Evolution of Multilocus Genetic Structure in *Avena hirtula* and *Avena barbata*

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ABSTRACT

Avena barbata, an autotetraploid grass, is much more widely adapted than *Avena hirtula*, its diploid ancestor. We have determined the 14-locus genotype of 754 diploid and 4751 tetraploid plants from 10 and 50 Spanish sites, respectively. Allelic diversity is much greater in the tetraploid (52 alleles) than in the diploid (38 alleles): the extra alleles of the tetraploid were present in nonsegregating heteroallelic quadriplexes. Seven loci were monomorphic for the same allele (genotypically *11*) in all populations of the diploid: five of these loci were also monomorphic for the same allele (genotypically *1111*) in all populations of the tetraploid whereas two loci each formed a heteroallelic quadriplex (*1122*) that was monomorphic or predominant in the tetraploid. Seven of the 14 loci formed one or more highly successful homoallelic and/or heteroallelic quadriplexes in the tetraploid. We attribute much of the greater heterosis and wider adaptedness of the tetraploid to favorable within-locus interactions and interlocus (epistatic) interactions among alleles of the loci that form heteroallelic quadriplexes. It is difficult to account for the observed patterns in which genotypes are distributed ecogeographically except in terms of natural selection favoring particular alleles and genotypes in specific habitats. We conclude that natural selection was the predominant integrating force in shaping the specific genetic structure of different local populations as well as the adaptive landscape of both the diploid and tetraploid.

AVENA barbata Pott ex Link (*Ab*) is an annual, predominantly self-fertilizing tetraploid grass (2n = 4x = 28 chromosomes) derived by polyploidization from the diploid (2n = 2x = 14 chromosomes) *Avena hirtula* Lag.-*Avena wiestii* Steud. complex (LADIZINSKY and ZOHARY 1968; RAJHATHY and THOMAS 1974). *A. hirtula* (*Ah*) and *A. wiestii* (*Aw*) are, respectively, the Mediterranean and desert ecotypes of a single biological species; the two ecotypes sometimes occur in mixed stands with each other and/or with *Ab*. Plants of *Aw* are typically small and slender whereas plants of *Ah* and especially *Ab* are usually larger and more robust. However, the three taxa are so similar morphologically that it is difficult to assign individuals unambiguously to a single group on morphological grounds alone. F_1 hybrids between *Ah* and *Aw* have regular meiosis (seven bivalents) and they are fully fertile. Meiosis is chaotic, however, in the rare triploid F_1 hybrids that result from natural intercrosses between the diploids and the tetraploid and the F_1 hybrid plants are nearly completely sterile; it therefore seems likely that *Ab* has been largely isolated reproductively from the two diploid taxa since it originated by polyploidization.

Cytogenetic studies have shown that *Ab* forms 14 bivalents at meiosis with greatest regularity which indicates that homoeologous pairing is suppressed in this near autotetraploid. LADIZINSKY (1973) has presented evidence suggesting that the suppression of pairing is due to a simple genetic mechanism that limits pairing to homologs of the same genome. Recent genetic studies of segregation patterns of allozyme variants (*e.g.*, HUTCHINSON *et al.* 1983a, 1983b; HAKIM-ELAHI and ALLARD 1983) have established that *Ab* behaves genetically as a fully diploidized tetraploid, *i.e.*, pairing is fully preferential within each of the two sets of seven pairs of homologous chromosomes and that no exchange of genetic materials occurs between corresponding chromosomes of the two homoeologous sets.

Ah and *Aw* are indigenous over the Mediterranean Basin, where they typically form small, sparse, disjunct stands. *Ah* is more common in coastal regions adjacent to the Mediterranean Sea and *Aw* is more common on the fringes of the North African and Middle Eastern deserts (*Aw* has not been observed in Spain). *Ab* is ubiquitous throughout the Mediterranean Basin and across the Middle East to Nepal. It thrives over a wide range of environmental conditions encompassing arid sites with shallow soils to well-watered sites with deep fertile soils. It often occurs in massive stands of millions of plants in undisturbed sites as well as in disturbed sites, *e.g.*, along roadsides and in cultivated fields; it has also been a highly successful colonizer in

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Mediterranean-like climates throughout the world. *Ab* is thus much more widely adapted, vigorous and successful in covering vast regions more or less continuously than its diploid progenitor.

Historical records indicate that *Ab* was introduced unintentionally to California from southwestern Spain (ROBBINS 1940; GARCIA *et al.* 1989) during the periods of exploration and colonization and that it spread rapidly, soon becoming a major component of the vegetation and a prized range grazing and wild hay species in all areas with Mediterranean-like climates (ROBBINS 1940). Studies of the population biology of *Ab* in California and Oregon (*e.g.*, CLEGG and ALLARD 1972, 1973; HAMRICK and ALLARD 1972; ALLARD *et al.* 1972; MILLER 1977; HAMRICK and HOLDEN 1979; HAKIM-ELAHI 1980; HUTCHINSON 1982; PIÑERO 1982; P. D. CLUSTER and R. W. ALLARD, unpublished data), in Israel (KAHLER *et al.* 1980), in Spain (GARCIA *et al.* 1989; PEREZ DE LA VEGA, GARCIA and ALLARD 1991; GARCIA *et al.* 1991) and in the Mediterranean Basin and the Middle East (PETERS 1989; R. W. ALLARD, unpublished data) have established that this species is presently differentiated into a number of ecotypes, each marked by a specific combination of alleles of 15 or more Mendelian loci that code for discretely recognizable morphological, allozyme and rDNA variants. These multiallelic configurations are distributed ecogeographically in patchwork patterns that are precise overlays of environmental heterogeneity, especially heterogeneity for available moisture and for temperature. In California each multilocus allelic configuration is monomorphic, or very nearly so, within its favored habitat. However, in boundary areas where two or more different habitats form areas of interface with each other (*e.g.*, along the margins of steams or in low areas that receive runoff water), polymorphism is the rule for the majority of loci. The genotypes of most individuals found within such polymorphic zones are identical to those of plants in the two (sometimes more) adjacent interfacing areas; however, some individuals in the polymorphic zones have genotypes made up of mixtures of alleles characteristic of adjacent monomorphic areas: gametic disequilibrium values are near maximal in such areas (*e.g.*, ALLARD *et al.* 1972; HAMRICK and HOLDEN 1979). The extent of the polymorphic zones expands and contracts from year to year with fluctuations in various environmental factors, especially available moisture. Also, the frequencies of different multilocus genotypes often shift strikingly within the polymorphic zones in step with year-to-year fluctuations in environmental factors, *e.g.*, shifts from near fixation of genotypes favored in arid habitats to near fixation of genotypes favored in mesic habitats, and vice versa, often take place in a single generation when a year of abundant rainfall follows a year of severe drought. Overall, the evidence is compelling that particular alleles of single loci, and more particularly specific multilocus genotypes, are under very strong selection and that selection is capable of rapidly reorganizing the multilocus structure of local populations to meet stresses imposed by short-term environmental changes.

Comparisons of present day Spanish and Californian gene pools on a locus-by-locus basis have shown that the two gene pools are closely similar to each other in allelic composition and in allelic frequencies (GARCIA *et al.* 1989). However, multivariate analyses have established that the two gene pools are very differently structured on a multilocus basis and that both rainfall and temperature have statistically significant effects on multilocus genetic structure in Spain (PEREZ DE LA VEGA, GARCIA and ALLARD 1991), as in California. Spanish rainfall-temperature combinations are, however, very numerous and they often intergrade over short distances so that patterns of association between habitats and genotypes are often difficult to identify. In the present study we determined the 14-locus allozyme genotypes of *Ah* and *Ab* plants collected in 10 and 50 Spanish sites, respectively, representing a number of distinctive ecogeographical regions extending from the northern plateau to southern Spain. The observed population genotype of each region differed from that of each other region and that of each site from that of each other site. The intricate patchwork patterns in which genotypes are associated with different regions and with different sites within regions lead us to the conclusion that natural selection favoring particular genotypes in different environments was the primary determinant of the ecogeographical distribution of genetic variability in both *Ah* and *Ab* as well as the internal genetic structure of each population. Earlier studies have established that several evolutionary factors in addition to selection, including mutation, diploidized tetraploidy (in *Ab*), the mating system of predominant self-fertilization, and frequent short- and long-distance migrations among populations, have also played significant roles in shaping genetic structure on both micro- and macrogeographical scales in these widely distributed species. However, among these evolutionary factors only natural selection favoring different genotypes in different environments acts directionally. We therefore conclude that natural selection has been the primary guiding force in shaping the internal multilocus genetic structure of populations and the adaptive landscape of both *Ah* and *Ab* throughout the range of both species. The arrays of 14-locus genotypes found in recently established colonial populations of *Ab* in California and Oregon are, however, completely different from those of the ancestral Spanish populations. This leads us to the further conclusion that natural selection, acting jointly with other evolutionary factors, is capable of quickly reshaping existing

