

Morphological variation in the *Chamaecytisus proliferus* (L.f.) Link complex (Fabaceae: Genisteae) in the Canary Islands

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FRANCISCO-ORTEGA, J., JACKSON, M. T., SANTOS-GUERRA, A. & FORD-LLOYD, B. V., 1993. **Morphological variation in the *Chamaecytisus proliferus* (L.f.) Link complex (Fabaceae: Genisteae) in the Canary Islands.** A multivariate study (Principal Component Analysis and Cluster Analysis, Ward's method) of 47 morphological traits from 164 populations of *Chamaecytisus proliferus* (L.f.) Link from the Canary Islands confirmed that this species complex is formed by seven morphological types. At least eight traits discriminated between these types. Patterns of variation follow a cline within Gran Canaria, Tenerife and La Palma. These results also show that morphological variation is greater in the eastern islands (i.e. Gran Canaria and Tenerife) than in the western islands (La Gomera, El Hierro and La Palma) and that no morphological differences are found between plants of typical tagasaste from wild and cultivated populations.

ADDITIONAL KEY WORDS: Biodiversity – fodder – legumes – Macaronesia – numerical taxonomy – shrubs – tagasaste.

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INTRODUCTION

The genus *Chamaecytisus* Link (Fabaceae: Genisteae) comprises 28 species which are found in Europe, the Near East, Morocco and the Canary Islands (Cristofolini, 1991). The species from the Canary Islands (*C. proliferus* (L.f.) Link) forms a taxonomic complex which has been regarded as a relic of the flora which spread along the Mediterranean basin during the Tertiary (Bramwell & Richardson, 1973; Polhill, 1976).

Taxonomic studies carried out by Acebes-Ginovés (1990) and Francisco-Ortega (1992) have suggested that this complex is formed by the seven morphological types listed in Table 1. Each of these types is found to be associated with different life-zones of the archipelago (Francisco-Ortega *et al.*, 1993b, c) and a summary of the ecological features of *C. proliferus* in the Canary Islands is also given in Table 1. Five morphological forms, namely typical tagasaste, escobon of El Hierro, white escobon of Gran Canaria and white escobon of Tenerife are found in those areas which are under the influence of the

TABLE 1. The seven morphological forms of *Chamaecytisus proliferus* (L.f.) Link after Acebes-Ginovés *et al.* (1991). Islands are coded as follows: H = El Hierro, P = La Palma, T = Tenerife, G = La Gomera, C = Gran Canaria

Taxon	Common name	Island	Ecology
1. <i>C. proliferus</i> (L.f.) Link subsp. <i>proliferus</i> var. <i>hierrensis</i> (Pitard) Acebes	Escobon of El Hierro	H	North: 700–1300 m, heath (<i>Erica arborea</i>) belt life-zone
2. <i>C. proliferus</i> (L.f.) Link subsp. <i>proliferus</i> var. <i>palmensis</i> (H. Christ) A. Hansen & Sunding	Typical tagasaste	P	North: 700–1300 m, heath belt and laurel (<i>Laurus azorica</i>) wood life-zones
3. <i>C. proliferus</i> (L.f.) Link subsp. <i>proliferus</i> var. <i>calderae</i> Acebes	White tagasaste	P	North: 1300–1200 m, south: 1000–2000 m, Canary pine (<i>Pinus canariensis</i>) forest life-zone*
4. <i>C. proliferus</i> (L.f.) Link subsp. <i>proliferus</i> var. <i>proliferus</i>	White escobon of Tenerife	T	North: 700–1300 m, heath belt and laurel wood life-zones
5. <i>C. proliferus</i> (L.f.) Link subsp. <i>angustifolius</i> (O. Ktze.) G. Kunkel	Narrow-leaved escobon	G T	North: 1300–2200 m, south: 700–2200 m, Canary pine forest life-zone
6. <i>C. proliferus</i> (L.f.) Link subsp., <i>proliferus</i> var. <i>canariae</i> (H. Christ) G. Kunkel	White escobon of Gran Canaria	C	North: 700–1300 m, heath belt and laurel wood life-zones
7. <i>C. proliferus</i> (L.f.) Link subsp. <i>meridionalis</i> Acebes	Escobon of southern Gran Canaria	C	North: 1300–2000 m, south 1300–2000 m, Canary pine forest life-zone

*In south restricted to La Caldera de Taburiente National Park.

north-eastern trade winds, whereas narrow-leaved escobon and escobon of southern Gran Canaria occur in zones which are not subjected to these winds.

Among these morphological forms typical tagasaste represents the most important non-ornamental cultivated plant which has its centre of origin in the Canary Islands. It is widely utilized in El Hierro, La Palma, La Gomera, Tenerife and Gran Canaria as a forage for livestock. The species was introduced into Australia and New Zealand at the end of last century (Francisco-Ortega *et al.*, 1991, 1992) where it is used as a fodder shrub for semi-arid regions with sandy soils.

Previous morphological and taxonomic reviews of the complex have been based on the study of single herbarium specimens and not on population samples (Acebes-Ginovés, 1990; Christ, 1888; Hutchinson, 1918; Kuntze, 1891). Name typification within the complex has been reviewed recently by Acebes-Ginovés (1990) and Santos-Guerra & Francisco-Ortega (unpublished).

Being closely related those infraspecific taxa which form a species complex or species group represent a taxonomic challenge which in the Canary Islands is enhanced by the fact that populations from the different infraspecific categories are usually found within a unique ecosystem or island. Their existence is likely to be due to adaptive factors or in some cases genetic drift, which has not provided sufficient diversification to warrant species distinction.

In this paper we present a morphological study based on material collected in the whole distribution range of *C. proliferus*. As a working taxonomy we use that recently given by Acebes-Ginovés, Del Arco Aguilar & Wildpret (1991). A revised taxonomy based not only on morphological data but also on flavonoid and isozyme profiles will be presented in a subsequent work. This study is part of an ecogeographical survey carried out within this species complex. For each of the populations in which morphological studies were carried out, germplasm was sampled (Francisco-Ortega *et al.*, 1990) and ecological (Francisco-Ortega *et al.*, 1993b, c), isozyme (Francisco-Ortega *et al.*, 1993) and plant phenolic studies (Francisco-Ortega, 1992) were also made. It is anticipated that the results presented here will stimulate further utilization of the genetic resources of *C. proliferus* and broader development of this species as a multipurpose shrub for subtropical regions.

