

## Genetic diversity in the *Chamaecytisus proliferus* complex (Fabaceae: Genisteae) in the Canary Islands in relation to *in situ* conservation

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### Summary

Electrophoresis was carried out for six isozyme systems on 175 accessions of the seven morphological forms of *Chamaecytisus proliferus* (L. fil.) Link (Fabaceae: Genisteae) from the Canary Islands. Previous studies have shown that there is clear differentiation into morphological and ecological forms. The underlying genetic variation as visualised by studying isozymes does not reflect this. While substantial genetic diversity can be identified, this was found to be as much within as between morphological forms. This genetic diversity was found to decrease from east to west, and reflects the pattern of variation remaining after colonisation of the individual islands, which is assumed to have progressed in the same direction. Subsequently, adaptive radiation has given rise to the overlying morphological variation as exhibited in the seven morphological forms.

In terms of *in situ* conservation, overall genetic diversity can be easily conserved in the abundant populations occurring in the east of the archipelago, while more attention is required for conservation of the much rarer morphological forms found in the west, despite their relative lack of isozyme diversity.

**Abbreviations:** ACO—aconitase, ADH—alcohol dehydrogenase, IDH—iscitrate dehydrogenase, MDH—malate dehydrogenase, PGD—6-phosphogluconate dehydrogenase, PGM—phosphoglucomutase, CA—cluster analysis, PCA—principal component analysis

### Introduction

Among a broad group of endemics, which are locally used as forage species in the Canary Islands, is tagasaste (*Chamaecytisus proliferus* (L. fil.) Link var. *palmensis* (Christ) Hansen & Sunding) (Fabaceae: Genisteae) which is widely cultivated in La Palma, La Gomera, Tenerife, Gran Canaria and El Hierro. It has also now achieved importance in some areas of New

Zealand and Australia where it has been under cultivation since late in the last century (Francisco-Ortega et al., 1991). Within the genus *Chamaecytisus*, tagasaste is the only species which is cultivated. Furthermore it represents the most important non-ornamental cultivated species with its centre of diversity and origin in the Canary Islands.

*Chamaecytisus proliferus* forms a complex of seven morphological forms (Table 1), each with a

Table 1. The seven morphological forms, of the *Chamaecytisus proliferus* complex in the Canary Islands after Acebes-Ginovés et al. (1991)

Taxon	Common name	Island	Ecology
1. <i>C. proliferus</i> ssp. <i>proliferus</i> var. <i>hierrensis</i> (Pit.) Aceb.			North: 700–1300 m, cliff belt with heath ( <i>Erica arborea</i> )
2. <i>C. proliferus</i> ssp. <i>proliferus</i> var. <i>palmensis</i> (Christ) Hans et Sund	Typical tagasaste	Wild in La Palma, cultivated elsewhere	North: 700–1300 m, cleared areas of heath belt and laurel ( <i>Laurus azorica</i> ) wood
3. <i>C. proliferus</i> ssp. <i>proliferus</i> var. <i>calderae</i> Aceb.	White tagasaste	La Palma	North: 1300–1200 m, south: 1000–2000 m, pine ( <i>Pinus canariensis</i> ) forest
4. <i>C. proliferus</i> ssp. <i>proliferus</i>	White escobon of Tenerife	Tenerife	North: 700–1300 m, cleared areas of heath belt and laurel wood
5. <i>C. proliferus</i> ssp. <i>angustifolius</i> (Ktoei) Kunkel	Narrow-leaved escobon	La Gomera and Tenerife	North: 1300–2200 m, south: 700–2200 m, pine forest
6. <i>C. proliferus</i> ssp. <i>proliferus</i> var. <i>canariae</i> (Christ) Kunkel	White escobon of Gran Canaria	Gran Canaria	North: 700–1300 m, cleared areas of heath belt and laurel wood
7. <i>C. proliferus</i> ssp. <i>meridionalis</i> Aceb.	Escobon of southern Gran Canaria	Gran Canaria	North: 1300–200 m, south: 1300–2000 m, pine forest

distinct ecological requirement (Acebes-Ginovés, 1990; Acebes-Ginovés et al., 1991; Francisco-Ortega, 1992) and associated with specific life-zones of each island (Table 1). The species follows the pattern of other Genisteae, and has been reported as tetraploid with  $2n = 4x = 48, 50, 52$  (Cristofolini, 1991).

