

# Genetic differentiation in endemic *Lobularia* (Brassicaceae) in the Canary Islands

Liv Borgen

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Patterns of genetic diversity were examined in five endemic subspecies of the *Lobularia canariensis* complex from six of the Canary Islands. The taxa are interfertile, insect-pollinated outbreeders with wind dispersal. Electrophoretic analysis revealed a high level of genetic polymorphism at ten loci coding soluble enzymes, with a mean of 2.38 alleles per locus, 73.7 % polymorphic loci, and a mean heterozygosity of 0.279. Excesses of homozygotes, indicating inbreeding, were observed in small populations. The average total diversity was high,  $F_{IT}=0.518$ . Among-population diversity,  $F_{ST}=0.318$ , contributed more to the total diversity than within-population diversity,  $F_{IS}=0.222$ . Little geographic or taxonomic patterning of the allozyme variation was observed. The mean genetic identity for pairwise comparisons of the 19 populations was 0.76, with a range of 0.51-0.96 and c. 17 % of the comparisons below 0.67 and c. 8 % above 0.90. The results contrast with the many cases of high genetic identities reported for populations of endemic plants on oceanic islands. High levels of allozyme divergence suggest a relatively old origin of the *L. canariensis* complex and a long period of isolation of some of the populations.

L. Borgen, Botanical Garden and Museum, University of Oslo, Trondheimsvn. 23B, N-0562 Oslo, Norway

## Introduction

Much data on genetic diversity in plants endemic to oceanic islands exist for Hawaii, with studies of genera of Asteraceae (Lowrey & Crawford 1985, Helenurm & Ganders 1985, Witter & Carr 1988), and of *Metrosideros* (Myrtaceae; Aradhya et al. 1991), *Gossypium* (Malvaceae; DeJoode & Wendel 1992), and *Silene* (Caryophyllaceae; Westerbergh & Saura 1994). These data and those for *Dendroseris* (Astereaceae) of the Juan Fernandez Islands (Crawford, Stuessy & Silva 1987) have revealed unusually high genetic identities between pairs of species, often 0.90 or above, i.e., as high as for conspecific populations in general. It has been suggested that speciation has been rapid and recent on oceanic islands like the Hawaiian archipelago (Crawford 1989). However, looking more closely into the details

of the results, there are differences between younger and older islands (Witter & Carr 1988, Westerbergh & Saura 1994). Crawford (1989) states: «If a similar pattern of greater divergence among species on older islands would be documented for other genera it would indicate that time is a critical, if not sole, factor in allozyme divergence».

Comparisons between Hawaii and the Canary Islands are interesting due to many similar circumstances: (1) a predominantly oceanic island situation, with (2) many endemic plant taxa that are often (3) long-lived, suffruticose perennials, mostly with (4) an out-crossed breeding system and (5) lacking internal barriers to gene exchange. One important difference between the two archipelagos is, however, the presumed difference in geologic age, with the oldest rocks being 6 Myr in the Hawaiian archipelago (MacDonald et al. 1983) and 25 Myr in the Canarian archipelago

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(Coello et al. 1992). One of my aims has therefore been to compare the genetic diversity in the Canary Islands with that in Hawaii.

The eastern Canary Islands, Lanzarote and Fuerteventura, are regarded as the oldest and possibly "continental" in character (Rothe & Schmincke 1968). The western islands appear to have a wholly oceanic and volcanic origin, and the westernmost, El Hierro and La Palma, are regarded as the youngest by most authors. While the oldest sedimentary rocks are of Cretaceous age, i. e. 70-80 Myr (Rothe 1968), no igneous rocks older than 25 Myr are known (Coello et al. 1992). According to Schmincke (1976) available data suggest that volcanic activity did not start prior to the Oligocene in the Mid-Tertiary. The potassium-argon dates by Abdel-Monem et al. (1971, 1972) seem to prove that the shields on the different islands did not form at the same time but periods of activity were overlapping on different islands: Fuerteventura 12-17 Myr BP, Lanzarote 5-11 Myr BP, Gran Canaria 10-16 Myr BP, Tenerife 5-7 Myr BP, and Gomera 8-12 Myr BP. Old as well as recent volcanic activity, with historic eruptions in the period 1585-1971 on Lanzarote, Tenerife, and La Palma (Schmincke 1976), has apparently played an important role in the development as well as the destruction of habitats for plant life.

Some elements in the endemic flora of the Canary Islands are considered relictual with affinities among the Tertiary flora of the Tethyan-Tertiary region (Wulff 1944, 1950, Meusel 1952, 1965, Takhtajan 1969, Bramwell 1972, 1976). The evidence to support this view comes from several independent fields, most importantly from the fossil record, with macrofossils of some representatives of the present day Macaronesian flora in Miocene and Pliocene deposits in the Mediterranean region (Saporta 1862-1874, Depape 1922). Many habitats in the Canary Islands have apparently survived more or less unchanged over a long period of geologic time as refugia for endemic, relictual taxa, particularly for the "laurisilva" species (cf. Bramwell 1976).

Few studies concerning genetic diversity in endemic Macaronesian plants have been published, i. e. for *Chamaecytisus* (Fabaceae; Francisco-Ortega et al. 1992) and *Argyranthemum* (Asteraceae; Francisco-Ortega et al. 1994, 1995). Therefore, studies related to the partitioning of genetic variation in endemic plants in Macaronesia are needed and the main aim of the present study has been to contribute such data.

The *Lobularia canariensis* (DC.) Borgen complex is endemic to the Macaronesian phytogeographical region (Sunding 1979). The complex is represented in the Salvage Islands, the Canary Islands, the Cape Verde Islands, and the Macaronesian enclave in SW Morocco. The Canary Islands constitute the main centre of diversity, with five of the nine currently recognized subspecies (Borgen 1987).

Four of the Canarian subspecies are perennial, suffruticose, chamaephytic dwarf shrubs: ssp. *canariensis*, ssp. *intermedia* (Webb) Borgen, ssp. *marginata* (Webb) Borgen, and ssp. *palmensis* (Christ) Borgen. The fifth, ssp. *microsperma* Borgen, is a herbaceous annual-biennial or, at most, a short-lived perennial therophyte. All have the chromosome number  $n=11$ , an outcrossed breeding system, and insect pollination. The small, light, more or less distinctly winged seeds are dispersed by wind.

The Canarian archipelago consists of seven islands and four islets situated in the Mid-Atlantic west of Southern Morocco between 27°37' and 29°23' N, and 13°20' and 18°16' W (cf. Fig. 1). All islands are mountainous and formed by old as well as recent volcanic activity, with deep ravines (barrancos), cliffs, and precipices.

