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The phytogeography of the *Chamaecytisus proliferus* (L. fil.) Link (Fabaceae: Genisteae) complex in the Canary Islands: a multivariate analysis

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Abstract

Chamaecytisus proliferus (L.fil.) Link (Fabaceae: Genisteae) represents a species complex in the Canary Islands. Floristic data from 147 releves from the whole complex were collected and analysed by classification (TWINSPAN) and ordination (DECORANA) methods. Results indicate that white escobon of Tenerife, escobon of El Hierro, white escobon of Gran Canaria and typical tagasaste in La Palma are associated with those plant communities from the north of these islands which are under the influence of the north-eastern trade winds. Narrow-leaved escobon in Tenerife and La Gomera, escobon of southern Gran Canaria and white tagasaste of La Palma are found in those areas which are not under the direct influence of these winds. Morphological forms from the more easterly islands (Gran Canaria and Tenerife-La Gomera) have the broadest ecological range and they have played an important role in the floristic changes which have taken place after the destruction of the forests in these islands. The highest priorities for *in situ* conservation should be given to wild populations of typical tagasaste, white escobon of Tenerife and escobon of El Hierro.

Abbreviations: International Board for Plant Genetic Resources (IBPGR), Detrended Correspondence Analysis (DECORANA), Operational Taxonomic Unit (OTU), Two Way Indicator Species Analysis (TWINSPAN)

Nomenclature: Hansen, A. & Sunding, P. 1985. Flora of Macaronesia. Checklist of vascular plants. 3rd ed. Sommerfeltia 1: 1–167; Acebes-Ginovés, J.R., Del Arco, M. & Wildpret, W. 1991. Revisión taxonómica del género *Chamaecytisus* (L. fil.) Link en Canarias. Vieraea 20: 191–202.

Introduction

The genus *Chamaecytisus* Link (Fabaceae: Genisteae) comprises approximately 28 species. The centre of highest diversity occurs in the Balkans where more than 15 species can be found (Cristofolini 1991). The number of species decreases towards the rest of Europe, the Near East, North Africa and the Canary Islands. *Chamaecytisus proliferus* (L.fil.) Link forms a taxonomic species complex in the Canary Islands (Fig. 1). Both Acebes-Ginovés (1990) and Francisco-Ortega (1992) reported seven morphological forms within this complex namely, white escobon of Tenerife (*C. proliferus* ssp. *proliferus sensu stricto*), narrow-leaved escobon (*C. proliferus* ssp. *angustifolius* (Kuntze) Kunkel), typical tagasaste (*C. proliferus* ssp. *proliferus* var. *palmensis* (Christ) Hansen & Sunding), white tagasaste (*C. proliferus* ssp. *proliferus* var. *calderae* J.R. Acebes), escobon of southern Gran Canaria (*C. proliferus* ssp. *meridionalis* J.R. Acebes), white escobon of Gran Canaria (*C. proliferus* ssp. *proliferus* var. *canariae* (Christ) Kunkel) and escobon of El Hierro (*C. proliferus* ssp. *proliferus* var. *hierrensis* (Pitard) J.R. Acebes).

Both kinds of tagasaste are endemic to the island of La Palma. Escobon of El Hierro, escobon of southern Gran Canaria, white escobon of Gran Canaria and white escobon of Tenerife are only found in their respective islands whereas narrow-leaved escobon occurs in Tenerife and La Gomera (Fig. 1).

Although originally from La Palma, typical tagasaste is also cultivated in El Hierro, La Gomera, Tenerife and Gran Canaria. The other six morphological forms are not cultivated but heavily pruned and grazed in their wild habitats (Pérez de Paz *et al.* 1986; Francisco-Ortega *et al.* 1990). White escobon of Gran Canaria has been reported to be semi-cultivated in some areas of north-western Gran Canaria (Hernández-González 1987; Francisco-Ortega *et al.* 1990) where it is used to feed livestock.

Tagasaste appears to follow the same pattern of domestication of other fodder species and although it is cultivated it cannot be regarded as a truly domesticated species (Harlan 1983). No clear morphological and agronomic differences exist between typical tagasaste plants from wild and from cultivated populations. This means that unlike many other more domesticated crops, tagasaste germplasm collected in the wild is of value as in many instances it can be used without having to resort to complex plant breeding procedures. The importance of germplasm from wild populations of this fodder species determines that ecogeographical studies within its distribution are extremely useful in the establishment of strategies for subsequent evaluation and utilisation of its plant genetic resources. Furthermore as the centre of origin and diversity of tagasaste is found within an archipelago, it is essential to consider the general patterns of island biogeography prior to any study on the phytogeography and plant genetic resources of this species.

Studies concerning the biogeography of the Canary Islands have been reported extensively elsewhere (e.g. Webb & Berthelot 1836–1850; Kunkel 1976; Bramwell 1979; Santos-Guerra 1983a; Rivas-Martínez 1987). Due to the oceanic position of the archipelago and the influence of the cold north-eastern and the hot north-western trade winds there is a stratification of different climates in the archipelago both in terms of altitude and orientation. This stratification is also reflected by the patterns of distribution of the vegetation of the Canary Islands in five different life-zones namely, infra-canarian zone (semi-desert scrub), thermo-canarian zone (arid scrub, *Laurus azorica* wood and heath belt), meso-canarian zone (*Pinus canariensis* forest), supra-canarian zone (high altitude scrub) and oro-canarian zone (only *Viola cheiranthifolia*). Within this ecological framework the other two factors which determine the patterns of biogeographical variation found in the Canary Islands are the obvious geographical isolation which exists between each island and the abrupt topography.

Habitat stratification in life-zones has produced several examples of adaptive radiation in the genera *Aeonium* (Lems 1960), *Argyranthemum* (Humphries 1976) and *Sonchus* (Alridge 1980). On the other hand geographical isolation due to