The value of isozymes for diversity and evolutionary studies at the infraspecific level has often been reviewed (e.g. Brown, 1990; Crawford, 1990). Isozyme studies have been of particular use in assessing patterns of plant evolution and speciation in islands (e.g. Wendel & Percy, 1990; Aradhya et al., 1991; Walters & Decker-Walters, 1991) where rapid speciation through adaptive radiation and vicariance has led to the development of high levels of morphological variation within usually narrow geographical boundaries.

In this paper we examine patterns of isozyme variation in relation to the complete range of distribution and morphology of *C. proliferus sensu lato*. Genetic variation within and between islands has been studied to confirm whether patterns deduced by studying morphology and ecology

are mirrored by isozyme patterns, and proposals regarding evolutionary development of the species within the Canaries are made. Effective conservation strategies are proposed.

### Materials and methods

Isozyme analysis was conducted on 175 accessions representing samples of wild, cultivated and semi-cultivated populations of *C. proliferus* (Francisco-Ortega & Jackson, 1990; Francisco-Ortega, 1992). They represent the complete range of ecogeographical variation found in this species complex. Seeds were collected in 1989 (Francisco-Ortega et al., 1990) and samples are now held in Centro Nacional de Recursos Fitogenéticos (Alcalá de Henares, Spain).

Enzyme extraction was carried out individually from at least ten mature embryos from each accession using the protocol of Nagamine et al. (1989). Horizontal starch gel electrophoresis was conducted following procedures given by Kephart (1990) using a 0.135 M tris 0.043 M citric acid solution as electrode buffer.

Six enzyme systems were selected after a preliminary survey of 12 enzymes, and these were aconitase (ACO), alcohol dehydrogenase (ADH), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD), and phosphoglucomutase (PGM). Staining for IDH, MDH and PGM were reported by Nagamine et al. (1989) and ACO, ADH and PGD by Wendel & Weeden (1989). Staining for ACO was modified by the elimination of agarose.

Zones of enzyme activity were identified numerically according to relative migration, those zones of activity producing the most anodal electrophoretic variants having the lowest numerical designation. Within each zone of activity, bands were also numbered from slower to faster migration in the gel. Genetic interpretation of isozyme phenotypes was based on a comparison of observed patterns of variation and knowledge of protein quaternary structures and subcellular

localisation previously reviewed by Weeden & Wendel (1989) and Crawford (1990). This has led to the definition of putative isozymes and allozymes and to the determination of accession allele frequencies.

Ordination of results was carried out by Principal Component Analysis (PCA). Each accession was regarded as an OTU and prior to the actual analyses, allele frequency values per accession were transformed (arcsine) and standardised to zero mean and standard deviation of 1.0. The statistical package CLUSTAN (Wishart, 1987) was used.

Following Wendel & Percy (1990) total variation (Ht) was divided into within and between morphological forms and island components (Hs and Dst respectively). The unbiased genetic distance and unbiased genetic identity (Nei, 1987) were also calculated. A similarity matrix of genetic distances and a dendrogram were obtained after a Cluster