The distributions of the subspecies among and within islands are partly allopatric, partly parapatric, with slight, but not consistent, differences in ecological preferences. Populations are found from sea level to 2000 m altitude (Borgen 1987). The plants grow mostly as chasmophytes in cliffs but also as ruderals in gravelly habitats and low altitude lava deserts. None of the subspecies are single island endemics. *Lobularia canariensis* ssp. *intermedia* is widespread, reported from four or five of the seven major islands. The others occur on two adjacent islands.

No intrinsic barriers to gene exchange exist between these taxa (Borgen 1987), and evolution is supposed to have occurred by means of gradual divergence in response to a geographic splitting by dispersal or vicariance events, partly in response to ecological gradients and shifts between habitats, i. e., by adaptive radiation. Selection pressure and genetic drift apparently operate on small local populations, resulting in morphological and physiological differentiation, even in geographically close localities.

## Material and methods

Nineteen populations of *Lobularia canariensis* from 6 of the 7 Canarian islands were surveyed (Tab. 1, Fig. 1). The mean number of individuals analysed per locus per population ranged from 10.6 to 50.5 (Tab. 2). Seeds were collected from individual plants in each population in 1989 and 1990, and the offspring from each mother were treated separately. Young leaves were used as enzyme sources. The extracting buffer consisted of 2.74 mM sodium metabisulfite, 2.84 mM diethyldithiocarbamic acid, 3.37 mM D,L-dithiothreitol, 5.0 mM ascorbic acid, 42.3 mM dibasic sodiumphosphate, 0.21 mM sucrose, 1.55 mM EDTA (disodium salt), 5 % w/v PVP-40, and 0.014 mM mercapthoethanol (modi-

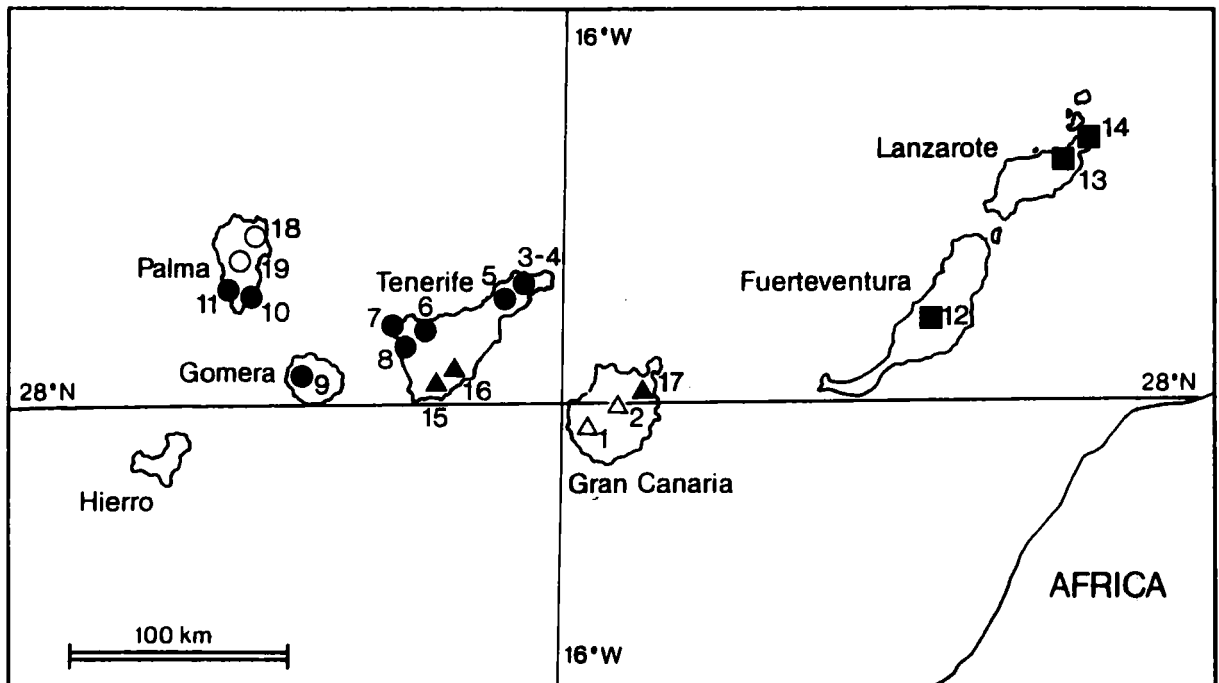


Fig. 1. *Lobularia canariensis* populations sampled in the Canary Islands. Nos. 1-2 (open triangles): ssp. *canariensis*; nos. 3-11 (black dots): ssp. *intermedia*; nos. 12-14 (black squares): ssp. *marginata*; nos. 15-17 (black triangles): ssp. *microsperma*; nos. 18-19 (open dots): ssp. *palmensis*.

fied after Morden et al. 1987).

The enzymes were run on 12 % (w/v) starch gels employing three buffer systems. System I consisted of (1) electrode buffer: 0.065 M L-histidine titrated to pH 6.5 with citric acid monohydrate and (2) gel buffer: one part electrode buffer plus three parts H<sub>2</sub>O. System II consisted of (1) electrode buffer: 0.30 M boric acid titrated to pH 8.1 with NaOH and (2) gel buffer: 0.083 M Tris titrated to pH 8.7 with citric acid monohydrate. System III consisted of (1) electrode buffer: 0.2 M boric acid, titrated to pH 8.3 with 1.0 M lithium hydroxide and (2) gel buffer: nine parts 0.05 M Tris, titrated to pH 8.3 with 1.0 M citric acid monohydrate plus one part electrode buffer.

System I was used to resolve aconitase (ACO), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), phosphoglucomutase (PGM), and 6-phosphogluconate dehydrogenase (6-PGD). System II was used to resolve aspartate aminotransferase (AAT), shikimate dehydrogenase (SKD), and catalase (CAT). System III was used to resolve aminopeptidase (AMP), glucose-6-phosphate isomerase (GPI), triosephosphate isomerase (TPI), and, eventually, as an alternative to system II, AAT. If more than one isozyme were present per enzyme, the most anodal one was designated 1, the next 2, etc. For each gene, the most anodal allozyme was labelled A, the next B, etc.

Procedures used for assaying enzymes followed protocols of Morden et al. (1987) except for TPI, which was stained with 6 ml 0.1 M Tris-HCl, pH 8.0, 54 ml H<sub>2</sub>O, 300 mg arsenic acid (sodium salt), 25 mg EDTA (disodium salt), 10 mg DHAP (lithium salt), 40 mg NAD, 20 mg ATP, 10 mg DHAP in filtrated solution with Dowex resin incubated at 37°C for 4 hrs and titrated to pH 4.5 with potassiumbicarbonate, 600 units glyceraldehyde-3-phosphate dehydrogenase, 20 mg MTT, and 2 mg PMS.

