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The relationship between degree of environmental heterogeneity and genetic polymorphism

1. INTRODUCTION

It has frequently been stated that the extent of genetic variation in populations is related to the degree of heterogeneity of the environment. The reasoning behind this notion was well expressed nearly a quarter century ago by DOBZHANSKY (1955):

> "no one genotype is likely to be a paragon of adaptability, superior to all other genotypes in all environments."

Hence:

> "the adaptedness of a Mendelian population may ... be advanced if it contains a variety of genotypes suited to different adaptive niches and facets on the environment which the population inhabits .... Granted that genetic variability is an instrumentality whereby Mendelian populations master environmental diversity ... populations which control a greater variety of ecological niches will be more variable than those having a limited hold on the environment."

Thus Dobzhansky proposed genetic diversity as an adaptive strategy by which populations cope with environmental heterogeneity and he postulated that genetic diversity would increase with increased heterogeneity of the environment.

The notion that regulation of genetic variability is a strategy by which Mendelian populations adapt to the spatial and temporal structure of the environment has been one of the most actively investigated areas in contemporary population biology. There is now a vast literature on this topic, a literature that has itself been extensively reviewed. Recent reviews of theoretical aspects include those of CHRISTIANSEN & FELDMAN (1975), FELSENSTEIN (1976), HADELER (1976), KARLIN (1976) and LEVIN (1976); and ANTONOVICS (1971), GOULD & JOHNSON (1972), HEDRICK *et al.* (1976), VALENTINE (1976) and WIENS (1976) have reviewed empirical studies. What is the present status of understanding of genetic variability as an adaptive strategy? HEDRICK *et al.* (1976) stated their conclusions as follows:

> "... a substantial amount of circumstantial evidence has accumulated indicating that genetic polymorphisms are related to environmental heterogeneity. There is, however, only a small amount of experimental evidence supporting the hypothesis that environmental heterogeneity is a major factor in maintaining genetic variation."

"Single-locus theory indicates that selection acting differentially in space, coupled with limited migration and/or habitat selection, will maintain a substantial amount of polymorphism .... There have been, however, few documented cases of this in laboratory or other situations where the magnitude and type of selection can be ascertained."

"... many papers will be written before it is clear what proportion of polymorphic loci is maintained or affected by environmental heterogeneity and how environmental differences result in genetic polymorphisms."

In short, the search for relationships between environmental heterogeneity and genetic diversity has not provided clear-cut evidence that such relationships exist.

This ambiguous result is, however, perhaps not surprising when we consider that most studies have treated adaptation in terms of single loci whereas there is an increasing body of evidence from multilocus studies of both natural and experimental populations (e.g. ALLARD *et al.* 1972; CLEGG *et al.* 1972; HAMRICK & ALLARD 1975; ALLARD *et al.* 1977; CLEGG *et al.* in press) that adaptation to specific environmental regimes depends on constellations of genes that act in different stages of the life cycle and affect many different morphological and physiological characteristics. If this is the case the entire genotype as an integrated system of interacting genes, rather than single loci, is the proper framework in which to examine genetic variability as an adaptive strategy. This is the topic considered in this paper. First, we will review the evidence that adaptation does in fact depend on synergistically interacting complexes of genes and show that multilocus Mendelian formulas can be written for ecotypes that occupy specific habitats. Then, we will analyze the question: Do the Mendelian formulas indicate whether there is a relationship between environmental heterogeneity and genetic variability?

2. MULTILOCUS ORGANIZATION

To identify the issues clearly, it is appropriate to discuss the theory of multilocus genetic organization briefly prior to considering experimental evidence that adaptation depends on integrated systems of genes, i.e. whether the genetic structure of populations features coadaptation in the sense of DOBZHANSKY (1955). The simplest model on which we can discuss the genetic basis of coadaptation is one involving just two loci, each with two alleles. Assume that the gametic types $A^{(1)}B^{(1)}$ and $A^{(2)}B^{(2)}$ produce genotypes that are superior in viability and that the alternative gametic types $A^{(1)}B^{(2)}$ and $A^{(2)}B^{(1)}$, produce selectively inferior genotypes. During the life cycle from zygote formation to reproductive maturity viability selection will favor individuals that carry the 11 and 22 combinations of alleles, causing their frequency to increase from early stages in the life cycle to the reproductive stage. If the two loci are unlinked, i.e. they are located on different

chromosomes or if they are located 50 or more crossover units apart on the same chromosome, free recombination will occur at gametogenesis and this will reduce the frequency of the favored combinations of alleles. Thus the recombination and segregation that occur during reproduction will undo the work of selection, and the association between the favored alleles will not persist. If, however, the loci are physically linked on the same chromosome, the suppression of recombination due to the linkage will tend to bind the concordant allelic complexes together. Theoretical studies (review in TURNER 1967) have shown that when the crossover value is small enough relative to the intensity of selection, stable nonrandom associations of alleles can develop and persist in the population; and if the linkage is very tight and selection sufficiently strong, the genetic variability will become so organized that only two among four possible gametic types, and only three among 9 possible genotypes, will occur in the population. In other words, the correlation between alleles will be complete ($|r| = 1$), and $|D'|$, the relative gametic phase disequilibrium (linkage disequilibrium) parameter will also take its maximum value of unity.

Theoretical studies have shown that any factor that restricts recombination will have an effect similar to linkage in binding concordant nonalleles together and that positive assortative mating in particular can lead to sharp restriction of recombination (JAIN & ALLARD 1966; WEIR & COCKERHAM 1973). This can be illustrated by considering two individuals with genotypes $A^1A^1B^1B^1$ and $A^2A^2B^2B^2$ in a predominantly selfing population. Due to the predominant selfing these individuals will produce only $A^1A^1B^1B^1$ and $A^2A^2B^2B^2$ progeny generation after generation and the A^1B^1 and A^2B^2 alleles will remain correlated within both lineages, just as if they were linked. But when hybridization occurs between the two lineages, producing the $A^1A^2B^1B^2$ heterozygote, segregation and recombination will occur, the A^1B^2 and A^2B^1 gametic types will be produced, and the association will be broken. When such intercrosses between lineages occur only once in 50 generations or more, as is the case in many plant species, it is obvious that the frequency of heterozygotes will be low and hence that recombination will be severely restricted because effective crossing over occurs only in heterozygotes and not in homozygotes.

It is helpful to have a quantitative measure of the restriction of recombination that is caused by linkage on the one hand and by mating system on the other hand, and for present purposes the rate at which D, the gametic phase disequilibrium parameter, converges to zero for <u>neutral</u> alleles is convenient. For two loci this rate is given by

$$1 - \frac{1}{2}\{\frac{1+\lambda+s}{2} + [(\frac{1+\lambda+s}{2})^2 - 2s\lambda]^{\frac{1}{2}}\},$$

in which λ is the amount of linkage ($0 \leq \lambda \leq 1$) and s is the probability ($0 \leq s \leq 1$) that an individual chosen at random in any generation is the offspring of a single individual in the previous generation ($t = 1-s$ is the

probability that it had two parents) (WEIR & COCKERHAM 1973). Note that λ and s enter this expression in the same way and that the magnitude of their effect on rate of decay of D is equal. With random mating (s = 0) and no linkage (λ = 0, or c = 0.5, where c is the crossover value), one half of any disequilibrium is lost in the next mating cycle. With random mating but tight linkage (λ = 0.98 or c = .01) only one percent of the disequilibrium is lost per generation. This is the well-known result that the asymptotic approach of D to zero for neutral alleles under random mating is at the geometric rate of (1-c) per generation so that D in any generation, t, is given by $D_{(t)} = (1-c)^t D_{(0)}$. With no linkage but 98 percent self fertilization, the rate of decay of D is also one percent per generation or 1/50 as large as with random mating and no linkage. And, when tight linkage is combined with heavy selfing, recombination is reduced to the point where little selection is required to hold favorable combinations of alleles together. With complete selfing no recombination will occur and all existing allelic combinations, both favorable and unfavorable, are expected to remain together indefinitely. Populations that reproduce by complete selfing are therefore not favorable for the study of coadaptation because all existing allelic combinations, whether favorable or unfavorable, will be locked together permanently. However, this problem appears to be hypothetical rather than real because, to our knowledge, no plant species is completely self fertilizing.

