Isozyme polymorphism in natural populations of *Avena canariensis* from the Canary Islands

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Nineteen populations of the diploid oat *Avena canariensis* were collected from Fuerteventura and Lanzarote of the Canary Islands. Electrophoretic surveys of genetic variation were carried out for six enzyme systems from which gene frequency, expected heterozygosity and unbiased genetic distance were calculated. Phenotype frequencies were scored representing nine variable loci. We recorded an average of 48.45 variable loci, 1.65 alleles/locus and an expected heterozygosity of 0.247. No heterozygotes resulting from outcrosses were found in any of the progeny. Plants from the central area of Fuerteventura tend to possess higher levels of variation than those from the northern part of Lanzarote. The population of Cs27 from northern Lanzarote was monomorphic but had peculiar allozyme, GOT-1S not being in the other populations. Cluster analysis showed three strongly differentiated groups were apparent, Cs26, Cs27 and the remainder. Each population appears to be adapted to a distinct microhabitat, especially soil condition.

INTRODUCTION

The diploid oat *Avena canariensis* ($2n = 2x = 14$) reported by Baum *et al.* (1973) is indigenous to some of the Canary Islands. Initially, *A. canariensis* was thought to occur in Morocco based on a single specimen collected in Casablanca by Ellaria in 1883 (Holmgren and Keuken, 1974). However, it is unlikely that this specimen is of *A. canariensis* and is almost certainly the newly described tetraploid *A. agadiriana* Baum *et Fedak* sp. nov., (Baum and Fedak, 1985). Thus, as far as is known, *A. canariensis* is restricted to the Canary Islands.

During 1985, J. M. Leggett, WPBS, U.K., G. Ladizinsky, Hebrew University of Jerusalem, Rehovot, Israel and P. Hagberg, Svalöf AB, Svalöv, Sweden, undertook a major collecting expedition sponsored by the International Board for Plant Genetic Resources, to the Canary Islands and Morocco to collect the wild species of *Avena*, particularly those species which were poorly represented in existing collections. The populations sampled greatly increases the available gene pool from which characters such as grain quality, yield and disease resistance etc., might be transferred to the cultivated crop.

By quantifying the range of available genetic diversity within and between wild populations of *Avena*, we can adjust our collection, evaluation and breeding strategies to obtain the maximum variation from any given wild population. Perhaps the most convenient method of assessing such variation is by conducting an electrophoretic separation of proteins

Nevo and his co-workers have recently made detailed electrophoretic surveys of the wild relatives of wheat (Nevo *et al.*, 1982) and barley (Nevo *et al.*, 1979, 1983, 1986), and Kahler *et al.* (1980) carried out a similar survey involving the wild oat *A. barbata*. The results of these investigations provided a better basis for the sampling and use of the wild germplasm. Craig *et al.* (1974) collected natural populations of *A. canariensis* from Fuerteventura Island and reported that this species has distinctive ecotypes, and is polymorphic in some morphological traits and in protein and esterase patterns.

In this paper, we report the results of an electrophoretic survey of a number of populations of the wild diploid oat *A. canariensis* collected on the Canary Islands of Fuerteventura and Lanzarote, and compare the genetic variability between the two islands. The manner in which the observed

Figure 1 Collection sites for *Avena canariensis* in the Canary Islands.

genetic variants are distributed and maintained is discussed.

MATERIALS AND METHODS

A. canariensis accessions were collected on the islands of Lanzarote and Fuerteventura of the Canary Island complex. Nine natural population samples of *A. canariensis* were collected on Fuerteventura and ten from Lanzarote. Collection sites

for *A. canariensis* in the Canary Islands are shown in fig. 1. The different habitats in which the nineteen populations were collected are described in table 1. Overall, the collection sites were dry and stony to a greater or lesser extent. The chippings referred to, were derived from inert volcanic debris, and had been placed on agricultural land to a depth of about 10 cm to reduce water loss due to evaporation. The altitude of the various collection sites varied, and some sites were on flat ground whilst others were on slopes of differing pitch.