MATERIAL AND METHODS

Morphological studies were based on analyses of dried herbarium specimens collected in the Canary Islands from 164 wild and cultivated sites, the collection being carried out during February–April 1989. Description of individual collection sites and further information concerning the ecology of these populations has been given previously by Francisco-Ortega & Jackson (1989) and Francisco-Ortega *et al.* (1993b, c). Morphological attributes were scored for pods, seeds, leaves and flowers. All the herbarium specimens were collected at the time of flowering. In order to check the general structure of fresh flowers a second visit to most of the populations was made in March 1991.

Ten plants were selected from each population, and for each specimen one mature leaf and one fully developed flower were selected randomly. Eleven morphological characters were scored on the leaves and 24 on the flowers (Table 2).

TABLE 2. *Chamaecytisus proliferus* morphological characters scored for taxonomic analysis. Continuous characters were measured in cm except ANGLE (degrees) and SEEWI (g). Leaf measurements were taken on the central leaflet. (1) = Five states in ascending order from 0 = glabrous to 5 = tomentose. For terminology of character states described here, see Stearn (1966)

Character	Character code	Character states
Central leaflet length	LEALE	Continuous
Central leaflet width	LEAWI	Continuous
Petiole length	PETLE	Continuous
Petiole width	PETWI	Continuous
Petiolule length	PEDLE	Continuous
Ratio of central leaflet length : distance from apex to widest point	LE/LO	Continuous
Ratio of central leaflet length : width	LE/WI	Continuous
Hairiness on leaf lower face	HAIRL	(1)
Hairiness on leaf upper face	HAIRU	(1)
Leaflet longitudinal posture	FOLDI	Coded as: 0 = not conduplicate 1 = conduplicate
Apex angle	ANGLE	Continuous
Standard petal length	STALE	Continuous
Standard petal width	STAWI	Continuous
Ratio of standard length : width	TL/TW	Continuous
Standard claw length	STACL	Continuous
Wing length	WINLE	Continuous
Maximum wing width	WINMA	Continuous
Minimum wing width	WINMI	Continuous
Wing claw length	WINCL	Continuous
Wing lobe length	WINLO	Continuous
Keel length	KEELE	Continuous
Keel width	KEEMA	Continuous
Keel claw length	KEECL	Continuous
Keel lobe length	KEELO	Continuous
Anther length	ANTLE	Continuous
Calyx length	CALLE	Continuous
Ovary length	OVALE	Continuous
Hairiness on central vein of standard petal	STACE	(1)
Hairiness on upper face of standard petal	STASI	(1)
Hairiness on upper edge of keel petal	KEEUP	(1)
Hairiness on upper edge of wing petal	WINUH	(1)
Hairiness on keel lobe	KEEHL	(1)
Hairiness on wing lobe	WINHL	(1)
Lobe of keel folded upwards	TAILK	Coded as: 0 = not folded 1 = folded
Orientation of standard petal	ORIEN	Coded as: 0 = not reflexed 1 = reflexed
Pod length	PODLE	Continuous
Pod width	PODWI	Continuous
Number of seeds per pod	SEEDN	Continuous
Seed breadth	SEEBR	Continuous
Seed length	SEELE	Continuous
Seed width	SEEWI	Continuous
Seed weight	SEEDG	Continuous
Ratio of seed length : width	SL/SW	Continuous
Ratio of seed width : breadth	SW/SB	Continuous
Aril length	ARLEN	Continuous
Aril width	ARWIN	Continuous
Seed colour	SEEDC	Coded as: 0 = not yellow 1 = yellow

Following germplasm collection during May–July 1989, ten pods were randomly selected from each of the collection sites, and 12 morphological attributes were recorded for each pod (Table 2).

Multivariate analyses were based on Cluster Analysis (CA) and Principal Component Analysis (PCA) of metric and ordinal discontinuous data. Therefore SEEDC, ORIEN, TAILK and FOLDI were not included in these analyses as they were multistate discontinuous traits. Character states were standardized prior to the analyses. Cluster Analysis was accomplished through hierarchical polythetic agglomerative classification using Ward's method (Ward, 1963). A similarity matrix, based on the squared Euclidian distance between OTUs was prepared prior to this classification. The cophenetic correlation coefficient (Sokal & Rohlf, 1962) was calculated as a measure of the distortion between the similarity matrices and dendrograms. Both CA and PCA were carried out with the CLUSTAN 3 package (Wishart, 1987).

In these analyses each population was regarded as an OTU and therefore mean values per population were used. Following PCA, those characters which accounted for most of the variation along the first two components were selected and these were the basis for univariate analysis. The range of variation of each of these characters was represented in bar diagrams following the procedures previously given by Abbott, Bisby & Rogers (1985). The statistical package MINITAB 7 was utilized for these univariate analyses (Anon., 1985) and actual values from each specimen were used for this purpose. Patterns of morphological variation for multistate discontinuous traits were studied in relation to germplasm provenance. A similar study was made with the other traits in order to detect which morphological attributes were related to the ecological and geographical features of each island.

In this study we have used estimates of a phenetic similarity rather than a cladistic approach in order to establish relationships between the various populations. Cladistic analysis is most appropriate and reliable for studies of macroevolution. In situations where variation is being studied which is adaptive at the population level, rather than evolutionary, and when the basis for that variation lies in gene and allele frequencies, then phenetic approaches are more appropriate.

RESULTS

Eight clusters were obtained after the hierarchical classification at a dissimilarity coefficient of 5.7 (Fig. 1). The cophenetic correlation coefficient was 0.74. The dendrogram obtained (Fig. 1) suggests a strong relationship between both tagasastes and escobon of El Hierro which were separated from the other morphological forms at a high dissimilarity coefficient of 106. Narrow-leaved escobon formed a clear group with two subgroups, whereas the two white escobons from Tenerife and Gran Canaria were grouped in two separate clusters linked at a phenetic distance of 6.2.