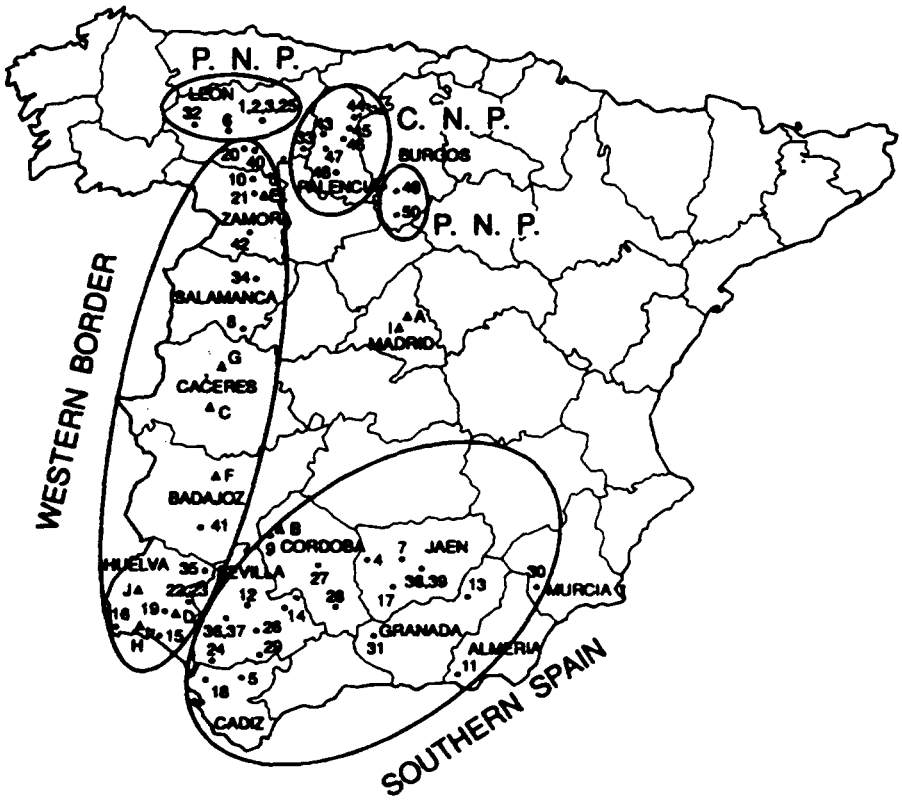

FIGURE 1.—Geographical locations of 10 populations of *A. hirtula* (A–I) and 50 populations of *A. barbata* (1–50). A, Alcobendas; B, Bélmez; C, Plasencia; D, Km 56; E, La Tabla; F, Mérida; G, Cáceres; H, Punta Umbria; I, Universidad; J, Valverde; 1, Agrícolas 83; 2, Agrícolas 84; 3, Agrícolas 85; 4, Andújar; 5, Arcos de la Frontera; 6, Astorga; 7, Bailén; 8, Béjar; 9, Bélmez; 10, Benavente; 11, Berja; 12, Carmona; 13, C-323; 14, Ecija; 15, Huelva; 16, Isla Cristina; 17, Jaén; 18, Jerez de la Frontera; 19, Km 56; 20, La Bañeza; 21, La Encina; 22, La Palma del Condado 84; 23, La Palma del Condado 85; 24, Las Cabezas de San Juan; 25, León; 26, Marchena; 27, Medina-Azahara; 28, Montilla; 29, Morón de la Frontera; 30, N-342A; 31, N-342B; 32, Ponferrada; 33, Sahagún; 34, Salamanca; 35, Santa Ollala; 36, Sevilla A; 37, Sevilla B; 38, Ubeda 84; 39, Ubeda 85; 40, Villamañán; 41, Zafra; 42, Zamora; 43, Saldaña; 44, Herrera de Pisuerga; 45, Alar del Rey; 46, Osorno; 47, Calzada de Los Molinos; 48, Monzón de Campos; 49, Lerma; 50, Aranda de Duero. C.N.P., Central Northern Plateau; P.N.P., Peripheral Northern Plateau.

genetic structures into novel structures that improve adaptedness.

MATERIALS AND METHODS

The materials of this study were 754 plants of *Ah* and 4751 plants of *Ab* collected in the sites shown in Figure 1. Most sites were occupied by thousands to tens of thousands of plants; hence, it is unlikely that random genetic drift had significant effects in shaping genetic structure within sites. Sampling was confined to a fairly central area about 100 m^2, containing ~3000 plants, that appeared to be most typical of each site. A single panicle was taken from about 100 randomly chosen plants located about 1 m apart on a grid pattern within the sampling area. A single seed was sown from each panicle and the resulting seedlings were assayed for 14 allozyme loci following electrophoretic procedures described in GARCIA *et al.* (1989). Designations of loci and alleles follow those of HUTCHINSON *et al.* (1983a) and GARCIA *et al.* (1989). However, to simplify discussion and to reduce the size of tables we have abbreviated the code for each allele to a single digit, *e.g.*, the code for allele *100* of each locus (the relative migration distance in mm of the first allele to be discovered at each locus) is *1*, the code for the second allele to be discovered is *2*, and so forth. Genotypes of *Ah* and *Ab* reflect their allelic composition, *e.g.*, *11* denotes the *100 100* homoallelic (homozygous) duplex of the diploid whereas *1111* and *1122* denote, respectively, the homoallelic (homozygous) *100 100 100 100* and the heteroallelic but homozygous *100 100 101 101* quadriplexes of the tetraploid. In Tables 5 and 6 the genotypes of the tetraploid have been further abbreviated to two digits, *e.g.*, *1111* and *1122* are denoted by *11* and *12*. Previous studies have shown that all populations of *Ah* and *Ab* are heavily self fertilizing and that all individuals are homozygous at a great majority of loci. Heterozygotes of all of the loci of this study are either two-banded or three-banded in the diploid and hence each allele can be distinguished unambiguously; we accordingly included the 13 heterozygotes in our sample of 754 diploid plants in estimating allelic frequencies but excluded these 13 individuals in estimating frequencies of homozygous diploid genotypes. In contrast three types of heteroallelic quadriplexes of the tetraploid have such closely similar electrophoretic phenotypes that progeny testing is required to distinguish among the types. As an example, the electrophoretic phenotype of the nonsegregating *100 100 104 104* double homozygote of the dimeric locus *Prx1* cannot be distinguished with certainty from the electrophoretic phenotypes of the *100 104 100 100* or *100 100 100 104* single heterozygotes, or from the *100 104 100 104* double heterozygote (ALLARD, MILLER and KAHLER 1978). However, it is known from previous studies that the combined frequencies of the three segregating genotypes is of an order of 50-fold to 100-fold smaller than that of the true-breeding homozygote. We consequently did not attempt to identify the segregating genotypes by progeny testing but scored all heteroallelic quadriplexes as double homozygotes; our estimates of the frequencies of nonsegregating heteroallelic quadriplexes given in Tables 1–3, 5 and 6 may thus be slightly biased on the high side.

RESULTS AND DISCUSSION

Allelic frequencies: Table 1 gives allelic frequencies estimated from data from 754 Spanish diploid plants (1,508 alleles) and 4,751 tetraploid plants (19,004 alleles). Considering the diploids first, the genotype of all 754 plants was *11* for three loci (*Pgm1*, *Got2*, *Pgd2*) and *22* for *Mdh1*. Thus, each of these four loci was completely monomorphic at all 10 Span-

TABLE 1

Allelic frequencies[a] in diploid and tetraploid Spanish wild oats

Locus	Allele 1	2	3	4	5	6	7
Pgm1	1.000						
	1.0000						
Got2	1.000						
	0.9991	0.0009					
Mdh2	0.996	0.004					
	0.9991	0.0009					
Got1	0.951	0.049					
	1.0000						
Pgi1	0.481	0.172		0.309	0.038		
	0.9375	0.0008	0.0096	0.0249	0.0270		
Mdh1		1.000					
	0.5002	0.4998					
Pgd2	1.000						
	0.5350	0.4439	0.0210				
Mdh3		0.859				0.138	0.003
	0.4234	0.5215	0.0275	0.0239	0.0036		
Acp2	0.836	0.034			0.130		
	0.2186	0.0559	0.2265	0.4989			
Pgd1	0.878	0.122					
	0.4870	0.3126	0.1975	0.0029			
Acp1	0.690	0.201			0.109		
	0.5397	0.4284	0.0146		0.0173		
Prx1	0.174	0.719		0.058	0.048		
	0.6196	0.2496	0.0742	0.0565			
Lap1	0.390	0.425	0.015	0.168	0.001		
	0.1671	0.4509	0.2991	0.0777	0.0051		
Est1	0.073	0.241		0.011	0.439	0.029	0.191
	0.0264	0.1808	0.3036	0.0049	0.3432	0.0220	0.1050

[a] The top number in pairs of numbers in each row gives the allelic frequency in *Ah* for one of the 14 allozyme loci whereas the bottom number in each pair gives the allelic frequency in *Ab*. Allelic frequencies for alleles *8*, *9* and *10* of *Est1* (not given in the body of the table) are 0.0073, 0.0048 and 0.0017, respectively, in *Ab*. Allele *8* of *Est1* was present in *Ah* in frequency 0.007, but alleles *9* and *10* were not present. Allele frequencies are based on assays of 754 plants (1,508 alleles) *Ah* and 4,751 plants (19,004 alleles) in *Ab*.

ish sites. Locus *Mdh2* differed slightly: the genotype was *11* for 751 plants and *22* for three plants (allelic frequencies 0.996:0.004 overall in Spain); nine sites were monomorphic for duplex *11* and one site was polymorphic for duplexes *11* and *22* (allelic and genotypic frequencies 0.96:0.04 at this site). The above five loci have been either completely monomorphic, or very nearly so, in all other diploid populations that have been sampled in the Mediterranean Basin and Middle East (PETERS 1989; GARCIA *et al.* 1991; R. W. ALLARD, unpublished data). The predominant alleles of each of these five loci apparently code for some essential function such that they confer superior survival ability relative to all other alleles that have arisen during the evolutionary history of the *Ah-Aw* complex. Evidently, none of the other alleles that have arisen in the diploid at these loci have been competitive with the predominant allele and none has survived except in inconsequential frequencies (*e.g.*, allele *2* of *Mdh2*). Present frequencies of alleles thus appear to provide a biologically meaningful measure of long-term survival values in the diploid of all alleles of these five loci. We consequently take the long-term survival values of the predominant alleles of loci *Pgm1*, *Got2*, *Pgd2*, *Mdh1* and *Mdh2* to be effectively 1.00 and the long-term survival values of all other alleles that have arisen at these loci through mutation to be very close to zero in each of the 10 Spanish populations sampled, as well as throughout the range of distribution of the diploid. The selective values of the mutants are, however, not necessarily close to zero although they are almost certainly lower on average than those of the surviving alleles.