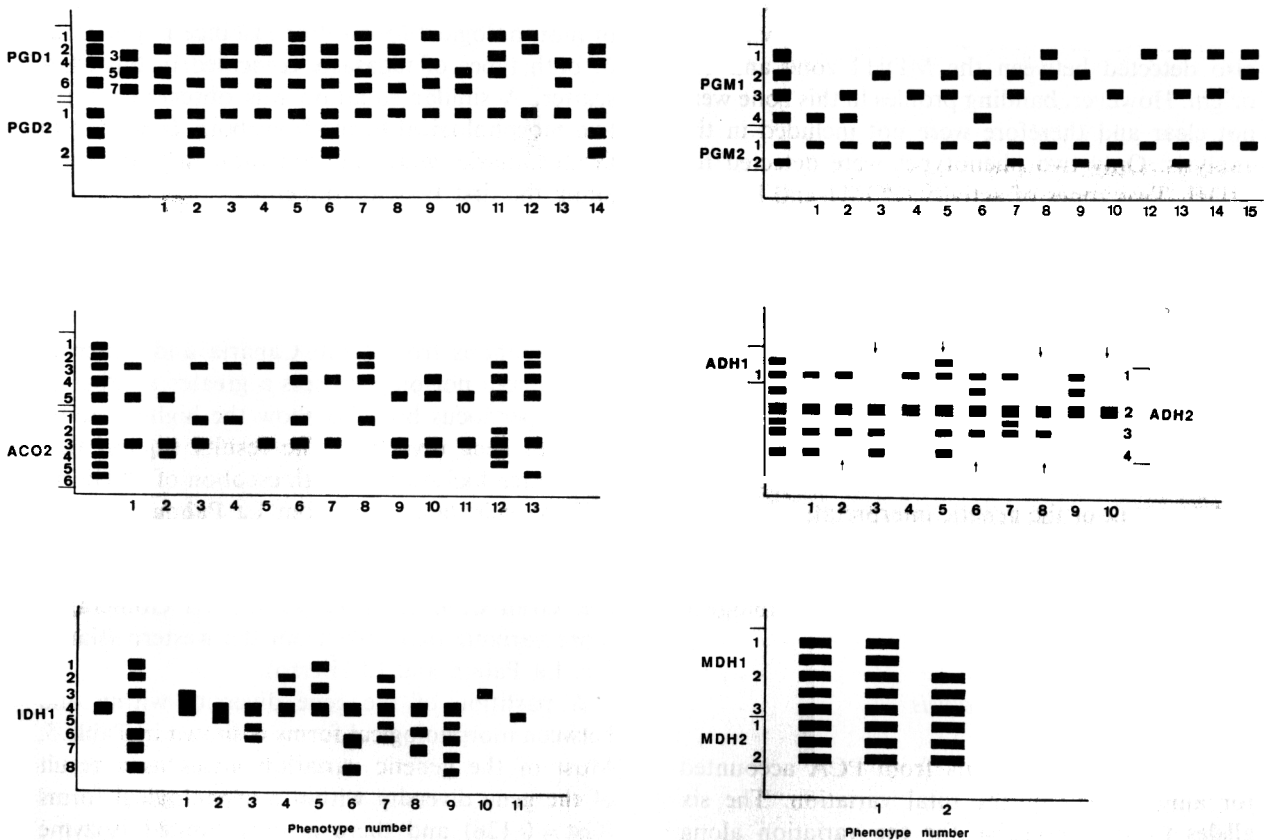


Fig. 1. Schematic illustrations of zymograms showing banding patterns in 175 accessions of *Chamaecytisus proliferus* for ACO, ADH, IDH, MDH, PGD and PGM. Selected phenotypes are also given. Null alleles are pointed.

Analysis (CA) (Unweighted Pair Group Arithmetic Average Clustering Method = UPGM) using NTSYS (Rohlf, 1988).

## Results

Ten putative loci were identified for the six enzymes studied and these are illustrated in Fig. 1. Two zones of activity (ACO1 and ACO2) were revealed for ACO system. Five alleles were detected for ACO1 and four for ACO2. Two zones of activity were observed for ADH (ADH1 and ADH2). Two alleles were identified for ADH1, one of which was regarded as null. Five alleles were recognised at ADH2. Alleles ADH1-1 and ADH2-1 had nearly the same electrophoretic mobility resulting in some overlapping of their regions of activity. Allele ADH2-2 was observed in all individuals. There was one zone of activity for IDH with a total of eight alleles. Two clear zones (MDH1 and MDH2) of enzyme activity were observed for the MDH system. Some activity was also detected between the MDH2 zone and the origin. However, banding profiles in this zone were not clear and therefore were not included in the analysis. Only two phenotypes were detected for MDH. Two zones of activity (PGM1 and PGM2) were identified for PGM system. Four alleles were detected at PGM1 and two at PGM2. Two zones of activity were identified for PGD (PGD1 and PGD2). Seven different bands were detected at PGD1 zone whilst only three bands were found at PGD2. A genetic interpretation of the banding patterns on PGD1 was not possible and therefore these data were not included in the multivariate analysis.

As a result of the genetic interpretation of these six isozyme systems, allele frequencies were calculated for accessions and for morphological forms. These are summarised for each morphological form in Table 2.

### *Principal Component Analysis*

The first two components from PCA accounted for almost 30% of the total variation. The six alleles most responsible for the variation along the first component were, with eigenvector values in brackets, PGM1-3 (0.44), ACO1-5 (-0.41),

PGM1-2 (-0.39), ACO2-5 (-0.36), ACO1-3 (0.18) and PGD2-2 (0.11). The six alleles with the highest eigenvector values along the second component were ACO1-4 (0.31), ACO2-2 (-0.28), ACO2-1 (-0.20), ACO1-2 (-0.13), PGD2-2 (-0.12) and ADH2-0 (-0.10).