Results from PCA are summarized in Table 3 and Figs 2 and 3. The first two components accounted for 37% and 19% of the total variance. As the variance contributed by the other factors decreased rapidly (Table 3) only the first two components are discussed here, and a scatter diagram is shown in Fig. 2. Populations which grouped together after CA also appeared in close proximity

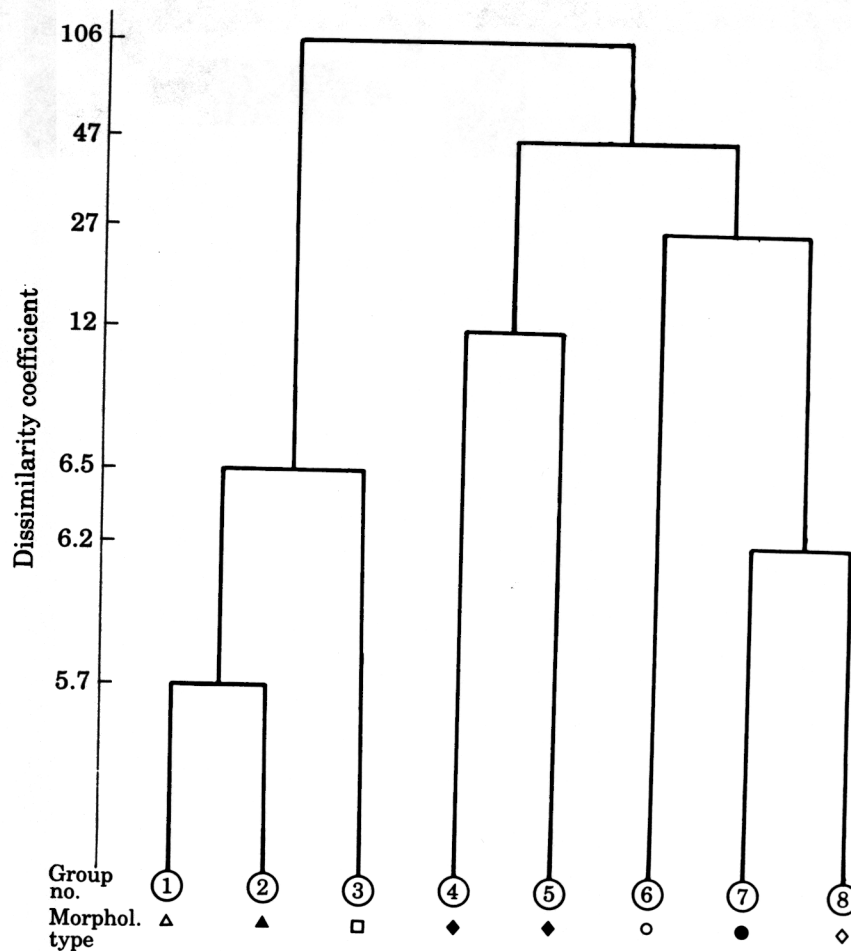


Figure 1. Dendrogram obtained after Cluster Analysis (Ward's method). Clusters are identified by numbers. Morphological forms coded as follows; (\square) escobon of El Hierro, (\blacktriangle) white tagasaste, (\triangle) typical tagasaste, (\blacklozenge) narrow-leaved escobon, (\circ) escobon of southern Gran Canaria, (\bullet) white escobon of Gran Canaria, (\diamond) white escobon of Tenerife.

in this diagram. Both types of tagasaste and escobon of El Hierro were found on the left side, whereas the remaining forms tended to group in the right zone of this diagram.

Character eigenvector values along the first two factors are summarized in Fig. 3. The five attributes responsible for maximum separation along the first component (with loadings in parentheses) were SEEDG (-0.24), STACE (-0.23), KEELE (0.25), PODWI (-0.24) and STASI (0.24). The five

TABLE 3. Eigenvalues, percentage variance and cumulative variance in Principal Component Analysis for 164 wild and cultivated populations of *Chamaecytisus proliferus* from the Canary Islands

Component	Eigenvalue	Percentage variance	Cumulative variance
1	14.75	37	37
2	7.26	19	56
3	3.31	8	64
4	3.13	7	71
5	2.06	5	76
6	1.04	2	78