For the interpretable isozymes, allelic frequencies were determined, and the proportion of loci polymorphic was calculated, with polymorphism taken as the presence of the most common allele in a frequency of 0.99 or less. Also the mean number of alleles per locus, including the monomorphic one, the observed and expected heterozygosities and the fixation indices were calculated. The calculations of the F-statistics were based on Wright (1965,1978) and Nei (1977). Chi-square tests were used to determine whether populations deviated from Hardy-Weinberg equilibrium expectations. The Levene (1949) correction for small sample size was employed in the chi-square analyses. Gene diversity statistics and standard genetic distances and identities were obtained using the method of Nei (1978). Matrices of genetic identities were used to construct a dendrogram according to the UPGMA method (Sneath

Tab. 1. Characteristics of the studied populations of *Lobularia canariensis* in the Canary Islands.

Population no.	Locality	Taxon	Population size	Habitat	m	Altitude	
						Latitude	Longitude
1	Gran Canaria: SW coast: Degollada de Veneguera	<i>ssp. canariensis</i>	ca. 50	Cliffs with <i>Euphorbia</i> shrub	400	15° 43' W	27° 54' N
2	Gran Canaria: Central mountains: Bco. de la Miña (betw. Cruz Tejada and Las Lagunetas)	<i>ssp. canariensis</i>	ca. 150	Cliffs with legume shrub	1280	15° 35' W	28° 0' N
3	Tenerife: NE coast: Anaga peninsula: mountain ridge betw. Bco. de las Huertas and Bco. Piedra Grande	<i>ssp. intermedia</i>	ca. 100	Cliffs with <i>Euphorbia</i> shrub	650	16° 11' W	28° 32' N
4	Tenerife: NE coast: Anaga peninsula: Rocque Suarez	<i>ssp. intermedia</i>	ca. 50	Cliffs with <i>Euphorbia</i> shrub	750	16° 12' W	28° 33' N
5	Tenerife: NE coast: Monte Guerra: El Boqueron	<i>ssp. intermedia</i>	ca. 100	Cliffs with <i>Erica-Myrica</i> shrub	450	16° 22' W	28° 30' N
6	Tenerife: NW coast: S of Icod el Alto	<i>ssp. intermedia</i>	ca. 50	Cliffs with <i>Euphorbia</i> shrub	430	16° 36' W	28° 22' N
7	Tenerife: NW coast: Teno peninsula: Punta de Teno: Bco Tamargo	<i>ssp. intermedia</i>	ca. 50	Cliffs with <i>Euphorbia</i> shrub	130	16° 54' W	28° 20' N
8	Tenerife: NW coast: Teno peninsula: Bco. de Masca	<i>ssp. intermedia</i>	ca. 80	Cliffs with <i>Euphorbia</i> shrub	950	16° 50' W	28° 18' N
9	La Gomera: W coast: La Carbonera SE of Arure	<i>ssp. intermedia</i>	ca. 50	Cliffs with <i>Erica-Myrica</i> shrub	850	17° 19' W	28° 08' N
10	La Palma: SE coast: Las Caletas	<i>ssp. intermedia</i>	ca. 50	Gravelly lava desert	540	17° 49' W	28° 29' N
11	La Palma: SW coast: Cresta del Gallo	<i>ssp. intermedia</i>	ca. 150	Gravelly slopes in pine forest	800	17° 50' W	28° 32' N
12	Fuerteventura: Macizo de Betancuria: SE of Vega de Rio de Palmas	<i>ssp. marginata</i>	18	Cliffs with <i>Euphorbia</i> shrub	450	14° 05' W	28° 23' N
13	Lanzarote: N coast: Peñas del Chache	<i>ssp. marginata</i>	ca. 200	Cliffs with <i>Nauplius</i> and <i>Euphorbia</i> shrub	650	13° 35' W	28° 07' N
14	Lanzarote: NW coast: W of Mirador del Rio	<i>ssp. marginata</i>	ca. 100	Gravelly slopes with <i>Launaea</i> and <i>Euphorbia</i> shrub	460	13° 30' W	29° 13' N
15	Tenerife: SE coast: Bco. del Callão NE of San Isidro	<i>ssp. microsperma</i>	ca. 150	Gravelly slopes with <i>Euphorbia</i> shrub along roadside	300	16° 33' W	28° 05' N

(Tab. 1 cont.)

Population no.	Locality	Taxon	Population		m	Altitude	
			size	Habitat		Latitude	Longitude
16	Tenerife: SE coast: N of Arico o Lomo de Arico	<i>ssp. microsperma</i>	ca. 100	Gravelly slopes with <i>Euphorbia</i> shrub along roadside	520	16° 30' W	28° 10' N
17	Gran Canaria: NE coast: Lomo Sabinal N of Jinamar	<i>ssp. microsperma</i>	ca. 100	Gravelly slopes with <i>Euphorbia</i> shrub	150	15° 24' W	28° 02' N
18	La Palma: NE coast: Bco. del Agua	<i>ssp. palmensis</i>	ca. 50	Cliffs in laurel forest	350	17° 47' W	28° 48' N
19	La Palma: Central mountains: Caldera de Taburiente: Cumbrecita	<i>ssp. palmensis</i>	ca. 50	Cliffs in pine forest	1200	17° 50' W	28° 41' N

& Sokal 1973). All calculations were made by the programme BIOSYS-1, release 1.7 (Swofford & Selander 1981).

## Results

### Iso- and allozymes

Seven enzymes, presumably encoded by ten loci, were resolved and interpretable throughout the material. All loci except Gpi-1 were polymorphic. The isozymes (and their allozymes) were called Amp-1 (A-F), Amp-2 (A-D), Gpi-1 (A), Gpi-2 (A-G), Idh-1 (A-C), Mdh-4 (A-D), Pgm-1 (A-D), Pgm-2 (A-F), Pgd-1 (A-D), and Tpi-1 (A-F).

Additional isozymes were not scored, either because they showed varying activity and/or resolution precluding interpretation (ACO, CAT, SKD) or complex phenotypes, presumably due to gene duplications (AAT, MDH, 6-PGD, TPI). Controlled crosses (not published) did not help verify the genetic interpretation of the putative duplications.