A scatter diagram with scores on the first two components is illustrated in Fig. 2. Results suggest that patterns of variation for some of the alleles are related to island provenance. They indicate that allozyme ACO2-1 was very common in La Palma whereas alleles ACO1-5 and ACO2-5 were almost exclusive to Gran Canaria. Accessions of escobon from Gran Canaria tended to have high negative values along the first component whereas populations from the rest of the archipelago had positive scores. Furthermore, accessions of wild tagasaste from La Palma and of escobon from El Hierro had negative values along the second component whilst escobons collected in Tenerife had positive scores.

There was no clear within island differentiation of morphological forms. For instance populations of both types of tagasaste coincided in this PCA scatter. A similar situation was observed for the two morphological forms from both Tenerife and Gran Canaria, which did not show distinct scores along the first two components.

### *Genetic diversity*

Results shown in Tables 2-4 indicate that the four escobons from Gran Canaria and Tenerife-La Gomera not only possess a greater number of alleles per locus but also show the highest values of total gene diversity. The results suggest that for the ten loci studied, both escobon of El Hierro and the wild tagasastes from La Palma were less variable than the other morphological forms, suggesting that germplasm from the eastern islands (i.e. Gran Canaria, Tenerife and La Gomera) is more variable than that from the western islands (i.e. La Palma and El Hierro).

A partition of the gene diversity within and between morphological forms is shown in Table 5. Most of the genetic variation arises as a result of the gene diversity within morphological forms ( $G_{st} = 0.126$ ) and there is only limited isozyme differentiation amongst the seven morphological forms.

Similar results were obtained after division of gene diversity into within and between island components (Table 6) as most of the total gene diversity is due to the variation found within each island ( $G_{st} = 0.113$ ). A comparison of results from Tables 5 and 6 indicate that for each locus Dst values were higher when the analysis was carried out on an island basis than when it was based on morphological forms. ACO1, ACO2 and

PGM1 loci had the highest Dst values. This supports the results from PCA, in which it was shown that allozymes from these loci yielded the clearest discrimination between islands.

#### Genetic distance and identity

Estimations of unbiased genetic distance between the seven morphological forms and between

Table 2. Allozyme frequencies at ten putative loci in *Chamaecytisus proliferus*. Frequencies are given by morphological form. Numbers of accessions are indicated in brackets. Morphological forms coded in Table 1

Locus	Allele	Morphological form						
		1 (2)	2 (44)	3 (6)	4 (5)	5 (62)	6 (18)	7 (38)
ACO1	1	0.00	0.00	0.00	0.00	0.01	0.00	0.01
	2	0.03	0.00	0.00	0.08	0.11	0.01	0.05
	3	0.53	0.79	0.87	0.47	0.43	0.35	0.30
	4	0.34	0.11	0.08	0.42	0.42	0.25	0.29
	5	0.10	0.10	0.05	0.03	0.03	0.39	0.35
ACO2	1	0.20	0.45	0.46	0.02	0.05	0.07	0.02
	2	0.17	0.07	0.06	0.41	0.39	0.08	0.13
	3	0.57	0.46	0.46	0.49	0.50	0.54	0.46
	4	0.00	0.00	0.01	0.02	0.01	0.04	0.07
	5	0.06	0.01	0.01	0.06	0.05	0.26	0.30
	6	0.00	0.00	0.00	0.00	0.00	0.01	0.02
ADH1	1	0.95	0.93	0.94	0.96	0.94	0.95	0.95
	0	0.05	0.07	0.06	0.04	0.06	0.05	0.05
ADH2	1	0.00	0.01	0.00	0.03	0.00	0.00	0.01
	2	0.50	0.51	0.50	0.52	0.51	0.56	0.57
	3	0.00	0.00	0.00	0.00	0.01	0.00	0.01
	4	0.42	0.23	0.50	0.31	0.14	0.21	0.17
	0	0.08	0.25	0.00	0.14	0.34	0.23	0.24
IDH1	1	0.00	0.02	0.00	0.00	0.01	0.01	0.02
	2	0.00	0.01	0.01	0.00	0.01	0.03	0.02
	3	0.00	0.04	0.02	0.00	0.02	0.01	0.02
	4	0.80	0.91	0.88	0.96	0.85	0.94	0.83
	5	0.00	0.00	0.00	0.02	0.02	0.00	0.02
	6	0.08	0.01	0.01	0.02	0.02	0.02	0.03
	7	0.12	0.01	0.08	0.00	0.01	0.00	0.06
	8	0.00	0.00	0.00	0.00	0.01	0.00	0.00
MDH1	1	0.00	0.02	0.01	0.00	0.02	0.03	0.06
	2	1.00	0.98	0.99	1.00	0.98	0.97	0.94
MDH2	1	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	2	0.50	0.50	0.50	0.50	0.50	0.50	0.50
PGD2	1	0.65	0.80	0.80	0.65	0.61	0.95	0.95
	2	0.35	0.20	0.20	0.35	0.39	0.05	0.05
PGM1	1	0.00	0.00	0.00	0.00	0.00	0.04	0.04
	2	0.00	0.08	0.17	0.25	0.24	0.66	0.73
	3	0.95	0.91	0.82	0.59	0.73	0.27	0.21
	4	0.05	0.01	0.01	0.16	0.03	0.03	0.02
PGM1	2	0.95	0.98	0.95	0.93	0.92	0.96	0.95
	2	0.04	0.02	0.05	0.07	0.08	0.04	0.05