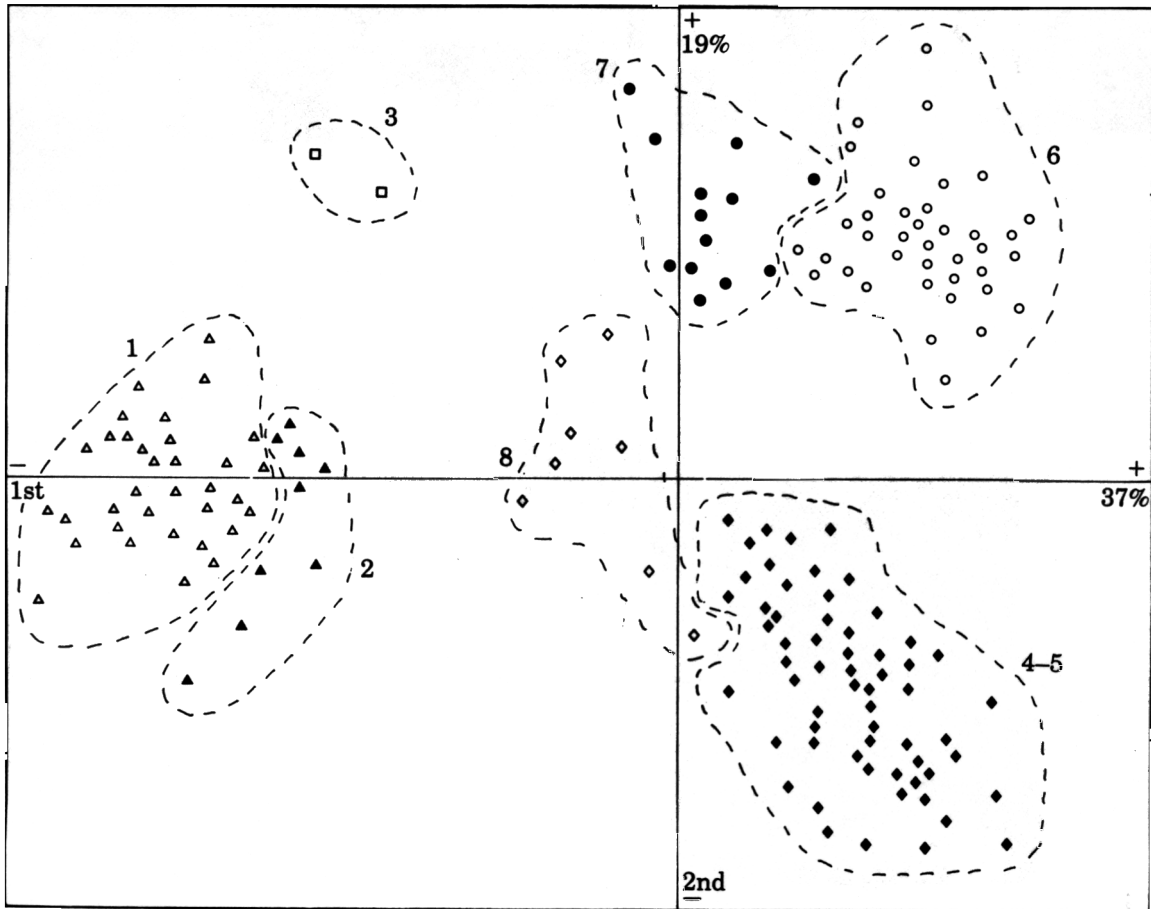


Figure 2. Scatter diagram obtained from the first two principal components. Morphological forms coded as in Fig. 1. The eight groups from Cluster Analysis are also shown.

characters which produced the highest separation along the second component were LE/WI (-0.32), WINLO (-0.28), ANGLE (0.28), HAIRU (0.24) and LE/LO (0.22).

These results agree with those obtained after CA: populations of both tagasastes and escobon of El Hierro had low negative values along the first component (Fig. 2), whereas those of narrow-leaved escobon had low negative scores on the first two components (Fig. 2). On the other hand the two morphological types from Gran Canaria tended to have large positive values along these two components whilst populations of white escobon of Tenerife were situated on the central region of the scatter diagram (Fig. 2).

Clear discontinuities between the morphological forms were detected in bar diagrams for those characters selected after PCA (Fig. 4). Most of the plants of narrow-leaved escobon had leaves with high values for the ratio of central leaflet length to central leaflet width (Fig. 4A). Leaf shape also distinguished escobon of southern Gran Canaria from the other morphological types as plants from this form tended to bear leaves with high scores for LE/LO (Fig. 4B). Similarly individuals of escobon of El Hierro, escobon of southern Gran Canaria and white escobon of Gran Canaria were distinct on the basis of leaf outline as they tended to possess large apex angles (Fig. 4C). Most of the individuals of typical tagasaste had more or less glabrous leaves, whereas those of escobon of El Hierro, typical tagasaste and the two escobons from Gran Canaria tended to have highly

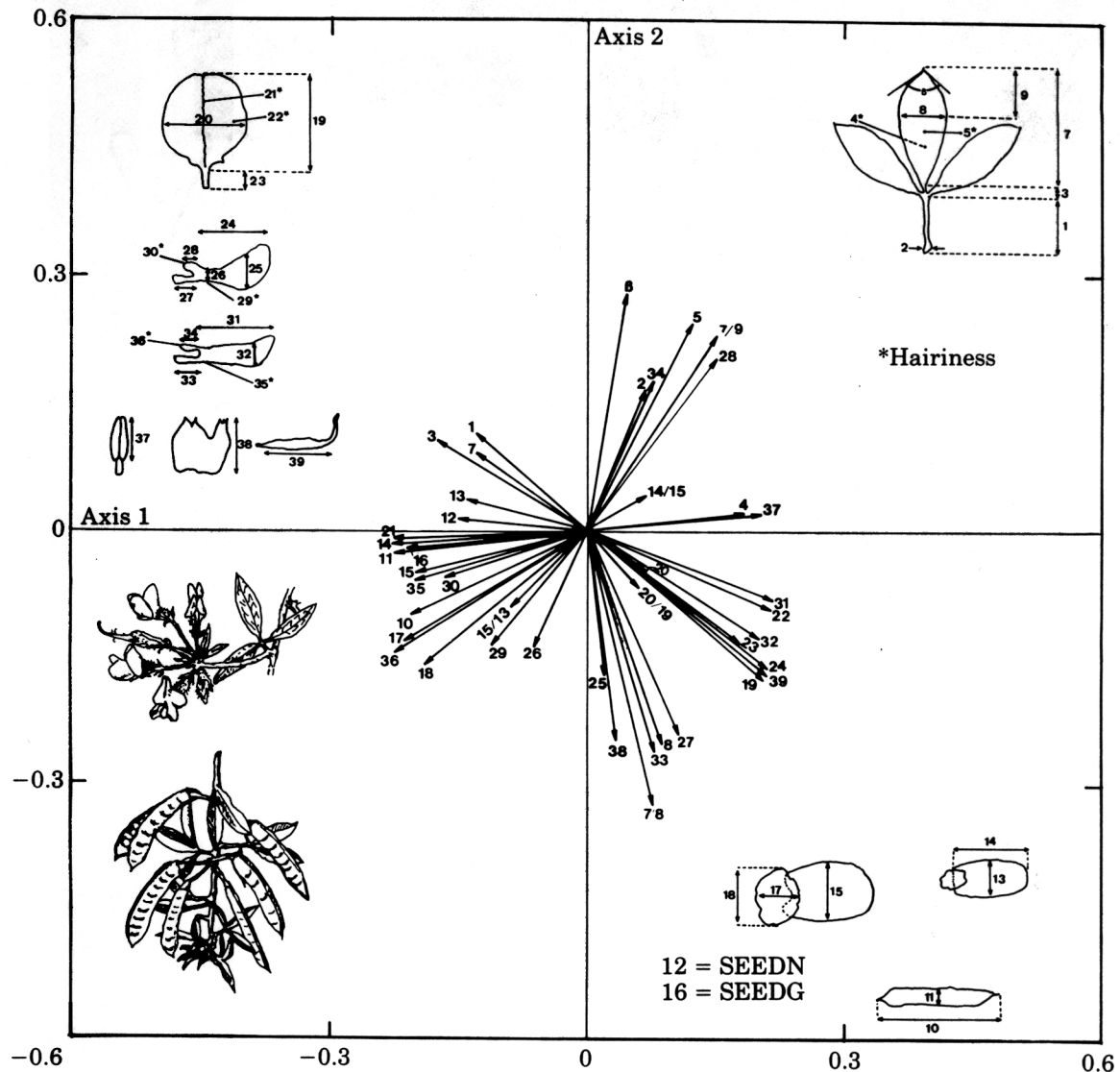


Figure 3. Eigenvector values on the first two axes after Principal Component Analysis. Arrows indicate eigenvector values for each character on each component. Numbers are given for each character which are illustrated on drawings of leaves, flower petals, seeds and pods.

pubescent leaves (Fig. 4D). It is noteworthy that narrow-leaved escobon and white escobon of Tenerife were extremely variable for this trait; many individuals of these morphological forms had highly pubescent to glabrous leaves (Fig. 4D).