The pattern of allelic variability differs for *Got1*. Although allele *1* of this locus is present in high frequency (f = 0.951) overall in Spain (Table 1), a second electrophoretically detectable allele (allele *2*) is present in one site and it was in fact more frequent at that site (f = 0.712) than allele *1* (f = 0.288). Thus, present frequencies indicate that the long-term overall survival values of alleles *1* and *2* of *Got1* are approximately 0.95 and 0.05, respectively, in the environment of Spain and that the long-term survival values of all other alleles than have arisen at this locus over the centuries are close to zero. Allele *2* and less frequently a third allele (allele *3*) of *Got1* have been

found in occasional populations throughout of range of distribution of the *Ah-Aw* complex, always in polymorphic association with allele *1*. Thus, alleles *2* and *3* are apparently not always mere morbid transients on their way to elimination by selection but they may contribute to overall population adaptedness in some habitats.

Patterns of within-site allelic variability in Spain and elsewhere in the Mediterranean Basin and Middle East are similar to that of *Got1* for four additional loci, *Mdh3*, *Acp2*, *Pgd1* and *Acp1*. In Spain (Table 1) one allele of each of these four loci was present in high frequency ($0.6 < f < 0.9$) and this most frequent allele overall was predominant or fixed in most sites. However, some sites were polymorphic for a second and sometimes for a third or fourth allele and one or another of these additional alleles was sometimes predominant or even fixed in occasional sites. This pattern of allelic variability suggests that a single allele of each of these four loci is nearly universally superior but that environments exist in which the long-term survival values of other alleles are superior to the usually predominant allele. The presence of two or more alleles of a single locus at some sites suggests that polymorphism may improve overall population fitness at those sites.

The four remaining loci, *Pgi1*, *Prx1*, *Lap1* and *Est1*, are extensively polymorphic (four to seven electrophoretically distinct alleles) in the diploid in Spain (Table 1). Three or more alleles of each of these loci were present in at least intermediate frequency in about half of the Spanish sites, as well as elsewhere throughout the range of the diploids. Evidently, the population genotypes that lead to optimum population fitness in most sites feature mixtures of alleles of these four loci.

Turning to *Ab*, it is apparent from Table 1 that allelic diversity is much greater in the tetraploid (52 alleles) than in its diploid progenitor (38 alleles). Thirty-four of the 38 alleles present in *Ah* were also present in *Ab* but 18 alleles not present in the *Ah* were present in *Ab*. Each of these 18 alleles appeared in the tetraploid as one of the pair of alleles present in nonsegregating heteroallelic quadriplexes; thus, the increased allelic diversity in the tetraploid relative to the diploid was consistently associated with formation of heteroallelic quadriplexes made up of at least one allele not present in the diploid. It is not possible for alleles that do not exist in the diploid to be incorporated into the tetraploid during episodes of polyploidization of diploid plants. Hence, contrary to widely held supposition, it seems likely that most heteroallelic quadriplexes stem from mutations that occurred in tetraploid *Ab* subsequent to its formation from *Ah* by chromosome doubling. Locus *Pgd2* serves as a model for the sequence of events that may have led to greater allelic diversity in *Ab* than *Ah*. The diploid *Ah-Aw* complex is monomorphic for allele *1* of *Pgd2*; consequently, the original quadriplex of *Pgd2* formed by chromosome doubling of a *11* duplex plant was almost certainly genotypically *1111*. Theory indicates that the chance that any mutant, including adaptively beneficial mutants, will become established in either a diploid or autotetraploid population is very small, especially in small populations (FISHER 1930; HALDANE 1936; LI 1955). However, population sizes are usually much larger in *Ab* than in *Ah* and it is likely that large numbers of novel mutants have appeared over time in one or the other of the two genomes of *Ab*, including individuals with genotype *1112* or *1211* for locus *Pgd2*. One-fourth of the selfed progeny of such singly heterozygous individuals are expected to be the highly heterotic nonsegregating *1122* quadriplex. The probability is thus much higher that such mutants would be incorporated into the tetraploid than the diploid and that this highly heterotic quadriplex would quickly sweep through the species, soon achieving its modern frequency of $f = 0.84$ (Table 2). Subsequent mutations in the near-ubiquitous *1122* quadriplex might, in similar manner, have produced the *2233* and *2222* quadriplexes of *Pgd2*, both of which found relatively small niches in which they were able to survive (Table 2).

Patterns of quadriplex formation differed for most of the 14 loci of this study (Tables 1 and 2). Three of the completely or nearly completely monomorphic loci of the diploid (*Pgm1*, *Got2*, *Mdh2*) formed only homoallelic quadriplexes that were completely or very nearly completely monomorphic for the same alleles as the diploid. *Got1*, which is monomorphic for duplex *11* in most populations of the diploid, but polymorphic for duplexes *11* and *22* in occasional populations, is monomorphic for homoallelic quadriplex *1111* in *Ab*; evidently allele *2* does not contribute to adaptedness of the tetraploid under any environmental conditions. In contrast, locus *Mdh1*, which is completely monomorphic in *Ah*, formed a single heteroallelic quadriplex (*1122*), that is monomorphic in all populations of *Ab*; clearly favorable interactions between alleles *1* and *2* of *Mdh1* contribute to the superior adaptedness of *Ab* in all environments. Locus *Pgd2*, which is also completely monomorphic in *Ah*, is similar to *Mdh1* in that it formed a highly successful heteroallelic quadriplex (*1122*, $f = 0.84$) but differs from *Mdh1* in that it also formed two homoallelic quadriplexes in the tetraploid, one (*1111*) moderately successful ($f = 0.12$) and the other (*2222*) much less successful ($f = 0.004$). The most successful quadriplexes of loci *Pgd1*, *Mdh3* and *Acp1* are also heteroallelic but one of the alleles involved is infrequent in the diploid (not absent as with *Mdh1* and *Pgd2*). The pattern for *Acp2* was still different in that this locus formed a highly successful heteroallelic quadriplex (*3344*) from two alleles, neither of which is present in the diploid; thus both

TABLE 2

Quadriplex frequencies[a] in Spanish *A. barbata*

Locus	Quadriplex													
	1111	*2222*	*3333*	*5555*	*1122*	*1133*	*1144*	*1155*	*2233*	*2244*	*2255*	*3344*	*3355*	*5577*
Pgm1	1.0000													
Got2	0.9981				0.0019									
Mdh2	0.9981				0.0019									
Got1	1.0000													
Pgi1	0.8783	0.0004		0.0019		0.0192	0.0490	0.0503		0.0008				
Mdh1	0.0004				0.9996									
Pgd2	0.1164	0.0042			0.8373				0.0421					
Mdh3	0.0004	0.0985			0.8461							0.0478	0.0072	
Acp2	0.0015					0.0004	0.4338		0.0002	0.1116		0.4525		
Pgd1	0.0183	0.0236	0.0055		0.5685	0.3690			0.0093	0.0002		0.0057		
Acp1	0.1120	0.0309		0.0013	0.7946	0.0293		0.0316			0.0004			
Prx1	0.2547	0.0154			0.4685	0.1484	0.1130							
Lap1	0.0223	0.1145	0.1204		0.2399	0.0495	0.0002		0.2911	0.1316	0.0103	0.0168		
Est1	0.0074	0.0116	0.1454	0.1398		0.0373		0.0008	0.1877		0.1473	0.0099	0.0368	0.2035

[a] Quadriplex frequencies not reported in the body of the table are: *Lap1 4444* (0.0034), *Est1 6666* (0.0017), *7777* (0.0025), *10101010* (0.0017), *2266* (0.0034), *3366* (0.0335), *3377* (0.0015), *3399* (0.0097), *5566* (0.0038), *5588* (0.0147).

alleles of this heteroallelic quadriplex evidently arose by mutation in *Ab*. The patterns for loci *Prx1*, *Lap1* and *Est1* were all similar in that each locus formed several moderately successful homoallelic as well as several heteroallelic quadriplexes from alleles that were generally moderately successful in the diploid. The pattern for *Pgi1* was unique: allele *1*, the most frequent in the diploid (f = 0.481), formed a homoallelic quadriplex (*1111*) that was much more successful (f = 0.88) in Spain (also throughout the range of distribution of *Ab*) than its homoallelic duplex (*11*) counterpart in the diploid. Alleles *2* and *5* formed less successful homoallelic quadriplexes and allele *1* combined with alleles *2*, *3* and *5* to form heteroallelic quadriplexes in *Ab*; however, these heteroallelic quadriplexes were highly successful only locally (one site each).

The above results show that homoallelic (homozygous) duplexes are the primary unit of allelic function in the diploid: heteroallelic (heterozygous) duplexes are too infrequent (f $\approx$ 0.01) to have much effect on immediate population fitness and selfing evidently reduces even the most heterotic heteroallelic (heterozygous) duplexes to very low frequency within a few generations. However, nonsegregating quadriplexes stabilized by fully preferential chromosome pairing within each of the two genomes are the primary unit of allelic function in the tetraploid. The majority of successful quadriplexes are heteroallelic: heteroallelism clearly increases the number of alleles of single loci that can be deployed simultaneously in adaptive diversifications within single individuals. Increased allelic diversity also has secondary implications involving two types of interactions that have potentially large effects on adaptedness and survivability: (1) interactions in the tetraploid among alleles of the same locus (intralocus interactions) completely stabilized through diploidized tetraploidy (ALLARD, MILLER and KAHLER 1978); (2) interlocus (epistatic) interactions in both diploid and tetraploid among alleles of different loci stabilized in various degrees by the mating system of nearly complete selfing (ALLARD 1975). We now examine geographical distributions for evidence concerning the direct and indirect effects of specific duplexes and quadriplexes on adaptedness under different environmental conditions in Spain.