Table 3. Summary statistics of genetic variability at ten isozyme loci in *Chamaecytisus proliferus*. Morphological forms coded in Table 1

	Morphological forms						
	1	2	3	4	5	6	7
Number of unique alleles	0	0	0	0	1	0	0
Polymorphic loci (%)	90	100	100	100	100	100	90
Mean number of alleles per locus	2.4	2.9	2.6	3.0	3.5	3.1	3.6
Total gene diversity	0.29	0.29	0.28	0.36	0.37	0.33	0.36

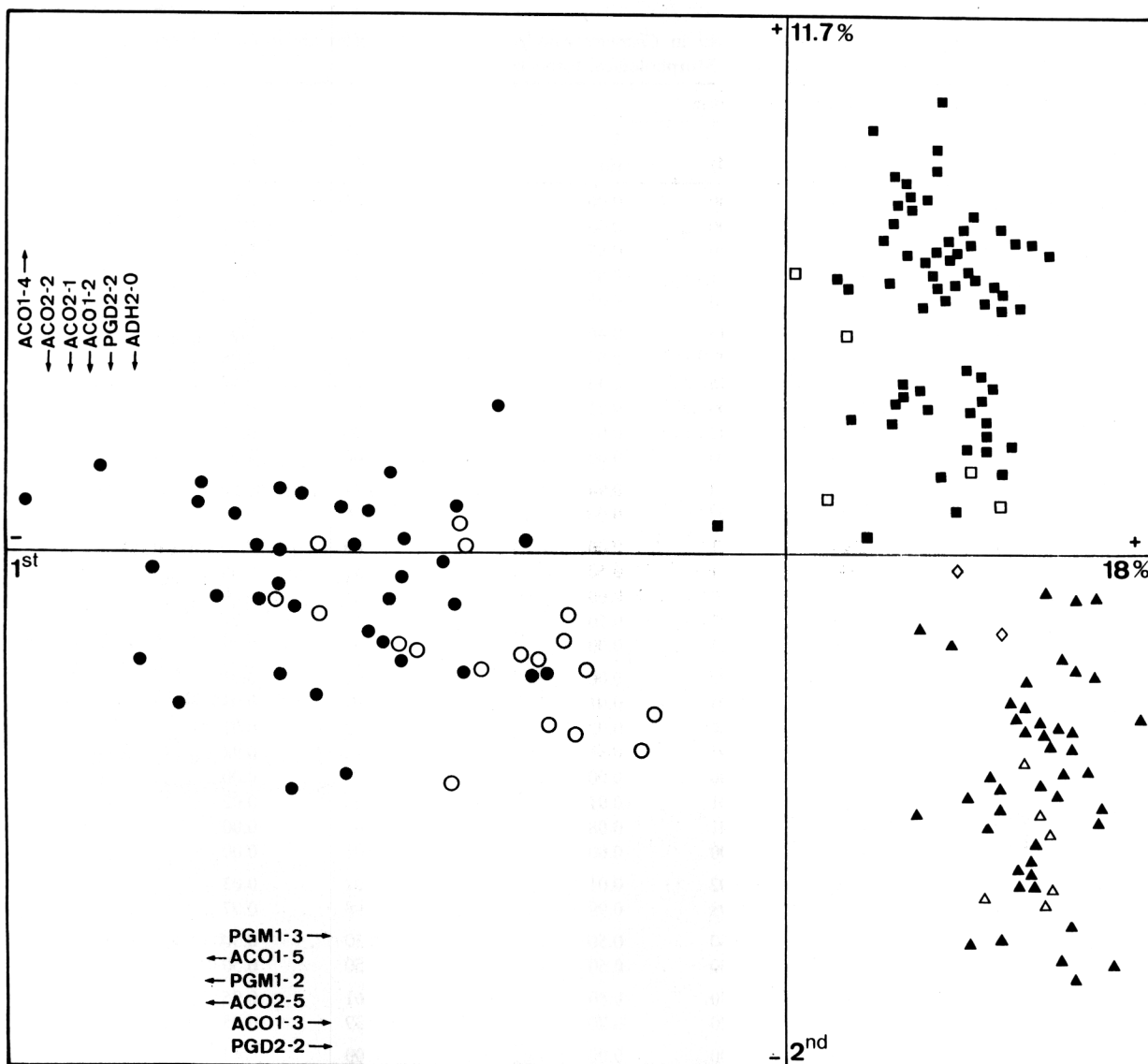


Fig. 2. Scatter diagram for the first two factors of Principal Component Analysis of 175 accessions of *Chamaecytisus proliferus*. Morphological forms coded as follows: escobon of El Hierro ( $\diamond$ ), typical tagasaste ( $\blacktriangle$ ), white tagasaste ( $\triangle$ ), white escobon of Tenerife ( $\square$ ), narrow-leaved escobon ( $\blacksquare$ ), white escobon of Gran Canaria ( $\circ$ ), escobon of southern Gran Canaria ( $\bullet$ ). Allele loadings along both factors are also given, arrows indicate whether eigenvector values are positive (right pointing arrows) or negative (left pointing arrows).

**Table 4.** Summary statistics of genetic variability at ten isozyme loci in *Chamaecytisus proliferus* from the Canary Islands. Results based on island provenance and status. 1 = El Hierro; 2 = La Palma; 3 = La Gomera; 4 = Tenerife; 5 = Gran Canaria

	1	2	3	4	5
Number of unique alleles	0	0	0	0	2
Polymorphic loci (%)	90	100	100	100	100
Mean number of alleles per locus	2.4	2.9	2.7	3.5	3.6
Total gene diversity	0.29	0.29	0.37	0.37	0.37

**Table 5.** Genetic differentiation of *Chamaecytisus proliferus* among its seven morphological forms. Based on allele frequencies from ten isozyme loci. Ht = Total gene diversity; Hs = average gene diversity within populations; Dst = average gene diversity between populations; Gst = gene diversity between populations, relative to Ht

Locus	Ht	Hs	Dst	Gst
AC01	0.667	0.537	0.130	0.195
AC02	0.684	0.561	0.123	0.180