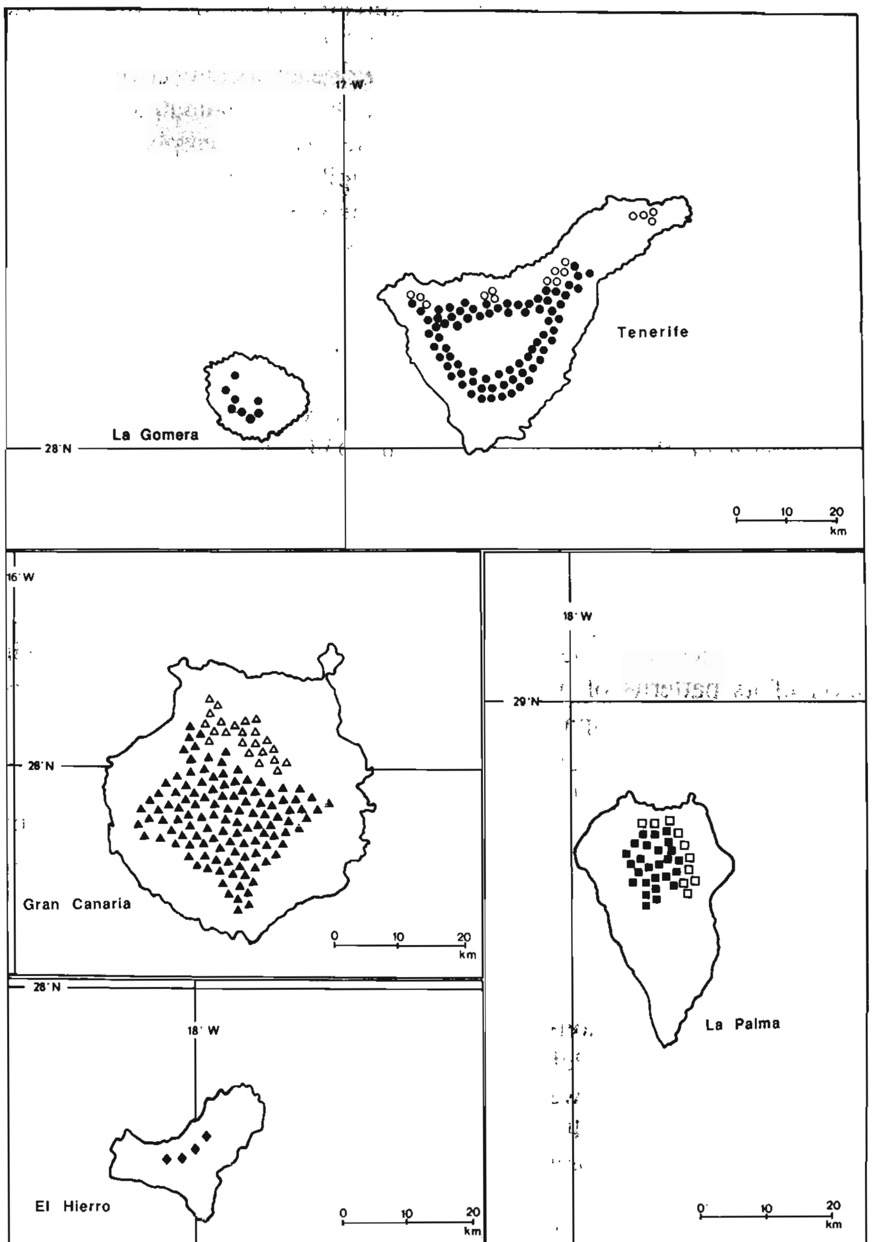

Fig. 1. The distribution of the seven morphological forms of *C. proliferus* (based on Acebes-Ginovés *et al.* (1991) and Francisco-Ortega (1992)). Taxa are coded as follows: ○ *C. proliferus* ssp. *proliferus* var. *proliferus*; ● *C. proliferus* ssp. *angustifolius*; △ *C. proliferus* ssp. *proliferus* var. *canariae*; ▲ *C. proliferus* ssp. *meridionalis*; ■ *C. proliferus* ssp. *proliferus* var. *palmensis*; □ *C. proliferus* ssp. *proliferus* var. *calderae* and ◆ *C. proliferus* ssp. *proliferus* var. *hierrensis*.

island topography and/or insular isolation has led to vicariance, examples of this evolutionary process being the patterns of morphological variation and ecology in the genera *Cheirolophus*, *Crambe* and *Limonium* (Bramwell 1972).

Previous reports on the phytogeography of *C. proliferus* (Ceballos & Ortuño 1951; Esteve-Chueca 1969; Sunding 1972; Rivas-Martínez 1987) were imprecise, as firstly they did not include the whole distribution range of the species, and secondly they were more concerned with the ecology of the life-zones of the archipelago rather than with the ecological characteristics and taxonomy of *C. proliferus* itself. Only recently has it been proposed (Acebes-Ginovés 1990) that typical tagasaste, white escobon of Gran Canaria, white escobon of Tenerife and escobon of El Hierro were linked to the laurel (*Laurus azorica*) wood and the heath (*Erica arborea*) formations from the north of these islands, whereas the other three morphological forms were in association with the plant communities of *P. canariensis*.

No multivariate analyses on the phytogeography of this species have been reported previously, and from our study both herbarium specimens and germplasm were collected from most of the localities of *C. proliferus* in the Canary Islands with the objective that an understanding of the phytogeography of this species would lead to a better interpretation of its patterns of morphological variation. In turn, it was anticipated that this would contribute to the ecogeographical characterization of the plant genetic resources of this fodder legume with a view to future conservation strategies.

Materials and methods

Floristic data from 147 wild populations of *C. proliferus sensu lato* from El Hierro, La Palma, La Gomera, Tenerife and Gran Canaria were collected from quadrats of approximately 40 x 40 m between March and September 1989. Populations from the whole distribution range of the species were sampled. They were separated by 3 km and were chosen following the north-south climatic gradient which exist within each island (Santos-Guerra 1984). Table 1 shows localities for which floristic lists were compiled. Further ecological information concerning each of these localities was given previously (IBPGR internal report 90/1), and indicated that the species thrives better on sandy soils with low salinity and pH values between 5 and 7. Furthermore populations were identified in areas where periodical frosts occur and in zones with low and high rainfall of 175 and 1200 mm respectively.

For each locality cover values of vascular plant species were estimated using the Braun-Blanquet scale. Special emphasis was placed upon the compilation of Canarian and Macaronesian endemics and of those species reported in previous works (e.g. Santos-Guerra 1983b; Rivas-Martínez 1987) as characteristic of each life-zone, since they are clearly related with both the ecology and historical biogeography of the Canary Islands. Numerical analyses were carried out on a matrix in which each quadrat was regarded as an OTU. Data from the Braun-Blanquet scale were transformed following Feoli-Chiapella & Feoli (1977). A classification of releves was obtained by the polythetic divisive method of TWINSPAN (Hill 1979a). Ordination of releves was accomplished using DECORANA (Hill 1979b) which avoids the curvilinear distortion known as "arch effect" which is produced with other techniques (e.g. Principal Component Analysis, Non-Metric Multidimensional Scaling, Reciprocal Averaging), when species diversity among sites follows environmental gradients (Jackson & Somers 1991). The CEP-PC package (Mohler 1987) was utilised to accomplish these multivariate analyses. In order to avoid between-island floristic vicariance effects, separate analyses were carried out for each island except for El Hierro where data were collected from only three populations. Simple descriptions of floristic compositions of these stands were used for interpretation of the ecological features of escobon of El Hierro.

Results

Tenerife

The hierarchical division of plant communities from TWINSPAN end groups, is given in Fig. 2a. Eight groups were recognised at the fifth division. These groups with their TWINSPAN indicator species are given in Table 2. Stands identified within each group are shown in Fig. 3.

Table 1. Localities of *Chamaecytisus proliferus* in the Canary Islands in which floristic studies were carried out.

