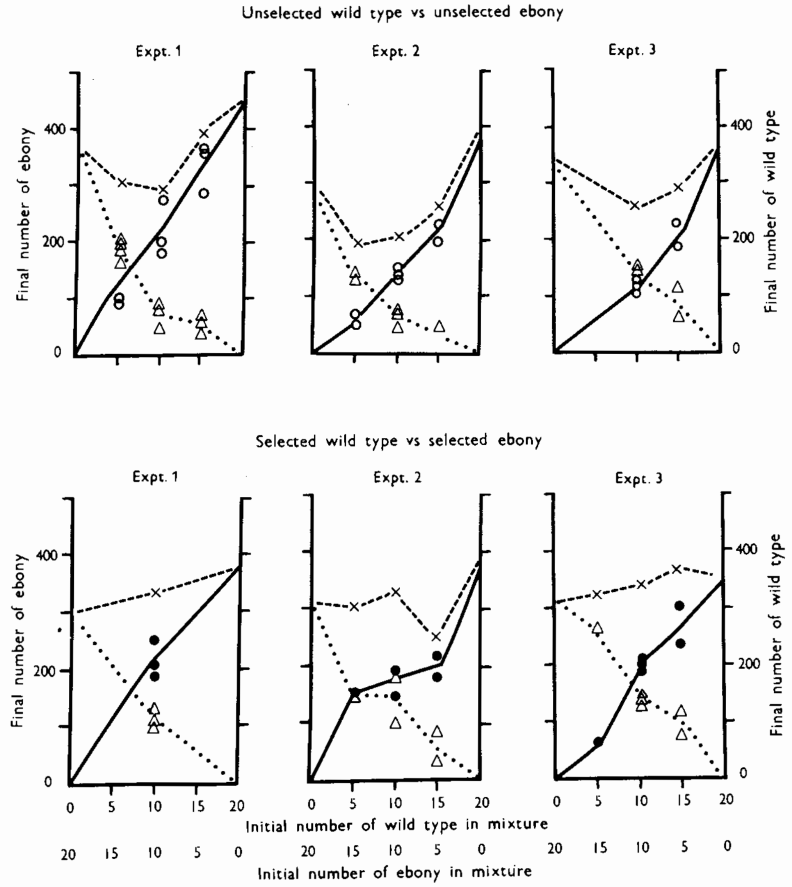

Fig. 6 Replacement series graphs snowing competitive relationships before and after selection for performance in non-interbreeding mixtures of ebony and wild type (Amherst) *Drosophila melanogaster*. Replacement series tests were carried out after 3, 4 and 4 generations in experiments 1, 2 and 3 respectively. Stocks used in experiments 1 and 2 were identical: in experiment 3 the basic stocks were outcrossed to 2 different wild type stocks to enhance their genetic variability (after Chen 1972).

differential resource utilization by one or both components and greater reproductive output of the mixture (Moore 1952; Seaton and Antonovics 1967; van Delden 1970; Barker 1973). Figure 6 illustrates some previously unpublished results obtained by Chen (1973); these results show an improved yield of the mixtures following selection and the development of frequency dependent relationships among the components. Almost as frequently, however, competitive performance remains unchanged (Sokal *et al.* 1970; Hedrick 1973) or in some cases even declines (Futuyma 1970; Ford 1972). Variable responses may result from the unpredictability inherent in any selection experiment, from the variety of initial competitive interrelationships that are possible or from the nature of the character itself. The ability of a population to perform well in mixture is probably a different kind of character from a simple quantitative trait because (a) it is likely to be an important fitness or yield component and populations may therefore show relatively little additive genetic variance for the character (b) it is undoubtedly often a complex trait and correlated responses may retard selection and (c) like other fitness traits it may be very susceptible to inbreeding depression (Ford 1972). Selection experiments are often characterized by small populations and selected individuals that are relatives, both of which lead to inbreeding depression.

Evidence in natural populations for these processes is circumstantial but compelling. Examples of 'character displacement' (Brown and Wilson 1956; Grant 1972) suggest coevolutionary responses among competitors in the direction of increased niche divergence. Explicit evidence for such coevolution may be difficult to obtain, since frequently changes in species composition are likely to be confounded with changes in environment. Therefore, it is perhaps not surprising that genetic changes in competitive relations have rarely been studied, either in established communities, during invasions or during ecological succession. Such changes are very pertinent to any discussion of communities as coevolved systems, and in need of investigation. We have little information on the degree to which spatial, temporal or other adjustments in resource partitioning are involved. Even the conflict between convergent adaptation to a common environment, and divergent adaptation to other members of the community, has never been explicitly investigated.