ADH1	0.103	0.104	0.001	0.010
ADH2	0.612	0.523	0.089	0.145
IDH1	0.240	0.217	0.023	0.090
MDH1	0.040	0.038	0.002	0.050
MDH2	0.500	0.500	0.000	0.000
PGD2	0.371	0.317	0.053	0.143
PGM1	0.509	0.346	0.163	0.320
PGM2	0.102	0.102	0.000	0.000
Mean	0.3837	0.328	0.056	0.126

islands are shown in Tables 7 and 8 respectively and the dendrograms obtained are illustrated in Figs 3 and 4. Results were in agreement with the outcome of the PCA and the dendrograms obtained after CA also reflected this situation. Figure 3 shows that germplasm from morphological forms with a common island origin grouped together in the same cluster. Cluster Analysis based on island provenance yielded a similar output

**Table 6.** Genetic differentiation of *Chamaecytisus proliferus* in the Canary Islands. Results based on allele frequencies from ten isozyme loci and on island provenance

Locus	Ht	Hs	Dst	Gst
AC01	0.667	0.520	0.147	0.220
AC02	0.684	0.607	0.077	0.112
ADH1	0.103	0.108	0.005	0.048
ADH2	0.612	0.587	0.024	0.039
IDH1	0.240	0.240	0.000	0.000
MDH1	0.050	0.040	0.002	0.040
MDH2	0.500	0.500	0.000	0.000
PGD2	0.370	0.360	0.010	0.027
PGM1	0.509	0.296	0.213	0.419
PGM2	0.102	0.095	0.007	0.068
Mean	0.384	0.335	0.049	0.113

**Table 7.** Unbiased genetic distance and unbiased genetic identities (Nei 1987) between the seven morphological forms of *Chamaecytisus proliferus* based on allele frequencies from 10 isozyme loci. Genetic identities are given in upper triangle, and genetic distances in the lower triangle. Morphological forms coded in Table 1

	Morphological form						
	1	2	3	4	5	6	7
1							
2	0.028	0.97	0.97	0.97	0.97	0.89	0.87
3	0.031	0.013	0.99	0.94	0.95	0.90	0.87
4	0.032	0.060	0.064		0.99	0.93	0.92
5	0.032	0.054	0.077	0.012		0.92	0.91
6	0.119	0.108	0.113	0.071	0.085		0.99
7	0.142	0.136	0.141	0.082	0.094	0.004	

(Fig. 4). Accessions from Gran Canaria were very distinct and in both analyses clustered apart from the other islands.