Forty-five alleles were scored (Appendix 1). Five alleles were unique to *ssp. intermedia* (Gpi-2 A & E, Mdh-4 D, Tpi-1 D & F), one (Pgm-1 D) to *ssp. marginata* and one (Pgm-2 C) to *ssp. microsperma*. Only four of the alleles were unique to single populations: Gpi-2 A occurred in low frequency (0.016) in population 3 (*ssp. intermedia* in Anaga on Tenerife); Pgm-1 D was present in low frequency (0.012) in population 14 (*ssp. marginata*, Lanzarote); Tpi-1 D occurred in low frequency (0.014) in population 8 (*ssp. intermedia* in Masca in Teno on Tenerife); Mdh-3 D occurred in high frequency (0.405) in population 9 (*ssp. intermedia*, Gomera). The other alleles showed varying frequencies throughout the populations.

### Genetic variation

The genetic variability in each population based on allele frequencies is given in Tab. 2. The mean number of alleles per locus ranged from 1.9 in population 5 to 2.9 in population 3 (both *ssp. intermedia* on Tenerife). The mean for all 19 populations was 2.38. The number of variable loci ranged from 6 (60 %) in populations 1 (*ssp. canariensis*, Gran Canaria), 4 and 5 (*ssp. intermedia*, Tenerife), 10 (*ssp. intermedia*, La Palma), and 12 (*ssp. marginata*, Fuerteventura) to 9 (90 %) in populations 6 and 8 (*ssp. intermedia*, Tenerife) and 19 (*ssp. palmensis*, La Palma), with a mean of 7.37 (73.7 %) for all populations.

The mean observed heterozygosity ranged from 0.121 in population 2 (*ssp. canariensis*, Gran Canaria) to 0.316 in population 18 (*ssp. palmensis*, La Palma), with a mean of 0.213 for all populations (Tab. 2). The mean expected heterozygosity ranged from 0.189 in population 2 (*ssp. canariensis*, Gran Canaria) to 0.371 in population 16 (*ssp. microsperma*, Tenerife), with a mean of 0.278 for all populations. The most variable population was no. 8, *ssp. intermedia* from Masca in Teno on Tenerife. Heterozygote deficiency was common. Significant deficiencies (chi-square test,  $p < 0.05$ ) were found in all nine polymorphic loci. The number of loci with significant deficiencies ranged from one to four per population and were different in different populations. Amp-1 and Amp-2 most frequently showed heterozygote deficiencies. Excesses in the number of heterozygotes were also observed, most frequently in populations 5, 10, 13, and 18, but a significant excess was observed only for Idh-1 in population 14.

The mean genetic variability in each subspecies is summarized in Tab. 3. The mean number of variable loci, mean number of alleles per locus, and the mean het-

Tab. 2. Genetic variability at 10 loci in 19 Canarian populations of *Lobularia canariensis*. No. = population number (cf. Tab. 1 and Fig. 1); N = mean sample size per locus;  $A_L$  = mean number of alleles per locus;  $A_p$  = mean number of alleles per polymorphic locus;  $A_s$  = number of observed alleles over all loci/number of loci; P = percentage of polymorphic loci (0.99 criterion);  $H_{OBS}$  = mean observed heterozygosity across loci;  $H_{EXP}$  = mean expected heterozygosity across loci, unbiased estimate (Nei 1978).

No.	N	$A_L$	$A_p$	$A_s$	P	$H_{OBS}$	$H_{EXP}$
1	10.6	2.1	2.7	2.0	60	0.178	0.286
2	29.8	2.1	2.6	2.4	70	0.121	0.189
3	30.6	2.9	3.4	2.9	80	0.210	0.318
4	19.4	2.3	3.2	2.1	60	0.154	0.274
5	20.0	1.9	2.5	1.9	60	0.150	0.196
6	31.4	2.8	2.9	2.7	90	0.242	0.298
7	20.8	2.5	3.0	2.4	70	0.178	0.259
8	34.9	2.9	3.0	2.8	90	0.237	0.303
9	20.8	2.2	2.5	2.2	80	0.255	0.327
10	24.8	2.2	3.0	2.2	60	0.185	0.203
11	50.5	2.4	2.6	2.3	80	0.241	0.300
12	17.0	2.0	2.4	2.0	60	0.206	0.265
13	32.6	2.1	2.4	2.1	80	0.188	0.215
14	37.9	2.5	3.1	2.5	70	0.201	0.241
15	45.9	2.4	3.0	2.4	70	0.237	0.298
16	45.1	2.6	3.0	2.6	80	0.301	0.371
17	32.0	2.1	2.6	2.1	70	0.209	0.258
18	33.5	2.5	2.9	2.5	80	0.316	0.359
19	28.1	2.7	2.9	2.6	90	0.242	0.347
Mean	29.8	2.38	2.83	2.35	73.7	0.213	0.278
SD	10.2	0.3	0.3	0.3	1.04	0.048	0.053
Min.	10.6	1.9	2.4	1.9	60	0.121	0.189
Max.	50.5	2.9	3.4	2.9	90	0.316	0.371

erozygosity were lowest in *ssp. canariensis* on Gran Canaria and highest in *ssp. palmensis* on La Palma.

### Genetic differentiation

Identity values in the pairwise comparisons of populations varied from  $I=0.513$  for populations 4 and 7 (*ssp. intermedia* from the Anaga and Teno peninsulas on Tenerife) to  $I=0.961$  for populations 10 and 13 (*ssp. intermedia*, La Palma and *ssp. marginata*, Lanzarote) (Tab. 4). Altogether 29 (c. 17%) of the pairwise comparisons had an  $I$  value  $< 0.67$ , nine of which represented within-taxon and 20 among-taxon comparisons. Only 13 (c. 8%) of the pairwise comparisons had  $I$  values  $> 0.90$ , eight of which were within-taxon and five among-taxon comparisons. The mean genetic identity for all pairwise comparisons of the 19 populations was 0.759. Thus, the lowest identities occurred among populations within Tenerife (populations 4 and 7, *ssp. intermedia*,  $I=0.513$ ; population 15, *ssp. microsperma*, and populations 7 and 6, respectively, of *ssp. intermedia*, with

$I=0.537$  and  $I=0.589$ ). The highest identities typically occurred among populations of the same taxon within a single island: 18 and 19 (*ssp. palmensis*, La Palma,  $I=0.921$ ), 10 and 11 (*ssp. intermedia*, La Palma,  $I=0.917$ ), 3 and 5 (*ssp. intermedia*, Tenerife,  $I=0.940$ ), 1 and 2 (*ssp. canariensis*, Gran Canaria,  $I=0.927$ ), and 13 and 14 (*ssp. marginata*, Lanzarote,  $I=0.921$ ). However, high identities were also observed between populations of different taxa within one island (2 and 17; *ssp. canariensis* and *ssp. microsperma* on Gran Canaria,  $I=0.922$ ), between populations of the same taxon on adjacent islands (12 and 13, *ssp. marginata* on Fuerteventura and Lanzarote,  $I=0.947$ ; 3 and 11, *ssp. intermedia* on Tenerife and La Palma,  $I=0.925$ ), and, surprisingly, between populations of different taxa on distant islands (13 and 10, *ssp. marginata* on Lanzarote and *ssp. intermedia* on La Palma,  $I=0.961$ ; 12 and 19, *ssp. marginata* on Fuerteventura and *ssp. palmensis* on La Palma,  $I=0.930$ ; 12 and 10, *ssp. marginata* on Fuerteventura and *ssp. intermedia* on La Palma,  $I=0.958$ ).