Acc. no.	Mo. fo.	Locality	Coordina.	I.	Alti.	Acc. no.	Mo. fo.	Locality	Coordina.	I.	Alti.
1	4	Anaga 1	28RCS7757	T	650	102	5	Madre Agua	28RCS4519	T	1700
2	4	Anaga 2	28RCS7655	T	730	103	5	El Río 1	28RCS4519	T	1550
13	3	Tenerra	28RBS1780	P	1000	104	5	Boca deTauce 1	28RCS3718	T	2000
14	3	Bombas de Agua	28RBS1881	P	1500	105	5	Boca deTauce 2	28RCS3520	T	1950
16	3	Los Cantos	28RBS1981	P	850	106	5	Chío	28RCS2927	T	1700
17	3	Dos Aguas	28RBS1878	P	500	107	5	Roque Cedro	28RCS3323	T	2100
18	3	Escuchaderos	28RBS2280	P	1550	108	5	El Junquillo	28RCS3122	T	1650
23	2	Los Tilos	28RBS2687	P	600	109	5	Gutiérrez 1	28RCS3126	T	1850
26	2	Marcos	28RBS2485	P	1500	110	5	Gutiérrez 2	28RCS3124	T	1700
30	5	Lomo Cedro	28RCS5842	T	1350	111	5	Erjos	28RCS2232	T	1100
31	5	Siete Ojos	28RCS5037	T	1150	113	5	Vergara 1	28RCS2732	T	1300
32	5	El Roque 1	28RCS5640	T	1450	114	5	Franquis	28RCS2333	T	1150
33	5	El Roque 2	28RCS5640	T	1500	115	5	Escobones	28RCS2330	T	1050
34	5	Aguamansa	28RCS5640	T	1500	116	5	El Estrecho	28RCS2530	T	1300
35	4	Tigaiga 1	28RCS4435	T	1400	117	5	Los Tomillos	28RCS2532	T	1300
36	4	Tigaida 2	28RCS4437	T	1300	118	5	El Hospital	28RCS2931	T	1600
38	6	Troya	28RDR4697	C	1100	122	5	Masca	28RCS2032	T	900
39	6	Lomo Picacho	28RDR4896	C	1000	123	5	La Fortaleza	28RCS4233	T	2000
40	6	Roque Grande	28RDR4794	C	1200	124	5	La Guancha	28RCS4033	T	1650
41	6	Lagunetas	28RDR4397	C	1200	125	5	Pinar Icod 1	28RCS3732	T	1550
43	7	Tejeda	28RDR4096	C	1200	126	5	Pinar Icod 2	28RCS3432	T	1650
45	6	Cueva grande	28RDR4496	C	1200	127	5	Pinar Icod 3	28RCS3232	T	1650
46	6	Lanzarote	28RDS4201	C	1200	128	5	El Charquido	28RCS5938	T	1300
47	6	Carpinterías	28RDS4303	C	800	129	5	El Corcho	28RCS5940	T	1450
48	6	Fontanales	28RDS3902	C	1200	130	5	Fuente Joco	28RCS5638	T	1960
51	6	El Pinar	28RDS3905	C	1000	131	5	La Crucita	28RCS5536	T	1850
52	6	Tres Cruces	28RDS3909	C	600	132	5	Las Arenas	28RCS5735	T	1450
53	6	Montaña Alta	28RDS3907	C	750	134	5	La Orotava 1	28RCS4933	T	1650
54	7	Tamadaba 1	28RDS3201	C	1200	135	5	El Portillo	28RCS4533	T	1850
55	7	Los Brezos	28RDR3599	C	1350	136	5	La Orotava 2	28RCS4733	T	1750
56	7	Artenara	28RDR3399	C	1000	137	5	La Orotava 3	28RCS5136	T	1400
57	7	Taurito	28RDR3187	C	850	138	5	Agando	28RBS8210	G	1000
58	7	Las Niñas	28RDR3388	C	950	139	5	Chipude	28RBS7611	G	1100
59	7	Pajonales	28RDR3589	C	900	140	5	Las Hayas 1	28RBS7513	G	1000
60	7	Inagua 1	28RDR2889	C	900	141	5	Las Hayas 2	28RBS7413	G	1000
61	7	Inagua 2	28RDR2890	C	1050	142	5	Igualero	28RBS7810	G	1200
62	7	Inagua 3	28RDR3892	C	1150	144	5	San Lorenzo	28RBS7908	G	1000
63	7	La Meca	28RDR4091	C	1350	145	5	Monte Torino	28RCS6644	T	755
64	7	Roque Nublo	28RDR3994	C	1200	146	5	La Cueva	28RCS5418	T	400
65	7	Temisas	28RDR4986	C	800	147	5	Las Chozas	28RCS5730	T	1600
66	7	Taidía	28RDR4589	C	950	148	5	Lomo Benito	28RCS5432	T	1800
67	7	Aguas Tunte	28RDR4390	C	1150	149	5	Güimar	28RCS5633	T	1600
68	7	Tirajana 1	28RDR4190	C	1200	150	5	Izaña 1	28RCS5128	T	2150
69	7	Cercados	28RDR3989	C	1150	151	5	Pinar Arico	28RCS4832	T	1900
70	7	Los Hornos	28RDR4193	C	1600	152	5	El Río 2	28RCS4721	T	1650
71	7	El Juncal	28RDR3692	C	1150	153	5	Izaña 2	28RCS5023	T	1650
72	7	Capellania	28RDR4885	C	650	154	5	El Contador	28RCS5117	T	700
73	7	Santa Lucía	28RDR4686	C	600	156	5	El Hospital	28RCS3129	T	1850
74	7	Tirajana 2	28RDR4387	C	950	157	5	Boca Tauce 3	28RCS3519	T	2000
75	7	Fataga 1	28RDR4485	C	700	158	5	La Colorada	28RCS3518	T	1950
76	7	Fataga 2	28RDR4483	C	450	159	5	Teresme	28RCS3307	T	1600
77	7	Fataga 3	28RDR4381	C	450	160	5	Pinar Tijoco	28RCS3322	T	2000
78	7	La Charca	28RDR4280	C	550	161	5	Llano Negro	28RCS3120	T	1700
79	7	Fataga 4	28RDR4379	C	400	162	5	Erques	28RCS3219	T	1600
80	7	Ayagaures	28RDR4081	C	350	163	5	Canal Fyffes	28RCS3218	T	1550
81	7	Arguineguín	28RDR3484	C	550	164	7	Los Pechos	28RDR4592	C	1850
82	7	Soria 1	28RDR3386	C	650	165	5	Encantadora	28RBS7817	G	450
83	7	Soria 2	28RDR3588	C	700	168	4	Santa Ursula	28RCS5440	T	1000
84	7	Chira	28RDR3786	C	950	170	5	Pinar Icod 4	28RCS3933	T	1575
85	7	Guayadeque 1	28RDR5489	C	450	179	1	Jinamar 1	28RBR0674	H	1150
86	7	Guayadeque 2	28RDR5090	C	900	180	4	Monte del Agua	28RCS2134	T	950
87	7	Infiernillo	28RDR5192	C	1000	183	1	Tabano	28RBR0271	H	1000
88	7	Los Marteles	28RDR4792	C	1500	217	2	Aguascae	28RBS2578	P	1000
90	7	Ventaiga	28RDR3795	C	1150	218	2	Los Hombres	28RBS1987	P	1200
91	6	Firgas	28RDS4406	C	700	222	3	Pico Nieve	28RBS2381	P	2000
92	6	Teror 1	28RDS4604	C	650	229	4	Las Yedras	28RCS7457	T	900
93	7	Guardaya	28RDR3898	C	1150	254	3	Tenerra 1	28RCS1780	P	1000
94	6	Teror 2	28RDS4601	C	800	255	3	Tenerra 2	28RBS1780	P	1000
95	7	Perralillo	28RDR3296	C	450	256	5	La Escalona	28RCS3512	T	900
96	7	La Coruña	28RDS3401	C	950	257	5	El Cherfe	28RCS2132	T	1050
98	7	Tamadaba 2	28RDS3400	C	1100	258	6	Monagas	28RDS4603	C	900
99	5	Los Quemados	28RCS3712	T	1200	259	6	Retamilla	28RDS3903	C	1500
100	5	Vilaflor	28RCS4014	T	1300	260	1	Jinamar 2	28RBR0674	H	1100
101	5	La Hondura	28RCS3917	T	1650						

Acc. no. = Accession number; Mo. fo. = Morphological form, coded as follows: 1 = escobon of El Hierro, 2 = typical tagasaste, 3 = white tagasaste, 4 = white escobon of Tenerife, 5 = narrow-leaved escobon, 6 = white escobon of Gran Canaria, 7 = escobon of southern Gran Canaria; Coordina. = Geographical coordinates on the Universal Transverse Mercator projection; I. = Island, coded as follows: H = El Hierro, P = La Palma, G = La Gomera, T = Tenerife, C = Gran Canaria; Alt. = Altitude.

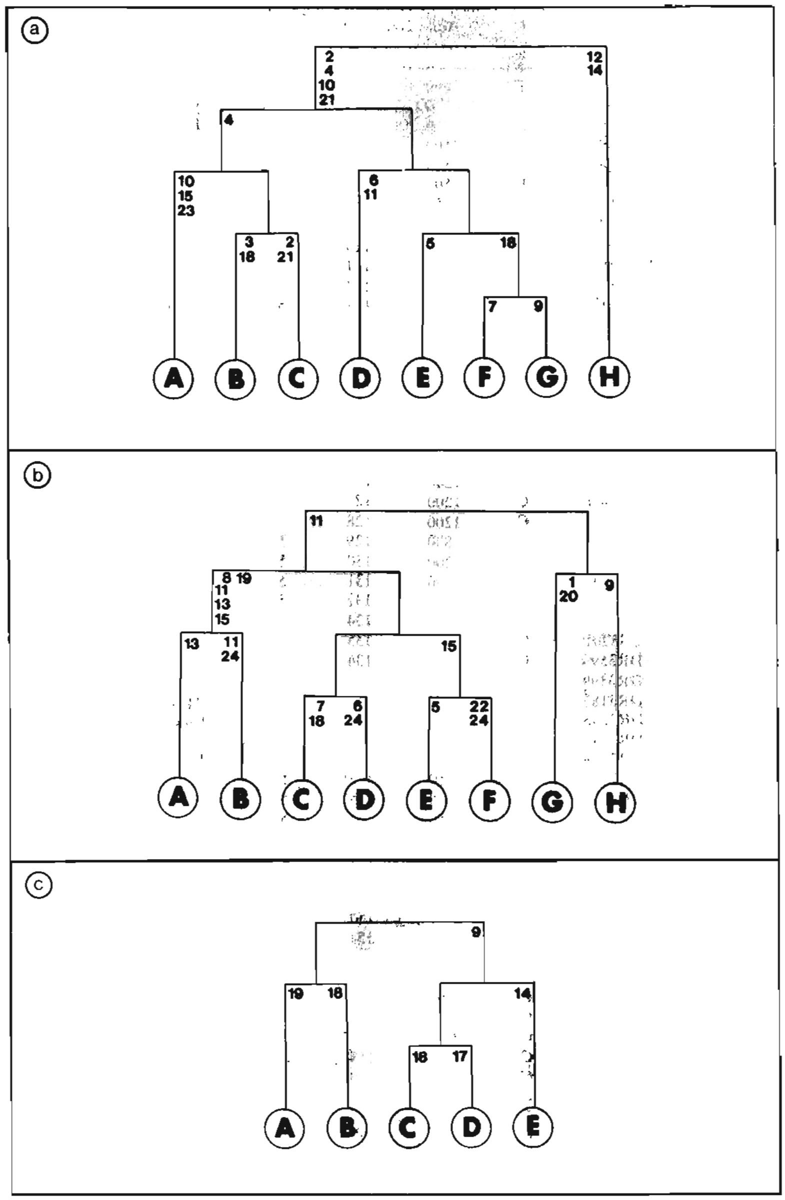

Fig. 2. TWINSPAN classification obtained for floristic data from Tenerife (a), Gran Canaria (b) and La Palma (c). The characteristic indicator species are also given (see species code number in Appendix A).