Results based on island provenance showed that germplasm from Tenerife is genetically close to La Gomera and suggested that accessions of narrow-leaved escobon from these two islands have similar patterns of isozyme variation and that La Gomera-Tenerife can be regarded as forming a group distinct from the others.

The dendrogram for the seven morphological forms (Fig. 3) suggests that escobon of El Hierro

**Table 8.** Unbiased genetic distance (Nei, 1987) between populations of *Chamaecytisus proliferus* based on allele frequencies from ten isozyme loci and island provenance. Genetic identities are given in upper triangle, and genetic distances in the lower triangle. 1 = El Hierro; 2 = La Palma; 3 = La Gomera; 4 = Tenerife; 5 = Gran Canaria

	1	2	3	4	5
1					
2	0.035	0.97	0.98	0.97	0.87
3	0.024	0.074	0.93	0.92	0.88
4	0.033	0.082	0.008	0.99	0.91
5	0.135	0.129	0.094	0.090	
6	0.027	0.011	0.053	0.053	0.013

is genetically close to both kinds of tagasaste. However, when the analysis was carried out on an island basis, escobon of El Hierro was more related to the forms found in Tenerife and La Gomera (Fig. 4) than to La Palma. These two different CA outcomes for germplasm from this island confirmed results from PCA (Fig. 2) as this island had an intermediate position between La Palma and Tenerife-La Gomera.

## Discussion

Studying isozyme diversity in the *C. proliferus* complex has indicated the existence of a high level of variability. None of the isozymes was monomorphic and on average there were more than two alleles per locus. Among the ten putative genetic loci studied, four of them (ACO1, ACO2, PGD2 and PGM1) clearly showed variation related to the geographical distribution of the species. High values of variation were detected within islands and within morphological forms, which suggests that genetic differentiation in *C. proliferus* is low. However, both PCA and CA based on Nei's genetic distance illustrated among island differ-

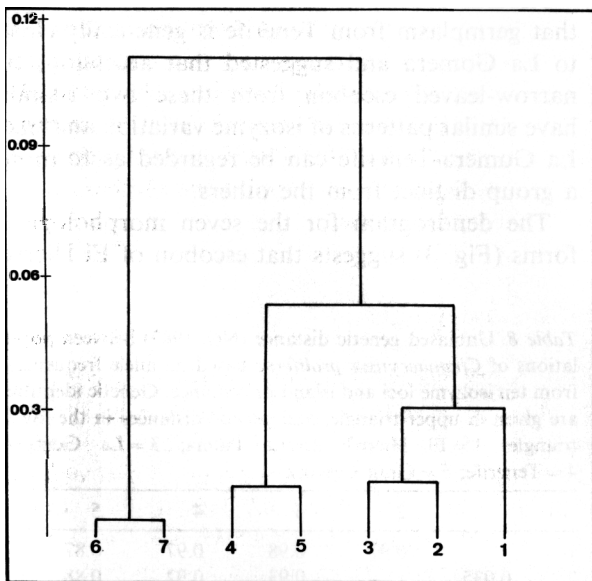


Fig. 3. Clustering dendrogram (UPGMA method) for the seven morphological forms of *Chamaecytisus proliferus* based on Nei's unbiased genetic distance for ten isozyme loci. Morphological forms coded in Table 1.

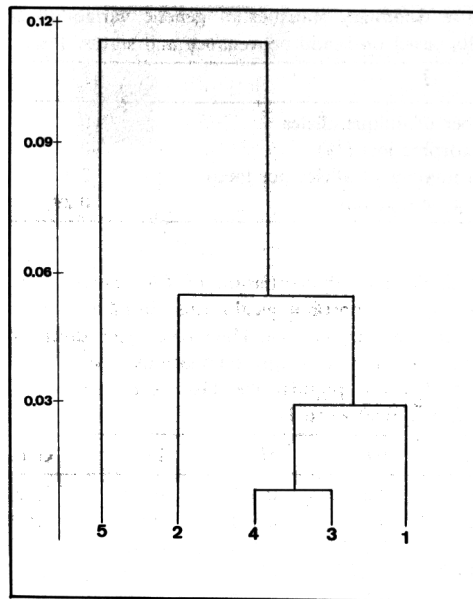


Fig. 4. Clustering dendrogram (UPGMA method) for *Chamaecytisus proliferus* populations based on Nei's unbiased genetic distance and island provenance for ten variable isozyme loci. Provenance is coded as follows: 1 = El Hierro; 2 = La Palma; 3 = La Gomera; 4 = Tenerife; 5 = Gran Canaria.

ences, and those alleles responsible for among island differentiation could be identified. Discrimination of any of the morphological forms was not possible by any of these analyses which suggests a greater genetical divergence of the complex among islands than among morphological forms.