Characters related to pod and seed size clearly separated the morphological forms from the islands furthest west (i.e. El Hierro and La Palma) from those of the most easterly islands (i.e. La Gomera, Tenerife and Gran Canaria), and this was reflected in the patterns of variation for PODWI (Fig. 4E) as the forms endemic to the eastern islands had pods which were larger in width.

Keel petal length varied both between and within islands (Fig. 4F). The morphological types from El Hierro and La Palma had small keel petals, a pattern which was also followed by the forms found in northern Tenerife (i.e. white escobon of Tenerife) and in the north of Gran Canaria (i.e. white escobon of Gran Canaria). Additional morphological distinction of escobon of southern Gran Canaria was also provided for WINLO, as plants of this form gave large scores for this trait (Fig. 4G).

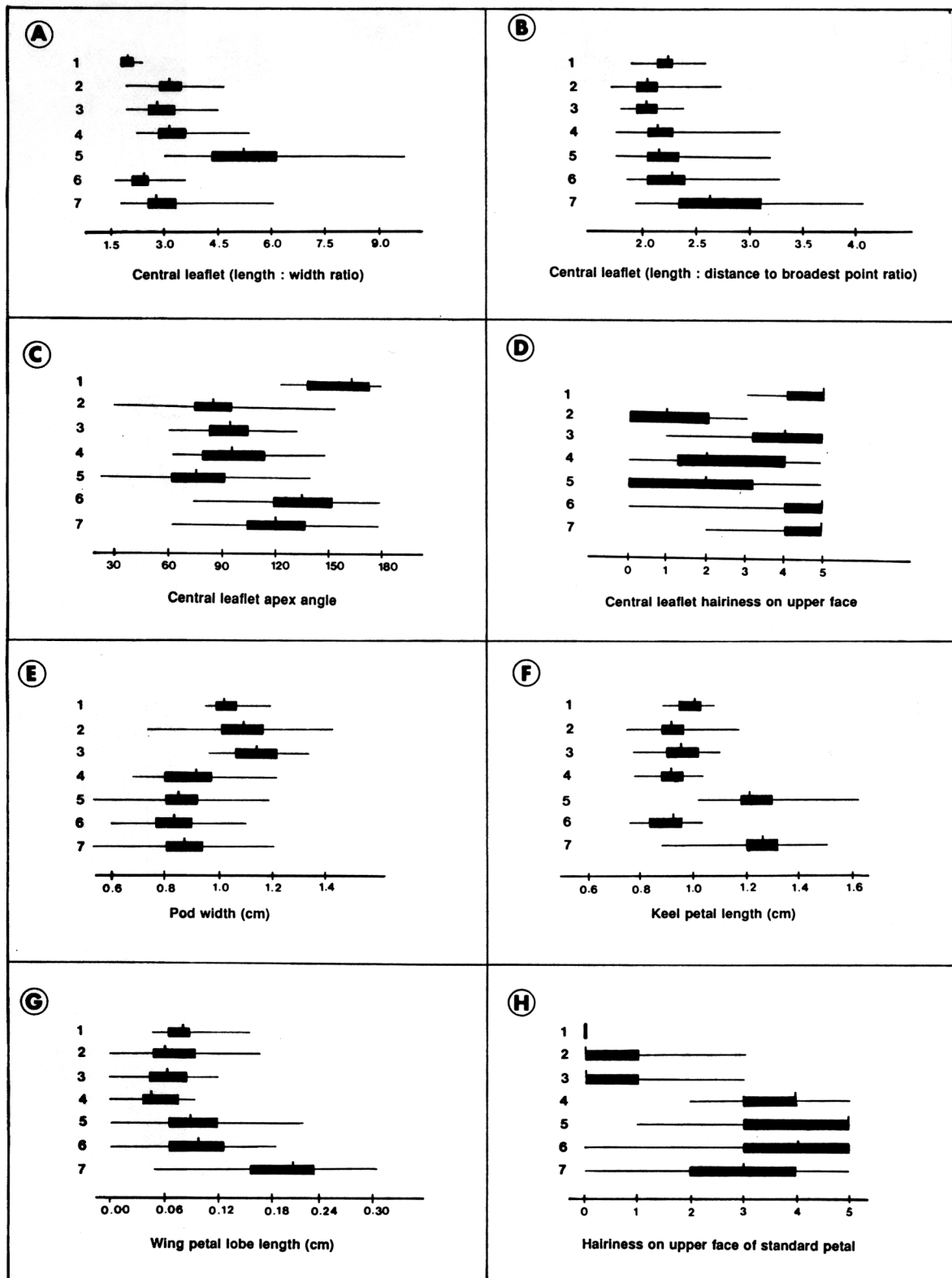


Figure 4. Ranges of variation for eight morphological traits in the seven morphological forms of *Chamaectysis proliferus*. Results based on the study of 1640 herbarium specimens, seeds and pods. The median is indicated and the broad line gives values between the first and third quartiles. The morphological forms are coded in Table 1. Morphological traits: A, LE/WI; B, LE/LO; C, ANGLE; D, HAIRU; E, PODWI; F, KEELE; G, WINLO; H, STASI.