End group A comprises those scrubs situated on northern and southern areas of the island at a mean altitude of 1850 m. Groups B, C, E and F were found both on northern and southern slopes of Tenerife and with an average altitude of 1600 m. Stands from end group D were only recorded on southern slopes at a mean altitude of 900 m. Both end groups G and H were located in northern Tenerife. The mean altitude for group G was of 1350 m whereas stands from group H were recorded at a mean altitude of 950 m.

An ecological interpretation of stands obtained

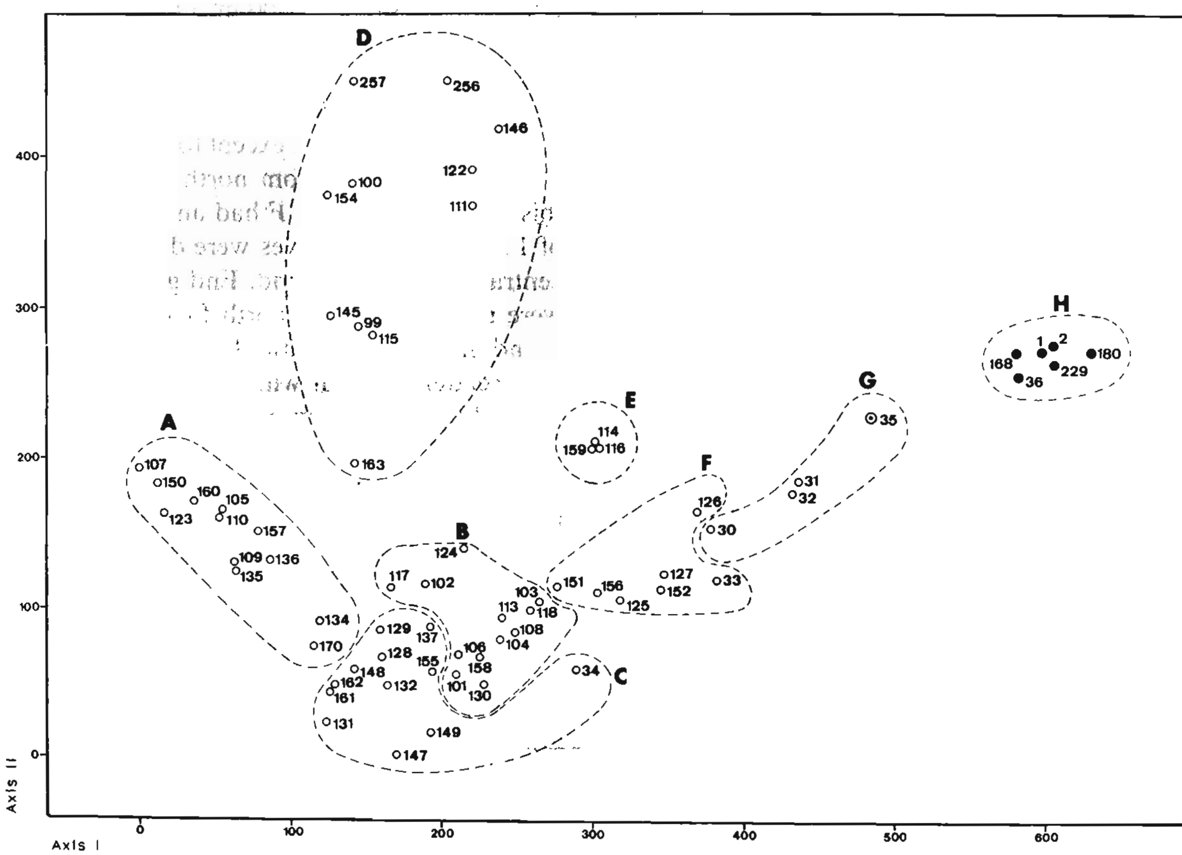

Fig. 3. DECORANA ordination for Tenerife. The eight TWINSPAN end groups are also given. Stands with white escobon of Tenerife are represented by closed circles; stands with narrow–leaved escobon are represented by open circles. Stands with intermediate plants are represented by open circle plus dot.

after hierarchical classification was achieved by their ordination through DECORANA. The scatter diagram for the first two DECORANA axes is illustrated in Fig. 3. TWINSPAN end groups G and H had high values along the first axis. Stands with white escobon of Tenerife were only detected in end group H, and one locality from end group G had plants intermediate between this morphological form and narrow-leaved escobon (Francisco-Ortega 1992). The other stands had lower scores on this axis and were of narrow-leaved escobon. End groups B, C, E and F were situated in the central zone of the scatter diagram. Geographically they occurred along a band which circled the island between 1100 and 1700 m in an area found within the meso-canarian zone.

The interpretation of these two axes was determined from the species scores along them, which are summarised in Table 3. Only characteristic species from the laurel wood and heath belt of northern Tenerife had large positive scores along the first axis whereas those species linked with high altitude zones (e.g. *Argyranthemum tenerifae* or *Nepeta teydea*) displayed low values on this axis. The separation of stands along the first DECORANA axis was associated with an altitudinal gradient which runs on the north of the island from the thermo-canarian zone towards the high altitude scrub.

Species from arid zones of southern Tenerife (e.g. *Euphorbia obtusifolia*) had high positive scores along the second axis whilst species associated with the Canary pine life-zone such as *Sideritis cretica* had low values on this axis (Table 3).

It was considered that this axis reflected a transect from the Canary pine area towards zones from southern Tenerife situated at low altitude.

Gran Canaria

Eight end groups were obtained at the fourth division after the TWINSPAN classification of releves from Gran Canaria, and they are illustrated in Fig. 2b. Stands which fell within each of these groups are given in Fig. 4. These groups with their TWINSPAN indicator species are given in Table 2.

Stands from TWINSPAN end group A were recorded on southern areas of the island at an average altitude 550 m. They have the most arid conditions of the whole complex. Releves from end group B were also located on southern slopes but a mean altitude of 800 m. End groups C and D had mean altitudes of 1040 m and 965 m respectively, and all the stands from these two groups were recorded in central and southern areas of Gran Canaria, except for localities 54, 98 and 96 which were from north facing slopes of this island. End group F had an average altitude of 1400 m and its releves were distributed in the central zone of the island. End groups G and H were recorded on the north facing slope of the island at an average altitude of 960 m.

A scatter diagram with values along the first two DECORANA axes is illustrated in Fig. 4. Releves from the centre of the island were distributed centrally on this diagram. Species from those areas of northern Gran Canaria found in an area which is under the influence of the trade winds had high values on the first axis while species from the arid south of Gran Canaria dis-