Comparisons of identity values within and among subspecies (Tab. 5) revealed high identities,  $>0.90$ ,

Tab. 3. Mean genetic variability at 10 loci in different subspecies of *Lobularia canariensis* in the Canarian archipelago. Mean heterozygosity is the unbiased estimate of Nei (1978).

Subspecies	No. of pops.	Mean sample size per locus	Mean no. of alleles per locus	Mean no. of variable loci	Mean heterozygosity
<i>canariensis</i> (SD) (range)	2	20.2 (9.6) (10.6-29.8)	2.1 (0) (0)	6.5 (0.5) (6-7)	0.238 (0.049) (0.189-0.286)
<i>intermedia</i> (SD) (range)	9	28.1 (9.6) (19.4-50.5)	2.5 (0.33) (1.9-2.9)	7.4 (1.7) (6-9)	0.275 (0.045) (0.196-0.327)
<i>marginata</i> (SD) (range)	3	29.2 (8.9) (17.0-37.9)	2.2 (0.22) (2.0-2.5)	7.0 (0.82) (6-8)	0.240 (0.020) (0.215-0.265)
<i>microsperma</i> (SD) (range)	3	41.0 (6.4) (32.0-45.1)	2.4 (0.21) (2.1-2.7)	7.3 (0.47) (7-8)	0.309 (0.047) (0.258-0.371)
<i>palmensis</i> (SD) (range)	2	30.8 (2.7) (28.1-33.5)	2.6 (0.1) (2.1-2.7)	8.5 (0.5) (7-9)	0.353 (0.006) (0.258-0.359)

within ssp. *canariensis* (0.927), ssp. *marginata* (0.918, range 0.886-0.947), and ssp. *palmensis* (0.921). The populations of ssp. *marginata* were from two islands; those of ssp. *canariensis* and ssp. *palmensis* from single islands. Within ssp. *microsperma*,  $I=0.812$ , the two populations on Tenerife were more similar,  $I=0.895$ , than either of them was to the population on Gran Canaria, with  $I=0.746$  and  $I=0.790$ , respectively. Within ssp. *intermedia*, with nine populations on three islands, the mean was low,  $I=0.751$ , with a range from  $I=0.513$  (populations 4 and 7) to  $I=0.940$  (populations 3 and 5). The values for the pairwise comparisons of the subspecies (Tab. 5) varied from  $I=0.689$  for *intermedia-microsperma* to  $I=0.828$  for *intermedia-marginata*. These means were thus lower than the means for the within-taxon comparisons, but the ranges were wide, from a low of 0.537 for *intermedia-microsperma*, populations 7 and 15, to a high of 0.961 for *intermedia-marginata*, populations 10 and 13.

The partitioning of genetic differentiation of populations was also analysed using F-statistics (Wright 1978) (Tab. 8). Mean total diversity ( $F_{IT}$ ) was 0.518; mean within-population diversity ( $F_{IS}$ ) was 0.222; and mean among-population diversity ( $F_{ST}$ ) was 0.381. The

amount of genetic differentiation among populations was quite high (cf. Hamrick & Godt 1989) but among population diversity contributed more to the total diversity than within population diversity. Hierarchical F-statistics indicated that most of the variation occurred among populations, irrespective of island or taxon.

The dendrogram based on Nei's (1978) unbiased genetic identity (Fig. 2) summarizes the similarity among populations. The branching pattern did neither correspond with geographical distribution nor with taxonomic entities. If drawing an imaginary phenon line at the similarity level of 0.87, above which level one usually finds populations belonging to the same species (Crawford 1989), ten clusters would appear. With a phenon-line at the similarity level 0.67, i. e. the grand mean for all pairwise comparisons of species within genera (Crawford 1989), only two main branches would appear: one with only population 7 (ssp. *intermedia* in Teno on Tenerife) and the other with all remaining populations. Genetically, population 7 appeared as remarkably distinct. The two populations of ssp. *palmensis* also formed one relatively distinct cluster. The two populations of the short-lived ssp. *microsperma*, 15 and 16 on Tenerife, clustered together but the third population

Tab. 4. Genetic identity and distance values for 19 Canarian populations of *Lobularia canariensis*. Below diagonal: Nei's (1978) unbiased genetic identity. Above diagonal: Nei's (1978) unbiased genetic distance. Pop. = population number (cf. Tab.1 & Fig.1)