The two morphological forms which exist in each island did not show any isozyme differentiation even though clear ecological and morphological differences exist between those forms found within each of La Palma, Tenerife and Gran Canaria (Acebes-Ginovés, 1990; Francisco-Ortega, 1992).

Furthermore, it was found that populations of escobon from Tenerife and escobon from Gran Canaria which grow under very similar ecological conditions (e.g. along the bottom of small ravines of the pine forest where soils are extremely sandy) and which are similar morphologically have different patterns of allozyme variation for ACO1, ACO2 and PGM1. These results, which are similar to those obtained when studying phenolic compounds (Francisco-Ortega, 1992), do indicate that genetic differentiation between islands has occurred.



The lack of genetic discontinuity between morphological forms also shows that the species is allogamous. All the allelic variation which was identified for any one island was, in some instances, also to be found in just one population from that island. Both Gottlieb (1981) and Crawford (1990) suggested that in outcrossing species there are usually similar allelic frequencies in separate populations because of gene flow both within and between populations. Only in those cases where some populations were isolated from each other would some alleles be present at higher frequencies. A high level of allogamy for *C. proliferus* was previously found by Webb & Shand (1985) and Woodfield & Forde (1987) based on reproductive biology and morphology respectively.

Of some importance is the question of how the biodiversity of the species is structured in the Canary Islands. Data from ecology and morphology indicate that variation decreases from east to west (Francisco-Ortega, 1992). Populations from the islands closer to the African continent (i.e. Tenerife and Gran Canaria) show greater morphological variation and wider ecological adaptation. Similar conclusions are drawn from the isozyme analysis. Genetic diversity in populations from Gran Canaria and Tenerife-La Gomera was larger than that observed in La Palma and El Hierro. Also, the only islands with unique alleles were those of Gran Canaria and Tenerife-La Gomera. Patterns of genetic diversity across the archipelago indicate that colonisation followed an east-west path where now, the oldest morphological forms, and the greatest diversity occurs in Gran Canaria.

It is clear that morphological differentiation has taken place and that morphological variants found in each island are likely to be derived from a common ancestor originating in proximity to mainland Africa. Indeed two species (i.e. *C. mollis* and *C. pulvinatus*) are found in the Atlas Mountains in Morocco. Localised ecological adaptation has produced the morphological variants found in each island through adaptive radiation. This has not been reflected yet in isozyme variation, where the patterns of genetic variation arising from the initial colonisation is still present.

Isozyme variation in *C. proliferus* in the Canary Islands follows a similar pattern to *Bidens* (Helenurm & Ganders, 1985) and *Tetramolopium*

(Lowrey & Crawford, 1985) in the Hawaiian Islands, and for *Dendroseris* (Crawford et al., 1987) in the Juan Fernandez Islands. It was found that these island endemics were highly variable for morphological and ecological traits but showed limited isozyme differentiation.

Strategies and priorities for *in situ* conservation of the species should take into consideration both levels of genetic variation as well as population abundance for each morphological form. Ecological studies (Francisco-Ortega, 1992) show that the most common morphological forms occur in Gran Canaria (i.e. escobon of southern Gran Canaria and white escobon of Gran Canaria) and Tenerife-La Gomera (i.e. narrow-leaved escobon). These three forms are extremely common in these islands, where they produce extensive scrubs. From the genetic diversity perspective, they should be given the highest priority for conservation because variation is greatest. It is fortunate therefore that these morphological forms (with the exception of white escobon of Tenerife) cannot be considered as endangered by any external factor.

The most rare forms exist in the wild in El Hierro (i.e. escobon of El Hierro), La Palma (i.e. typical tagasaste and white tagasaste) and Tenerife (i.e. white escobon of Tenerife). It is believed that these morphological forms should actually receive the greatest attention in terms of conservation as these are the most rare morphological forms within the complex. The establishment of the Canarian network of wild reserves (Anon., 1987) has facilitated the conservation *in situ* of most of the populations of these three morphological forms.

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