Geographical distribution of allozyme duplexes and quadriplexes: In examining associations between genotypes and environments it is convenient to represent long-term survival values, which are correlated with present frequencies, in the form of topographic maps (WRIGHT 1932, 1951, 1965). In constructing topographies we plotted all duplexes or quadriplexes of a single locus as points on a plane Cartesian coordinate system. The ordinate erected at each point within a given site was the observed frequency of the duplex or quadriplex at that site. Thus, the locus was represented on a surface above the base plane by one or more points reflecting the present frequency (long-term survival value) of the duplexes or quadriplexes of the locus in each site. Fourteen single-locus topographies (one per locus) were constructed for *Ah* and also for *Ab*; 10 collection sites were represented on each topography for the diploid and 50 for the tetraploid. The topographies are too extensive to report in full; consequently, we have prepared a summary of the distribution data in tabular form (Table 3) from which the main features of the topographies can be inferred (duplexes and quadriplexes present in frequencies <0.02 are omitted from this table).

The topographies fall into five groups. Group I includes loci *Pgm1*, *Got2* and *Mdh2*, all of which are

TABLE 3

Geographical distribution of allozyme duplexes and quadriplexes

Locus	Duplex or quadriplex	Overall frequency	No. of sites in which: Present[a]	Most frequent	Fixed
Pgm1, Got2	*11*	1.00	10/10	10/10	10/10
Mdh2	*1111*	1.00	50/50	50/50	50/50[b]
Mdh1	*22*	1.00	10/10	10/10	10/10
	1122	1.00	50/50	50/50	49/50[b]
Got1	*11*	0.95	10/10	9/10	9/10
	22	0.05	1/10	1/10	
	1111	1.00	50/50	50/50	50/50
Pgi1	*11*	0.48	8/10	7/10	3/10
	22	0.17	3/10	1/10	1/10
	44	0.31	5/10	2/10	1/10
	55	0.04	2/10		
	1111	0.88	50/50	46/50	31/50
	1133	0.02	1/50	1/50	
	1144	0.05	9/50	2/50	
	1155	0.05	14/50	1/50	
Pgd2	*11*	1.00	10/10	10/10	10/10
	1111	0.12	10/50	3/50	1/50
	1122	0.84	49/50	47/50	24/50
	2233	0.04	14/50		
Mdh3	*22*	0.86	9/10	9/10	7/10
	66	0.14	2/10	1/10	1/10
	2222	0.10	11/50	2/50	1/50
	1122	0.85	49/50	47/50	26/50
	3344	0.05	13/50	1/50	
Pgd1	*11*	0.88	10/10	9/10	6/10
	22	0.12	4/10	1/10	
	1111	0.02	11/50	1/50	
	2222	0.02	6/50	1/50	
	1122	0.57	45/50	30/50	8/50
	1133	0.37	36/50	17/50	5/50
Acp2	*11*	0.84	10/10	9/10	6/10
	22	0.03	2/10		
	55	0.13	2/10	1/10	
	1144	0.43	37/50	24/50	8/50
	2244	0.11	18/50	5/50	
	3344	0.45	41/50	21/50	6/50
Acp1	*11*	0.69	9/10	6/10	4/10
	22	0.20	5/10	2/10	
	55	0.11	3/10	2/10	1/10
	1111	0.11	17/50	3/50	1/50
	2222	0.03	12/50	1/50	
	1122	0.79	48/50	44/50	24/50
	1133	0.03	2/50	1/50	1/50
	1155	0.03	7/50	1/50	
Prx1	*11*	0.17	4/10	1/10	1/10
	22	0.72	7/10	7/10	4/10
	44	0.06	2/10	1/10	
	55	0.05	1/10	1/10	1/10
	1111	0.25	27/50	12/50	4/50
	2222	0.02	2/50	1/50	
	1122	0.47	41/50	26/50	13/50
	1133	0.15	19/50	7/50	2/50
	1144	0.11	12/50	4/50	1/50
Lap1	*11*	0.39	9/10	4/10	2/10
	22	0.43	6/10	4/10	1/10
	44	0.17	5/10	2/10	
	1111	0.02	6/50	1/50	
	2222	0.11	13/50	6/50	1/50
	3333	0.12	15/50	4/50	1/50
	1122	0.24	31/50	15/50	2/50
	1133	0.05	16/50	1/50	
	2233	0.29	32/50	16/50	6/50
	2244	0.13	19/50	7/50	1/50
	3344	0.02	7/50		
Est1	*11*	0.07	4/10	1/10	
	22	0.24	8/10	2/10	
	55	0.44	8/10	5/10	2/10
	66	0.03	1/10		
	77	0.19	3/10	2/10	
	3333	0.15	25/50	6/50	1/50
	5555	0.14	24/50	8/50	
	1133	0.04	10/50	1/50	
	2233	0.19	27/50	7/50	2/50
	2255	0.15	24/50	9/50	1/50
	3355	0.04	16/50	2/50	
	3366	0.03	6/50	3/50	
	5577	0.20	19/50	11/50	4/50

[a] Present in frequency ≥0.02.
[b] Population 15 of *Ab* included nine plants (f = 0.09) with quadriplexes *Got2 1122* and *Mdh2 1122* and population 9 of *Ab* included two plants (f = 0.04) with quadriplex *Mdh1 1111*.

monomorphic for the *11* duplexes and *1111* quadriplexes in all 10 diploid and all 50 tetraploid sites. The single-locus topography of each of the three loci of group I features a single monolithic column (relative height 1.00) located at sites A-I and 1–50, respectively. Two-locus and three-locus topographies for *Pgm1*, *Got2* and *Mdh2* feature identical two-element or three-element columns at each site. This result indicates that these three loci, whether considered singly or jointly, have identical survival values in all Spanish sites sampled and that no epistatic interactions occur among loci in either the diploid or tetraploid genetic backgrounds. Group II includes the *11* and *22* duplexes of *Pgd2* and *Mdh1* whereas group III includes the *1111* and *1122* quadriplexes of *Got1* and *Mdh1*, respectively. All of these duplexes and quadriplexes are monomorphic at all sites (A-I, 1–50); thus, each single-locus topography features an identical monolithic column at each site, indicating that the survival values are identical at all Spanish sites sampled. However, the topographies of these duplexes and quadriplexes, unlike those of group I, differ in the diploid and tetraploid: the *11* duplex of *Pgd2* is monomorphic in the diploid but this locus is polymorphic for its quadriplexes in the tetraploid, the *1122* quadriplex of *Mdh1* is heteroallelic, and duplex *11* of *Mdh1* is not present in the diploid (Table 3). Thus, although ploidy level affects survival ability of these

duplexes and quadriplexes, it does so identically in all 10 diploid and all 50 tetraploid sites. This is surprising because most of the sites differ widely respecting various environmental factors (*e.g.*, rainfall, temperature, slope, edaphic features) that have large differential effects on the survival values of most of the duplexes of the group IV and the quadriplexes of group V loci.

Group IV is made up of the 27 duplexes of the nine loci that are polymorphic in at least one of the 10 diploid sites (Table 3; only duplexes present in overall frequency ≥0.02 are listed in this table). Locus *Got1* is monomorphic for duplex *11* in nine sites but polymorphic for duplexes *11* and *22* (f = 0.288:0.712) in one site (site B). The topography for *Got1* thus features a single monolithic column (height 1.00) at nine sites and one two-element column (heights 0.288 and 0.712) at site B. Survival of duplexes *11* and *22* in polymorphic association at this site implies that a mixture of the two duplexes, rather than fixation of either duplex *11* or *22*, gives optimum fitness, *i.e.*, that mixture increases the carrying capacity of the site above levels that would prevail if the site were occupied by either duplex *11* or *22* alone. Mechanisms that have been proposed for such enhancement of fitness include: (1) site patchiness, including patches that favor duplex *11* and patches that favor genotype *22*; (2) that different genotypes (say *11* and *22*) make different and/or nonsimultaneous demands on limiting resources (*e.g.*, water) such that each genotype obtains more resources when it grows in intimate association with other genotypes than it would in pure stand. ALLARD and ADAMS (1969) have presented experimental evidence that supports hypothesis 1 in some cases and hypothesis 2 in other cases.

The topography of locus *Pgi1* is more typical of the nine loci of group IV than that of *Got1* (the topography of *Got1* is by far the least complex topography of the group IV loci). The topography of *Pgi1* is characterized by single monolithic columns in five sites (duplex *11* fixed in sites B, D, E, duplex *44* fixed in site F, and duplex *22* fixed in site J), two two-element columns (duplexes *11* and *22* polymorphic in site H and duplexes *11* and *44* in site A), and three three-element columns (duplexes *11*, *55* and *44* polymorphic in sites G and I; duplexes *11*, *22* and *44* polymorphic in site C). The topographies of the nine loci of group IV thus indicate, in contrast to those of the loci of groups I, II and III, that the survival abilities of specific duplexes as well as those of mixtures of duplexes differ from site to site, *i.e.*, that interactions among genotypes and environments have complex effects on fitness. Among the 90 (9 × 10) locus-by-site combinations of the Group IV loci, 49/90 (54%) were monomorphic and 41/90 (46%) were polymorphic, suggesting that monomorphism for a single duplex led to optimum fitness slightly more frequently than mixtures of two more duplexes.