It is important to note a difference in the effect of restriction of recombination due to linkage and that due to inbreeding. Linkage keeps combinations of alleles involving loci that are physically close on the same chromosome from breaking up; but it does not preserve allelic combinations for loci located on different chromosomes. Inbreeding, in contrast, restricts recombination between all loci, whether on the same or different chromosomes. Theory therefore predicts that as the level of inbreeding increases the entire genotype will become more closely bound together and hence that inbreeding may be a very efficient mechanism for organizing the whole of the gene pool into an integrated system. It also follows that inbreeding populations should be much more favorable than random mating populations for investigating coadaptation experimentally. This is because all loci in inbreeding populations behave as if they are linked in some degree and, consequently, it is unnecessary to search for difficult-to-find closely linked loci upon which to base experiments designed to detect nonrandom associations of alleles.

The introduction of electrophoretic techniques into population genetics have provided a means by which precise multilocus Mendelian formulas can be written for ecotypes that occupy specific habitats. This is now possible because electrophoretic banding patterns can be identified precisely with genotype so that all individuals can be scored unambiguously as a homozygote or heterozygote at each locus. We will now illustrate the results of electrophoretic analysis of population structure on a multilocus basis with

examples taken from our own studies of the Slender Wild Oat, *Avena barbata* Brot. The mating system of this species, one of approximately 98 percent of self fertilization, is nearly ideal for studies of coadaptation, because this amount of inbreeding is expected to protect favorable complexes of alleles from break up due to segregation while at the same time leaving ample free genetic variability for evolutionary change in response to spatial and/or temporal variations in the environment.

3. *AVENA BARBATA*

A. barbata was introduced into California from the Mediterranean basin approximately 250 years ago. Records indicate that its spread was rapid and that it soon became a prominent component of grass and oak-savanna communities in California. *A. barbata* is a tetraploid (2N = 4X = 28) winter annual that germinates with the first wetting rains in the fall and continues to grow throughout the winter. It does not survive hard frost; hence it is not unexpected that it is found only in areas where mean minimum January temperatures remain about -4°C (Fig. 1). Also, there are limitations to its drought resistance and it does not occur in areas where mean annual rainfall is less than 250 mm, also indicated on Fig. 1. These two parameters appear to identify the major climatic limitations to the distribution of the species in California.

In 1972 CLEGG & ALLARD reported the results of a survey of allelic variability at five enzyme loci and two loci governing morphological variants in 16 populations of *A. barbata* in California. This survey showed that all populations in southern California and the semiarid grasslands bordering the central valley are monomorphic for all of the seven loci assayed. Furthermore, all populations are fixed for the same allele at each of these seven loci. In other words only a single homozygous genotype occurs in this large geographical area encompassing about half of the area of California. This survey also showed that this same genotype is the exclusive one in populations occupying the most xeric sites in northern California, e.g. sites on steep slopes with western exposure. On the other hand, populations occupying the most mesic habitats in northern California (e.g. bottomland sites with deep dark soil) are monomorphic and fixed for a genotype carrying the opposite set of alleles at these seven loci. However, the great majority of habitats in northern California are intermediate between the xeric and mesic extremes and populations occupying these intermediate habitats were found to be polymorphic for the seven loci. Furthermore, allelic frequencies in the intermediate habitats were found to be closely correlated with degree of xerism, i.e. the frequency of the "xeric" set of alleles increased with increasing xerism of the habitat.

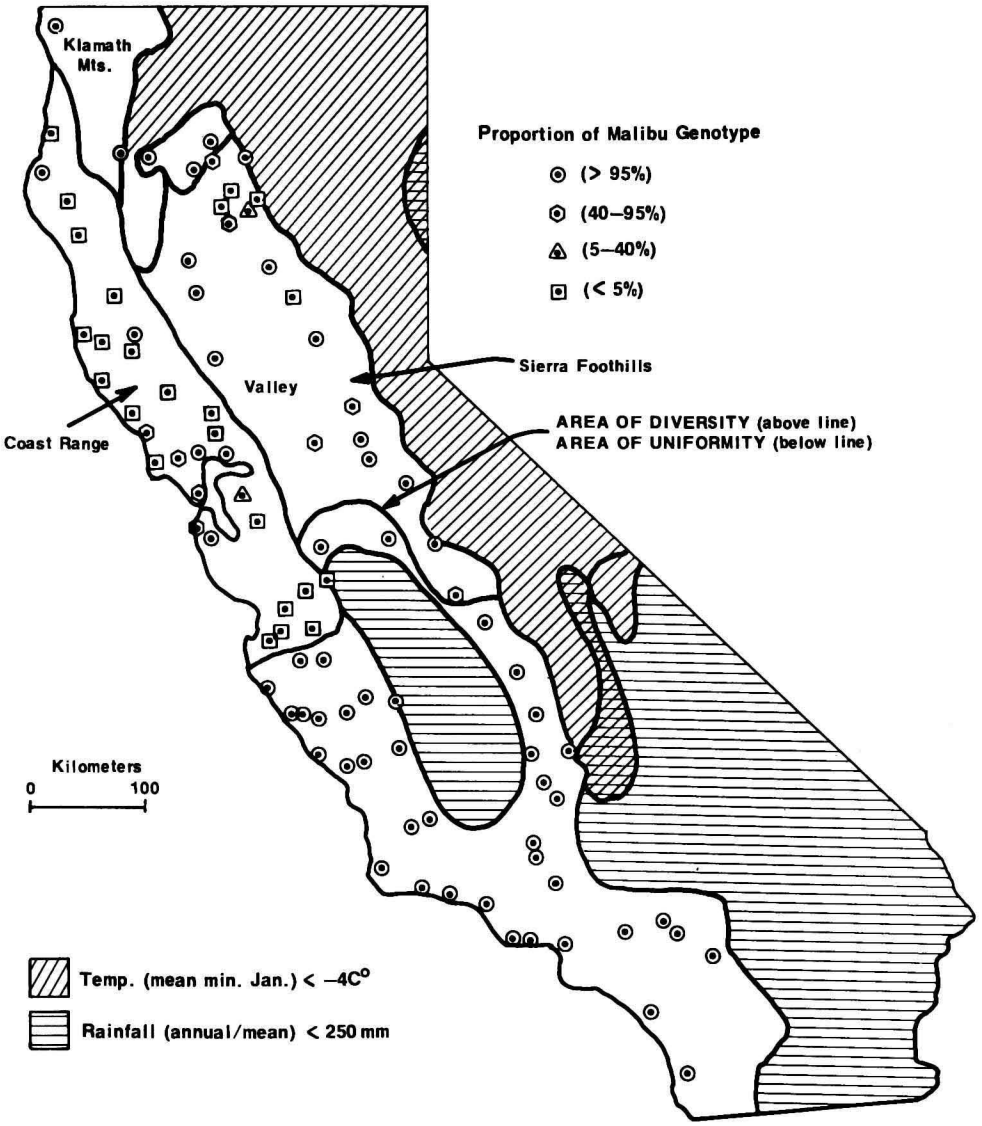

FIG. 1. Avena barbata *collection sites in California, factors limiting distribution, proportion of Malibu type, and genetic regions* (MILLER *in preparation*)