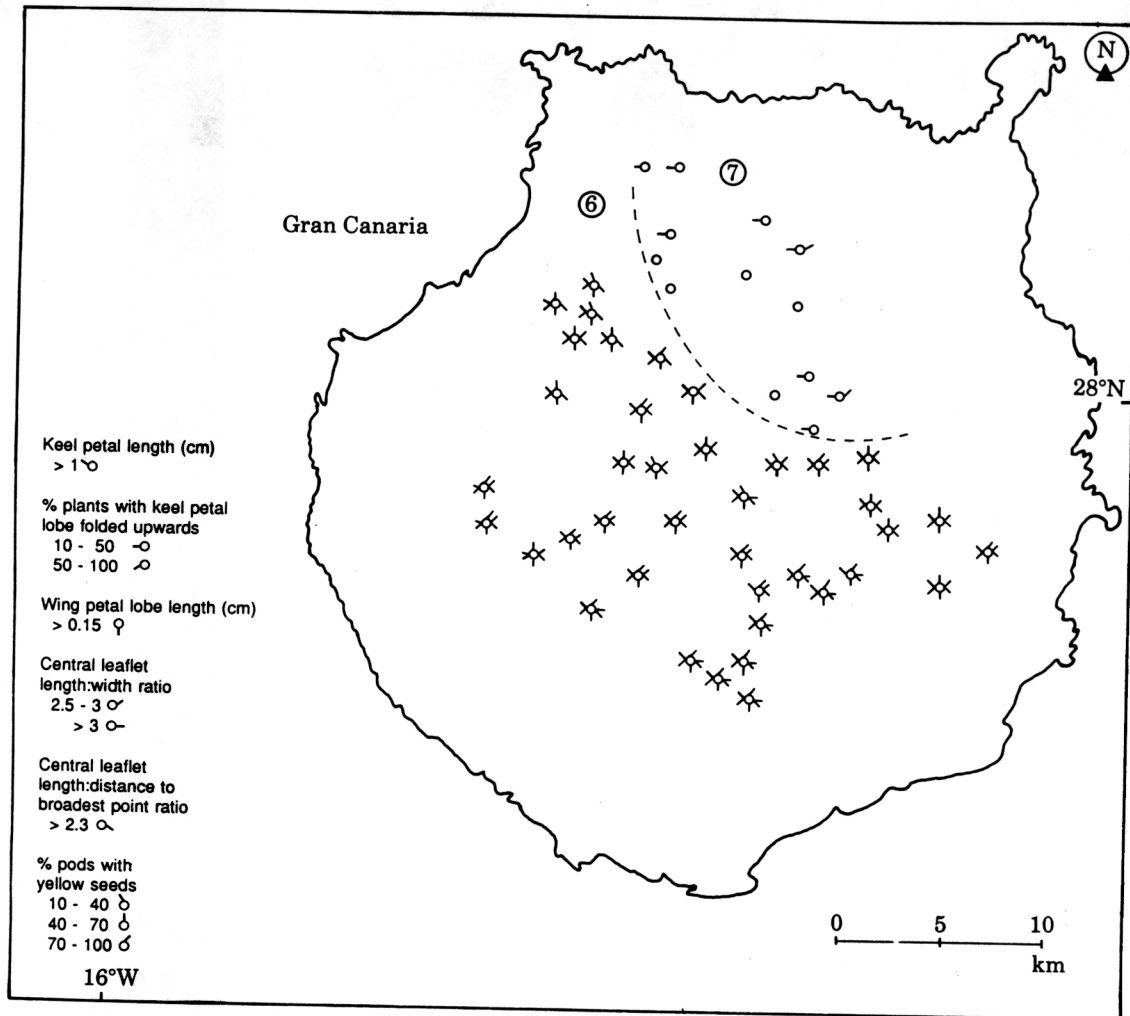


Figure 5. Geographical distribution of morphological attributes in different wild populations of *Chamaecytisus proliferus* from Gran Canaria. 6, White escobon of Gran Canaria; 7, escobon of southern Gran Canaria.

Besides seed and pod characters, the other morphological trait which contributed to separation of the taxa from El Hierro and La Palma from those found in the other islands was the degree of hairiness on the upper face of the standard petal. Most flowers of plants from these two islands possessed petals which were glabrous to almost glabrous (Fig. 4H). In contrast, individuals of the other four morphological types had flowers with highly pubescent standard petals.

Variation in leaf outline followed a cline in both Gran Canaria and Tenerife (Figs 5, 6). Populations from the low altitude areas of northern Tenerife (i.e. white escobon of Tenerife) and from northern Gran Canaria (i.e. white escobon of Gran Canaria) were largely made up of plants with broad leaves. A similar pattern was followed by LE/LO in Gran Canaria (Fig. 5), as values for this trait increased from north to the south.

Variation in two other leaf traits followed gradients in Tenerife; they were the percentage of plants with conduplicate leaves per population and leaf pubescence (Fig. 6). Most of the plants of narrow-leaved escobon collected in southern and western Tenerife had glabrous and conduplicate leaves; a pattern which was also followed by all the populations from La Gomera. Plants of white