Group V is made up of 43 quadriplexes of the nine loci that are polymorphic in at least one of the 50 tetraploid sites (Table 3). The numbers of sites in which the various quadriplexes appeared and their frequencies in the 50 sites varied widely. A few of the quadriplexes were found in only one of the 50 sites (*e.g.*, quadriplexes *1133* of *Pgi1* and *2222* of *Prx1*) whereas other quadriplexes were widely distributed (*e.g.*, quadriplex *1111* of *Pgi1* was present in all 50 sites, most-frequent in 46/50 and fixed in 31/50 sites). In contrast, quadriplex *1133* of *Pgi1* was found only in site 8 (f = 0.97, polymorphic with quadriplexes *2222* and *1111* in f = 0.02 and 0.01, respectively). This suggests that site 8 is unique regarding some environmental factor or factors that affect long-term survival ability. The sites in which a given quadriplex was found were often clustered within given regions. As an example quadriplex *5577* of *Est1* was found in only two regions, the northern plateau and southwestern Spain. In the northern plateau quadriplex *5577* was fixed or most frequent in eleven sites (43–48, 33, 1, 2, 25, 50) and it was in intermediate frequency (f = 0.26) in site 3. It was present in low frequencies in five sites in Southwestern Spain clustered in the Provinces of Cádiz (site 5, f = 0.01), Sevilla (site 26, f = 0.06), Córdoba (site 28, f = 0.03; site 27, f = 0.14) and Jaén (site 4, f = 0.01). The many cases in which quadriplexes were associated nonrandomly with sites located within environmentally similar regions provide evidence that particular quadriplexes are well adapted in some regions and in some specific sites within regions whereas other quadriplexes are better adapted in other regions and sites.

The nine-locus topographies of the loci of group V differ from those of loci of groups I–IV in two major ways: (1) they are consistently much more complex, indicating that interactions among genotypes within sites are more intricate than in groups I–IV; and (2) the topographies differ more from site to site, indicating that genotype-environment interactions are also much more complex. Among the 450 (9 × 50) locus × site combinations, 175 (39%) were monomorphic and 275 (61%) were polymorphic (Table 3); evidently, monomorphism for a single quadriplex led to optimum fitness in about 1/3 and polymorphism in about 2/3 of cases. As in the diploid, within-site environmental patchiness and/or favorable interactions among genetically different plants may have been responsible for enhancement of fitness in the polymorphic populations. However, a different type of interaction, not available in the diploid, is possible in the tetraploid, namely heterotic within-cell or within-tissue interactions among different molecular products of different pairs of alleles in the two genomes of heteroallelic quadriplexes. The greater allelic diver-

TABLE 4

Most-frequent 14-locus genotypes in 10 populations of *Ah*

Population	Locus															
	Pgm1	*Got2*	*Mdh2*	*Got1*	*Pgi1*	*Mdh1*	*Pgd2*	*Mdh3*	*Acp2*	*Pgd1*	*Acp1*	*Prx1*	*Lap1*	*Est1*	N^a	f^b
E	*11*	*11*	*11*	*11*	*11*	*22*	*11*	*22*	*11*	*11*	*55*	*55*	*11*	*55*	1	1.00
G	*11*	*11*	*11*	*11*	55^p	*22*	*11*	*22*	55^p	11^p	22^p	22^p	22^p	22^p	34	0.17
C	*11*	*11*	*11*	*11*	22^p	*22*	*11*	22^p	11^p	22^p	11^p	*22*	11^p	55^p	36	0.12
F	*11*	*11*	*11*	*11*	*44*	*22*	*11*	*66*	*11*	*11*	*11*	*22*	*22*	*55*	1	1.00
B	*11*	*11*	*11*	22^p	*11*	*22*	*11*	*22*	*11*	*11*	22^p	*22*	44^p	55^p	3	0.71
J	*11*	*11*	*11*	*11*	*22*	*22*	*11*	*22*	*11*	*11*	*11*	*11*	*11*	77^p	2	0.93
D	*11*	*11*	*11*	*11*	*11*	*22*	*11*	*22*	*11*	*11*	55^p	44^p	44^p	11^p	13	0.45
H	*11*	*11*	*11*	*11*	11^p	*22*	*11*	22^p	55^p	*11*	*11*	22^p	11^p	77^p	17	0.21
A	*11*	*11*	*11*	*11*	44^p	*22*	*11*	*22*	*11*	11^p	*11*	*22*	22^p	55^p	8	0.51
I	*11*	*11*	11^p	*11*	44^p	*22*	*11*	*22*	11^p	22^p	11^p	22^p	22^p	22^p	20	0.26

[a] Number of 14-locus genotypes observed at each site.
[b] Frequency within site of the most frequent 14-locus genotype.
[p] Site polymorphic for 14-locus genotypes due to polymorphism at loci indicated.

sity stabilized by diploidization in the tetraploid apparently not only allows for increased exploitation of favorable intralocus interactions but also increases opportunities for increased exploitation of epistatic interactions among alleles of different loci. In the diploid, *e.g.*, in a plant genotypically *11* for *Lap1* and *55* for *Est1*, no heteroallelic intralocus interactions are possible (excluding rare heterozygotes, *e.g.*, *Lap1 12*, resulting from rare outcrosses) and only one epistatic interaction is possible, *11* × *55*. However, in the tetraploid, *e.g.*, in a plant genotypically *2233* for *Lap1* and *5577* for *Est1*, two intralocus interactions (*22* × *33* and *55* × *77*) and four pairwise interlocus (epistatic) interactions are possible (*22* × *55*, *22* × *77*, *33* × *55* and *33* × *77*); four of the six combinations were present in the Spanish populations in significant frequencies (Tables 2 and 3), indicating that these four interactions were favorable. Many higher-order interactions are also possible. In the next two sections we examine the frequencies of the 14-locus genotypes in different diploid and tetraploid sites to identify interlocus combinations that have been successful in Spain and intralocus and interlocus combinations that have been successful in *Ab* in Spain and in California.

Geographical distribution of 14-locus genotypes in Ah: In total, 107 14-locus genotypes were observed in the 10 populations of *Ah*. Comparisons of the arrays of 14-locus genotypes present in the 10 sites showed that the population genotype at each site differed from that at each other site. The data are too extensive to be reported in full; however, the main features of within-population as well as interpopulational differentiation can be deduced from Table 4, which lists the single most-frequent 14-locus genotype (presumably the best adapted genotype at each site) and also identifies the monomorphic and polymorphic loci in each population. Two populations (E, F) were monomorphic at all 14 loci, *i.e.*, only one 14-locus genotype was present (f = 1.00) in each population. The 14-locus genotype of these two populations differed at five loci (*Pgi1*, *Mdh3*, *Acp1*, *Prx1*, *Lap1*). Obviously, all of the genetic differences between populations E and F were interpopulational and none were intrapopulational. Within-population 14-locus genotypic diversity varied from very small for population J (only two 14-locus genotypes present in f = 0.93 and 0.07, respectively) to substantial for populations G, C, H and I (several 14-locus genotypes present, the most frequent in f ≥ 0.26). However, among-population variability was larger than within-population variability even in these most variable diploid populations. The within-population genetic structure of each of the 10 diploid populations differed from that of each other population and each population was sharply differentiated from each other populations, evidently due to different selective pressures imposed by differences in environment at the several sites. Taking into account the very large population sizes at each site, and the frequent and extensive migrations among sites, it seems likely that very little of the observed genetic differences within or among populations resulted from genetic drift.

Multivariate log-linear analyses (FIENBERG 1980; ZHANG, SAGHAI MAROOF and ALLARD 1990) of the full diploid data set (SÁENZ DE MIERA 1989) showed that disequilibrium values are high in all 10 populations and that all loci of this study are tied together through complex networks of overlapping two-locus, three-locus and higher-order epistatic interactions. Alternatively, the lower-order interactions may be a consequence of the full 14-locus structure or the structure of the entire genome. The mating system of *Ah* is favorable for the development and maintenance of patchwork patterns of epistatic interlocus combinations of alleles that provide for local high adaptedness. The 1% of within-population outcrossing leads

to heterozygosity, segregation and recombination that produces novel interlocus allelic combinations upon which continued evolutionary change depends; it also allows migrant alleles and new mutants to be integrated quickly into the population genotype. The 99% of selfing causes all loci, whether located on the same or different chromosomes, to behave as if they are linked with crossover values ≤0.01, thus restricting recombination sufficiently to protect favorable interlocus combinations from being broken up by segregation before they can be integrated into the populations (ALLARD 1975). Populations E and F provide examples of populations in which disequilibrium values are maximal for all 14 loci (only one 14-locus genotype present but a different one in each population). Disequilibrium is near maximal in three populations (A, B, D) and high in the five remaining populations.

Geographical distribution of 14-locus genotypes in Spanish and Californian populations of Ab: Applications of discrete log-linear techniques to analyses of associations among the allozyme loci with each other and with environmental factors (PÉREZ DE LA VEGA, GARCÍA and ALLARD 1991) have shown: (1) that disequilibrium values are high among the 14 allozyme loci in *Ab*; (2) that the 14 loci are tied together through overlapping two-locus, three-locus and higher-order interactions or as a consequence of the full 14-locus structure or the structure of the entire genome; (3) that differences in rainfall and temperature affect multilocus genetic structure at two-locus and higher-order levels. Comparisons of the arrays of 14-locus genotypes show that the population genotype of each of the 50 populations of *Ab* differed from that of all other sites. The number of 14-locus genotypes observed in *Ab* (>440) is much larger than in *Ah* and the data are far too extensive to be reported in full. However, the main features of intrapopulational genetic diversity can be deduced from Table 5 in which are given the most-frequent 14-locus genotype and its frequency in each site; Table 5 also lists the 14-locus genotypes that are monomorphic within each of the five principal habitats in which *Ab* occurs in California and Oregon.