In spite of the inconsistencies of experimental data, and the weakness of evidence from natural populations, several conclusions can be drawn that are pertinent to the agronomist:

(a) The interrelationships of species mixtures may not be permanent: shifts in competitive ability will occur as a result of natural selection. This may not necessarily result in increased agronomic yield.

(b) Selection for beneficial interactions, so that mixtures yield more than pure stands, is theoretically possible, but response is not certain and may be complex.

(c) Alternative resource utilization is 'coevolutionary'. Random mixing of varieties will be unlikely, *per se*, to generate beneficial combinations. Selection among existing varieties of combinations showing overcompensatory effects may be less successful than explicit selection for such effects (Allard and Adams 1969).

(d) Even where mixtures may not outyield pure stands for any one season or site, they may have better overall stability in the face of temporal and spatial variations of the environment.

MIXTURES IN A HETEROGENEOUS ENVIRONMENT

Different resources used by two components of a mixture may not be physically separated. An extreme case is where both use one resource but with differing efficiencies at different concentrations (e.g. Stewart and Levin 1973). Alternatively, the resources may be separated in space and time. Where two components occupy unique 'niches' in the environment the reproductive output of the mixture is the sum of that of the components. Models of situations that fall between these extremes, so called 'multiple niche models', have recently become common in the population genetics literature (see Christensen and Feldman 1975). These models assume that some genotypes are favored in one niche, others in different niches and that the number of individuals in a niche is held constant (i.e. density dependent factors act independently in the separate niches but act equally with regard to the genotypes). Different amounts and types of migration between the niches can be assumed (see Dickinson and Antonovics 1973a). In terms of such models, ecologists have lagged behind geneticists and only recently have the conditions for equilibrium been defined when two non-interbreeding competing components occupy alternative niches (Levin 1974). The primary conclusion of these multiple niche models, and one that is still not generally appreciated by many biologists, is that gene flow between two populations (particularly at low levels) may retard, but does not necessarily prevent, divergence between them. And if a population is faced with a heterogeneous environment, selection for different alleles in different environments will maintain allelic variation in the population.

Evidence that these processes are important has come from studies of populations at ecotones (e.g. Antonovics and Bradshaw 1970) and in heterogeneous habitats (Snaydon 1970). The most detailed study of adaptation to microhabitats has been that on *Plantago lanceolata* growing in a very small segment of grassland (Watson 1974). Heterogeneity was defined by vegetation height, which often reflected changes in community composition (Fig. 7). The positions of plants of *P. lanceolata* in this segment were noted and they were then removed and cloned prior to transplanting them in standard greenhouse and garden conditions. Following growth for over a year, measurements showed that with regard to leaf length, growth habit and inflorescence length, the plants were genetically adapted to the vegetation height from which they came. Other characters (leaf width, spike length and leaf number) showed significant genetic variance but were not correlated with the measured heterogeneity.

Over evolutionary time the consequences of a heterogeneous environment may be increased phenotypic plasticity (generalized genotypes), genetic polymorphism or genetic divergence among sub-habitats. In these ways, the members of the population can become adapted to a wider range of micro-environments, with a resulting increase in the reproductive output of the population. In an agronomic context, where a mixture is frequently reconstituted *de novo*, the conditions under which the mixture will have a greater reproductive output than a pure stand in a heterogeneous environment are rather restricted. It will occur: (a) if the two genotypes generate their own heterogeneity by using different resources when in competition (these situations have been discussed above); (b) if we can place the correct genotype in the correct microenvironment or, more generally, if there is

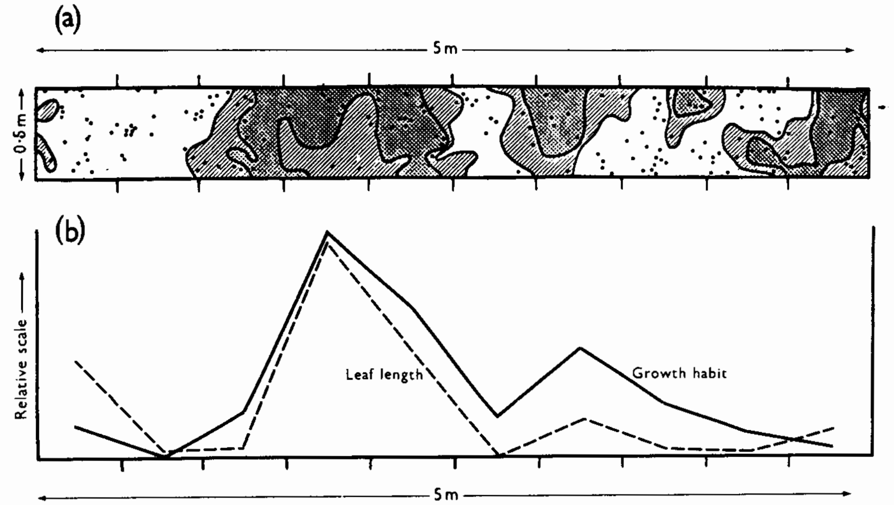

Fig. 7 Diagram showing relationship between vegetation height and genetic microdifferentiation in *Plantago lanceolata.* (a) Contour map of vegetation height (average of readings taken at 3-monthly intervals over 2 years) where unshaded = 0–7·5 cm, hatched = 7·5–10 cm and cross-hatched = 10–20 cm; dots indicate positions of sampled plants. (b) Mean leaf length (dotted line) and growth habit (solid line) of sampled plants after cloning and cultivation under standard conditions. Vertical scale is relative, based on average of 2 times of measurement in both greenhouse and garden conditions.

habitat selection (perhaps preferential growth) by the genotypes; (c) if competition within the mixture improves the adaptation to each microenvironment. This latter situation has two components: (i) Selection may be dependent on the presence of other genotypes in that microniche. If, in each microniche, only one individual can survive, and only one individual or individuals of like genotype land, there can be no differential survival; but if different genotypes land, then there may be differential survival. Thus, the more seeds that are sown, the greater is the probability that each niche will contain a range of genotypes, including the optimum genotype for that niche. An interbreeding version of this model (Dickinson and Antonovics 1973b) showed that even with completely random dispersal and random variation of the niches, greater genotype environment correlation resulted from greater seed density. (ii) The intensity of selection may itself depend on the intensity of competition: at greater densities selection is likely to be higher.

As a result of these two processes 'correct' genotypes may assort into correct niches with a resultant increase in yield. If plants are sown in pure stands at high densities there is usually, but not invariably, plant mortality (Palmblad 1968; White and Harper 1970), a process termed self-thinning (Harper 1961). The death of particular individuals may be determined by 'chance' factors such as time of emergence or size of initial seed reserves (Sagar 1960, quoted in Harper 1961; Ross 1968, quoted in White and Harper 1970). However, genetic differences within the population may also be responsible for this mortality, particularly since plants are static and therefore selection pressures are severe (Bradshaw 1972). Indirect evidence that genetic changes may result from self-thinning comes from rapid genetic changes in populations established for only a few years (Charles 1964; Crossley and Bradshaw 1968) and from microdifferentiation in annuals (Allard *et al.* 1972).

To investigate genetic changes during self-thinning I mixed seed of 4 contrasting populations of *P. lanceolata* to create a genetically variable seed pool; the mixed population was sown in seedling flats at high density and the plants were either left uncut or cut twice per week to a height of 3 cm. The percentage of seedlings that had died after 6 months was 47 and 19% in the uncut and cut treatment respectively. At the end of 6 months of this pretreatment, plants were sampled from the population in the flats and transferred to the field for 1 growing season under a uniform regime of no cutting. Another group of plants was sampled from the flats after 13 months pretreatment and grown for a further year in the greenhouse without cutting. After these extra periods of growth a number of morphological characteristics of the surviving plants were examined. The samples from the 2 cutting regimes differed in leaf length for the 6 month pretreatment group and in leaf length, growth habit, inflorescence number and height for the 13 month pretreatment group (Table 1). These differences were probably the result of genetic changes during self-thinning since several of the characteristics examined are known to be inherited (Barber *et al.* 1968) and the 'experimental population' was deliberately constituted to enhance genetic variation.

Table 1
Effects of cutting pretreatments on the morphology of surviving *Plantago lanceolata* plants subsequently grown under standard conditions either in the field for 1 growing season or the greenhouse for 1 year (means of 20 plants). Habit grade scored on a range of 1–5 for prostrate to upright.

	Plants Grown in Field (cutting pretreatment for 6 months)		Plants Grown in Greenhouse (cutting pretreatment for 13 months)	
	Cuttings per Month		Cuttings per Month	
	0	8	0	8
Leaf number	142·3	128·9	19·1	17·4
Leaf length (cm)	37·2	30·4*	8·5	5·8*
Leaf width (mm)	30·1	27·7	14·1	13·6
Habit grade	3·2	3·3	2·2	1·5*
Inflorescence Number	107·8	103·9	3·1	6·3*
Inflorescence Height (cm)	58·9	55·0	27·4	18·9*

*Difference significant, $P < \cdot 05$.

Genetic change by self-thinning is potentially a very important process of adaptation in plant populations. High species density may accentuate phenotypic and genetic differences between individuals and result in extreme selection pressures. Density stress among juvenile individuals is also likely to be very localized so that the surviving genotypes will be determined by the conditions at each microsite. Such adaptation can clearly occur within a single generation by screening appropriate individuals from a genetically variable seed input. The above process, termed 'sieve selection' (Antonovics *et al.* 1973), may be a widespread phenomenon (Bradshaw 1972). The precise adaptation in *P. lanceolata* described earlier

(Watson 1974) might have its basis in such a process: mortality in the seedling to juvenile stage (0–3 months) was *c.* 60% and a removal experiment showed that juveniles and adults were under density stress (Watson and Antonovics, unpublished data).

Indeed the great 'excess' of seed production, and the high seedling mortality characteristic of plant populations (e.g. Sharitz and McCormick 1973), may have as much a genetic as an ecological basis. The 'cost' resulting from mortality of seedlings through self-thinning may be offset by greater precision and speed of genetic adaptation, leading to improved individual adult survival, growth and seed production. Dickinson and Antonovics (1973b) have shown, theoretically, that a higher seed density should result in a greater genotype environment correlation since there is a greater probability that the appropriate genotype will land in an appropriate microhabitat. This stochastic component would act synergistically with the genetic effects of self-thinning to maximize adaptation and, consequently, population seed output. There is need to document such processes in natural populations and to define more precisely, under experimental and agronomic circumstances, the relation between the 'cost' of self-thinning and the 'benefit' of local adaptation and its interaction with density, environmental heterogeneity and breeding system.

Temporal variation is likely to be as important as spatial heterogeneity. The demonstration that many perennials have a relatively short life span (Harper 1967; Antonovics 1972; Sarukhan and Harper 1973; Sarukhan 1974) and the demonstration of 'plant movement' by sequential mapping of pasture communities (Lieth 1960) suggests that 'permanent' pastures may, in fact, be extremely fluid, characterized by rapid turnover, internal microsuccession and, above all, temporal variation. However, the process of community change in such dysclimax vegetation has never been quantified. One possible approach is to use a repeated point cover technique to study 'community demography' (Fowler, unpublished data); this is less subjective than outline maps, and transition probabilities for species to species shifts can be obtained.

CONCLUSIONS

The discussion has been based on rather simple models of species interactions. MacArthur (1970), when referring to the Lotka–Volterra models, stated 'More realistically, the equations should include higher order terms and perhaps higher derivatives, the effects of seasonality and patchy environments, age distributions, time lags, and the like; but ecologists have found it interesting to see what consequences even these simplified equations may have.' It is encouraging therefore that even such simple models of fundamental, almost axiomatic, interest to the student of natural populations are consequential for processes occurring in nature, and that they do give guidelines to the applied agronomist.

Many of the simple assumptions of these models do not pertain to pastures: for those with a high proportion of perennial species more realistic models should include overlapping generations, asexual reproduction, a dormant seed pool, and should take into account spatial and temporal heterogeneity. Recent progress in integrating genetic and demographic models has led to the possibility of such comprehensive descriptions. We can now think of populations changing simultaneously in size and genetic constitution. Differential fitness can be measured in terms of age specific mortality, reproduction and the nature of the contribution to the following generation. This contribution may be by seed or vegetative propagation and the contributions may differ in timing or quality. Seeds may or may not enter dormancy; they may be inbred or outbred; and they may compete with relatives or with unrelated members of the population.

In brief, there is now sufficient theoretical background in population biology to quantify complexity, rather than shrug off the problem as being insurmountable. The consequences of this are that there must be increasing cooperation between theoretical and applied ecologists. The imagination is too fertile for unbridled exploration of the consequences of extensive parameterization. The student of natural populations is generally interested in long-term equilibrium states of complex systems, whereas the agronomist is additionally interested in maximization of yield, yet has the advantage of working with simpler systems. They both have an important role to play in guiding and thereby benefiting from theoretical developments in population biology.

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