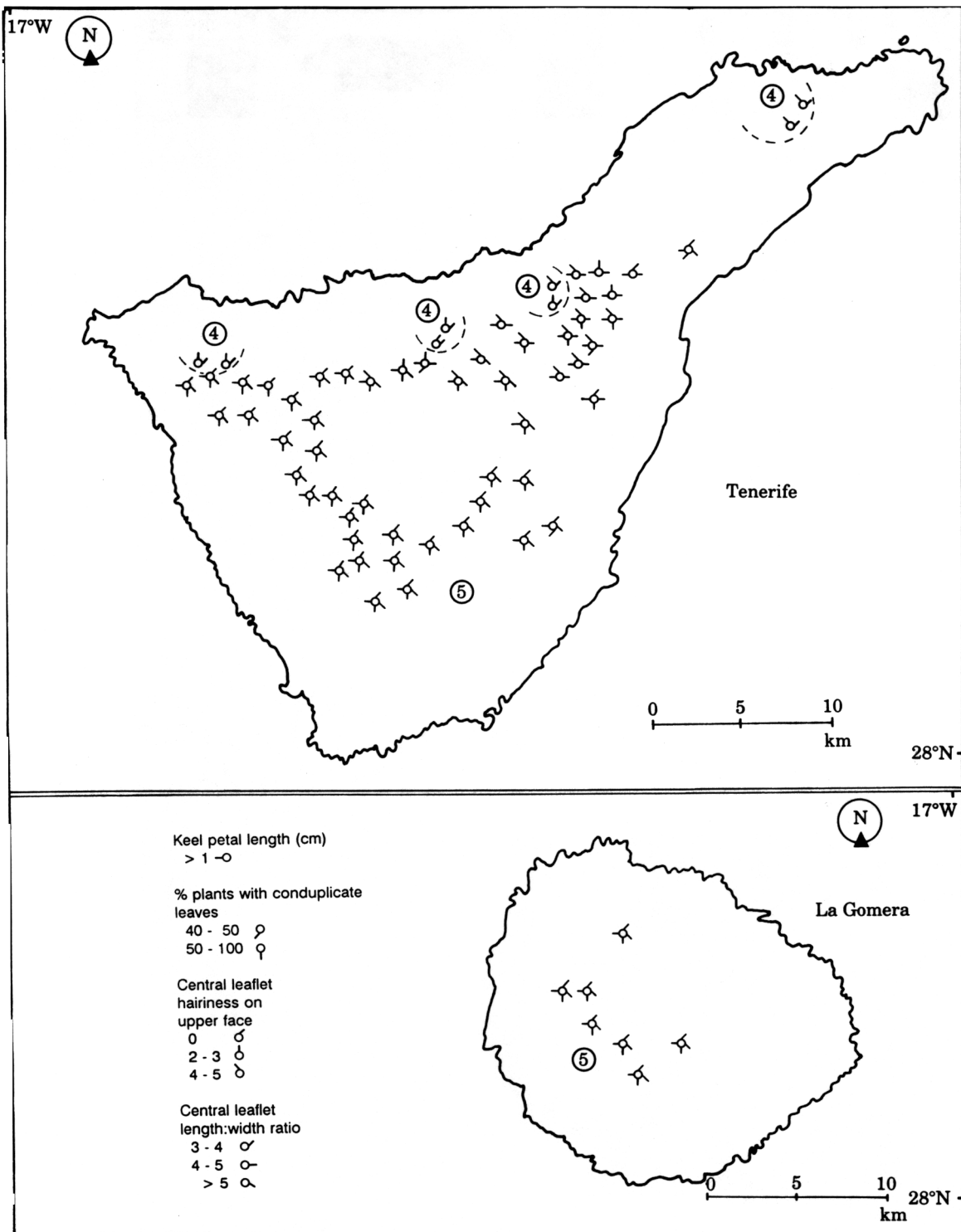


Figure 6. Geographical distribution of morphological attributes in different wild populations of *Chamaecytisus proliferus* from Tenerife and La Gomera. 4, White escobon; 5, narrow-leaved escobon.

escobon of Tenerife never had conduplicate leaves and most of the plants possessed highly pubescent leaves (Fig. 6).

A similar transect was detected for the percentage of pods with yellow seeds as this value increases in Gran Canaria from north to south (Fig. 5). TAILK also followed a cline in this island; all the populations of escobon of southern Gran

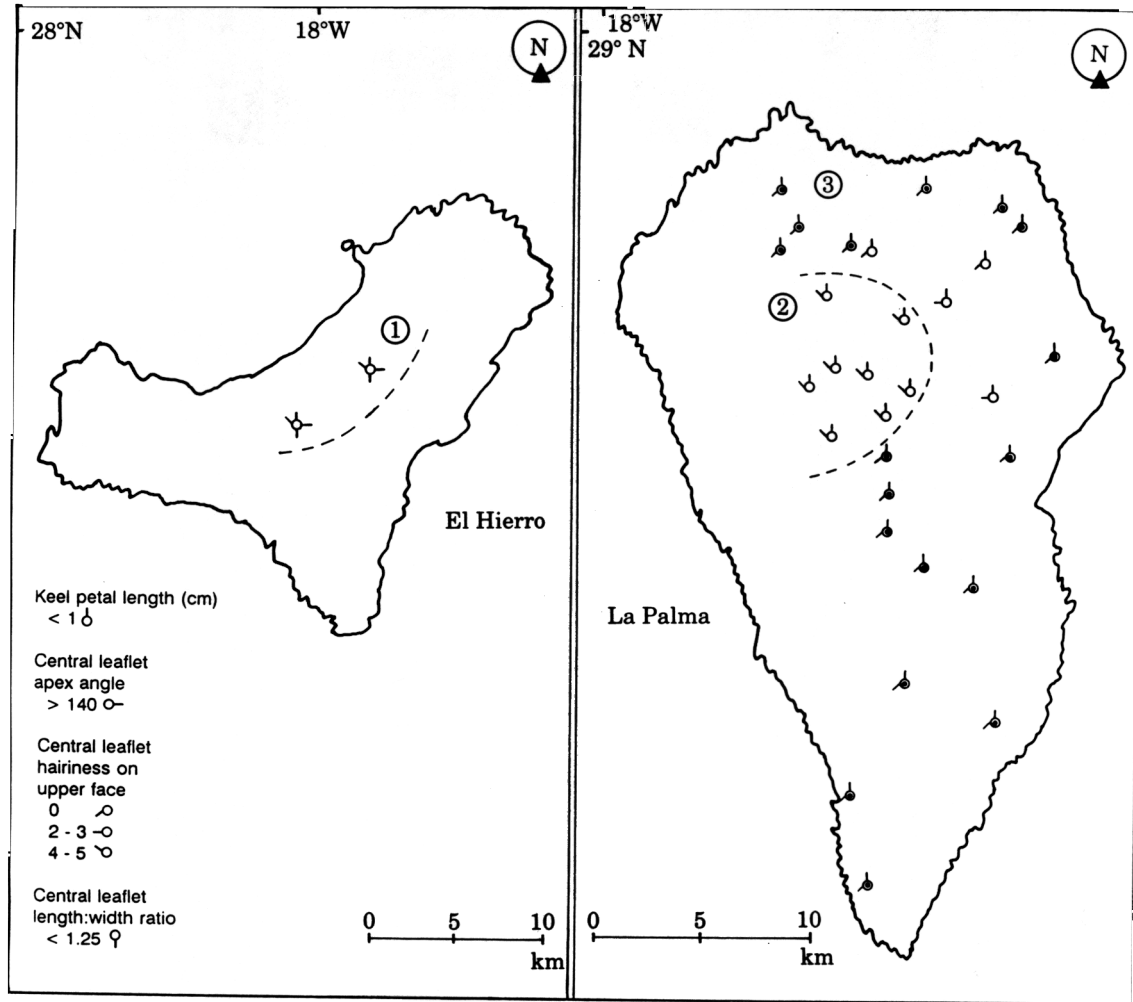


Figure 7. Geographical distribution of morphological attributes in different wild populations of *Chamaecytisus proliferus* from La Palma and El Hierro. 1, Escobon of El Hierro; 2, white tagasaste; 3, typical tagasaste. Filled circles show cultivated collection sites of tagasaste.

Canaria had a majority of individuals with the extreme of the keel petal lobe folded upwards (Fig. 5).

Plants with large keel petals were only found in La Gomera and in the south of Tenerife and Gran Canaria (Figs 5–7). Populations from the rest of the archipelago always had small keel petals. This trait did not follow a cline in La Palma where the two types of tagasaste were distinguished from each other on the basis of leaf hairiness. A cline was also detected for wild populations of La Palma (Fig. 7), with plants from the pine forest having pubescent leaves and those from the laurel wood glabrous leaves.

The most important flower attribute which was observed in the field was the actual disposition of the standard petal with respect to the whole flower. Some plants had the standard petal folded backwards (reflexed position) whilst others had it folded forwards. From the study of dry herbarium specimens it was not always obvious what kind of standard existed in each individual, so that in order to check patterns of variation for this character further field studies were carried out in March 1991.

These observations suggest that all plants of escobon of El Hierro, white escobons and both types of tagasaste had the standard petal folded forwards,

whereas those of narrow-leaved escobon had reflexed standard petals. Even though in almost all the populations of escobon of southern Gran Canaria there were individuals with both kinds of flowers on the same plant, all these populations had plants with many of their flowers with the standard petal reflexed, and this feature was not observed at all in any population of white escobon of Gran Canaria.

DISCUSSION

Multivariate analyses give results which support the recognition of the seven morphological types previously described by Acebes-Ginovés (1990) and Acebes-Ginovés *et al.* (1991) for *C. proliferus*. In addition, seed, leaf and flower attributes are identified which clearly discriminate, not only between these seven forms but also between islands. Furthermore, some morphological characters follow a continuous gradient in Gran Canaria, Tenerife and La Palma.

It is obvious just from field observations that for some characters (i.e. seed and pod size, hairiness on standard petal) differences exist between islands but not within islands, and that the variation for these particular traits is not related to the contrasting ecological differences (i.e. life-zones) which exist within each island. Based on the patterns of variation for these characters and on results of the CA and PCA, the *C. proliferus* complex can be divided into two 'broad morphological groups'. The first of these groups is composed of the three forms occurring in the western islands of El Hierro and La Palma, made up of plants bearing large seeds and pods, and having almost glabrous standard petals. Morphological types from the most eastern islands (La Gomera, Tenerife and Gran Canaria) are included in the second 'broad morphological group' where individuals possess highly pubescent standard petals, and small seeds and pods.

A relationship between geography and diversity could be established. Morphological diversity is found to be greater in Gran Canaria and Tenerife than in the other islands. At least six characters (keel petal length, keel petal lobe folded upwards, wing petal lobe length, seed colour, leaf shape) either follow an ecological cline from north to south, or differentiate between the two morphological types from Gran Canaria, the island situated furthest east. In Tenerife four traits (keel petal length, leaf hairiness, leaf shape and conduplicate leaves) are related to ecological features of the island. However, only one morphological type is found in the most westerly island of El Hierro, and the two types of tagasaste which are endemic to La Palma can only be distinguished on the basis of leaf hairiness.

Despite the fact that plants of escobon of southern Gran Canaria have flowers with standard petals both in a reflexed position and folded backwards, it is clear that flower traits yield the clearest discontinuities among the morphological forms found within Tenerife and Gran Canaria. Plants from the north were found to have smaller keel petals and ovaries as well, with their wings folded inwards resulting in the concealment of the style. This 'non-exposition' of the style is reinforced by the fact that the standard petal of this kind of flowers is folded forwards. In contrast, individuals of narrow-leaved escobon and escobon of southern Gran Canaria have flowers with a totally different structure, and they possess larger keels and ovaries which allow both the style and anthers to be

exposed. This feature of displaying the stigma is reinforced morphologically by the fact that all the plants of narrow-leaved escobon and many of the individuals of escobon of southern Gran Canaria have their standard petal reflexed. The occurrence of two different flower structures in the north and south of Gran Canaria and Tenerife could be a mechanism restricting gene flow between them, and is another example of how morphological differentiation is greater in the eastern islands.

The decrease of morphological diversity from Gran Canaria towards El Hierro evident from the multivariate analyses has been detected using isozymes (Francisco-Ortega *et al.*, 1993a), ecological data (Francisco-Ortega *et al.*, 1993b) and also by analysing juvenile morphological characters (Francisco-Ortega *et al.*, 1993d). Populations from Gran Canaria and Tenerife have the highest values for Nei's index of genetic diversity and it is only in these islands that 'endemic allozymes' are reported (Francisco-Ortega *et al.*, 1993a). Furthermore, the species thrives under a wider range of ecological conditions in Gran Canaria and Tenerife than in the other islands (Francisco-Ortega *et al.*, 1993b, c).

One of the main features of fodder crops is that usually there are very few obvious morphological differences between plants from cultivated and wild populations (Harlan, 1983). This applies to *C. proliferus* where individuals of typical tagasaste collected from cultivated sites did not differ morphologically from those collected as wild plants. Peasant farmers from La Palma give the name 'tagasaste mollar' to those plants which are tender and easier to prune. However, wild plants of white tagasaste were also found in La Caldera de Taburiente which peasant farmers from this National Park also call 'tagasaste blanco mollar'.

The hypothesis of a monophyletic origin for each island and the assumption that the types from Tenerife and Gran Canaria are evolutionarily the oldest provides an explanation for the patterns of morphological variation of *C. proliferus*. The two morphological forms from the two eastern islands have had a longer time to achieve greater differentiation. They have surpassed the early ecotypic stage of speciation and can now be regarded as being in an advanced stage of taxonomic differentiation.

Types from La Palma and El Hierro have had less time to achieve any sharp morphological differentiation. This is especially reflected in La Palma where morphological forms from the pine forest and the laurel wood have similar flower structures and can only be distinguished on the basis of leaf hairiness. They may be in an early stage of speciation in a phase which can be regarded as close to ecotypic.

Results have indicated that the *C. proliferus* complex is highly variable for the traits studied here. Morphological variation with taxonomic value has been identified and it seems that some of the traits are related to the ecogeography of the species. Furthermore, it has been shown that morphological variation for *Chamaecytisus* in the Canary Islands follows a pattern previously reported for other insular endemics such as *Erigeron* (Compositae) in the Juan Fernandez Islands (Valdebenito, Stuessy & Crawford, 1992), *Gossypium* (Malvaceae) in the Galapagos Islands (Wendel & Percy, 1990) or *Tetramolopium* (Compositae) in the Hawaiian Islands (Lowrey & Crawford, 1985). In all these cases morphological variants have arisen through rapid speciation after initial colonization and isolation in each island.

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