The most clear-cut regional pattern in Spain is that of the cold high-elevation (850–950 m) central northern plateau region. It can be seen from Table 5 that the same 14-locus genotype was most-frequent in each of the seven sites (43–48, 33) of that region (Figure 1). This regionally most-frequent 14-locus genotype was monomorphic in population 43 and nearly monomorphic in population 45; these two populations occupy some of the highest and/or most exposed among the seven sites of the region. The frequency of this regionally most-frequent genotype dropped off at lower elevations and in less-exposed sites and its frequency fell to 0.68 in site 46. In areas peripheral to this central region in the northern part of the Spanish Meseta (plateau) the frequency of this 14-locus genotype fell to 0.56 in site 25, located to the westward of the central region, and it was entirely absent in sites 1, 2 and 3 located a few km to the west of site 25, and in sites 49 and 50 located to the southeast of the central region at slightly lower elevation (~800 m). This pattern suggests that this particular 14-locus genotype confers superior adaptedness under the coldest conditions but that it is a less effective competitor under the more temperate conditions of peripheral areas. In sites 1 and 2 the predominant 14-locus genotype of the central northern plateau was replaced as the most-frequent genotype by a 14-locus genotype (Tables 5 and 6) that differed from the "cold-tolerant" genotype only at locus *Acp2* (quadriplex *3344* replaced quadriplex *1144*); this genotype was also third most-frequent (f = 0.24) in site 3 (Table 6). However, several other 14-locus genotypes differing from the "cold tolerant" genotype at five to seven loci were also present in populations 1, 2 and 3 (Table 6); thus, the apparently slight changes in environment that occurred in the transition from site 25 to sites 1, 2 and 3 were evidently responsible for the major restructuring of the 14-locus population genotype in the latter sites. Environmental conditions at the sites occupied by populations 6 and 32, located in west-central and extreme western León province, respectively, are very different from each other and also from those of sites 1, 2 and 3: population 6 occupies a cold infertile site (elevation ≈ 870 m) whereas the site occupied by population 32 (elevation ≈ 540 m) lies in a fertile well-watered valley in which *Ab* occurs in dense lush stands. Population 6 is monomorphic for a single 14-locus genotype (f = 1.00); however, 39 different 14-locus genotypes are present in population 32 in f > 0.01 (the single most-frequent genotype is present in f = 0.20). Evidently, natural selection sorted out a particular 14-locus genotype that is uniquely adapted under the harsh environmental conditions of site 6 and also integrated many different 14-locus genotypes into a complex unified entity that provides optimum adaptedness in the more benign environment of site 32.

Each of the 14 populations extending from site 40 (Province of León) southward along the western border of Spain to population 16 (Province of Huelva) occupies a site that is very different environmentally from each other site (elevation varies from 960 to 7 m; rainfall, temperature, edaphic and other characteristics also vary widely from site to site). Within-site 14-locus genotypic variability was small in nearly all of these 14 populations: only one 14-locus genotype (f = 1.00) was present in site 21 and a single 14-locus genotype was predominant (f ≥ 0.50) in nine populations (8, 20, 19, 34, 23, 10, 40, 41, 22). Only population 15 (elevation 7 m) was conspicuously polymor-

TABLE 5

Most-frequent 14-locus tetraploid genotypes in Spain and California

Site	Locus														f[a]
	Pgm1	*Got2*	*Mdh2*	*Got1*	*Pgi1*	*Mdh1*	*Pgd2*	*Mdh3*	*Acp2*	*Pgd1*	*Acp1*	*Prx1*	*Lap1*	*Est1*	
Central Northern Plateau															
43	11	11	11	11	11	12	12	12	14	13	12	11	23	57	1.00
45	11	11	11	11	11	12	12	12	14	13[p]	12	11[p]	23	57	0.99
44	11	11	11	11	11	12	12	12	14	13[p]	12	11	23	57	0.81
48	11	11	11	11	11	12	12[p]	12	14[p]	13[p]	12	11	23	57[p]	0.90
47	11	11	11	11	11	12	12	12	14	13[p]	12	11[p]	23[p]	57[p]	0.78
46	11	11	11	11	11	12	12	12	14[p]	13[p]	12	11	23	57[p]	0.68
33	11	11	11	11	11	12	12[p]	12[p]	14[p]	13[p]	12	11[p]	23[p]	57[p]	0.91
Peripheral Northern Plateau															
1	11	11	11	11	11	12	12[p]	12[p]	34[p]	13[p]	12[p]	11[p]	23[p]	57[p]	0.35
2	11	11	11	11	11	12	12[p]	12[p]	34[p]	13[p]	12[p]	11[p]	23[p]	57[p]	0.48
3	11	11	11	11	11	12	12[p]	12[p]	14[p]	12[p]	11[p]	12[p]	22[p]	23[p]	0.33
25	11	11	11	11	11	12	12[p]	12[p]	14[p]	13[p]	12[p]	11[p]	23[p]	57[p]	0.56
6	11	11	11	11	11	12	12	22	14	12	12	14	12	23	1.00
32	11	11	11	11	11[p]	12	12[p]	12[p]	34[p]	12[p]	12[p]	11[p]	22[p]	33[p]	0.20
49	11	11	11	11	14[p]	12	12	12	14[p]	11[p]	12[p]	13[p]	24[p]	55[p]	0.43
50	11	11	11	11	11	12	12	12	14	13	13	12	33	57	1.00
Western Border															
40	11	11	11	11	11	12	11[p]	22[p]	34[p]	12	12[p]	14[p]	33[p]	23[p]	0.85
20	11	11	11	11	11	12	12	12	34	12	12[p]	12	22[p]	33[p]	0.80
10	11	11	11	11	11	12	11	12	34	12	12	12	33	25[p]	0.58
21	11	11	11	11	11	12	12	12	14	12	11	12	22	33	1.00
42	11	11	11	11	11	12	12[p]	12[p]	34[p]	12[p]	12	12	22[p]	33[p]	0.34
34	11	11	11	11	11	12	12	12	34[p]	13	12	12	22[p]	25[p]	0.78
8	11	11	11	11	13[p]	12	12	12	34[p]	22[p]	12[p]	12	12	25[p]	0.78
41	11	11	11	11	11[p]	12	12	12[p]	34[p]	12[p]	12	22[p]	23[p]	23[p]	0.71
35	11	11	11	11	11[p]	12	12[p]	12[p]	34[p]	23[p]	12	12[p]	13[p]	22[p]	0.34
22	11	11	11	11	11	12	12	12	24[p]	13	12	13[p]	24[p]	55[p]	0.56
23	11	11	11	11	11	12	12	12	24[p]	13[p]	12	13	24	33[p]	0.62
19	11	11	11	11	11	12	12[p]	12	34[p]	13	12	12[p]	22[p]	36[p]	0.79
15	11	11[p]	11[p]	11	11	12	23[p]	12	24[p]	34[p]	12[p]	13[p]	24[p]	55[p]	0.28
16	11	11	11	11	11	12	12	12	34[p]	12	12	12[p]	24[p]	39[p]	0.49
Southern Spain															
18	11	11	11	11	11	12	12	12	14[p]	12[p]	12	13	24[p]	55[p]	0.67
5	11	11	11	11	11	12	12[p]	12	34[p]	12[p]	12	13[p]	12[p]	55[p]	0.49
24	11	11	11	11	11[p]	12	23[p]	12[p]	14[p]	12	12[p]	13[p]	12[p]	23[p]	0.35
29	11	11	11	11	11[p]	12	12	12[p]	34	12	12	12	23	13[p]	0.62
26	11	11	11	11	14[p]	12	12[p]	12	24[p]	12[p]	15[p]	12[p]	13[p]	25[p]	0.19
37	11	11	11	11	11[p]	12	12[p]	12[p]	34[p]	12[p]	11[p]	11[p]	34[p]	23[p]	0.13
36	11	11	11	11	11[p]	12	12[p]	12[p]	34[p]	12[p]	15[p]	12[p]	12[p]	36[p]	0.32
12	11	11	11	11	14[p]	12	12	12	14	12[p]	11[p]	12	11[p]	33[p]	0.89
14	11	11	11	11	11[p]	12	12	34[p]	34	12[p]	12	11[p]	23[p]	23[p]	0.26
28	11	11	11	11	11[p]	12	12	34[p]	34	12[p]	12	12[p]	12[p]	33[p]	0.25
27	11	11	11	11	11[p]	12	12[p]	12	14[p]	12[p]	12[p]	12	12[p]	55[p]	0.39
9	11	11	11	11	15[p]	12[p]	12[p]	12[p]	34	13[p]	12[p]	12	12[p]	34[p]	0.32
4	11	11	11	11	11[p]	12	12[p]	12[p]	24[p]	12[p]	11[p]	11[p]	24[p]	55[p]	0.35
7	11	11	11	11	11[p]	12	12[p]	12[p]	24[p]	13[p]	12[p]	14[p]	12[p]	35[p]	0.56
17	11	11	11	11	11	12	11[p]	12	14[p]	12[p]	12[p]	14[p]	12[p]	23[p]	0.29
38	11	11	11	11	11[p]	12	12	12[p]	34[p]	12[p]	12[p]	12[p]	12[p]	25[p]	0.33
39	11	11	11	11	11[p]	12	12	12[p]	14[p]	12[p]	12[p]	12[p]	25[p]	55[p]	0.25
31	11	11	11	11	11	12	12	12[p]	34	12[p]	11[p]	12	23[p]	25[p]	0.63
11	11	11	11	11	11	12	12[p]	34[p]	14[p]	12	22[p]	13[p]	23[p]	25[p]	0.52
13	11	11	11	11	11	12	12	12	14[p]	12[p]	12	13[p]	12[p]	23	0.41
30	11	11	11	11	11	12	12[p]	12	14[p]	13[p]	12	12	23[p]	25	0.82
California and Oregon															*rDNA genotype*[b]
Xeric	11	11	11	11	11	12	12	12	34	11	12	13	12	35	13,10,8,7
Jasper Ridge	11	11	11	11	11	12	12	12	34	12	12	13	12	35	12,8,7
Hopland	11	11	11	11	11	12	12	12	34	12	12	13	12	35	10,8,7
Mesic	11	11	11	11	11	12	12	12	34	22	13	12	13	55	15,9,8,7
Jenner	11	11	11	11	11	12	12	12	34	12	13	12	13	55	12,10,8,7,3

[a] Frequency within site of the most-frequent 14-locus genotype.
[b] rDNA genotype, P. D. CLUSTER and R. W. ALLARD, unpublished data.
[p] Site polymorphic for 14-locus genotype due to polymorphism at loci indicated.