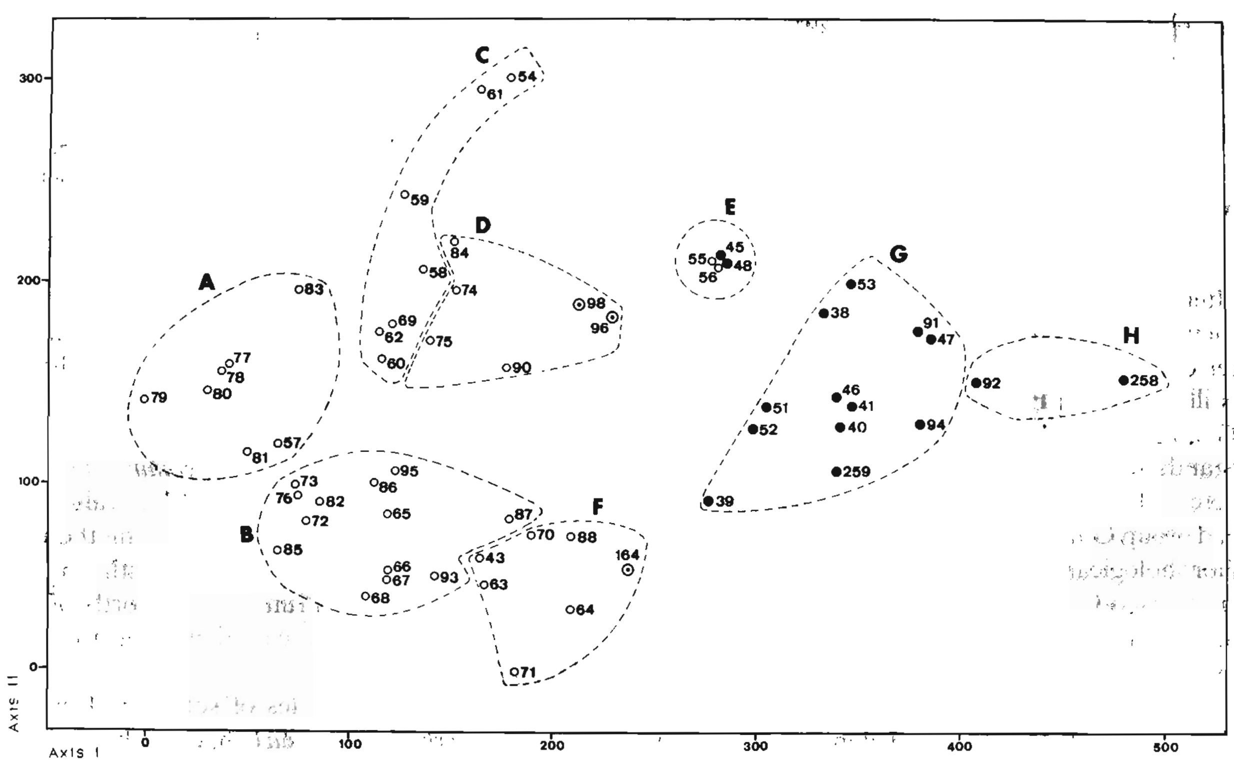

Fig. 4. DECORANA ordination for Gran Canaria. The eight TWINSPAN end groups are also given. Stands with white escobon of Gran Canaria are represented by closed circles; stands with escobon of southern Gran Canaria are represented by open circles. Stands with intermediate plants are represented by open circle plus dot.

Table 2. Characterization of TWINSPAN end groups within *Chamaecytisus proliferus* from Tenerife, Gran Canaria and La Palma.

TWINSPAN end group	Indicator species	Ecological characterization
Tenerife		
A	*Spartocytisus supranubius* *Erysium scoparium* *Nepeta teydea*	High altitude scrub of narrow-leaved escobon and *S. supranubius*. *Pinus canariensis* was recorded occasionally
B	*Pinus canariensis* *Bystropogon origanifolius*	Open pine forest with a rich understorey with species such as *Sideritis cretica* and *Micromeria hyssopifolia*
C	*Adenocarpus viscosus* *Sideritis cretica*	Scrubs of *Chamaecytisus/Adenocarpus*
D	*Cistus monspeliensis* *Euphorbia obtusifolia*	Scrubs in arid areas of southern Tenerife. Two stands were found in abandoned cultivated sites
E	*C. proliferus* ssp. *angustifolius*	Dense scrub of narrow-leaved escobon
F	*Cistus symphytifolius*	Dense pine forest with narrow-leaved escobon as an understorey species
G	*Erica arborea*	Dense Canary pine-heath forest
H	*Laurus azorica* *Ilex canariensis*	Sunny cliffs of the laurel wood area. Only stand 180 has plants inside the 'real' laurel wood
Gran Canaria		
A	*Kleinia neriifolia*	Low altitude scrubs in arid zones of southern Gran Canaria
B	*Euphorbia obtusifolia* *Teline microphylla*	Scrubs from southern Gran Canaria. Similar to end group A but at higher altitude. Five stands were found in abandoned cultivated sites
C	*Pinus canariensis* *Cistus symphytifolius*	Canary pine forest. Half of the stands had a rich understorey
D	*Cistus monspeliensis* *Teline microphylla*	Scrubs from southern Gran Canaria similar to end group D from Tenerife
E	*C. proliferus*	Dense scrubs of white escobon of Gran Canaria or escobon of southern Gran Canaria
F	*Teline microphylla* *Sideritis dasygnaphalla*	Scrubs in central zones of Gran Canaria. Three stands in abandoned cultivated sites
G	*Adenocarpus foliolosus* *Senecio webbii*	Scrubs of white escobon of Gran Canaria and *Adenocarpus* from northern Gran Canaria. Two stands in abandoned cultivated sites
H	*Erica arborea*	Open and sunny areas of the heath belt
La Palma		
A	*Rumex lunaria*	Rather dense scrubs along the bottom of the gorges of Caldera de Taburiente. Canary pine was found occasionally and the stands have the most sandy soils of the complex
B	*Pinus canariensis*	Canary pine forest. Three localities in La Caldera de Taburiente and one on high altitude zones of northern La Palma
C	*Pinus canariensis*	Transition between heath belt and pine forest. Tagasaste was found as an understorey species in open areas
D	*Festuca agustini* *Phyllis nobla*	Cliffs of gorges of northern La Palma in transition zones between the heath belt and the pine forest
E	*Laurus azorica*	Open zones of the laurel wood on slopes of a gorge

Table 3. Ten species which had the highest and the lowest values along the first two DECORANA axes in releves from Tenerife.

DECORANA 1		DECORANA 2	
Ranunculus cortusifolius	630	*Euphorbia atropurpurea*	496
Teline canariensis	629	*Kleinia neriifolia*	492
Hypericum glandulosum	627	*Lavandula canariensis*	475
Ilex canariensis	626	*Periploca laevigata*	466
Laurus azorica	625	*Rumex lunaria*	441
Echium wildpretii	– 28	*Carlina xeranthemoides*	– 27
Spartocytisus supranubius	– 32	*Sideritis cretica*	– 46
Nepeta teydea	– 34	*Rumex maderensis*	– 53
Descurainia bourgeauana	– 70	*Argyranthemum foeniculaceum*	– 73
Argyranthemum tenerifae	– 73	*Descurainia lemsii*	– 81
Eigenvalue	0.823		0.632

played low scores on this axis (Table 4). These data revealed that the first DECORANA axis shows a gradient from those zones of northern Gran Canaria which receive the influence of the north-eastern trade winds towards low altitude areas from the south of this island. Stands of white escobon of Gran Canaria (TWINSPAN end groups G and H) were the only ones which displayed high positive scores along the first DECORANA axis, the two releves from the "pure" laurel wood and the heath belt having the highest values on this axis. Furthermore, localities 96, 98 and 164 had plants with morphological characters intermediate between white escobon and escobon of southern Gran Canaria (Francisco-Ortega 1992). They also had intermediate values along the first DECORANA axis.

Canary pine forest releves and scrubs of *Cistus monspeliensis-Teline microphyla* had positive values along the second axis whereas those stands from the high altitude zone of central Gran Canaria had the lowest scores on the second axis. This pattern was also followed by the species scores which are summarised in Table 4, as those species linked to the pine forest had high positive values on this axis whilst species which occur at high altitude displayed negative scores along it. The second DECORANA axis represented a

Table 4. Ten species which had the highest positive and negative values along the first two DECORANA axes in releves from Gran Canaria.

DECORANA 1		DECORANA 2	
Hypericum grandifolium	543	*Cistus symphytifolius*	409
Laurus azorica	538	*Pinus canariensis*	391
Hypericum canariense	528	*Cistus monspeliensis*	316
Senecio webbii	488	*Micromeria lanata*	311
Erica arborea	455	*Reseda luteola*	275
Kickxia scoparia	– 50	*Sideritis dasygnaphala*	– 65
Campylanthus salsoloides	– 53	*Argyranthemum adauctum*	– 72
Neochamaelea pulverulenta	– 61	*Echium decaisnei*	– 89
Artemisia ramosa	– 83	*Pterocephalus dumetorus*	– 129
Lycium intricatum	– 88	*Descurainia preauxiana*	– 136
Eigenvalue	0.659		0.378

transition between the plant communities from the centre of the island, towards the Canary pine forest zone found at low altitudes. It is noteworthy that it is likely that in the past the plant communities of central Gran Canaria also had *P. canariensis* as a common species. However intensive deforestation has meant that it has vanished from this area (Santos-Guerra & Fernández-Galván 1980).

La Palma

The hierarchical classification yielded five TWINSPAN end groups at the third division (Fig. 2c and Table 2). Releves which fell within each end group are illustrated in Fig. 5.