Table 1 Habitat of the natural populations of *Avena canariensis* from Fuerteventura and Lanzarote in the Canary Islands

Site	Altitude (m)	Habitat	Slope	Population size
Cs9*	150	Path of watercourse	flat	intermediate
Cs10	200	Clay soil cultivation	rolling	intermediate
Cs13	250	Stony soil	rolling	small
Cs14	100	Stony soil	flat	intermediate
Cs15	90	Sandy and dusty soil	flat	intermediate
Cs16	200	Dust and clay soil	flat	intermediate
Cs17	500	Rocky	steep	intermediate
Cs18	300	Stony, clay, dust hollows	flat	intermediate
Cs19	200	Stony roadside	flat	intermediate
Cs20	25	Stony clay and ash roadside	flat	small
Cs21	125	Stony abandoned terraces	flat	large
Cs22	125	Chippings	flat	intermediate
Cs23	50	Chippings stony	flat	large
Cs24	150	Rocky, severe	flat	small
Cs25	350	Chippings and stony	steep	small
Cs26	350	Chippings	rolling	intermediate
Cs27	450	Stony	rolling	intermediate
Cs28	150	Chipping, watercourse	flat	intermediate
Cs29	300	Rocky	steep	intermediate

* Nine populations (Cs9–Cs19) are from Fuerteventura. Ten populations (Cs20–Cs29) are from Lanzarote.

Sampling

A. canariensis in the Canary Islands stores a considerable amount of genetic variation at least partly correlated with ecological factors (Craig *et al.*, 1974). There is no single region rich in diversity within Fuerteventura but rather local, sporadic and regional patterns of differentiation involving different populations or areas. Therefore, collection of smaller samples in as many localities as possible is desirable in *A. canariensis*.

We have made the samplings of *A. canariensis* in natural and disturbed habitats in the xeric upland at elevations of from 25 to 500 m. Individual plants of *A. canariensis* were collected at random from 19 populations in May 1985 around the two islands. In each site, one spikelet was collected from about 30–50 plants at least 1 metre apart along a transect of over one hundred metres. Seedling progeny from a first floret of the spikelet from a total of 475 (19 populations $\times$ 25 plants from the seed collected) different plants was planted in 5 inch pots. However, 70 plants were dead or were unsuitable for electrophoresis. Therefore, the 405 different plants were actually assayed at the first generation. Moreover, a genetic analysis on *Pgi*, *Got*, *Est* and *Lap* loci was carried out by using 294 plants in the F₂ populations from the crosses between different genotypes.

Electrophoretic procedures

A horizontal starch gel was employed to separate the electrophoretic variants of six enzyme systems, esterase (EST), glutamate oxaloacetate-transaminase (GOT), phosphoglucosomerase (PGI), leucine aminopeptidase (LAP), superoxide dismutase (SOD) and benzoyl arginine aminopeptidase (BAP). The electrophoresis was carried out according to Scandalios (1969), and Hayward and McAdam (1977) with some modifications.

Approximately 3 cm sections of young actively growing leaf material was crushed in two drops of Tris-HCl buffer (pH 7.2, 0.05 M) containing 0.01 ml mercaptoethanol per 50 ml. The gels were run at 200 V, 38 mA under 4°C for 4–5 hours. The banding patterns were detected using slight modifications of assays described by Shields *et al.* (1983).

Genetic diversity

The genotype of each plant was inferred for allozyme loci by interpretation of electrophoretic assay of the leaves of 20–25 plants from each

population. Gene diversity or expected heterozygosity (H) was calculated for populations as follows: $H = 1 - \sum X_i^2$ where X_i is the frequency of the i th allele. Because sampling was balanced for loci and within population, pooling over loci within populations was performed without weighting. Variation among populations was assessed using unbiased genetic distance (UGD) as defined by Nei (1978). The matrix of UGD's formed the basis for a sort of linkage average cluster analysis, unweighted pair group mean analysis (UPGMA).