TABLE 6

Fourteen-locus genotypes[a] of Northern Spain

Site	N[b]	Locus									Freq[c]	N[d]
		Pgi1	*Pgd2*	*Mdh3*	*Acp2*	*Pgd1*	*Acp1*	*Prx1*	*Lap1*	*Est1*		
						Central Northern Plateau						
43	84	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	1.00	1
45	91	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.99	2
	1					*12*		*22*			0.01	
44	79	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.81	
	17					*12*					0.17	3
	2					*33*					0.02	
48	87	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.90	
	8				*34*	*12*				*55*	0.08	4
	1 (2)										≤0.01 each	
47	72	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.78	
	18					*12*		*12*	*22*	*33*	0.20	4
	1 (2)										≤0.01 each	
46	54	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.68	
	10					*12*				*13*	0.13	
	8					*12*				*23*	0.10	7
	4				*34*						0.05	
	1 (3)										≤0.01 each	
33	78	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.91	
	7		*11*	*22*	*34*	*12*		*14*	*33*	*23*	0.08	3
	1					*12*					0.01	
						Peripheral Northern Plateau						
1[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	
	66				*34*						0.35	
	53		*11*	*22*	*34*	*12*		*14*	*33*	*23*	0.28	
	43					*12*	*11*	*12*	*22*	*33*	0.23	14
	10				*34*	*12*		*12*	*22*	*25*	0.05	
	5		*11*	*22*	*24*	*12*		*14*	*13*	*23*	0.03	
	3		*11*	*22*		*12*		*14*	*13*	*23*	0.02	
	1 (8)										≤0.01 each	
2[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	
	86				*34*						0.48	
	43		*11*	*22*	*34*	*12*		*14*	*33*	*23*	0.24	
	27					*12*	*11*	*12*	*22*	*33*	0.15	9
	11				*34*	*12*		*12*	*22*	*25*	0.06	
	9		*11*	*22*	*24*	*12*		*14*	*13*	*23*	0.05	
	1 (4)										≤0.01 each	
3[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	
	68					*12*	*11*	*12*	*22*	*33*	0.32	
	66		*11*	*22*	*34*	*12*		*14*	*33*	*23*	0.32	23
	49				*34*						0.24	
	1 (20)										≤0.01 each	
25[e]	48	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.56	
	20		*11*	*22*	*34*	*12*		*14*	*33*	*23*	0.23	
	12		*11*			*12*		*14*	*13*	*23*	0.14	7
	3		*11*			*12*		*12*	*13*	*25*	0.04	
	1 (3)										≤0.01 each	
6[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	1
	90			*22*		*12*		*14*	*12*	*23*	1.00	
32[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	
	19				*34*	*12*		*12*	*22*	*33*	0.20	
	16		*11*		*34*	*12*	*11*		*33*	*35*	0.16	
	9		*11*		*34*	*12*	*11*		*33*	*13*	0.09	
	4				*34*	*12*			*33*	*55*	0.04	
	4			*22*	*34*	*12*			*33*	*55*	0.04	
	4				*34*	*12*			*33*	*35*	0.04	39
	3				*34*	*12*		*12*		*33*	0.03	
	3		*11*		*34*	*12*			*33*	*35*	0.03	
	2		*11*	*22*	*34*	*12*			*13*	*13*	0.02	

TABLE 6—*Continued*

Site	N[b]	Locus									Freq[c]	N[d]
		Pgi1	*Pgd2*	*Mdh3*	*Acp2*	*Pgd1*	*Acp1*	*Prx1*	*Lap1*	*Est1*		
	2			*22*	*34*	*12*		*12*	*12*	*23*	0.02	
	2		*11*		*34*	*12*		*14*	*33*	*35*	0.02	
	2			*11*	*34*	*12*		*12*	*22*	*33*	0.02	
	1 (27)										≤0.01 each	
49[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	
	42	*14*				*11*		*13*	*24*	*55*	0.43	
	17						*13*	*12*	*34*	*55*	0.18	
	5				*34*		*13*	*12*	*33*	*55*	0.05	
	5					*12*					0.05	
	4				*34*		*13*	*12*	*34*	*55*	0.04	20
	3	*14*				*11*	*13*	*13*	*24*	*55*	0.03	
	3	*14*						*13*	*24*	*55*	0.03	
	3				*34*	*11*		*13*	*33*	*55*	0.03	
	3					*11*	*13*	*12*	*33*	*55*	0.03	
	2					*11*		*13*	*24*	*55*	0.02	
	1 (10)										≤0.01 each	
50[e]	00	*11*	*12*	*12*	*14*	*13*	*12*	*11*	*23*	*57*	0.00	1
	100						*13*	*12*	*33*		1.00	

[a] Loci *Pgd1*, *Got2*, *Mdh2* and *Got1* are fixed for quadriplex *1111* and locus *Mdh1* is fixed for quadriplex *1122* in all Northern Spanish sites; these loci are consequently not included in this table.
[b] Number of individuals with indicated 14-locus genotype.
[c] The most-frequent 14-locus genotype of the Central Northern Plateau region is indicated in the first row for each site and the frequencies of other 14-locus genotypes are given below.
[d] Number of different 14-locus genotypes observed at each site.
[e] Peripheral Northern Plateau sites.

phic (the single most-frequent 14-locus genotype was present in f = 0.28). In contrast, among-population genetic variability was large, *i.e.*, each of the 14 populations was sharply differentiated genetically from each other population.

The 21 sites extending eastward from population 18 (Province of Cádiz) across southern Spain to population 30 (Province of Murcia) are much more similar respecting altitude, temperature, rainfall and various other environmental characteristics than the 14 western-border sites. Most of the populations occupying these sites were extensively polymorphic (a single 14-locus genotype was clearly predominant, f > 0.80, in only two of the 21 populations, populations 12 and 30). Although the population genotype of each of the 21 populations differed from that of each other population, in many cases the same 14-locus genotypes were present in several populations but in frequencies that differed from population to population. Thus, in general, genetic differentiation among the southern populations was less distinct than in other regions and the differentiation was often due to frequency differences rather than to the presence *vs* the absence of specific 14-locus genotypes.

Table 5 also lists the predominant 14-locus allozyme and multiallelic rDNA genotypes found in five environmentally distinctive areas in California and Oregon. A great majority of populations within each of these environmentally distinct areas are monomorphic for a single 14-locus allozyme genotype and also for a different multiallelic rDNA genotype (CLEGG and ALLARD 1972; P. D. CLUSTER and R. W. ALLARD, unpublished data). None of the above predominant 14-locus allozyme or multiallelic rDNA genotypes has been observed in ancestral Spanish populations, which indicates that they arose in the recently established colonial populations. Evidence from experimental populations of inbreeding plants (ALLARD 1988; ALLARD *et al.* 1992) has established: (1) that multilocus selection, acting in concert with other evolutionary forces, is capable of rapidly breaking up existing multilocus allelic associations and reorganizing the original allelic ingredients into novel arrangements adapted to different environmental challenges; (2) that selection, in combination with diploidized tetraploidy, is capable of rapidly integrating new beneficial mutants into local populations. Locus *Acp1* of *Ab* appears to provide an example of rapid integration of a new mutant allele in natural populations. Quadriplex *1133* of this locus is fixed in the Californian mesic and Jenner habitats. However, allele *3* and quadriplex *1133* are infrequent in Spain and confined to a region (sites 49 and 50) located >700 km northeast of the southwestern Spanish ports from which explorers and colonists departed for the Americas. It therefore seems unlikely that allele *3* or quadriplex *1133* reached California from Spain but that allele *3* arose anew by mutation in California and that quadriplex *1133* also developed anew in the colonial populations. Quadriplex *1122* is presently the most frequent quadriplex in Spain and also in California, where it is monomorphic or very nearly so in the extensive California xeric, Hopland and Jasper Ridge habitats. Consequently, it seems likely that the *1122* quadriplex was the most frequent quadriplex in the original introductions from Spain and that, since its introduction from Spain, it has continually been the most frequent quadriplex of *Acp1* in California. Historical records indi-

cate that population numbers of *Ab* in California had reached many millions of plants annually by the mid-1800s, so that at least some mutations from allele *2* to allele *3* were likely to have occurred in quadriplex *1122* to produce quadriplex *1133*. The *1133* quadriplex is clearly highly heterotic in the cool, well-watered Californian mesic habitat, which is closely similar to the moist habitats of Spanish sites 49 and 50 located along the banks of the Río Arlanza and Río Duero, respectively. We therefore postulate that quadriplex *1133* became established and supplanted its ancestral *1122* quadriplex in one or more mesic sites in California from which it spread, primarily by seed migration, into all mesic habitats throughout California and also into Oregon. We also postulate that the evolution of the present day mesic genotype in California involved much more than simple insertion of the new *1133* quadriplex into an existing 14-locus genotype: the new quadriplex may also have triggered the reorganizational changes that occurred at loci *Prx1*, *Lap1* and *Est1* and among the rDNA variants (Table 5). In this connection note that the 14-locus genotypes found in the Californian mesic and Spanish sites 49 and 50 differ for loci *Prx1*, *Lap1* and/or *Est1*.

CONCLUSIONS

In this study we determined the multilocus allozyme genotypes of populations of diploid *Ah* and of *Ab*, its tetraploid descendant, from 10 and 50 ecologically diverse sites in Spain. The multilocus genetic structure of the population of *Ah* and *Ab* from each site differed from that at each other site: this brings into focus the primary importance of local environments in shaping the internal genetic structure of each local population and thus also the adaptive landscapes of both species in Spain.