A scatter diagram with values along the first two DECORANA axes is shown in Fig. 5. Stands recorded within the laurel wood-heath belt zone had high positive values on the first axis. Populations sampled on the bottom of some of the wide gorges of La Caldera de Taburiente National Park had high negative values along the first DECORANA axis. This situation was also reflected by the species scores on this axis which are summarised in Table 5, as those species linked to the laurel wood zone (e.g. *Laurus azorica*) had positive values along this axis whilst species mainly found on the scrubs of La Caldera de Taburiente gorges (e.g. *Bystropogon origanifolius*) had negative scores. Stands which had typical tagasaste showed the highest scores on the first DECORANA axis. The separation of stands along this axis was associated with a gradient which ran from northern La Palma towards the interior of La Caldera de Taburiente.

The second DECORANA axis was related with changes in the floristic composition of the Canary pine communities. Stand 26 had the highest positive value on this axis and it was recorded on a cliff, in an area where the pine forest was not so dense. This was confirmed by the fact that species such as *Festuca agustini* and *Gonospermum canariensis* had positive values along the second axis (Table 5). Stands 254 and 255 were found in those areas of the pine forest of La Caldera de Taburiente, which meant that species related to the thermo-canarian zone such as *Erica arborea* had low values on this axis (Table 5).

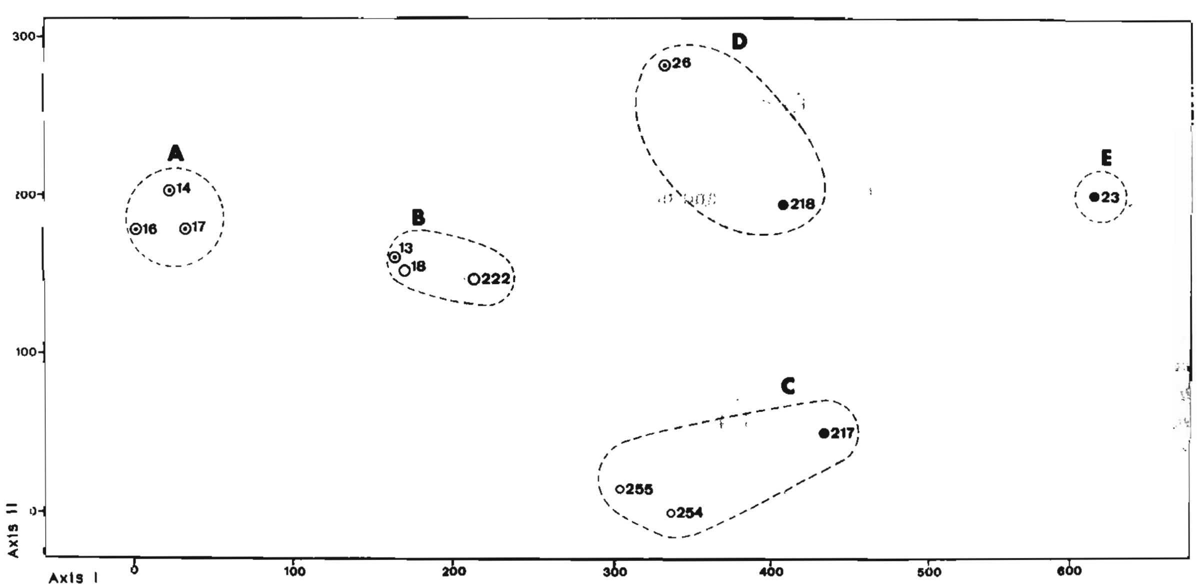

Fig. 5. DECORANA ordination for La Palma. The five TWINSPAN end groups are also given. Stands with typical tagasaste are represented by closed circles; stands with white tagasaste are represented by open circles. Stands with intermediate plants are represented by open circle plus dot.

Table 5. Ten species which had the highest positive and negative values along the first two DECORANA axes in releves from La Palma.

DECORANA 1		DECORANA 2	
Laurus azorica	673	*Tinguarra montana*	383
Teline stenopetala	673	*Festuca agustini*	383
Hypericum grandifolium	673	*Silene pogonocalyx*	366
Myrica faya	590	*Gonospermum canariense*	358
Erica arborea	585	*Helianthemum broussonetii*	335
Paronychia canariensis	−82	*Lotus hillebrandii*	39
Lobularia palmensis	−82	*Andryala webbii*	39
Spartocytisus filipes	−89	*Erica arborea*	−85
Bystropogon origanifolius	−91	*Rubus ulmifolius*	−90
Senecio palmensis	−111	*Sideritis bolleana*	−104
Eigenvalue	0.821		0.401

Four stands from La Caldera de Taburiente had plants of white tagasaste and typical tagasaste growing together (Francisco-Ortega 1992). However in these localities white tagasaste was always dominant. Furthermore, this morphological form was never detected within the laurel wood life-zone.

La Gomera

All the stands of narrow-leaved escobon from La Gomera were associated with *Cistus monspeliensis*, and were similar to the scrubs from low altitude zones of southern Tenerife. The hierarchical classification yielded two end groups at the first division.

The first end group (TWINSPAN end group A) had *Erica arborea* as characteristic species whereas the second (TWINSPAN end group B) had *Artemisia thuscula* and *Micromeria lepida*. The two releves from end group A had also other characteristic species from the heath-belt and laurel wood plant communities (e.g. *Myrica faya* and *Ilex canariensis*) however these two sites were not within the limits of the actual laurel wood or heath belt.

A scatter diagram for the first two DECO-

Table 6. Ten species which had the highest positive and negative values along the first two DECORANA axes in releves from La Gomera.

DECORANA		DECORANA 2	
Micromeria lepida	258	*Sonchus ortunoi*	348
Euphorbia obtusifolia	238	*Phagnalon saxatile*	220
Kleinia neriifolia	201	*Adenocarpus foliolosus*	188
Artemisia thuscula	194	*Phagnalon saxatile*	125
Polycarpaea divaricata	169	*Hypericum grandifolium*	99
Bystropogon origanifolius	−165	*Hyparrhenia hirta*	−35
Bituminaria bituminosa	−221	*Carlina salicifolia*	−98
Ilex canariensis	−234	*Andryala pinnatifida*	−159
Myrica faya	−234	*Dittrichia viscosa*	−178
Erica arborea	−250	*Micromeria varia*	−317
Eigenvalue	0.233		0.101

RANA axes (Fig. 6) showed that populations from TWINSPAN end group A had low values along the second axis and were regarded as being more influenced by the northern trade winds. All the localities, with the exception of one (population 165), were below 1200 m altitude, and in the southern areas of the island. Population 165 was in the north west of the island but at an altitude of 450 m. This distribution was in agreement with the species scores along the first axis (Table 6). Those species usually found in areas which have the influence of the trade winds (e.g. *Myrica faya*) had large negative scores on the first axis. High positive values were only obtained for arid areas (e.g. *Kleinia neriifolia* or *Euphorbia obtusifolia*). This axis showed a transition within the *Cistus monspeliensis* scrub from semi-arid areas to those which receive the effect of the trade winds.

It was difficult from the data set to obtain an ecological interpretation for the second DECORANA axis, which separated stands 139 and 142 at one end and stands 138 and 140 at the other (Fig. 6). However floristic species scores (Table 6) indicate that the legume shrub *Adenocarpus foliolosus* which is also a member of the Genisteae had high positive scores along the second axis whereas *Micromeria varia* had low negative values on this axis.