Pop.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	-	0.075	0.337	0.216	0.422	0.287	0.424	0.170	0.248	0.338	0.356	0.284	0.245	0.301	0.223	0.211	0.139	0.386	0.229
2	0.927	-	0.368	0.392	0.354	0.255	0.346	0.139	0.127	0.251	0.282	0.221	0.184	0.214	0.345	0.303	0.081	0.396	0.284
3	0.714	0.692	-	0.139	0.061	0.274	0.445	0.348	0.491	0.161	0.078	0.189	0.228	0.121	0.439	0.319	0.376	0.214	0.273
4	0.806	0.676	0.871	-	0.253	0.463	0.667	0.369	0.526	0.188	0.180	0.224	0.226	0.264	0.272	0.282	0.317	0.304	0.234
5	0.656	0.702	0.940	0.777	-	0.198	0.389	0.354	0.511	0.118	0.102	0.147	0.138	0.107	0.482	0.385	0.310	0.281	0.288
6	0.750	0.775	0.761	0.629	0.821	-	0.287	0.185	0.438	0.259	0.285	0.178	0.164	0.159	0.530	0.310	0.256	0.350	0.266
7	0.654	0.708	0.641	0.513	0.678	0.750	-	0.283	0.412	0.450	0.337	0.472	0.419	0.306	0.622	0.504	0.467	0.475	0.567
8	0.844	0.870	0.706	0.691	0.702	0.831	0.754	-	0.258	0.162	0.255	0.166	0.117	0.116	0.399	0.405	0.276	0.440	0.262
9	0.781	0.881	0.612	0.591	0.600	0.645	0.662	0.772	-	0.315	0.324	0.322	0.342	0.316	0.488	0.441	0.189	0.369	0.331
10	0.714	0.778	0.851	0.829	0.888	0.772	0.637	0.850	0.730	-	0.086	0.042	0.039	0.058	0.414	0.414	0.238	0.266	0.178
11	0.701	0.754	0.925	0.836	0.903	0.752	0.714	0.775	0.723	0.917	-	0.119	0.169	0.105	0.418	0.363	0.261	0.183	0.205
12	0.753	0.802	0.828	0.799	0.863	0.837	0.624	0.847	0.724	0.958	0.888	-	0.055	0.121	0.364	0.285	0.173	0.173	0.072
13	0.783	0.832	0.796	0.798	0.871	0.849	0.658	0.889	0.711	0.961	0.844	0.947	-	0.082	0.387	0.378	0.173	0.397	0.209
14	0.740	0.808	0.886	0.768	0.898	0.853	0.737	0.890	0.729	0.944	0.900	0.886	0.921	-	0.470	0.392	0.304	0.321	0.283
15	0.800	0.708	0.645	0.762	0.617	0.589	0.537	0.671	0.614	0.661	0.658	0.695	0.679	0.625	-	0.111	0.293	0.420	0.292
16	0.810	0.739	0.727	0.754	0.680	0.734	0.604	0.667	0.643	0.661	0.696	0.752	0.686	0.675	0.895	-	0.228	0.264	0.242
17	0.870	0.922	0.686	0.728	0.733	0.774	0.627	0.759	0.828	0.788	0.770	0.841	0.841	0.738	0.746	0.790	-	0.304	0.193
18	0.680	0.673	0.807	0.738	0.755	0.705	0.622	0.644	0.691	0.766	0.833	0.842	0.672	0.725	0.657	0.768	0.738	-	0.082
19	0.795	0.753	0.761	0.791	0.750	0.767	0.567	0.770	0.718	0.837	0.815	0.930	0.811	0.753	0.747	0.785	0.824	0.921	-

of ssp. *microsperma*, 17 on Gran Canaria, clustered with the populations of ssp. *canariensis* on Gran Canaria, plus the La Gomera population of ssp. *intermedia*. The remaining populations of ssp. *intermedia*, together with those of ssp. *marginata*, formed a confusing branch in the dendrogram, from both a taxonomic as well as a geographic perspective.

## Discussion

The allozyme variation in *Lobularia canariensis*, assessed by means of polymorphic loci, alleles per locus, and heterozygosity, is high compared with other plant species in general (Gottlieb 1981, Hamrick & Godt 1989, Hamrick 1989) and other island plant endemics in particular (see Tab. 7 and references therein, and De-Joode & Wendel 1992). Compared to most other groups of endemic plants on oceanic islands, the I-values (Tab. 8) for the pairwise comparisons of the five subspecies of *L. canariensis* are relatively low (mean 0.759). The values indicate rather extensive genetic differentiation among the populations of the Canarian subspecies of *L. canariensis* compared to other island endemics. In the Hawaiian archipelago, only some *Dubautia* (Asteraceae) species of the n=14 group on the oldest island, Kauai, show lower I-values (Witter & Carr 1988). In the Juan Fernandez Islands, similar low I-values are reported for some species of *Robinsonia* (Asteraceae; Crawford et al. 1992) and *Wahlenbergia* (Campanulaceae; Crawford et al. 1990).

The genetic identities between pairs of populations of *L. canariensis* are highly variable, with a range from

0.513 to 0.961 (Tab. 4). Among the five Canarian subspecies, ssp. *intermedia* is more variable than the others. The mean genetic identity among the nine *intermedia* populations is 0.751 (Tab. 5). The identity is particularly low, 0.513, between the Anaga population (no. 4) and the Teno population (no. 7) on Tenerife. According to Schmincke (1976), the shield of Tenerife is of variable age. In the extreme east and west regions, Anaga and Teno, the mountain massifs are of old Tertiary (Miocene-Pliocene) origin. These rocks, mainly basalts, are regarded as the oldest in Tenerife, presumably formed some 5-7 Myr ago (Schmincke 1976). The two regions are floristically very rich (Bramwell & Bramwell 1974) and were probably less affected by later volcanic eruptions than the intermediate regions. The Anaga and Teno peninsulas may thus be considered as floristic and faunistic refugia and irradiation centers (cf. Machado 1976). The low genetic identity between populations in Anaga and Teno indicates a long period of separation and isolation and supports the refugia hypothesis for the two regions. The divergence of the populations in Teno and Anaga may have occurred within a similar time frame as the *Dubautia* species on Kauai, Hawaii, which have diverged to a minimum of I=0.43 within a maximum of 5-6 Myr (Witter & Carr 1988). The species on Kauai are postulated to be the oldest *Dubautia* species in Hawaii (Carr & Kyhos 1986), and the data of Witter & Carr (1988) indicate that time is a critical factor for allozyme divergence. Data for *L. canariensis* seem to give further support to this hypothesis.

Westerbergh & Saura (1994) also found that the degree of heterozygosity increases with the age of the environments occupied by populations of *Silene* in Ha-



Tab. 5. Matrix of Nei's (1978) unbiased genetic identity averaged among and within subspecies of *Lobularia canariensis*. Ranges in brackets.

Subspecies	No. of pops.	1	2	3	4	5
1. canariensis	2	0.927	-	-	-	-
-		-	-	-	-	-
2. intermedia	9	0.747 (0.654-0.881)	0.751 (0.513-0.961)	-	-	-
				-	-	-
3. marginata	3	0.786 (0.740-0.832)	0.828 (0.624-0.961)	0.918 (0.886-0.947)	-	-
					-	-
4. microsperma	3	0.808 (0.708-0.922)	0.689 (0.537-0.828)	0.726 (0.625-0.841)	0.812 (0.746-0.895)	-
						-
5. palmensis	2	0.725 (0.673-0.795)	0.741 (0.567-0.837)	0.789 (0.672-0.930)	0.753 (0.657-0.824)	0.921 -

waii. According to their calculations, the age difference of 1.5 Myr between Maui and Hawaii would result in at least 0.5 more alleles per locus, a value in accordance with their actual observations (Westerbergh & Saura 1994). They also found a correlation between the genetic distances of the populations and the geological age of the areas. The largest distance between any of the *Silene* populations was  $D=0.288$  between populations of *S. struthioloides* in the islands of Maui (0.5 Myr old) and Hawaii (2 Myr old). Compared to a distance of  $D=0.667$  between the most distant populations of *L. canariensis* ssp. *intermedia* from the 5-7 Myr old Anaga and Teno peninsulas on Tenerife, time again appears crucial for the accumulation of allozyme differences.