The genetic systems of both the diploid and the tetraploid are highly interactive. Beneficial interlocus (epistatic) interactions at the two-locus, three-locus and higher-order levels, stabilized in various degrees by restriction of recombination due to predominant selfing, are common in *Ah* and even more common in *Ab*. Four among 50 Spanish populations of *Ab* and two among 10 Spanish populations of *Ah* are fixed for a single 14-locus genotype; however, the majority of Spanish populations of both *Ah* and *Ab* are polymorphic for different multilocus genotypes which suggests that interactions at the interplant level may also contribute to superior adaptedness.

Allelic diversity is greater in the tetraploid (52 alleles) than in the diploid (38 alleles). The extra alleles of the tetraploid were always present in nonsegregating heteroallelic quadriplexes. Seven of the 14 loci of this study were monomorphic for a single duplex, or very nearly so, in all populations of the diploid. Five of these seven monomorphic loci of the diploid formed homoallelic quadriplexes (genotypically *1111*) featuring exactly the same alleles present in the diploid. However, two of the seven monomorphic loci of the diploid each formed a highly successful nonsegregating heteroallelic quadriplex (genotypically *1122*) featuring the predominant allele of the diploid, together with a second allele not present in the diploid. The seven remaining loci of this study were polymorphic in the diploid and each of these loci formed one or more successful homoallelic quadriplexes and also one or more successful heteroallelic quadriplexes, often featuring alleles that were not present in the diploid.

The diploidized tetraploidy of *Ab* increases the chances for favorably interacting newly arisen mutants in quadriplexes to become established in local populations. This in turn increases allelic diversity and hence opportunities for beneficial epistatic interactions with alleles of other loci. Frequent short- and long-distance transfers of seeds from place to place, principally through agricultural activities, rapidly spread novel alleles and genotypes from population to population. Outcrosses occur between migrants and residents of the recipient populations, leading to segregation and recombination that produces novel multilocus genotypes upon which evolutionary change depends. The large changes in genotypic frequencies that have been observed within local populations in single generation intervals in *Ah*, *Ab* and other heavily selfing species suggests that natural selection quickly purges populations of alleles and genotypes that do not contribute to superior population adaptedness and at the same time may integrate other alleles and genotypes into the population genotype in ways that lead to a better-functioning whole. "Adaptive valleys" resulting from immigration of unfit individuals are evidently of short duration. Also "adaptive peaks" often shift substantially with annual fluctuations of various features of environment (ALLARD *et al.* 1992). Interactions among several evolutionary forces—natural selection, mutation, diploidized tetraploidy, the mating system—are complex. However, it is difficult to account for the intricate patterns in which specific multilocus genotypes are distributed in space other than in terms of natural selection favoring specific multilocus genotypes under specific sets of environmental conditions. We therefore conclude that natural selection was the main integrating force in shaping the internal genetic structure of local populations as well as in shaping the adaptive landscapes of *Ah* and *Ab* in Spain and elsewhere, and that the restructuring often takes place in short periods of time.

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LITERATURE CITED

ALLARD, R. W., 1975 The mating system and microevolution. Genetics **79:** 115–126.

ALLARD, R. W., 1988 Genetic changes associated with the evolution of adaptedness in cultivated plants and their wild progenitors. J. Hered. **79:** 225–238.

ALLARD, R. W., and J. P. ADAMS, 1969 Population studies in predominantly self-pollinated species. XIII. Intergenotypic competition and population structure. Am. Nat. **103:** 621–645.

ALLARD, R. W., R. D. MILLER and A. L. KAHLER, 1978 The relationship between degree of environmental heterogeneity and genetic polymorphism, pp. 49–73 in *The Structure and Functioning of Plant Populations*, edited by A. H. J. FREYSEN and J. W. WALDENDORP. North Holland Publ. Co., Amsterdam.

ALLARD, R. W., G. R. BABBEL, M. T. CLEGG and A. L. KAHLER, 1972 Evidence for coadaptation in *Avena barbata*. Proc. Natl. Acad. Sci. USA **69:** 3043–3048.

ALLARD, R. W., Q. ZHANG, M. A. SAGHAI MAROOF and O. M. MUONA, 1992 Evolution of multilocus genetic structure in an experimental barley population. Genetics **131:** 957–969.

CLEGG, M. T., and R. W. ALLARD, 1972 Patterns of genetic differentiation in the Slender Wild Oat species *Avena barbata*. Proc. Natl. Acad. Sci. USA **69:** 1820–1824.

CLEGG, M. T., and R. W. ALLARD, 1973 Viability *versus* fecundity selection in the slender wild oat, *Avena barbata*. Science **181:** 667–688.

FIENBERG, S. E., 1980 *The Analysis of Cross-classified Categorical Data*. MIT Press, Cambridge, MA.

FISHER, R. A., 1930 *The Genetical Theory of Natural Selection*. Claredon Press, Oxford.

GARCÍA, P., F. J. VENCES, M. PÉREZ DE LA VEGA and R. W. ALLARD, 1989 Allelic and genotypic composition of ancestral Spanish and colonial Californian gene pools of *Avena barbata*: evolutionary implications. Genetics **122:** 687–694.

GARCÍA, P., M. I. MORRIS, L. E. SÁENZ DE MIERA, R. W. ALLARD, M. PEREZ DE LA VEGA, *et al.*, 1991 Genetic diversity and adaptedness in tetraploid *Avena barbata* and its diploid ancestors *Avena hirtula* and *Avena wiestii*. Proc. Natl. Acad. Sci. **88:** 1407–1411.

HAKIM-ELAHI, A., 1980 Temporal changes in the population structure of the slender wild oat (*Avena barbata*) as measured by allozyme polymorphisms. Ph.D. Dissertation, University of California, Davis.

HAKIM-ELAHI, A., and R. W. ALLARD, 1983 Distribution of homeoalleles at two loci in a diploidized tetraploid: leucine aminopeptidase loci in *Avena barbata*. J. Hered. **74:** 379–380.

HALDANE, J. B. S., 1936 The amount of heterozygotes to be expected in an approximately pure line. J. Genet. **31:** 375–391.

HAMRICK, J. L., and R. W. ALLARD, 1972 Microgeographical variation in allozyme frequencies in *Avena barbata*. Proc. Natl. Acad. Sci. USA **69:** 2100–2104.

HAMRICK, J. L., and L. R. HOLDEN, 1979 Influence of microhabitat heterogeneity on gene frequency distribution and gametic phase disequilibrium in *Avena barbata*. Evolution **33:** 521–533.

HUTCHINSON, E. S., 1982 Genetic markers and ecotypic differentiation in *Avena barbata*. Pott ex Link. Ph.D. Dissertation, University of California, Davis.

HUTCHINSON, E. S., A. HAKIM-ELAHI, R. D. MILLER and R. W. ALLARD, 1983a The genetics of the diploidized tetraploid *Avena barbata*: acid phosphatase, esterase, leucine, aminopeptidase, peroxidase, and 6-phosphogluconate dehydrogenase loci. J. Hered. **74:** 325–330.

HUTCHINSON, E. S., S. C. PRICE, A. L. KAHLER, M. I. MORRIS and R. W. ALLARD, 1983b An experimental verification of segregation theory in a diploidized tetraploid: esterase loci in *Avena barbata*. J. Hered. **74:** 381–383.

KAHLER, A. L., R. W. ALLARD, M. KRZAKOWA, C. F. WEHRHAHN and E. NEVO, 1980 Associations between isozyme phenotypes and environment in the slender wild oat (*Avena barbata*) in Israel. Theor. Appl. Genet. **56:** 31–47.

LADIZINSKY, G., 1973 Genetic control of bivalent pairing in the *Avena strigosa* polyploid complex. Chromosoma **42:** 105–110.

LADIZINSKY, G., and D. ZOHARY, 1968 Genetic relationships between diploids and tetraploids in series *Eubarbatae* of *Avena*. Can. J. Genet. Cytol. **10:** 68–81.

LI, C. C., 1955 *Population Genetics*. University of Chicago Press, Chicago.

MILLER, R. D., 1977 Genetic variability in the slender wild oat *Avena barbata* in California. Ph.D. Dissertation, University of California, Davis.

PÉREZ DE LA VEGA, M., P. GARCÍA and R. W. ALLARD, 1991 Multilocus genetic structure of ancestral Spanish and colonial Californian populations of *Avena barbata*. Proc. Natl. Acad. Sci. USA **88:** 1202–1206.

PETERS, I., 1989 Allozyme and ribosomal DNA spacer-length polymorphisms in Mediterranean collections of *Avena barbata* Pott. ex Link. Ph.D. Dissertation, University of California, Davis.

PIÑERO, D., 1982 Correlations between enzyme phenotypes and physical environment in California populations of *Avena barbata* and *Avena fatua*. Ph.D. Dissertation, University of California, Davis.

RAJHATHY, T., and H. THOMAS, 1974 Cytogenetics of Oats (*Avena* L.). Misc. Publ. Genet. Soc. Canada: No. 2.

ROBBINS, W. W., 1940 Alien plants growing without cultivation in California. Calif. Univ. Agric. Exp. Sta. Bull. 637.

SÁENZ DE MIERA, L. E., 1989 Muestreo y estructura genética de poblaciones españolas del género *Avena*. Dissertation, Universidad de León, León.

WRIGHT, S., 1932 The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proc. VI Internat. Cong. Genet. **1:** 356–366.

WRIGHT, S., 1951 The genetical structure of populations. Ann. Eugen. **15:** 323–358.

WRIGHT, S., 1965 Factor interaction and linkage in evolution. Proc. Roy. Soc. Lond. B **162:** 80–104.

ZHANG, Q., M. A. SAGHAI MAROOF, and R. W. ALLARD, 1990 Worldwide pattern of multilocus structure in barley determined by discrete log-linear multivariate analyses. Theor. Appl. Genet. **80:** 121–128.

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