El Hierro

The three stands of escobon of El Hierro were located on the cliffs of El Golfo caldera in the north of this island at an altitude of 1000 m. These stands were clearly linked to the heath belt

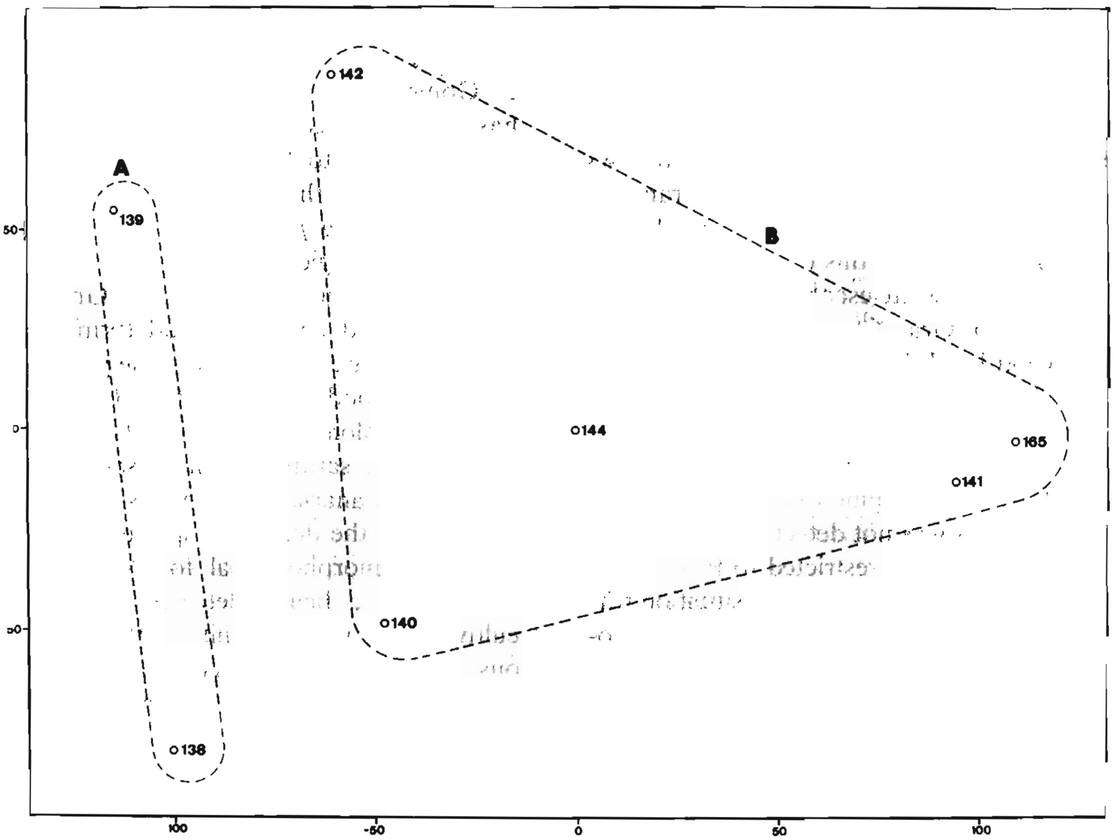

Fig. 6. DECORANA ordination for La Gomera. The two TWINSPAN end groups are also indicated

and species usually found on cliff plant communities such as *Greenovia aurea*, *Silene sabinosae* or *Tolpis proustii* were also recorded. It was never observed forming dense scrubs and could not be regarded as a common species. No populations of *C. proliferus* were associated with the pine forest, despite the extensive floristic survey carried out in the south of the island.

Discussion

Chamaecytisus proliferus should be regarded as a species which grows under a broad range of ecological conditions. Previous reports (Ceballos & Ortuño 1951; Esteve-Chueca 1969; Sunding 1972 and Rivas-Martínez 1987) which indicated that the whole complex is restricted to the Canary pine life-zone have been misleading. The different morphological forms of the complex are also found in the thermo-canarian zone, and some populations were also identified towards the high altitude scrub of Tenerife or in the semi-arid infracanarian zone from the south of Tenerife and Gran Canaria. The classification and ordination of the stands demonstrate that the species follows an ecological cline through Tenerife, Gran Canaria and La Palma, with distinct morphological forms in the extremes of this cline. Typical tagasaste in La Palma, white escobon of Tenerife and white escobon of Gran Canaria are only located in laurel wood/heath belt zones of these islands, whereas white tagasaste in La Palma, narrow-leaved escobon in Tenerife and escobon of southern Gran Canaria have their distribution range linked with the Canary pine forest area.

Such a gradient was not detected in El Hierro, where *C. proliferus* was restricted to the cliffs of the heath belt of El Golfo. A similar situation was found in La Gomera, where narrow-leaved escobon was always associated with *Cistus monspeliensis*, forming a kind of scrub which also occurred in localities of southern Tenerife. However, some of the stands from La Gomera had species such as *Erica arborea* or *Myrica faya* which were not found in their homologues from the south of Tenerife. These species usually occur in northern areas which are under the influence of the trade winds (Santos-Guerra 1984), a situation previously described by Fernández-Galván (1983), in La Gomera, an island with lower altitude than La Palma, Tenerife and Gran Canaria, and where the trade winds can have a great influence on some slopes of the south. This factor coupled with the fact that there are no real pine forest formations in the island, means that in the south there are zones which reflect a transition between the heath belt and plant communities from arid zones. In relation to that, one of the main features of *C. proliferus* in La Gomera is that it was never located within the true laurel wood zone. Acebes-Ginovés (pers. comm.) considers it likely that a form of *C. proliferus* similar to the white escobon of Tenerife or Gran Canaria could exist on the cliffs of the laurel wood of this island. Despite the survey carried out during field studies and interviews with farmers and forest rangers from the area, such a morphological form was never found. The fact that narrow-leaved escobon was never observed within the limits of the laurel wood of La Gomera confirms that this morphological form has achieved ecological differentiation, and is clearly adapted to dry areas which were not under the influence of the north-eastern trade winds.

Chamaecytisus proliferus does not conform to the same ecological trends in each island. The two morphological forms from Gran Canaria were observed colonising and forming massive scrubs in all areas where both the pine forest and the laurel wood have vanished. On some occasions, this colonising ability has led to the formation of dense scrubs in which escobon of southern Gran Canaria or white escobon of Gran Canaria are the dominant species. Furthermore, these two morphological forms also exhibit a weedy habit, being detected on abandoned cultivated sites. This ability to thrive under various ecological conditions was only shown by narrow-leaved escobon in Tenerife where this morphological type also forms dense scrubs (TWINSPAN end group E) and grows on abandoned cultivated sites. All the other morphological forms have a more restricted ecological range; white escobon of El Hierro, white escobon of

Tenerife and typical tagasaste were only observed on cliffs and sunny areas of the laurel wood/heath belt.

White tagasaste was confined to the pine forest of northern La Palma and to La Caldera de Taburiente and did not show the weedy habit of its ecologically homologous narrow-leaved escobon and escobon of southern Gran Canaria. Although it was observed as an understorey species of the pine forest it shows a tendency to form dense scrubs along the bottoms of the numerous gullies which dissect the huge eroded caldera of the La Caldera de Taburiente. This morphological form was observed neither in the pine forest of southern La Palma nor linked to low altitude plant communities of *Euphorbia obtusifolia* or *Kleinia neriifolia*. These distribution patterns represent a more restricted ecological range than escobon of southern Gran Canaria or narrow-leaved escobon.

Results shown here indicate that the ability of the species to grow under wider ecological conditions is demonstrated more in the eastern islands (Gran Canaria and Tenerife-La Gomera) than in the western islands (La Palma and El Hierro). This accords with previous studies of genetic diversity, based on results from ten isozyme loci, where only populations from the eastern islands had unique alleles and also the highest values of Nei's index of genetic diversity (Francisco-Ortega 1992). Similarly, it was also in those islands where a greater number of morphological variants were detected (i.e. morphological clines for seed colour, juvenile characters, leaf shape and keel petal length in Gran Canaria and for leaf hairiness, leaf shape and keel petal length in Tenerife). These results suggest that there is a relationship between germplasm provenance and ecogeographical variation measured in terms of ecology, morphology and allozymes. In this relationship, germplasm from the eastern islands was more variable than that collected in the western islands.

There is another major consequence of the high colonising ability of narrow-leaved escobon, escobon of southern Gran Canaria and white escobon of Gran Canaria. These morphological forms have played an important role during the floristic changes which the pine forests of Tenerife and Gran Canaria and the laurel wood/heath belt of Gran Canaria have suffered because of human impact since the conquest of the Canary Islands, late in the 14th century. Then intense pastoralism and agriculture resulted in large-scale deforestation (Parsons 1981). Once such forests were cut down these forms of *C. proliferus* colonised the area and formed scrub, as the habitats became sunnier and competition with other species was dramatically reduced. Furthermore, wild *C. proliferus* is broadly utilised as a fodder plant. In our study, 80% of the stands were found to have heavily pruned escobon shrubs (Francisco-Ortega 1992). This means that only in exceptional cases can *C. proliferus* form a dense shrub. Its competition with other species of the scrub and its colonisation ability and its density is severely reduced by its utilisation as fodder by peasant farmers. Eventually the scrub is not so dense and a ground layer is mainly formed by *Micromeria* spp., *Bystropogon origanifolius* or *Sideritis* spp. In the few places where escobon is not pruned it has become the dominant species, and even in some situations other shrubs, such as *Adenocarpus* spp. which have similar ecological requirements to *C. proliferus* could barely compete with escobon. Our observations indicate that prior to the massive destruction of the Canary pine forest and the laurel wood, *C. proliferus* may have been found mainly in those areas where the forest was not so dense, such as along the small and numerous ravines which dissected the forest, or on cliffs where taller trees are not dominant. It is also perceived that due to the abrupt and rough geography of the islands the species could find many ecological niches because of these features where it thrived in association with other species of the forest.

We also find that *C. proliferus* should be regarded as a pyrophytic species. Many young plants of narrow-leaved escobon, tagasaste and escobon of southern Gran Canaria were observed growing in stands which had been burnt recently and this is confirmed by Pérez de Paz *et al.* (1986). Being a pyrophyte *C. proliferus* grows better on habitats which become sunnier with less competition from other species. Furthermore, as *P. canariensis* is able to continue growth after a fire, a real scrub has not actually replaced the pine forest, and only some young plants of *C. proliferus* have survived in competition with the Canary pine. Therefore an equilibrium, in which fire is one of the regulators, is established between *C. proliferus* and *P. canariensis*.

From a combined ecogeographical and genetic resource perspective the seven morphological types of *C. proliferus* have different ecological requirements and effective *in situ* conservation and utilisation of the plant genetic resources of the species needs to take account of its phytogeography. The two morphological forms endemic in Gran Canaria, and narrow-leaved escobon in Tenerife and La Gomera are not endangered species. Also they can withstand continuous pruning by farmers and many of their plant communities have arisen as a result of human intervention upon the forest. As a consequence of the rather limited distribution range of white tagasaste most of its populations are confined to La Caldera de Taburiente National Park where they correctly have an *in situ* conservation status. Other priorities for *in situ* conservation should be focused towards the other three morphological forms, namely typical tagasaste, white escobon of Tenerife and escobon of El Hierro. They have restricted ecological requirements and also have lower adaptation to those disturbed habitats which have arisen after deforestation.

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Appendix A

TWINSPAN characteristic species for Tenerife, Gran Canaria and La Palma.

1. *Adenocarpus foliolosus*
2. *Adenocarpus viscosus*
3. *Bystropogon origanifolius*
4. *Carlina xeranthemoides*
5. *Chamaecytisus proliferus s.l.*
6. *Cistus monspeliensis*
7. *Cistus symphytifolius*
8. *Echium onosmifolium*
9. *Erica arborea*
10. *Erysimum scoparium*
11. *Euphorbia obtusifolia*
12. *Ilex canariensis*
13. *Kleinia neriifolia*
14. *Laurus azorica*
15. *Micromeria benthamii*
16. *Nepeta teydea*
17. *Phyllis nobla*
18. *Pinus canariensis*
19. *Rumex lunaria*
20. *Senecio webbii*
21. *Sideritis cretica*
22. *Sideritis dasygnaphalla*
23. *Spartocytisus supranubius*
24. *Teline micropylla*
25. *Festuca agustini*

References

Acebes-Ginovés, J.R. 1990. Contribución al estudio de los géneros *Chamaecytisus* Link y *Dorycnium* Mill en el archipiélago canario (Ph.D. Thesis, unpublished). Universidad de La Laguna, La Laguna, Tenerife.

Alridge, A.E. 1980. Anatomy and evolution in Macaronesian *Echium* (Boraginaceae). Plant Syst. Evol. 138: 9–22.

Bramwell, D. 1972. Endemism in the flora of the Canary Islands. In: Valentine, D.H. (ed), Taxonomy, phytogeography and evolution, pp. 258–294. Academic Press, London.

Bramwell, D. (ed) 1979. Plants and islands. Academic Press, London.

Ceballos, L. & Ortuño, F. 1951. Estudio sobre la vegetación y la flora de las Canarias occidentales. Instituto Forestal de Investigaciones y Experiencias, Madrid.

Cristofolini, G. 1991. Taxonomic revision of *Cytisus* Desf. sect. *Tubocytisus* DC. (Fabaceae). Webbia 45: 187–219.

Esteve-Chueca, F. 1969. Estudio de las alianzas y asociaciones del orden *Cytiso-Pinetalia* en las Canarias orientales. Bol. R. Soc. Esp. Hist. Nat. Secc. Biol. 67: 77–104.

Feoli-Chiapella, L. & Feoli, E. 1977. A numerical phytosociological study of the summits of the Majella massive (Italy). Vegetatio 34: 21–39.

Fernández-Galván, M. 1983. Esquema de la vegetación potencial de la isla de La Gomera. In: Comunicaçoes apresentadas ao II Congreso Internacional pro Flora Macaronesica 19–25 Junho de 1977, pp. 269–293. Funchal.

Francisco-Ortega, J. 1992. An ecogeographical study within the *Chamaecytisus proliferus* (L.fil.) Link complex (Fabaceae: Genisteae) in the Canary Islands (Ph.D. Thesis, unpublished). The University of Birmingham, Birmingham.

Francisco-Ortega, J., Jackson, M.T., Santos-Guerra, A. & Fernández-Galván, M. 1990. Genetic resources of the fodder legumes tagasaste and escobon (*Chamaecytisus prolif-*

erus (L.fil.) Link *sensu lato*). FAO/IBPGR Pl. Genet. Resources Newsl. 81/82: 27–32.

Harlan, J.R. 1983. The scope for collection and improvement of forage plants. In: McIvor, J.G. & Bray, R.A. (eds), Genetic resources of forage plants, pp. 3–14. Commonwealth Science and Industrial Research Organization, East Melbourne.

Hernández-González, M. 1987. Comarca Guía-Juncalillo, estudio forrajero (B.Sc. Thesis, unpublished). Universidad Politécnica de Las Palmas Gran Canaria, La Laguna, Tenerife.

Hill, M.O. 1979a. TWINSPAN – A fortran program for arranging multivariate data in an ordered two-way table classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithaca, New York.

Hill, M.O. 1979b. DECORANA – A fortran program for detrented correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, New York.

Humphries, C.J. 1976. A revision of the Macaronesian genus *Argyranthemum* Webb ex Schultz Bip. (Compositae-Anthemidae). Bull. Br. Mus. (Nat. His.) Bot. 5: 145–240.

Jackson, D.A & Somers, K.M. 1991. Putting things in order: the ups and downs of detrended correspondence analysis. Am. Nat. 137: 704–712.

Kunkel, G. (ed) 1976. Biogeography and ecology in the Canary Islands. W. Junk, The Hague.

Lems, K. 1960. Botanical notes on the Canary Islands II. The evolution of plant forms in the Canary Islands: *Aeonium*. Ecology 41: 1–17.

Mohler, C.L. 1987. Cornell ecology programs. Microcomputer Power, Ithaca.

Parsons, J.J. 1981. Human influences in the pine and laurel forest of the Canary Islands. Geogr. Rev. 71: 253–271.

Pérez de Paz, P.L., Del Arco, M., Acebes-Ginovés, J.R. & Wildpret, W. 1986. Leguminosas forrajeras de Canarias. Cabildo Insular de Tenerife, Santa Cruz de Tenerife.

Rivas-Martínez, S. 1987. Memoria del mapa de series de vegetación de España 1:400,000. Instituto para la Conservación de La Naturaleza, Madrid.

Santos-Guerra, A. 1983a. Vegetación y flora de La Palma. Editorial Interinsular Canaria, Santa Cruz de Tenerife.

Santos-Guerra, A. 1983b. Vegetación de la region macaronésica. In: Comunicaçoes apresentadas ao II Congreso Internacional pro Flora Macaronesica 19–25 Junho de 1977, pp. 185–203. Funchal.

Santos-Guerra, A. 1984. Flora y vegetación. In: Afonso, A. (ed), Geografía de Canarias. Vol.1, geografía física, pp. 258–294. Editorial Interinsular Canaria, Santa Cruz de Tenerife.

Santos-Guerra, A. & Fernández-Galván, M. 1980. Vegetación. In: Afonso, L. (ed), Atlas básico de Canarias, pp. 38–47. Interinsular Canaria, Santa Cruz de Tenerife.

Sunding, P. 1972. The vegetation of Gran Canaria. Universitetsforlaget, Oslo.

Webb, P.B. & Berthelot, S. 1836–1850. Histoire naturelle des Iles Canaries. Paris.