Tab. 6. Genetic differentiation of populations of *Lobularia canariensis* by F-statistics (Wright 1978) at nine variable loci.

Locus	F <sub>IS</sub>	F <sub>IT</sub>	F <sub>ST</sub>
Amp-1	0.315	0.491	0.257
Amp-2	0.423	0.509	0.149
Gpi-2	0.022	0.454	0.442
Idh-1	0.175	0.509	0.406
Mdh-4	0.146	0.346	0.235
Pgm-1	0.334	0.721	0.581
Pgm-2	0.135	0.589	0.524
Pgd-1	0.066	0.477	0.440
Tpi-1	0.116	0.477	0.408
Mean	0.222	0.518	0.381

Mutations, migrations, selection, and genetic drift are the main evolutionary processes that in combination with factors like population sizes, distribution patterns, life history traits, and reproductive strategies influence the genetic structure of plant populations (Ayala 1975, Hamrick 1989, Hamrick & Godt 1989). Behind radiations on oceanic islands, selection and genetic drift are cited as the two main evolutionary processes (Crawford, Witkus & Stuessy 1987) but while different kinds of selection are important in the evolution of morphological differentiation, polymorphisms at the molecular level are claimed to be selective neutral (Kimura 1984). Thus, allozyme variation is determined by the processes of mutations, migrations, and genetic drift, of which drift presumably is the most important one in an oceanic island situation. The low levels of allozyme divergence previously reported in many endemic plants on oceanic islands are mainly ascribed to genetic bottlenecks associated with colonization, small population sizes, and recent speciation (see Crawford 1989, DeJooode & Wendel 1992). While unique, often fixed, alleles due to mutation events seem to characterize old and relictual species, like those of *Mabrya* (Scrophulariaceae) in SW USA and Mexico (Elisens & Crawford 1988), time has only occasionally been long enough to make the slow accumulation of new mutations a major process behind allozyme divergence in island endemics, like the Hawaiian *Dubautia* species of the n=14 group (Witter & Carr 1988).

In *L. canariensis*, relatively few alleles are unique and none of these are fixed. Only four are unique to single populations; three in populations of ssp. *intermedia* from Anaga, Tenerife (no. 3), Teno, Tenerife (no. 8), and Gomera (no. 9); and one in a population of ssp.

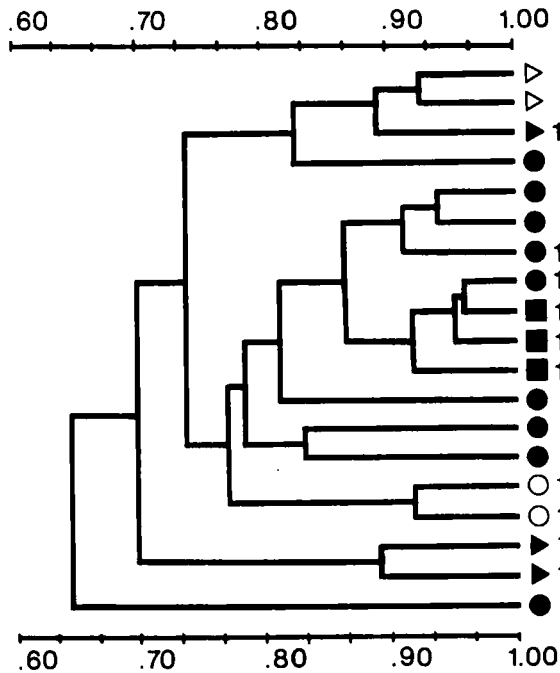


Fig. 2. Genetic relationship between 19 Canarian populations of *Lobularia canariensis* based on 10 loci and Nei's (1978) unbiased genetic identity as coefficient for the UPGMA dendrogram. Nos. 1-2 (open triangles): ssp. *canariensis*; nos. 3-11 (black dots): ssp. *intermedia*; nos. 12-14 (black squares): ssp. *marginata*; nos. 15-17 (black triangles): ssp. *microsperma*; nos 18-19 (open dots): ssp. *palmensis*.

*marginata* on Lanzarote (no. 14). The Anaga and Teno peninsulas on Tenerife, as well as Gomera, are areas characterized by a long period of geological stability (Schmincke 1976), and these areas have probably been isolated for a longer period of time than many of the other areas in the Canary Islands. Allozyme divergence in *L. canariensis* thus seems to reflect a long-lasting stability and isolation of habitats. On the subspecies level, five alleles are unique to ssp. *intermedia*, one to ssp. *marginata*, and one to ssp. *microsperma*. On the species level, seven alleles are unique to *L. canariensis*, compared to four in the mediterranean *L. maritima* (Borgen 1995). These figures demonstrate that some mutations have occurred in *L. canariensis* subsequent to the colonization of the islands, but mutations alone cannot explain the observed pattern of genetic differentiation.

In Robinsonia in the Juan Fernandez Islands, the relatively high contemporary species divergency is partly explained as a possible result of several colonizers carrying considerable variation to the islands (Crawford et al. 1992). The Canary Islands are much closer to Africa than the Juan Fernandez Islands to S America. The island of Fuerteventura is situated only ca. 100 km off the coast of Morocco and the prevailing wind direction is from the

mainland to the islands. Thus, multiple colonizations early in the history of *L. canariensis* may have brought much variation to the archipelago and this may explain some of the genetic variation observed today. In *Robinsonia*, gene diversity is highest in the two most common species, with values comparable to those of continental species with similar life history attributes (Crawford et al. 1992). The allozyme structure in *L. canariensis* and the widespread ssp. *intermedia* in particular, is also more similar to the structure in widespread, polymorphic mainland species than to the structure in isolated insular species, and the reason for this may partly be historical.

In addition to alleles that are unique to single subspecies of *L. canariensis*, some occur in different pairs of subspecies. Mdh-3 A is shared by ssp. *canariensis* and ssp. *microsperma*; Tpi-1 B by ssp. *intermedia* and ssp. *palmensis*; whereas three alleles, Amp-1 A, Idh-1 A, and Pgm-1 A, are shared by ssp. *intermedia* and ssp. *microsperma*. As previously suggested for *Robinsonia* (Crawford et al. 1992), the distribution of particular alleles between various pairs of subspecies may indicate sorting during the process of radiation.