RESULTS

The banding patterns and allelic designations for nine polymorphic loci observed in nineteen natural populations of *A. canariensis* on the Canary Islands are shown in figs 2–5 and fig. 6. The most anodal band (fastest mobility) is designated "F", the least anodal (slowest) "S", and an intermediate between fast and slow is designated "M". The extremely fast or slow band whose frequencies were quite low, are designated "FF" and "SS" respectively. The null allele which makes no enzymatic product is shown as "N" in LAP and EST. An allele at the monomorphic locus is designated "A".

Monomorphic enzymes

Two enzyme systems BAP and SOD were monomorphic in all plants examined. Only a single band was resolved in the BAP system, whilst two were resolved in the SOD system.

Polymorphic enzymes

Four of the enzyme systems studied were found to be polymorphic for at least one locus:

Esterase (EST)

There were three zones of activity on EST gels; EST-1, EST-2 and EST-3, which migrated anodally. *Est*-3 had much more variation than the other loci of *Est*. *Est*-1 and *Est*-2 showed two types of double bands. Both of the slow-migrating bands showed strong activity, but the converse was the case in the fast-migrating bands. *Est*-3 showed three bands. The SS isozyme was found in only one plant of the Cs 15 population.

Figure 2-5 Photographs of the zymogram phenotypes at loci encoded by two dimeric and two monomeric enzymes in *A. canariensis*; anodal direction is above.

Figure 2 EST allozymes at three loci, *Est-1*, *Est-2* and *Est-3*.

Figure 3 GOT allozymes at two loci, *Got-1* and *Got-3*.

Figure 4 PGI allozymes at two loci, *Pgi-1* and *Pgi-2*.

Figure 5 LAP allozymes at two loci, *Lap-2* and *Lap-3*.

Glutamate oxaloacetate-transaminase (GOT)

Three zones of activity were found for GOT. Three bands were present in the GOT-3 region which indicates a dimeric enzyme. GOT-2 was monomeric and faint in our samples and is not described in this study. GOT-1 showed only two bands, but the slower one was found only in population Cs 27 and the faster one was found in all the other populations.

Figure 6 Banding patterns and their allelic designations for nine polymorphic loci observed in *A. canariensis*. Character under band refers to the variant at that allozyme locus.

Phosphoglucoseisomerase (PGI)

Two zones of activity were detected with this enzyme system. The most anodal isoenzyme according to Gottlieb (1981) is located only in the chloroplast, and is specified by *Pgi-1*. Two bands were produced by both the *Pgi-1* and *Pgi-2* loci.

Leucine aminopeptidase (LAP)

Three zones of activity were observed for LAP. Three single and three double bands were observed for LAP-2 and LAP-3 respectively, and both involved null alleles. The most rapidly migrating band "FF" of LAP-2 and LAP-3 were found in only two plants from populations Cs 13 and Cs 15. *Lap-1* produces one band which was monomorphic. LAP is considered to be a monomeric enzyme.

Allele frequencies

The frequencies of the individual alleles at each of the thirteen loci are presented in table 2. Progeny derived from each adult individual in nature were assayed electrophoretically in polymorphic populations. No heterozygous individuals were found in any of the arrays at the first generation. The "F" allele at the *Est-1* locus was often observed in four of the nine populations from Fuerteventura Island, although the frequencies were relatively low. Of the ten populations from Lanzarote, only Cs 25 exhibited the "F" allele at a low frequency. The "F" allele at the *Got-3* locus was frequently

Table 2 Allozyme frequency at 13 loci in the 19 natural populations of *Avena canariensis*

Locus	Allele	Population name																	
		Cs9	Cs10	Cs13	Cs14	Cs15	Cs16	Cs17	Cs18	Cs19	Cs20	Cs21	Cs22	Cs23	Cs24	Cs25	Cs26	Cs27	Cs29
<i>Est-1</i>	F	0.29	0.00	0.00	0.05	0.00	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
	S	0.10	0.10	0.24	0.24	0.29	0.24	0.19	0.10	0.10	0.00	0.14	0.22	0.05	0.14	0.14	0.00	0.00	0.00
	N	0.61	0.90	0.76	0.71	0.71	0.71	0.76	0.90	0.90	1.00	0.86	0.78	0.95	0.86	0.76	1.00	1.00	1.00
<i>Est-2</i>	F	0.57	0.57	0.38	0.67	0.52	0.57	0.38	0.67	0.52	0.77	0.42	0.13	0.57	0.00	0.14	0.00	1.00	0.19
	S	0.00	0.10	0.05	0.00	0.00	0.05	0.05	0.00	0.00	0.18	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.05
	N	0.43	0.33	0.57	0.33	0.48	0.38	0.57	0.33	0.48	0.05	0.29	0.87	0.43	1.00	0.86	1.00	0.00	0.76
<i>Est-3</i>	F	0.52	0.19	0.00	0.00	0.10	0.38	0.33	0.48	0.48	0.05	0.19	0.17	0.10	0.00	0.00	0.00	1.00	0.05
	S	0.48	0.81	1.00	1.00	0.86	0.62	0.67	0.52	0.52	0.95	0.81	0.83	0.90	1.00	1.00	0.00	0.00	0.95
	SS	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Got-1</i>	F	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
<i>Got-3</i>	F	0.04	0.00	0.48	0.00	0.19	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00
	M	0.95	0.52	0.48	0.76	0.52	0.24	0.86	0.81	0.86	0.05	0.57	0.96	0.90	1.00	0.90	0.05	1.00	0.63
	S	0.00	0.48	0.05	0.24	0.29	0.76	0.14	0.10	0.14	0.95	0.43	0.04	0.10	0.00	0.10	0.00	0.00	0.38
<i>Pgi-1</i>	F	0.95	0.86	0.48	0.29	0.67	0.86	0.76	0.90	0.81	0.91	0.95	0.96	0.33	1.00	0.95	1.00	0.71	0.14
	S	0.05	0.14	0.52	0.71	0.33	0.14	0.24	0.10	0.19	0.09	0.05	0.04	0.67	0.00	0.05	0.00	0.29	0.86
<i>Pgi-2</i>	F	0.00	0.00	0.00	0.00	0.00	0.05	0.38	0.00	0.05	0.00	0.05	0.00	0.05	0.29	0.81	0.00	0.00	0.63
	S	1.00	1.00	1.00	1.00	1.00	0.95	0.62	1.00	0.95	1.00	0.95	1.00	0.95	0.71	0.19	1.00	1.00	0.38
	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>Lap-1</i>	FF	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lap-2</i>	F	0.33	0.48	0.43	0.24	0.29	0.62	0.38	0.48	0.62	0.82	0.62	0.87	0.10	0.81	0.90	0.29	0.90	0.88
	S	0.00	0.00	0.52	0.48	0.14	0.19	0.10	0.19	0.33	0.05	0.14	0.04	0.57	0.05	0.00	0.00	0.10	0.43
	N	0.67	0.52	0.00	0.29	0.57	0.19	0.52	0.33	0.05	0.14	0.24	0.09	0.33	0.14	0.10	0.71	0.00	0.10
<i>Lap-3</i>	FF	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	F	0.66	0.43	0.00	0.29	0.43	0.14	0.48	0.29	0.05	0.14	0.10	0.05	0.28	0.14	0.10	0.71	0.00	0.14
	S	0.05	0.10	0.00	0.00	0.14	0.05	0.05	0.05	0.00	0.00	0.14	0.04	0.05	0.00	0.00	0.00	0.00	0.00
	N	0.29	0.48	1.00	0.71	0.38	0.81	0.48	0.67	0.95	0.86	0.76	0.91	0.67	0.86	0.90	0.29	1.00	0.86
<i>Sod-1</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>Sod-2</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>Bap-1</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

observed in the Cs 26 population and is ubiquitous on the island of Fuerteventura. The plants from Cs 27 were very different from the other populations, having a later heading date, prostrate growth habit and pubescence. This population also has a unique "S" allele at the *Got-1* locus. Dimorphic differentiation of Cs 29 was detected from the observations of EST-2, EST-3, PGI-1 and GOT-3 isozymes, which are positively correlated with morphological characters, especially heading date and leaf morphology. In population Cs 29, early and late flowering types were observed. The early type always had EST-3S, EST-2N, GOT-3M and PGI-2F isozymes, whilst the late type had EST-3F, EST-2F, GOT-3S and PGI-2S. The same general trend was observed in the other populations. Several plants in Cs 17, Cs 21 and Cs 24 in which the bands GOT-3M and PGI-2S were observed also exhibited late maturity and leaf pubescence.

Genetic variability

Table 3 shows the genetic variability at thirteen loci in all the populations, and was calculated from

the allozyme frequency in table 2. The number of alleles per locus varied from 1.15 (Cs 27) to 1.92 (Cs 15, Cs 16 and Cs 17), and the means of each island were 1.76 for Fuerteventura and 1.54 for Lanzarote. The difference of the means between two islands was statistically significant at 0.05 level. The variable loci expressed as a percentage, had a positive correlation with the number of alleles per locus, and the mean number of variable loci of the Fuerteventura populations was much higher than the populations from Lanzarote. To facilitate comparisons of degrees of polymorphism, a measure of heterozygosity would be useful. The mean expected heterozygosity per population varied from 0.05 to 0.28. The averages over all loci in each island are 0.226 in Fuerteventura and 0.127 in Lanzarote. The means between them were significantly different at 0.001 level.

Three parameter values, variable loci, number of alleles per locus and expected heterozygosity, indicate that the populations of Fuerteventura are genetically much more variable than those of Lanzarote. However, Lanzarote's populations have a more unique allozyme banding patterns

Table 3 Genetic variability at 13 loci in the 19 natural populations of *A. canariensis*

Site	No. of plants examined	Variable loci (per cent)	No. of alleles per locus	Unbiased heterozygosity	Unbiased genetic distance		
					Mean	Range	S.D.
Cs9	21	53.8	1.69	0.21	0.11	0.03-0.23	0.06
Cs10	21	53.8	1.69	0.23	0.07	0.01-0.24	0.06
Cs13	21	38.5	1.62	0.19	0.10	0.04-0.29	0.06
Cs14	21	46.2	1.62	0.21	0.10	0.00-0.28	0.07
Cs15	21	53.8	1.92	0.27	0.08	0.01-0.29	0.06
Cs16	21	61.5	1.92	0.24	0.09	0.02-0.22	0.06
Cs17	21	61.5	1.92	0.28	0.07	0.03-0.25	0.06
Cs18	21	53.8	1.77	0.21	0.07	0.01-0.16	0.04
Cs19	21	61.5	1.69	0.19	0.07	0.01-0.21	0.05
Mean		53.8	1.76*	0.226***	0.084*		
Cs20	22	46.2	1.62	0.10	0.13	0.02-0.28	0.07
Cs21	21	61.5	1.85	0.22	0.07	0.01-0.22	0.05
Cs22	23	53.8	1.69	0.11	0.08	0.01-0.24	0.05
Cs23	21	61.5	1.77	0.20	0.10	0.00-0.27	0.07
Cs24	21	30.8	1.38	0.10	0.10	0.01-0.31	0.07
Cs25	21	53.8	1.62	0.12	0.14	0.03-0.35	0.08
Cs26	21	15.4	1.15	0.06	0.19	0.09-0.53	0.09
Cs27	21	15.4	1.15	0.05	0.27	0.14-0.53	0.08
Cs28	21	38.5	1.54	0.12	0.12	0.02-0.29	0.07
Cs29	24	53.8	1.62	0.19	0.10	0.03-0.22	0.06
Mean		43.1	1.54*	0.127***	0.134*		

* and ***, Significant difference of means between two islands at 0.05 and 0.001 levels, respectively.

than the populations from Fuerteventura. Populations Cs 25, Cs 26 and Cs 29 were collected in the mountainous region of Lanzarote (altitude 350-450 m). In Fuerteventura, Cs 13 also came from a stony habitat and showed a relatively lower gene diversity than the others from volcanic ash, chipping covered or cultivated areas. Population Cs 17 was collected from a rocky, steeply sloping habitat at a relatively high altitude in Fuerteventura, and showed the highest expected heterozygosity (0.28), number of alleles per locus (1.92) and variable loci (61.5 per cent).

Genetic distance

The genetic distance coefficients were calculated for all population comparisons according to Nei (1978) and the means and ranges are given in table 3. The ranges for Cs 27 and Cs 26 are from 0.14 to 0.53 (mean 0.27) and from 0.09 to 0.53 (mean 0.19), respectively. A UPGMA cluster analysis was performed using the unbiased genetic distance, and the resulting dendrogram is presented in fig. 7. A major dichotomy separates Cs 26 and Cs 27 from the remaining populations and secondary minor clusters separate the populations Cs 24,

Cs 25 and Cs 29 from Lanzarote's mountain area, and the populations Cs 9, Cs 10 and Cs 15 from the southern part of Fuerteventura. The populations from Fuerteventura are relatively

Figure 7 Dendrogram resulting from a linkage average cluster analysis (UPGMA). Coefficient used is Nei's (1978) unbiased genetic distance.

tightly clustered, whilst the remaining populations are separated.

DISCUSSION

The debate whether allozyme variation in natural populations is selectively meaningful or adaptively neutral (Lewontin, 1974) is still going on. This problem has both theoretical and practical implications. If neutral then the abundant allozyme polymorphisms found in natural populations of plants and animals are predominantly of interest only as genetic markers. If however this variation is largely adaptive, it may be of use in plant breeding programmes.

The electrophoretic evidence from 405 plants of *A. canariensis* from the Canary Islands, in which more than 13 loci and 30 alleles were detected has suggested that the amounts of genetic polymorphism varies nonrandomly between loci, populations, habitats and life zones. Although these populations originated from a relatively small area, the range of variation in electrophoretic traits was greater than the variation found in other species of oats examined by other workers (Marshall and Allard, 1970; Allard *et al.*, 1978).

Natural populations of diploid *A. canariensis* on the island of Fuerteventura in the Canary archipelago are polymorphic in morphological characteristics and in electrophoretic patterns (Craig *et al.*, 1974). The "FF" allele in *Lap-2* of population Cs 13, the "SS" allele in *Est-3* and the "FF" allele in *Lap-3* in population Cs 15 occurred at very low frequencies (0.05) compared to the ubiquitous "S" and "F" alleles.

Harris *et al.* (1977) and Ward (1977), have shown that multimeric enzymes are significantly less variable than monomeric enzymes. In our study of *A. canariensis* we also found that EST and LAP were more variable than PGI or GOT. Marshall and Allard (1970) reported that electrophoretic variation in *A. fatua* was genetically more variable than the observed in *A. barbata* for the isozymes esterase, phosphatase and leucine aminopeptidase, and their provisional estimates indicated that 31 per cent of loci in *A. barbata* and 54 per cent of loci in *A. fatua* were polymorphic for electrophoretic variants. By comparison, the mean variable loci recorded in *A. canariensis* was 48.5 per cent.

A simple method of assessing the degree of outcrossing in apparently self-fertilized plants is given by Marshall and Broué (1973). It requires

only that a plant population be polymorphic for a diallelic locus. According to the formula the degree of outcrossing will be zero when no heterozygotes are observed. No heterozygotes were detected in any of the populations of *A. canariensis* studied here, indicating that the amount of outcrossing which occurs in *A. canariensis* is very low indeed, especially when compared to the Californian population of *A. barbata* studied by Marshall and Allard (1970), where outcrossing was recorded from 0.1 per cent to more than 7 per cent. The levels of heterozygosity expected assuming Hardy-Weinberg equilibrium in the *A. canariensis* populations ranged from 0.05 to 0.28, and averaged (over all loci in each of the islands) 0.226 in Fuerteventura and 0.127 in Lanzarote, which are substantially higher than the mean values for the *Avena* species *A. fatua* 0.06 and *A. barbata* 0.03 reported by Marshall and Allard (1970), but somewhat lower than the outcrossing species such as *Zea mays* 0.251 (Doebley *et al.*, 1985). Significant differences between observed and expected proportion of heterozygous individuals in *A. canariensis* probably reflects inbreeding in this species. The disparity between these sets of results seems to be due to the fact that *A. canariensis* has become highly adapted to various microhabitats in the Canary Islands.

In autogamous species, linkage disequilibrium decays very slowly, even for unlinked loci, so that allozymes may hitch-hike with any locus in the genome (Hedrick, 1980), and allozyme frequency disparity between ecotypes will persist for many generations regardless of its origin (Hedrick and Holden, 1979). Kahler *et al.* (1980) inferred that modification of the mating system has been the major strategy by which *A. barbata* adjusts its system of genetic variability to allow response to changing evolutionary circumstances. In *Gailardia pulchella* two particular allozymes (ADH-2f and PGM-1c) have been shown to be associated with specific soil characteristics and edaphic factors (Heywood and Levin, 1985; Heywood, 1986).

In the present study, distinctive ecotypes were located at the periphery of the elevation gradient and ecotypes differing morphologically were distributed along the gradient. A tall, early, erect and glabrous ecotype occurred at the lowest elevation, and a shorter, very late, prostrate and pubescent type occurred at the highest elevations. The early maturing types were distributed throughout the islands and were adapted mainly to disturbed habitats along ditches and roadsides. The later maturing types were collected in the southern part of Fuerteventura and the northern part of Lanzarote,

mainly at high elevations in habitats that were basically undisturbed by cultivation. Clearly, the two ecotypes which are morphologically and isoenzymatically distinguishable from one another exist in the same population Cs 29 and are sympatrically isolated from one another by mainly the difference in flowering date.

Three populations (Cs 25, Cs 26 and Cs 27) were collected in a relatively small area in the northern part of Lanzarote but the genetic distances between them were quite large. The unbiased genetic distance between Cs 26 and Cs 27 was 0.53 which is almost equivalent to the degree of the genetic differentiation between sibling species in *Drosophila willistoni* (Ayala *et al.*, 1974). This value indicates that about 53 allelic substitutions per 100 gene loci have occurred in their separate evolution.

Nevo *et al.* (1979, 1981) have surveyed the genetic diversity and environmental associations in wild barley and wheat. The range of genetic distances between populations in these autogamous species was less than we observed in *A. canariensis*.

Some of the populations (Cs 24, Cs 25 and Cs 27) observed in this study differed by a relatively large chromosome translocation which was detected cytologically by observing multivalents at meiosis of interpopulation hybrids (Morikawa unpublished data). One instance of rapid speciation involves the two diploid species *Clarkia lingulata* and *C. biloba*, which are native to California (Gottlieb, 1973). Both the species are similar in external morphology except petal shape. However, their chromosomal configurations differ by a translocation and several inversions. These species remain genetically quite similar with genetic distance of 0.128 (Ayala, 1982). The speciation in *A. canariensis* involved the dissimilar genetic distances among populations, which means that it took a relatively longer time to separate the two ecotypes than *C. lingulata*. However, both the species are similar to each other in involving chromosomal differentiations.

Thus, we may conclude that *A. canariensis* is differentiated in its chromosome architecture, and its allozyme composition, and has a number of unique polymorphic genotypes which are restricted to a relatively small area.

Acknowledgements We wish to thank Drs Hugh Thomas and M. D. Hayward, Welsh Plant Breeding Station, U.K., for valuable suggestions during the preparation of this paper and their critical reading of the manuscript.

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