In the topographically diverse coast range of northern California, changes from mesic to xeric habitats frequently take place over very short distances and, to determine whether the remarkable correspondence between allelic frequencies that occurs over most of California is repeated on a micro-geographical scale, detailed studies were made of some populations that span transitions from mesic to xeric vegetational associations in distances of 200 meters or less (HAMRICK & ALLARD 1972; ALLARD *et al.* 1972). The results

revealed a consistent pattern of change in allelic frequencies correlated with environment. A typical result was obtained on a hillside transect, designated CSA, located about one mile north east of Calistoga in the Napa Valley. In a distance of less than 200 meters, the habitat on this hillside changes from highly mesic on the valley floor at the bottom to highly xeric on the steep west-facing slope at the top of the hillside. Although the increase in xerism is fairly regular up the hillside, there are some deviations from regularity associated with local topography, such as a small well-watered depression in the hillside. It was found that allelic frequencies tracked the environment almost exactly on this hillside transect: "mesic" alleles decreased steadily from the mesic bottom to the xeric top, except in those local areas where the habitat did not follow the general trend of increasing xerism. Correlation coefficients between alleles at pairs of loci are all of the order of 0.90 and significant statistically. Thus as the "mesic" allele at any locus changed in frequency a similar change in frequency occurred in "mesic" alleles at the other loci, and these changes in allelic frequency reflected changes in degree of xerism with remarkable precision.

To determine the extent to which these loci are inherited as a unit requires that sufficiently large samples be taken from individual populations to permit comparisons of observed enzyme five-locus gametic frequencies with expected frequencies computed as products of observed single-locus frequencies. When such studies were made in polymorphic populations, it was found that two among the $2^5 = 32$ possible 5-locus gametic types were in great excess over expectations based on single-locus allelic frequencies. These were the two gametic types characteristic of xeric and mesic habitats, respectively. There was, of course, a corresponding deficiency among the remaining 5-locus gametic types and it is interesting that this deficiency tended to be greatest for the more extreme recombinants relative to the two favored types. The relative gametic phase disequilibrium parameter (D'), averaged over pairs of loci, usually took more than 50 per cent of its maximum possible value showing that these five loci, while highly correlated in their inheritance, are by no means completely associated. Thus "leakage" in the system provides free genetic variability for quick response to temporal changes in the environment and for opportunistic colonization of unusual habitats. Allozyme frequencies for the same five loci have been examined in Mediterranean populations of *A. barbata* and the two complexes found in California have not been found. The patterns of coadaptation, correlated with environment, that are found in California have therefore developed since the introduction of this species more than two centuries ago.

In addition to the enzyme loci and the morphological variants, several quantitative characters have been studied both in nature and in common garden experiments (HAMRICK & ALLARD 1972, 1975). These studies show that individuals homozygous for the mesic and xeric complex of enzyme alleles, taken from the

same population, differ in time to maturity, stature, tillering capacity, outcrossing rates and other quantitative characters. Thus loci governing these quantitative characters are also components of the gene complexes marked by the enzyme loci. Measurement characters, such as height and time to maturity, are almost certainly governed by many genes of small effect and these genes are presumably distributed over many chromosomes. The xeric and mesic gene complexes therefore include loci located on several chromosomes and most likely on all of the N = 14 chromosomes of *A. barbata*. This provides experimental support for the theoretical prediction that restriction of recombination due to inbreeding helps in holding together favorable associations of alleles of unlinked loci. It also shows that the distribution of *A. barbata* in typical grassland and oak savanna habitats in California can be accounted for in large part on the basis of two ecotypes with Mendelian formulas that can be specified in terms of the enzyme loci. Populations that occupy extreme xeric habitats are made up exclusively of the ecotype whose genetic formula is identified by the multilocus homozygous xeric set of allozymes. Populations occupying extreme mesic habitats have Mendelian formulas marked by the homozygous mesic set of allozymes. Populations that occupy intermediate habitats are polymorphic and large populations are expected to contain all of the $3^5 = 243$ possible genotypes specified by the five enzyme loci. This is because the average level of heterozygosity at any locus is about 4 per cent and this level of heterozygosity provides for sufficient recombination to allow all 32 possible gametic types to appear in each population in each generation. However, the important point is that the "xeric" and "mesic" homozygotes are both found in much higher frequency in polymorphic populations than predicted on the basis of expectations calculated as products of the five single-locus genotypic frequencies. The observed excesses of these two homozygotes in segregating populations provide strong evidence that they represent interacting complexes of genes favored by selection. LEWONTIN (1974) did not take the genetic facts into account in discussing *A. barbata* and he was led to the erroneous conclusion that the selfing that occurs in this species results in "lack of recombination". This in turn led him to conclusions regarding multilocus associations of alleles that are at variance with both theoretical expectations and the observed results.

4. ADDITIONAL PATTERNS OF GENETIC AND GEOGRAPHICAL VARIABILITY

The distribution of genetic variability in *A. barbata* in California has more recently been mapped much more precisely by examining 97 additional populations (Fig. 1) and extending the number of loci assayed from seven to 35. This more extensive study provides additional information concerning the allelic composition and the geographical distribution of the "xeric" complex of alleles and it also shows that seven additional correlated complexes of genes each

marked by a specific Mendelian formula for enzyme loci, occur in specific habitats.

Perhaps the most striking feature of the more detailed study is the impressive confirmation it provides for the homozygosity of the xeric complex of enzyme loci in the more arid regions of Southern and Central California: it shows that the xeric genotype is in fact fixed for all of the 35 loci analyzed, i.e. all populations in this region are made up exclusively of the same 35-locus homozygote. This genotype has been designated the Malibu genotype after one of the sites in Southern California in which it occurs.

Analysis of electrophoretic genotypes in the 97 additional populations distributed over California reveal a striking pattern of variation for the Malibu genotype. As shown in Fig. 1, all populations in the southern half of the range of *A. barbata* in California are fixed for this genotype. This area is consequently designated the area of uniformity. The remainder of the range is designated the area of diversity because the frequency of the Malibu genotype varies widely and additional multilocus genotypes appear. The area of diversity can be broken into four main subregions based on geography and frequency of the Malibu genotype: (1) the Sacramento Valley and Sierra foothills in which populations are sometimes polymorphic and the frequency of the Malibu type usually exceeds 40 per cent; (2) two local areas within the valley-foothill region in which Malibu is absent; (3) the Klamath mountains where all populations are fixed or nearly fixed for Malibu; and (4) the coast and the coastal ranges in which a great diversity of types occur.

Is the Malibu genotype highly adapted to xeric conditions as suggested by earlier work? Evidence on this point comes from samples taken from paired locations located less than 100 meters apart within six sites where there was visible ecological differentiation. The paired locations were rated subjectively as to degree of xerism on the basis of exposure, slope, drainage and associated vegetation. Samples were then taken and scored electrophoretically, with the results given in Table 1.

TABLE 1. *Frequency of the Malibu complex in paired mesic and xeric subpopulations located less than 100 meters apart* (MILLER *unpublished*)

Location	Mesic subsite	Xeric subsite
Balls Ferry*	0.00	0.00
Del Loma	1.00	1.00
Paicines	0.00	1.00
Hooker Creek	0.00	1.00
Weott	0.00	1.00
Bells Station	0.00	0.26

* does not contain Malibu complex

One site (Del Loma) was highly xeric and both subdivisions were fixed for the Malibu genotype. In another site (Balls Ferry) the Malibu genotype did not occur. However, in three of the four remaining sites, the xeric subsites were fixed for the Malibu genotype and in the fourth site (Bells Station), which was judged to be generally mesic, only the more xeric subsite contained the Malibu genotype.