The variability among populations of ssp. *intermedia* blurs the slight tendency to some geographic and/or taxonomic pattern which otherwise could be superimposed on the dendrogram (Fig. 2). Most strikingly, the Teno population (no. 7) forms a branch of its own. Although circumscribed as belonging to ssp. *intermedia* due to corresponding flower morphology, i. e. small flowers with spatulate, creamy petals (Borgen 1987), the Teno population (no. 7) deviates in leaf morphology from all other Canarian populations and coincides with one of the Cape Verde taxa, ssp. *spathulata*. Several varieties have in fact been described in order to accommodate the slight morphological differentiation among populations of the widespread ssp. *intermedia* (Christ 1888, Pitard & Proust 1908), a variation that hardly merits recognition as formal taxonomic units (Borgen 1987). Perhaps ssp. *intermedia* is an example of incipient speciation. If populations remain isolated, new, distinct taxa may eventually evolve from the highly variable gene pool of ssp. *intermedia*.

In terms of allozymes, not only ssp. *intermedia* but also ssp. *microsperma* is variable. The two Tenerife populations, nos. 15 and 16, are fairly similar,  $I=0.895$ , and constitute one branch in the dendrogram (Fig. 2). The third *microsperma* population, no. 17 on Gran Canaria, is more identical to the other populations on Gran Canaria, nos. 1-2 of ssp. *canariensis* ( $I=0.870$  and  $0.922$ ) than to the Tenerife populations of ssp. *microsperma* ( $I=0.746$  and  $0.790$ ). The allozyme data may suggest a polytopic origin and parallel evolution, that is independent origins from the ssp. *canariensis* gene pools in Gran Canaria and Tenerife. Unfortunately, populations of ssp. *canariensis* on Tenerife were not available in this investigation.

Tab. 7. Genetic variability in Canarian *Lobularia canariensis* compared with endemic Hawaiian groups of plants.  $P_{TOT}$  = frequency of all loci polymorphic in at least one taxon.  $P$  = frequency of polymorphic loci per population.  $A_L$  = mean number of alleles per locus per population.  $A_p$  = mean number of alleles per polymorphic locus.  $H_{EXP}$  = mean expected heterozygosity averaged over all loci and all populations.

Plant group and origin	$P_{TOT}$	$P$	$A_L$	$A_p$	$H_{EXP}$	Reference
<i>Lobularia</i> , Canary Islands	0.90	0.74	2.38	2.83	0.278	This paper
Madiinae, Hawaii	1.00	0.24	1.29	2.20	0.075	Witter & Carr 1988
<i>Tetramolopium</i> , Hawaii	0.27	0.07	1.09	2.13	<0.010	Lowrey & Crawford 1985
<i>Bidens</i> , Hawaii	0.26	0.12	1.16	2.47	0.045	Helenurm & Ganders 1985
<i>Silene</i> , Hawaii	0.48	0.20	1.29	-	0.057	Westerberg & Saura 1994

Within the remaining three subspecies, *canariensis*, *marginata*, and *palmensis*, the I-values range from 0.918 to 0.927 and are thus comparable to values reported for conspecific populations. The two *palmensis* populations form a distinct cluster (Fig. 2). While Schmincke (1976) claims that the origin of La Palma is recent, at most 2 Myr, other geologists (e. g., Kogarko pers. comm.) suggest possibly a much older origin. Each of the populations of ssp. *palmensis* is relatively polymorphic (Tab. 2). *Lobularia canariensis* ssp. *palmensis* is the «shrubbiest» member of the genus and grows in supposedly relictual vegetation types, i. e. the laurel and pine forests. In some genera with more extensive adaptive radiation than *Lobularia* (e. g., *Argyranthemum*, Humphries 1979), the assumed most ancestral members also occur within these vegetation types. My data suggest that ssp. *palmensis* has existed in the Canary Islands for a sufficient period of time for the accumulation of fair amounts of allozyme polymorphism. Although rare on Tenerife (populations not investigated), the occurrences on Tenerife could be older than those on La Palma, given that Tenerife is the older of the two islands. This age difference is not evident from the genetic data, however, as the variability on La Palma as a whole is higher than on any of the other islands. My data may thus support an older age of La Palma than has been claimed in the literature (cf. Schmincke 1976).

Geologically, one of the easternmost islands, Fuerteventura, is claimed to be the oldest in the archipelago (Coello et al. 1992). Sedimentary rocks of Cretaceous origin similar to those known from the nearest coast of southwestern Morocco are found on Fuerteventura (cf. Schmincke 1976) but available data suggest that the volcanic activity did not start prior to the Oligocene in the Mid-Tertiary 25 Myr ago (Coello et al. 1992). Lanzarote and Fuerteventura may be continental in origin (cf. Rothe & Schmincke, 1968, Sunding 1979; but see Schmincke 1976). *Lobularia canariensis* ssp. *marginata* occurs on some of the older mountain massifs on Fuerteventura and Lanzarote as well as in SW Morocco. *Lobularia canariensis* ssp. *marginata* is morphologically distinct and shares some morphologic

traits, i. e. many seeds per silicle and broad seed wings, with the widespread Mediterranean species *L. libyca* of the presumably monophyletic  $n=11$  group of *Lobularia*. In the perspective of historical plant geography, ssp. *marginata* may be the most ancestral taxon in the *L. canariensis* complex. Analyses based on cladistics and cladistic biogeography also support this hypothesis (Borgen 1996). Allozyme data, on the other hand, are slightly contradictory. The populations of ssp. *marginata* are less variable than most of the other populations (Tab. 2) but a unique allele was observed in one of them. Quite surprisingly, the ssp. *marginata* populations (nos. 12, 13, and 14) cluster closely together with one of the populations, no. 10, of ssp. *intermedia* from one of the westernmost, geographically most distant islands, La Palma (Fig. 2). This east-west connection is difficult to explain but could be due either to inter-insular dispersal, i.e. gene flow, genetic drift in the ancestral gene pool, or parallel mutations.

Gene flow can be estimated according to Wright's (1951) formula:  $F_{ST} = 1/(4Nm + 1)$ , where  $N$  is the effective population size and  $m$  is the number of migrants per population. Wright (1951), who based his  $F_{ST}$  value on all loci, showed that unless  $Nm < 1$  no population differentiation is likely to occur. For the Canarian populations of *L. canariensis*, calculations according to Wright's formula gives a  $Nm$  of 0.406. Thus, population differentiation is expected. A  $F_{ST}$  value of 0.381 compared to a  $F_{IS}$  value of 0.222 also indicates a certain amount of population differentiation and does not support extensive gene flow among populations but even slight gene flow might be enough to blur population distinctions. A trend to inter-insular long distance dispersal is reported in the Macaronesian composite genus *Argyranthemum*, based on chloroplast DNA restriction site data and nuclear r-DNA sequence data (Francisco-Ortega, Jansen & Santos-Guerra 1995). Also in *Lobularia* it is likely that some inter-insular gene flow (i.e. seed dispersal by wind) combined with complete infra-specific cross compatibility, has contributed to the complexity of the genetic variation pattern.

The relatively high fixation within populations,

Tab. 8. