CHAPTER 11

Genetic variation and environmental variation: expectations and experiments

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We may think of the evolution of genetic systems as a course of evolution which, although running parallel to and closely integrated with the evolution of form and function, is nevertheless separate enough to be studied by itself.
(Stebbins, 1950)

11.1 INTRODUCTION

Because the diversity of genetic systems (defined as those characteristics of the organism influencing the rate of genetic recombination) is much greater in plants than in animals, such systems have been of particular interest to students of plant evolution. Ever since the work of Darlington (1939), it has been realized that the evolutionary forces acting on genetic systems are likely to be different from those acting on more conventional morphological and physiological traits. For example, a particular chromosome number or recombination frequency may have very little direct impact on the physiological functioning of the organism, on its survival and fecundity, but may have a marked effect on the evolutionary potential of the descendants of that individual. As Stebbins (1950) states, 'Hence in discussing the selective value of genetic systems we must consider primarily the advantages a particular system gives to the progeny of those who have it ... the immediate advantages or disadvantages of the system are of secondary importance.' In the early works of Darlington, Huxley, Mather and Stebbins, the hypothesis was proposed that particular genetic systems result from a compromise between the need for constancy so as to preserve adaptation to the immediate contemporary environment and the need for flexibility in the face of changing environments to which the species will
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became exposed in the future. This idea was so forceful in its elegance and in its explanatory power that it became engrained in evolutionary biology more as a paradigm of how genetic systems actually do evolve, rather than as a hypothesis requiring rigorous formulation and testing. As a result the idea that genetic variation is in some sense an adaptation for coping with environmental variation and change has become an idea that pervades not only introductory texts, but also our evolutionary consciousness. It has also received support from a homomorphism of ideas between ecology and genetics. Environmental variation and diversity are seen as essential (and desirable) ingredients of ecological systems: surely then the genetic variation we see in organisms is there to adapt the organism to such environmental variation.

What we want to do in this chapter is to continue in the Stebbinsian tradition of examining closely the relationship between genetic variation and environmental variation. However, we wish to do so less from a comparative standpoint, but more from an experimental perspective. This we believe is in keeping with the rapid change in evolutionary biology that is bringing the science closer in methodology to other traditionally more experimental sciences such as developmental biology and physiology. Plants, given their experimental convenience, have a large role to play in this change.

First, we present a straw-man, the intent of which is to defuse any glib assumptions that genetic variation is necessarily an adaptation to environmental variation. Secondly, we outline some specific hypotheses that have been proposed for 'short-term' advantages to sexual reproduction in varying environments: this is because we feel such hypotheses are amenable to direct experimental test, whereas 'long-term' hypotheses are much less so. We emphasize however that such hypotheses are still crude, unquantified word-models, and that indeed we have few quantitative models that can serve as a focus for precise experimental quantification of the selective forces acting on genetic systems. Third, we emphasize that there has been considerable confusion about the concept of environment: this has served both to divert our thoughts into inappropriate directions as well as to distort our experimentation into focusing on inappropriate (and often overly complex) measurements. Finally, we present the results of an experiment which not only illustrates some of these pitfalls, but which illustrates the necessary, but not necessarily sufficient, conditions for genetic variation to be favored in a variable environment. In brief, the hypotheses generated by Ledyard Stebbins and other plant evolutionary biologists many years ago still demand our attention today: we are perhaps only now developing the conceptual and experimental tools that can examine these ideas both critically and creatively.
11.2 A STRAW-MAN

Consider a habitat which is a mosaic patchwork of two soil types (uncontaminated vs. metal contaminated soil?) which we will call white and grey (Fig. 11.1). Let this mosaic be occupied by a haploid organism, such that genotype A survives in the grey microsites and genotype a in the white microsites. Then we can ask: will an individual be favored if it produces only A type or only a type progeny (asexually) or will it be favored if it produces a 50:50 proportion of A and a. Let us assume that the progeny are dispersed at random over the microsites. It is evident that the progeny of an individual that produces only A or a will have 50% survival (Fig. 11.1). However, it is also evident (Fig. 11.1) that the individual that produces two types of offspring will have no advantage, since A and a will each fall in the wrong microsite 50% of the time. There is thus no overall advantage to an individual with a genetic system that produces variable as opposed to uniform progeny.

The point of this straw-man is twofold. First, the facile presumption that genetic variance is 'adaptive' for environmental variance is clearly erroneous. We need to have precise hypotheses, where assumptions are explicitly stated, before the more generalized idea can be tested. (Most biologists could easily modify the above model, such that the variable progeny would be favored, for example, by assuming competition in microsites, such that the best genotype for that site wins.) Secondly, given that the numbers of individuals that occupy each microsite are limited, the straw-man model would maintain genetic variance in a population but would still not provide an individual advantage to variable progeny. Thus the observation of a correlation between genetic variation and environmental variation is also insufficient proof that environmental variation provides the selective forces for genetic systems that promote variation.
11.3 TOWARDS WORD-MODELS

The past decade has seen a re-structuring of our ideas on the evolution of genetic systems. Although it is generally agreed that many such systems may not have a large physiological cost (and hence 'direct' fitness effect) on the individual, it has been pointed out that there are major costs to outcrossing and sexual reproduction in terms of gene-transmission (Williams, 1975; Lloyd, 1980a,b; Uyenoyama, 1984). Concomitantly, physiological costs associated with outcrossing and sexual reproduction (such as costs of mate attraction) have also been re-emphasized. Because these transmission costs are large, yet sexual reproduction is a widespread phenomenon, commonly occurring throughout nearly every major group of eukaryotes, theoreticians have offered a large variety of models to account for the advantages of sex and recombination (summarized in reviews by Ghiselin, 1974; Williams, 1975; Maynard Smith, 1978; Lloyd, 1980a; Bell, 1982). These models all seek to find 'short-term' (i.e. single-generation) advantages in terms of the number of progeny that reproduce again in the following generation. Such advantages are often termed 'individual advantages' to contrast them with advantages that may accrue to the population (or 'group') as a whole. Use of the term 'individual advantage' is somewhat misleading, since it is most often assumed that the individual possessing a particular genetic system still has no advantage in terms of survival or offspring number, but that the advantage is accrued by the immediate progeny of that individual. Most of such 'short-term' selection models fall into two classes, those involving frequency-dependent selection and those involving changing or unpredictable environments.

The first class of models argue that sex will be favored if there is an advantage to being genetically different from the majority genotype (Levin, 1975; Jaenike, 1978; Glesener, 1979; Lloyd, 1980a; Hamilton, 1980; Price and Waser, 1982; Tooby, 1982). Such minority types are more likely to escape pathogens and predators. We have obtained experimental evidence in the grass Anthoxanthum that sexual individuals indeed have a substantial fitness advantage as a result of frequency-dependent selection (Antonovics and Ellstrand, 1984; Schmitt and Antonovics, 1986b). Under high sibling densities, genetically variable sexual progeny will also be favored because of reduced competition as a result of resource partitioning among diverse genotypes (Maynard Smith, 1978; Young, 1981; Price and Waser, 1982). Minority genotypes will compete less with each other if they use differing resources. However, we found no evidence for this in Anthoxanthum; fitness differences for sexual and asexual progeny did not increase with increasing density (Ellstrand and Antonovics, 1985).

The second class of models argues that the production of genetically variable progeny will be advantageous when environments are variable in
time and space. In the case of temporal variation, individuals that produce variable progeny will be favored if the environment encountered by these progeny is likely to be different from that of the parents. Environmental states may change from generation to generation so as to be negatively autocorrelated (Maynard Smith, 1978), or environments may change over time in some directional manner (Treichman, 1976). Genetic variation may also be favored because it provides a mechanism of 'bet-hedging' in the face of environmental unpredictability. Different genotypes may be favored at different times, so resulting in a lower variance in fitness over time. Since such fitness values over time are integrated as the geometric mean rather than as the arithmetic mean (Gillespie, 1977; Lacey et al., 1983), those genetic systems reducing variance (even at the expense of mean performance) would be favored.

In the case of spatial variation, one can envisage a continuum between one extreme where environments are so highly heterogeneous that all possible habitats are encountered with about equal probability in every generation (fine-grained environments sensu Levins, 1968), and the other extreme where environments change gradually over space so that new environments are only encountered in successive generations of dispersal (coarse-grained environments). In the former case, variable progeny will be favored if the appropriate genotype can either choose (behaviorally or by differential growth) the appropriate habitat (Maynard Smith, 1978; Bell, 1982), or if sub-competition or differential mortality results in the appropriate genotype displacing other genotypes in a given microsite (Maynard Smith, 1978; Williams and Mitton, 1973; Bulmer, 1980; Taylor, 1979; Barton and Post, 1986). In the case of gradually changing spatial environments, individuals that produce variable progeny will be favored if the environment encountered by these progeny is likely to be different from that of the parents. The gradually changing spatial environment models converge on those relating to temporal variation, in the sense that successive generations encounter different environments in space, rather than in time.

The difficulty with all these heterogeneous environment hypotheses is one of degree. Do environments in nature in fact change sufficiently enough and consistently enough to sustain sexual reproduction in this way? What do we mean by 'enough'? What environmental parameters should we measure? Indeed how can these models be operationalized so as to be amenable to experimental test? How can the selective forces acting on genetic systems be measured?

11.4 THE CONCEPT OF THE ENVIRONMENT

Whereas the concept of fitness has received extensive attention from both philosophers and empiricists interested in evolution, the concept of the
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environment has received only minimal or passing interest (Brandon, 1986). Yet for the theory of natural selection to have explanatory power with regard to how adaptations originate, the concept of environment is as important as that of fitness. The reason is simple and can be easily illustrated by an example. If we grew one plant on good soil, and another on poor soil, the one on good soil would probably survive better, grow larger, and have more seed. Although we might be tempted to say one plant had a greater 'fitness' than the other, we are in this case referring to properties of the environment rather than to properties of the phenotypes of those plants which would explain their differential success. (We assume phenotypes are not 'choosing' different soils.) In other words for the theory of natural selection to have explanatory power, we must compare the fitness of different phenotypes in identical environments. Conversely, two environments can be thought of as homogeneous (with regard to selection) if their effect on the relative fitness of phenotypes is the same. It is within such selectively homogeneous environments that differential fitness is the result of properties of the organism and within which the theory of natural selection therefore has explanatory power.

It is almost irresistibly tempting, in view of its popular usage, to equate environment with some measure of conditions external to the organism. Indeed whole fields of endeavour, the environmental sciences, are concerned with this. In biology however, we should recognize that there are really three quite disparate ways in which we can measure the environment, and these measures may produce quite different scales of heterogeneity (Fig. 11.2). The 'external environment' reflects properties of the environment that are measurable externally, without any necessary involvement of the organism itself. This type of environment is equivalent to the popular usage alluded to above.

The 'ecological environment' reflects properties of the external environment that influence the organism's contribution to population growth, or its reproductive value sensu Fisher (1930). This environment is measurable in terms of the demographic performance of individuals. It therefore follows that the scale of heterogeneity that is present will depend on the organisms (whether they be individuals, populations or species) used as the 'measuring instruments' (Antonovics, Clay and Schmitt, 1987). The use of organisms as environmental measuring instruments was first pioneered by Clements and Goldsmith (1924), although in these studies the focus was often the external environment, with the organism used as an inexpensive instrument which could be calibrated against more complex measuring instruments indicating the external environment.

The 'selective environment' reflects properties of the external environment that influence the differential contribution of genotypes to subsequent generations. This environment is measurable in terms of the fitness (in a
The concept of the environment

1 External environment

[Graph showing molybdenum level vs. distance]

2 Ecological environment

[Graph showing reproductive value vs. distance]

3 Selective environment

[Graph showing fitness vs. distance with two lines, P₁ and P₂]

Fig. 11.2 Schematic illustration of how external, ecological and selective environments may show different scales of heterogeneity. We assume that molybdenum levels only reduce the performance of the organism when they are above a threshold, and that two phenotypes, P₁ and P₂, within the species react differentially only to extremely low molybdenum levels.

relative sense) of genotypes, and environmental heterogeneity is indicated by differential performance of genotypes in different regions or at different times (i.e. by genotype × environment interactions). The scale of environmental heterogeneity will therefore depend on the genotypes used to measure it. Curiously, but obviously, if two genotypes used to measure an environment are identical, then the selective environment for these genotypes will be uniform!

Two points should be noted. The first point is that the selective environment although measurable by the use of genotypes as 'phytometers', will also have correlates (often causal) with the ecological and external environments. The second point is that ideas can be expressed and quantified in
terms of the selective environment, perhaps the experimentalist need only
take measurements of this one type of environment, and can safely ignore
the other types so perhaps simplifying his task.

When we speak of the evolution of genetic systems, in heterogeneous
environments, with which type of environment should we be primarily
cconcerned? We will argue that our concern should be with none of the
above (in their entirety), but with a subclass of the selective environment.

11.5 AWAY FROM WORD-MODELS

In this section, we return to two of the models of short-term advantages of
sex in heterogeneous environments, and use them to illustrate how, at least
in principle, these word-models can be operationalized into experimentally
testable hypotheses. We have chosen the two models because they relate to
large-scale variation in time or space and therefore represent our simplest,
or perhaps most naive, expectations as to the type of environmental
variation that may favor genetic variation.

Maynard Smith’s ‘hot genes, wet genes’

Maynard Smith (1978) developed a scenario whereby increased recombin-
atlon between two gene loci would be favored in a temporarily varying
environment. At one locus, the \( A \) allele confers higher fitness in hot
environments while the \( a \) allele confers higher fitness in cold environments.
At the other locus, the \( B \) allele has a higher fitness when the environment is
wet whereas the \( b \) allele has the higher fitness when it is dry. If hot/wet or
cold/dry environments alternate with hot/dry and cold/wet environments,
then direct translation of gene effects as above would favor the cis combina-
tions \((AB, ab)\) alternatively with the trans combinations \((Ab, aB)\) thus
favoring greater recombination among these loci. While this model is very
explicit, as Maynard Smith admits, it is also very contrived. As a conse-
quenCe it is hard to ‘imagine’ how it would work in nature. More to the point,
it is difficult to see how it could be tested, not so much in principle, as in
practice. Specific genes with specific environmental effects would have to be
identified, their fitness effects established under a range of environments,
and those environments then measured over successive time intervals.

Williams’ ‘cod–starfish model’

Williams (1975) pointed out that the genetic variance of sexually produced
progeny is likely to be greater than the variance of asexually produced
progeny. If the environment now changes such that only extreme progeny
types are favored, it is more likely that a sexual progeny array would
contain these extreme phenotypes. Sexual reproduction would thus be favored. This model, in contrast to that of Maynard Smith is extremely general, and in practice difficult to test because of this. One would need knowledge of what factors in the environment are changing (one may measure many, but miss the important one), one would need to know which phenotypes give a high performance in those environments, and one would need to know something about the heritability as well as within progeny genetic variance of those phenotypes.

Both these models are phrased explicitly or implicitly in terms of 'external environments'. However, an essential ingredient for these two models, indeed a necessary condition for them to work, is that there is genotype—environment interaction in fitness, i.e. that the environment be 'selectively heterogeneous'. Both models can be translated to fitness effects of genotypes in different environments. By way of illustration (Fig. 11.3), we have done this

![Diagram](image)

**Fig. 11.3** Diagram showing how the greater fitness of a sexually produced offspring array in the face of a temporally changing environment subsumes an underlying genotype—environment interaction in fitness over time, i.e. a selective environment that is variable in time.
explicitly for the 'cod–starfish model'. When this translation is carried out (as well as from intuitive reasoning) it is evident that we need a particular extreme form of genotype–environment interaction for the models to work.

We can recognize two types of genotype–environment interaction, namely those of the 'crossing type' and those of the 'non-crossing type' (Fig. 11.4). In the non-crossing type, the genetic correlation of phenotypes between environments will be positive and genetic variance will be high relative to genotype–environment interaction. In the crossing type, the genetic correlation of phenotypes between environments will be negative and genetic variance will be low relative to genotype–environment interaction. It can be shown (Shaw, 1986; after Tachida and Mukai, 1985) that a genotype–environment interaction variance component can be expressed as a function of the variances in the individual environments and the genetic correlation among environments. For the two-environment case:

$$2V_{GE} = (V_1 - V_2) + V_1 V_2 (1 - R)$$

where $V_{GE}$ = genotype–environment interaction variance;

$V_1, V_2$ = genetic variance in environments 1 and 2, respectively; and

$R$ = genetic correlation among environments.

Then,

$$V_{GE} - V_G = V_1 V_2 (1 - R) - V_1 V_2,$$

where $V_G = (V_1 + V_2)/2$, or total genetic variance.

From this it follows that if $V_{GE} < V_G$, then $R > 0$ and the genotype–environment interaction is of the non-crossing type. Alternatively if $V_{GE} > V_G$, then $R < 0$ and the genotype–environment interaction is of the crossing type.

For there to be an advantage to genetic variation in heterogeneous environments it is necessary that there be a crossing genotype–environment interaction in fitness. This is indicated empirically either by a negative genetic correlation in fitness across environments (see Via and Lande, 1985, for further discussion of this concept) or by a genotype–environment interaction effect that is greater than the genotype main effect. In other words, the environment not only has to be selectively heterogeneous but it has to be heterogeneous in a rather extreme way. While a crossing type of genotype–environment interaction in fitness is necessary for there to be selection for a 'more open genetic system' in a heterogeneous environment, it is clearly not a sufficient condition, particularly given that there may be transmission costs associated with such genetic systems. It is unclear from such generalized models exactly how large a particular genotype–environment interaction in fitness would have to be to favor a more open breeding system. Nor is it clear that this is even the correct way to phrase the issue. Perhaps we should instead be assessing the degree to which the
Fig. 11.4 Diagram showing difference between non-crossing and crossing genotype-environment interactions, and how this difference results in a positive and negative genetic correlation across environments.

descendants of a particular individual (with a particular genetic system) encounter a selective environment that is heterogeneous in space and time, and what the expected fitness is from the observed responses of the range of genotypes produced by that individual versus the expected fitness from a range of genotypes produced by an alternative genetic system (which could be imposed experimentally). It is probably true that we do not know for any genetic system whether the naturally occurring one generates a greater 'short-term' fitness than say a more open or more closed system.

We next describe an experiment carried out very early in our research program on the success of genetically variable vs. genetically uniform progeny. The experiment was naive in its goals: we simply wished to know whether different genotypes of Anthoxanthum responded differently to spatial environmental heterogeneity. We chose vegetation composition as our main measure of such heterogeneity, since not only was this an environmental variable that in all likelihood affected the performance of Anthoxanthum but it could also be documented relatively easily, without extensive instrumentation. We use this experiment both to illustrate the
existence of genotype–environment interactions as well as to illustrate, after the event, the pitfalls of failing to distinguish external from selective environments.

11.6 AN EXPERIMENT

In 1978, we simulated dispersal of asexual progeny across a spectrum of environments normally encountered by a population of the perennial, self-incompatible grass, *Anthoxanthum odoratum* L., and asked if the environments were heterogeneous, whether the fitness of *Anthoxanthum* was affected by these environments, and whether different genotypes of *Anthoxanthum* reacted differently to different environments. We thus made separate measures of heterogeneity of the ‘external’, ‘ecological’ and ‘selective’ environments in this field. We further asked whether and at what scale genotype × environment interactions were greater than genotype main-effects, since such effects would have to be present for there to be an advantage to genetic variation in a heterogeneous environment.

Plants of *A. odoratum* were collected in May 1978 from a mown field on Duke Campus, Durham, North Carolina (see Fowler and Antonovics, 1981; Antonovics and Ellstrand, 1984, for further details). Collections were made from the area studied by Fowler and Antonovics (1981) and Fowler (1981); 22 genotypes of *Anthoxanthum* were randomly sampled as single tillers, grown in the greenhouse and cloned. In November 1978, 50 tillers of each genotype at the 3–4 leaf stage were individually weighed, and planted into paper tubes filled with soil from the field site. The tubes were 1 cm diameter and 5 cm long, and were made by sewing together folded strips of filter paper (see also Antonovics and Primack, 1982). The planted tillers were kept in the greenhouse for one week during which time they started to root. They were then transplanted into the field; a hole was made in the ground using an apple corer, the paper tube inserted, and the soil pushed back around the tube. The surrounding vegetation was left completely undisturbed. Each plant (hereafter referred to as a ‘transplant’) was marked with a plastic coated wire ring and a plastic toothpick.

The 22 cloned genotypes were planted 20 cm apart in random order in a linear array within each of 50 blocks, there being one transplant per genotype per block. These blocks were themselves arranged contiguously in a linear fashion along three transects spanning the field and approximately centered around the original collection site (Fig. 11.5). Over the next three years, the transplants were scored in May for tiller number and inflorescence number, and in November for tiller number. The ‘environment’ around each transplant was measured in May 1979 in terms of the surrounding vegetation, using a hexagonal 37-point cover grid (Fig. 11.6), with a spacing of 2 cm between points. The grid consisted of two layers of cross wires, with
by-passing life-history stages that could be critical. And while a quantitative genetics approach could circumvent some of this problem by calculating the fitness performance of lines derived from within sibship crosses, it is not entirely clear the extent to which additive vs. non-additive components of variance are important in adaptation of progeny arrays to unpredictable environments. Such an indirect quantitative genetics approach would also be extremely labor intensive.

The connection between genetic variance and environmental variance has been largely an intuitive rather than explicit concept, particularly as far as developing an understanding of how and when open genetic systems provide a short-term advantage in spatially or temporally varying environments. While a number of mathematical and word models have been presented, these models have been difficult to translate into experimental tests of particular hypotheses. Conceptually, there has been confusion between the external measurable environment, the environment as it influences the organism, and the selectively heterogeneous environment. Environments are only selectively heterogeneous if different genotypes have different relative fitnesses in those environments. The ingredients that would be required for genetic variation among a progeny array to be favored have been proposed theoretically, but even for the most obvious cases (e.g. simple spatial or temporal variation) we have no comprehensive quantitative theory couched in terms measurable by the ecological geneticist. Practically, we still need to develop tissue culture technology to obtain replicates of individual genotypes, and to translate such technology into a natural population context so the critical experiments can be performed. Stebbins' (1950) exhortation that the evolution of genetic systems is a subject 'separate enough to be studied by itself' is as true today as it was then. We have barely begun to scratch the surface of many of the major and critical questions in the evolutionary biology of plant breeding systems, and the issue is likely to remain a challenge that will require the integrated efforts of theoreticians, field biologists, and biotechnologists.

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11.9 REFERENCES


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