Fig. 2 gives an overlay of the frequency of the Malibu genotype on annual rainfall data for California. This figure shows that the dividing line between the area of uniformity and the area of diversity is the 500 mm rainfall line,

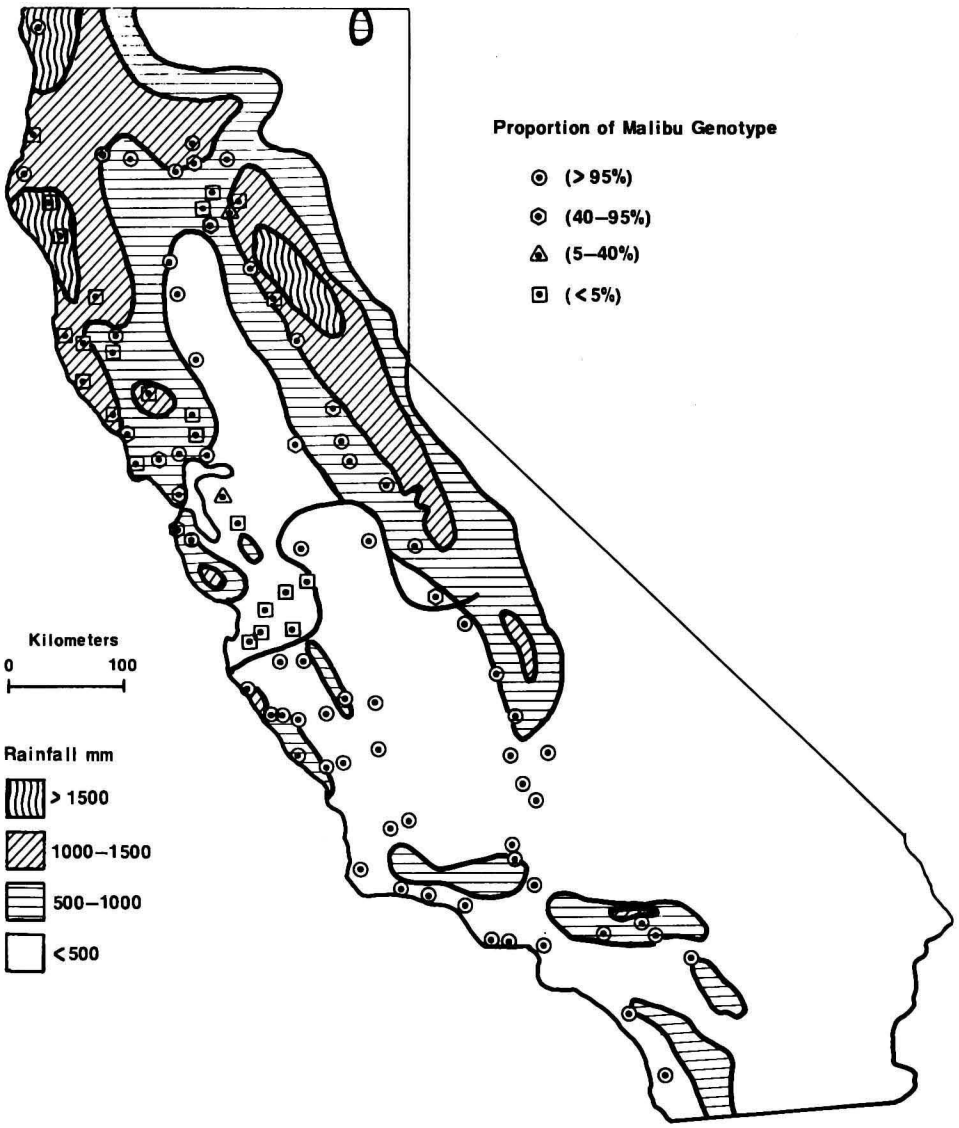

Fig. 2. *Mean annual rainfall and the distribution of the Malibu genotype in California* (MILLER *in preparation*)

i.e. all polymorphic populations and all non-Malibu populations occur above the 500 mm line. There is one exception: the area to the east of Monterey Bay where non-Malibu types occur in an area with less than 500 mm of rainfall. This is a very foggy area in which fog drip is known to be an important supplement to the light rainfall in the growing of specialty crops. The distribution of the Malibu type thus suggests a model for the relationship between environment and genotype. Malibu is an ecotype highly adapted to dry areas. However, once a moisture threshold is reached, other genotypes become competitive. Local factors can be very important. In the Klamath Mountains, for example, most populations are fixed or nearly fixed for the Malibu genotype, even though rainfall exceeds 1000 mm. In this area, however, *A. barbata* is restricted to very steep south- and west-facing slopes with shallow or sandy soils, i.e. to habitats that are extremely xeric despite the high rainfall.

Fig. 3 gives the distribution of several additional correlated complexes of alleles that were observed in the area of diversity. In this figure the different allelic complexes are given in code. There are three major groups of genotypes: (1) the Malibu complex, the basic xeric type for which all alleles are coded 1; (2) the mesic complex of the early studies; and (3) the Geyserville complex, which was found in only a single population in the early studies. Two variants occur within each the Malibu and mesic complexes, and three variants in the Geyserville complex, bringing the total number of major complexes to seven. In four locations a complex mixture of genotypes was found. Note that populations with a particular complex of alleles are usually widely dispersed geographically and when two nearby populations have the same complex of alleles, they are usually separated geographically by a population with a different genotype. The distribution of allelic complexes thus suggests a mosaic pattern rather than clinal changes in the environment.

5. ENZYME DIVERSITY IN ISRAEL

Thirty-one populations collected over a wide geographical area have been assayed electrophoretically for seven enzyme systems to determine patterns of enzyme variability in *A. barbata* in Israel (KAHLER *et al.* in preparation). Phenotypic frequencies were scored in nine zones of enzyme activity, probably representing 27 loci. The results show that all loci are polymorphic in Israel and that extensive variability occurs both among populations and within populations. Each population differed from each other population with respect to enzyme genotype and no population was monomorphic for all enzyme loci. In Israel *A. barbata* is therefore more variable genetically than it is in California.

Principal component and multiple regression analyses were used to determine whether there are correlations between environmental parameters and enzyme

GENOTYPIC COMPLEXES										
B	Is	6Pg	Lap	E_1	E_2	E_3	Cp	Ap	P	Code
1	1	1	1	1	1	1	1	1	1	11
1	2	1	1	1	1	1	1	1	1	12
2	2	2	2	2	1	2	1	2	2	21
1	2	1	2	2	1	2	1	2	2	22
2	2	3	1	5	2	2	2	3	1	31
1	2	3	1	3	2	2	2	3	1	32
2	2	2	3	4	2	2	2	3	1	33
								Other Genotypic Complexes		40

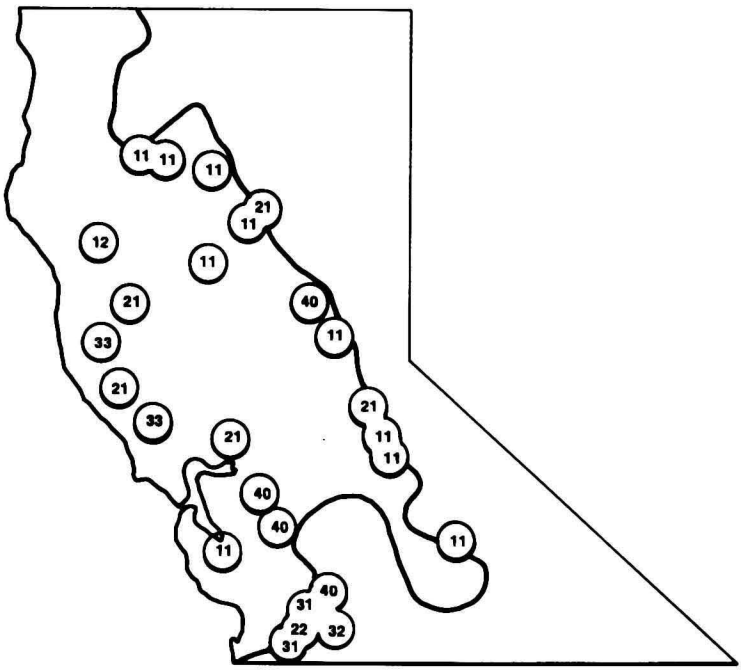

FIG. 3. *Distribution of* Avena barbata *genotypic complexes in the area of diversity* (MILLER *in preparation*)

phenotypes in Israel. It was found that temperature related variables and, to a lesser degree, moisture regime variables are correlated with particular enzyme phenotypes. In six out of seven instances temperature related variables were moderately to highly correlated with phenotypic frequencies and in three of seven cases there were moderate associations with moisture regime variables. Temperature and moisture are clearly important factors in adaptation in both

Israel and California, although temperature appears more directly implicated in Israel and moisture more implicated in California.

When an overlay was made of phenotypic frequencies on map locations in Israel, it was found that populations with high frequencies of particular phenotypes were widely dispersed geographically. Also, when phenotypic frequencies were similar in nearby populations, a population with a very different phenotypic frequency was usually located in between. Thus, as in California, isozyme frequency variations appear to reflect a mosaic pattern rather than clinal changes in environmental variability. The importance of this observation is that clinal patterns of genetic variability can arise through drift of neutral alleles (KARLIN & RICKTER-DYN 1976) whereas mosaic patterns are difficult to explain except on the basis of selection.

6. ENVIRONMENTAL HETEROGENEITY AND GENETIC VARIABILITY

We are now in a position to address the question we set out to analyze: Do multilocus Mendelian formulas indicate whether a relationship exists between environmental heterogeneity and genetic variability? To answer this question we must establish: (1) that populations occupying different habitats in an area differ genetically; and (2) that the observed genetic differences are related to variations in the environment of these habitats. With respect to the first of these issues, the multilocus Mendelian formulas make it clear that the extent of genetic variability differs widely from area to area for *A. barbata*. The entire southern half of California is an area of genetic uniformity in which all populations contain the same 35-locus homozygous enzyme genotype. Israel, in contrast, is an area of genetic variability: all of the enzyme loci assayed are variable and all of the populations surveyed are polymorphic for some loci. The northern half of California differs from both southern California and Israel with respect to genetic variability. In this area some populations are monomorphic and some are polymorphic; further, the polymorphic populations differ widely in degree of polymorphism.

This brings us to the second issue above, i.e. whether these observed differences in genetic variability can be related in a meaningful way to variations in the environment. Unfortunately, we do not know which aspects of the environment are pertinent in most cases. However, the above data provide information concerning the way *A. barbata* perceives the environments of various areas. In Israel each of the 31 populations surveyed has its unique multilocus enzyme genotype and the populations also differ substantially from each other with respect to within-population genetic variability. The observed genetic differences among the populations indicate that the environment differs from place to place in Israel, i.e. that *A. barbata* perceives the environment as spatially heterogeneous, or coarse grained, in the sense of LEVINS & MacARTHUR (1966). The genetic variability within all populations indicates

that they also perceive the local environment as coarse grained, either spatially on a microscale or temporally. Correlations with temperature and moisture suggest that these are two of the environmental factors implicated. However, too little is known about environmental heterogeneity in Israel to relate it to the observed genetic variability in any meaningful way other than to say that *A. barbata* perceives the environment as heterogeneous on both macro- and microgeographical scales and that the adaptive strategy adopted is one of genetic variability.

The southern half of California is the opposite case from Israel with respect to extent of genetic variability. All of the 35 loci assayed were monomorphic for the same set of alleles and these loci therefore perceive the environment as fine grained. This region, taken by itself, therefore also provides little information concerning the relationship between environmental heterogeneity and genetic variability other than indicating that genetic uniformity can be a workable adaptative strategy even in an area as large, topographically diverse, and environmentally heterogeneous as the southern half of California.

The northern half of California is an area of genetic diversity in which populations from different places are often strikingly different from each other genetically. Several coadapted allelic complexes occur in this area, indicating that *A. barbata* perceives the environment of northern California as spatially heterogeneous on a macrogeographical scale.

Let us now focus on one pattern that is particularly useful in relating genetic variability to variations in the environment. This is the pattern of monomorphism and polymorphism associated with the xeric (Malibu) and mesic complexes of alleles of the grassland and grass-oak savanna habitats, which are the typical habitats of *A. barbata* in California.

In southern California all populations are fixed for the xeric complex but in the northern half of California most populations are polymorphic. However, some populations in the north are monomorphic. Populations that occupy xeric sites, such as those located on steep slopes with thin rocky soils, are monomorphic for the xeric Malibu complex of southern California. Populations that occupy mesic sites, such as well-watered meadows with deep soils, are monomorphic for an opposite set of alleles, the mesic set. The monomorphic populations thus occupy identifiable habitats which they perceive to be environmentally homogeneous. The question to be asked is whether the sites occupied by polymorphic populations, which the populations perceive as coarse grained, are visibly more heterogeneous environmentally than sites occupied by monomorphic populations. Evidence has already been cited that this is the case and a recent detailed mapping of the CSA hillside (HAMRICK, unpublished) provides striking support that the habitats occupied by polymorphic populations are in fact conspicuously heterogeneous on a microgeographical scale.

The CSA hillside is transitional between two vegetation types. The bottom of the hillside is a well-watered grassland area with deep dark soil. The top of the hillside, less than 200 meters distant, is a steep west-facing slope with rocky light-colored soil occupied by mixed patches of brush and grass. Total change in altitude is about 30 meters. *A. barbata* occurs in 23 patches on the hillside (Fig. 4), each of which was classified into one of five

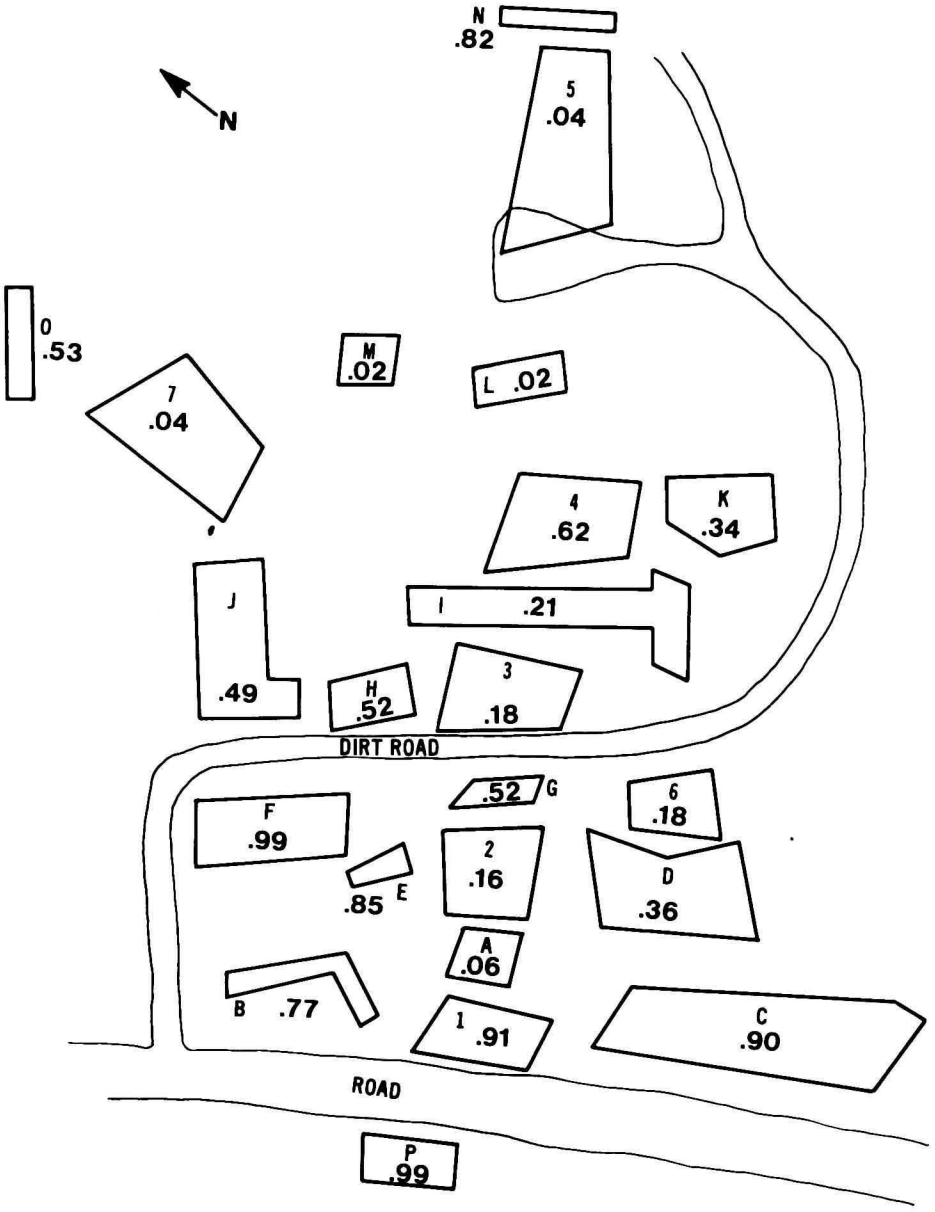

FIG. 4. *Distribution of* Avena barbata *in 23 locations on the CSA transect. Decimal fractions give genetic identity values (Nei) for each patch with the "mesic" complex of alleles. The environment classification of each patch is given in Table 2* (HAMRICK *unpublished*)

environmental categories (mesic, intermediate mesic, intermediate, intermediate xeric, xeric) on the basis of its topographical, soil, and vegetational features. Two of the patches (2 and 4) were subdivided into 6 subsites, each of which was classified environmentally (Fig. 5). This environmental classification showed that, although xerism increased from the bottom to the top of the hillside, the environment of the hillside is a very complex mosaic of micro-habitats. A genetic classification of the hillside was obtained by

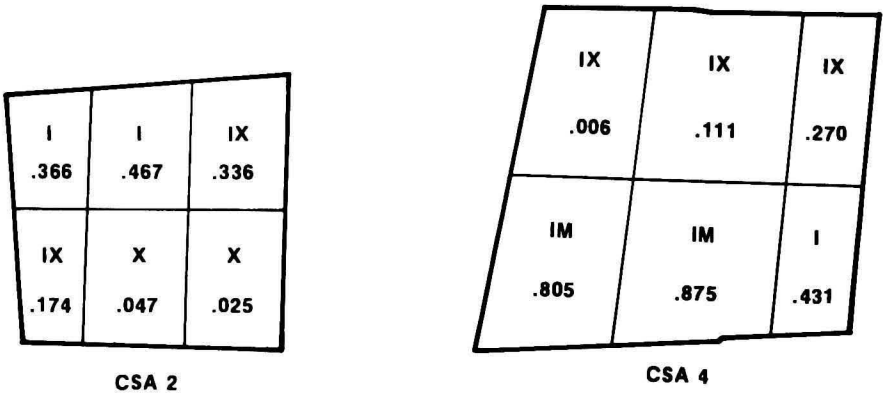

FIG. 5. *Subdivisions of the CSA2 and CSA4 sites. Letters give the environmental classification:* X, *xeric;* IX, *intermediate xeric;* I, *intermediate;* IM, *intermediate mesic. Decimal fractions give genetic identity values (Nei) for each subdivision with the "mesic" complex of alleles* (HAMRICK *unpublished*)

assaying samples of *A. barbata* taken from each of the 23 patches for allozyme genotype. The results, given in Fig. 4 and Table 2, show that the frequency of mesic and xeric alleles differ sharply from place to place on the hillside and also that the agreement between the environmental and the genetic classifications is very close. Agreement was also very close between the environmental and genetic classifications for the subsites of CSA2 and CSA4, as shown in Fig. 5.

A polymorphic index, defined as

$$\text{P.I.} = \frac{1}{m} \sum_{i=1}^{m} \sum_{j=1}^{n_i} p_{ij}(1-p_{ij}),$$

where m is the number of loci, n is the number of alleles per locus, p_{ij} is the frequency of the j^{th} allele at the i^{th} locus, was calculated as a measure of genetic variability. This index is equivalent to the probability of heterozygosity at a locus, assuming Hardy-Weinberg equilibrium; thus with two

TABLE 2. *Genetic identity values (Nei) with the "mesic" genotype for each of the 23 patches on the CSA transect* (HAMRICK *unpublished*)

Mesic	Intermediate mesic	Intermediate	Intermediate xeric	Xeric
F (.99)	B (.77)	O (.53)	D (.36)	6 (.18)
P (.99)	4 (.62)	H (.53)	K (.34)	3 (.18)
I (.91)		G (.52)	I (.21)	2 (.16)
C (.90)		J (.49)		A (.06)
E (.85)				7 (.04)
N (.82)				5 (.04)
				M (.02)
				L (.02)

alleles at each locus, as in the present case, this polymorphic index can take values between zero and 0.5. Actual P.I. values were found to be zero or near zero for the environmentally uniform mesic and xeric sites at the bottom and top of the hillside, respectively. Along the transect P.I. values were found to be correlated with the degree of heterogeneity of the local environment and they reached values of 0.46, which is near the maximum possible value of 0.50, in the environmentally most heterogeneous locations on the hillside, such as CSA4.

These results thus provide strong evidence that *A. barbata* perceives the environment of this hillside as spatially heterogeneous and that the extent of genetic variability is very closely correlated with the degree of spatial heterogeneity of the environment. It should be noted that the balance between mesic and xeric factors of the environment fluctuates with the differences in amount and distribution of rainfall that occur from year to year in California. Thus, in extremely dry years, the most mesic patches no longer appear uniform environmentally but become visibly heterogeneous. Similarly, in wet years more xeric patches also become visibly more heterogeneous. It is therefore evident that environmental heterogeneity has a temportal as well as a spatial component.

7. ADAPTIVE STRATEGIES IN *AVENA BARBATA*

Theoretically the most efficient strategy for coping with heterogeneous environments is the development of an "all-purpose" genotype with sufficient phenotypic plasticity to perform well in each of the environments that is likely to be encountered. The observed monomorphism for electrophoretically detectable variants in extreme xeric and mesic habitats indicates that genetic

uniformity is in fact one of the adaptive strategies that has been adopted by *A. barbata*.

In this connection it should be noted that *A. barbata* is a diploidized tetraploid, i.e. that regular bivalent formation occurs between the 7 pairs of chromosomes of each of the two ancestral genomes, giving 14 chromosome pairs of meiosis. This has important implications concerning genetic variability that are illustrated in Fig. 6 in terms of the genetics of the enzyme 6-phosphogluconate dehydrogenase (6-PDGH). Two types of families are

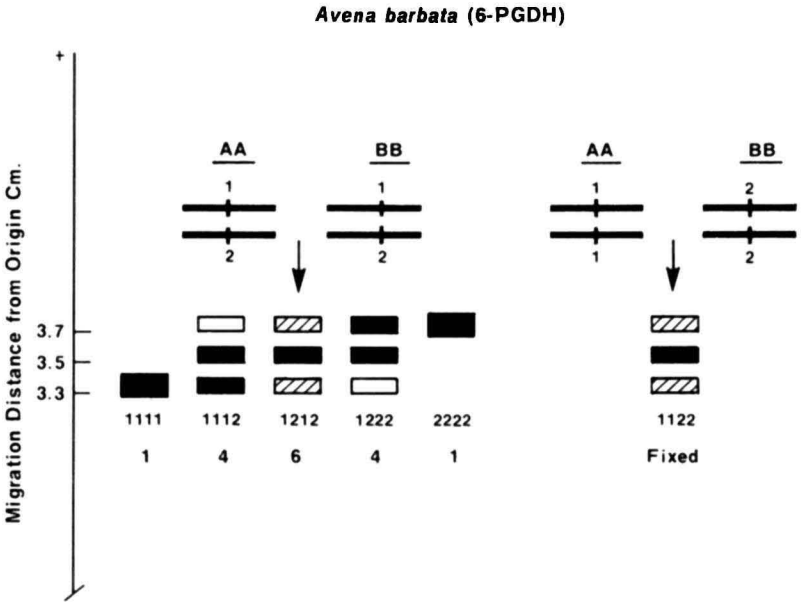

FIG. 6. *Diagramatic representation of "fixed heterozygosity" for 6-PGDH in* Avena barbata. *Left: duplicated 6-PDGH locus is heterozygous for alleles 1 and 2 in both genomes, giving a two-locus segregation (1/16, 4/16, 6/16, 4/16, 1/16). Right: Genome A is homozygous for allele 1 and Genome B is homozygous for allele 2, leading to formation of a fixed intercistronic "hybrid" enzyme* (KAHLER *et al. in preparation*)

found when plants with one of the phenotypes of this enzyme (designated $A_1A_2B_1B_2$ and $A_1A_1B_2B_2$ in Fig. 6) are self pollinated and progeny tested: some families segregate in a 1/16:4/16:6/16:4/16:1/16 ratio whereas other families include only individuals like the maternal parent. The explanation is the $A_1A_2B_1B_2$ maternal individuals are heterozygous in both genomes, and hence segregation in their progeny follows a two-locus pattern, while $A_1A_1B_2B_2$ maternal individuals are homozygous in both genomes, and there is no

segregation. $A_1A_1B_2B_2$ individuals, which are homozygous for different alleles in their two ancestral genomes, thus form a hybrid enzyme of intercistronic origin and they are fixed for all three forms of the enzyme. There is substantial evidence to indicate that biochemical diversity due to this "fixed heterozygosity" is high in *A. barbata*. The key point is that populations that have been judged to be devoid of genetic heterogeneity on the basis of enzyme phenotypes, such as the populations in the area of enzyme locus uniformity, may in fact be little less diverse biochemically than polymorphic populations. Hence caution is called for in interpreting the results of electrophoretic surveys of genetic variability especially in polyploids. Further, increasing evidence that evolution by gene duplication is a common phenomenon indicates that this caveat should also be heeded in studies involving diploids, particularly when the formal genetics of the enzyme variants have not been worked out, as has usually been the case.

There is another reason for suspection that populations monomorphic for electrophoretically detectable variants are not entirely devoid of genetic variability: studies of measurement characters made long before electrophoretic methods were used in population genetics show that there is extensive variability for such characters both within and between populations (ALLARD unpublished). In these studies seeds collected from random individuals in nature were sown in replicated common garden experiments and the resulting progenies were measured for continuously varying characters, such as flowering time and height. Significant differences were found in progeny means which indicates that the populations are genetically variable respecting quantitative characters. In addition responses were obtained when plus and minus selection was practiced within progenies derived from single plants. Response to such selection provides clear evidence that at least some of the loci governing each measurement character are heterozygous in the natural populations. These common garden experiments also showed that the mean value for each population differed significantly from the mean of each other population, and hence that each population differs genetically from each other population respecting measurement characters. The adaptive strategy adopted with respect to the measurement characters is therefore one of genetic variability. This illustrates the point that different adaptive strategies may be adopted for different loci and that no single class of loci, such as the enzyme variants, or those governing measurement characters, gives a complete picture of the relationship between environmental heterogeneity and genetic variability.

The area of diversity in northern California illustrates another adaptive strategy that has been adopted by *A. barbata*. In the southern half of California all 35 enzyme loci are monomorphic and in northern California many of these are also monomorphic in all populations. However, the remaining enzyme loci are polymorphic in many populations in northern California. Thus, on one side of environmental threshold associated with the 500 mm rainfall

line, the adaptive strategy is one of genetic uniformity for all enzyme loci while, on the other side of this line, the strategy is a mixed one featuring genetic uniformity for some loci and genetic variability for other loci. In Israel all of the enzyme loci are variable. Hence, with respect to the enzyme loci, Israel represents the extreme case in which the adaptive strategy is one of genetic variability for all enzyme loci.

The area of diversity in California illustrates still another adaptative strategy that has been adopted by *A. barbata*, namely the strategy of evolving different multilocus complexes of genes for the colonization of habitats that differ from the standard grassland and oak savanna habitats in which the species typically occurs in California. Seven major coadapted complexes have been identified thus far and almost certainly additional complexes will be found as the genetic mapping of *A. barbata* proceeds in California. In Israel every population of *A. barbata* appears to be genetically different. Thus the evolution of ecotypes adapted to specific habitats, each marked by a particular set of enzyme alleles, has evidently proceeded further in Israel, where *A. barbata* is endemic, than in California where it is a recent introduction.

8. CONCLUSIONS

The studies reviewed indicate that adjustment of genetic variability is a strategy by which populations of *A. barbata* cope with variations in the environment. However, the results also show that relationships between environmental heterogeneity and genetic variability are complex and that identification of patterns of relationship requires information concerning the genetic system on a multilocus basis together with detailed coordinate information concerning the responses of populations to the environment.

9. ACKNOWLEDGEMENT

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VAN DELDEN (Groningen): Have you investigated whether there is variation in the amount of selfing in the different parts of your populations? Looking at the large-scale variation pattern, you find one homozygous genotype in the south and in the xeric environments. I can imagine that in the polymorphic regions the amount of outbreeding is higher, causing a higher degree of polymorphism. This is also suggested by the data, derived from the small-scale variation, on genetic identities. These values were very low for the xeric environments, and could have been caused by genetic drift. In that case the differentiation between the populations from these xeric patches could have been brought about by drift instead of local differentiation due to selection in different environments.

ALLARD: Thank you very much for asking that question. I left out something I did not intend to leave out. When you are doing population genetics the first thing you have to do is mating systems, and that should include *Drosophila* and other species. The reason is that the mating system is rarely random mating and of course here we absolutely have to know what the mating system is, so we always do the mating system first. With respect to mating system, *Avena barbata* is about 98 per cent selfed and about 2 per cent outcrossed on the average, but this varies a great deal. In the more xeric habitats it is a tenth of one per cent outcrossing and in the more mesic habitats it can go up to about 10 per cent outcrossing, so there is a great variation. This brings up another thing I forgot to mention. I talked about electrophoretic genotypes in relation to habitat. We have also studied these with respect to metric characters such as the size of the roots (and incidentally the xeric type has a much larger root system than the mesic type), and with respect to plant stature, maturity data, and a whole series of other things, including mating systems. One of the things associated with the xeric electrophoretic genotype, the handle we can use to get hold of this, is that the mating system is one with a smaller amount of outcrossing than is the mesic type. This is part of this whole complex of things.

VAN DELDEN: Do you think this has a genetic basis or is it environmentally induced?

ALLARD: No, it is genetic, because what we have done is take this back to a common garden experiment. While the mating system is obviously not the same as in nature, because we take it in a different environment, the difference we observe in nature remains in the common garden experiment. So in this experiment we can show that there is a genetic component to this. These xeric and mesic complexes have a whole series of things associated with them The electrophoretic variance is the handle that allows us to identify a whole series of measurement character differences that we were not able to proceed with before. They were there but were rather indefinite, and it is very hard to pick them up unless you have some framework to look at. Concerning your

question whether the differences could be due to drift, the answer is that in no way this could be due to drift.

ANONYMOUS (1): Is there some physical or perhaps functional reason for the deviation from random mating of the gene complexes in barley populations? Are there some chromosomal complexes or genetic mechanisms that distort the random distribution of gametic types?

ALLARD: No, there is no problem of that kind. The whole thing is due to the mating system operating on the population level. If you take heterozygotes from the populations and self them and you do the standard sort of genetic analysis, you get perfectly good 1:2:1 ratios, and so on. There are no disturbances in meiosis, no meiotic drive, and no other genetic disturbances. This is purely associated with the mating system. We looked at this very carefully, and there is no reason to think that other things are involved.

ANONYMOUS (1): You used NEI's formula for genetic similarity, but there are genotypic associations, could HEDRICK's genotypic identity be more relevant biologically?

ALLARD: We have computer programs for these calculations and we routinely calculated not only NEI's genetic-distance measure but also HEDRICK's one, which is on a genotypic basis rather than on a gene-frequency basis. We also did the one that ANTHONY EDWARDS worked out. The answer is that they all tell you the same thing, the values are very close. The reason that I used NEI's measure is that most people who work with animals use it.

ANONYMOUS (2): Would you care to comment on whether or not there is a positive relationship between niche width and genetic variability? It seems to me that *Avena* is a weed and occurs in all kinds of habitats, so it has to be broad-niched.

ALLARD: First of all, *Avena barbata* is really not very weedy. *Avena fatua* or *Avena sterilis* is a real weed, but *Avena barbata* is not.

ANONYMOUS (2): But it is still broad-niched, because there is such a variety of habitats that it occurs in.

ALLARD: After GRIMES' discussion yesterday I have some hesitation about commenting very much on this. Let me compare *Avena barbata* with *Avena fatua*; that might possibly give you some indications. *Avena fatua* is a hexaploid and you migh expect that it would have more buffering, more biological diversity. It is also more heavily inbreeding than *Avena barbata*. It is also much more of a generalist; it occurs in a very wide range of habitats. The interesting thing about it is that it is also more polymorphic, despite the lower outcrossing rate, despite its having more phenotypic plasticity, at least you might guess it might have in terms of the biochemical diversity. But it is much more polymorphic than *Avena barbata*; much less phenomorphic. So again you have to be very careful about making broad generalizations. Each case seems to be pretty much unique in itself. There are some patterns that show up, but you really ought to know quite a bit about the situations before you

say very much about such things as niche width, at least in genetic terms.

ANONYMOUS (3): How can you be sure, since California is a very large state, that the history of the species is not important. You might, given the way it has been colonized, have had very discrete founder events, because the situation in Israel seems to be really difficult to interpret.

ALLARD: A great deal is known about the introduction of *Avena barbata* and many other species of the Mediterranean basin, because during the exploration period there were historians along. Very shortly thereafter, botanists came. So the mission period is very well documented. There were massive, multiple introductions of *Avena barbata*, because there was a great deal of trade back and forth, particularly with Spain, but also with other parts of the Mediterranean. I might say that we have got hold of samples of other places than just Israel, and the complexes we see here do not occur in the Mediterranean basin, at least we have not found them in very extensive sampling. So what has happened in California has been an evolution to suit the particular circumstances of our super-Mediterranean climate. We have a more Mediterranean climate than the Mediterranean.

LEVIN (Texas): The idea of fixed heterozygosity, as you pointed out, is a very intriguing possibility which offers the plant all kinds of biochemical plasticity. I was wondering if you considered looking at fixed heterozygosity over habitats, to see whether there is a relationship in that respect?

ALLARD: That is one of the things we are looking at now in *Avena barbata* but also in another group of species: the *Festucas*. Here we have diploids, tetraploids, and hexaploids. All we can say so far is that *Festuca microstachys,* which is very widely distributed and has a great variety of habitats, is a hexaploid. The species that is almost certainly the diploid ancestor is, however, very narrowly distributed; it occurs only in a few specialized habitats in California. Whether in fact the fixed heterozygosity, which is very much greater in *Festuca microstachys,* has anything to do with it, is a question. But at least the result here, and in many other species too, suggests that fixed heterozygosity does have something to do with broadening the ability to handle broader niches.

LEVIN: In view of your interpretation of selection for the differences that you pointed out, have you calculated selective coefficients?

ALLARD: We have done this a number of times. We have a huge paper in preparation right now, for which we took the whole life cycle apart. We took viability selection, that is, selection from the time of zygote formation to reproductive maturity, as one part of the life cycle. As another part we took from reproductive maturity to zygote formation. That is a very complicated part of the life cycle and it turns out that the selection in it goes in different intensities and at different directions for the same locus in different parts of the life cycle. Thus, there is one set of alleles favoured in viability selection and the opposite set is favoured in gamete formation.

So this is a very complicated area, as TIMOTHY PROUT has pointed out for animal populations.

LEVIN: What kind of values do you get in terms of selection coefficients?

ALLARD: There are 20 to 30 to 40 per cent differences between allele one *versus* allele two, except that what happens at one locus depends very much on what happens at the second locus and what happens at the third locus and so on. The single locus data can be very misleading.

ANONYMOUS (4): Have you tried to map your populations, or one part of your populations, in order to see if the partition of your different genotypes is random from one year to the other?

ALLARD: That is another thing I intended to mention and forgot. I talked mostly about spatial heterogeneity, but it is very clear that there is also temporal heterogeneity. For example, this year in California we are having a drought that is probably as bad as the one in Britain last year, and we had one the year before. It is very clear that the CSA hillside, for example, was very xeric last year and this year. We have mapped this over ten years now and there are fluctuations in the genotypes associated with the amount of rainfall. A moisture parameter keeps coming out and there are fluctuations over time. But there is an average for any particular little part of the habitat. The populations fluctuate around that particular average, depending on what the environment was the previous year.

VALDERON (Montpellier): Is there any evidence concerning the physiological significance of the enzymes you are working with in the electrophoretic studies?

ALLARD: We regard the eletrophoretic variance as very nice marker genes and I am not very interested in getting into the argument of specifically what they do, particularly the systems that we work with. If we worked with such enzymes as alcohol dehydrogenase or amylase, that might be another matter. But for the enzymes we work with we have no clue and furthermore we are not about to put out the amount of work it would mean to try to get a clue. Partly because we suspect we would fail, but mostly because we want them as markers to study mating systems and migration and the standard parameters of population genetics. I would be very happy if somebody else would take this on, but we are not about to do it.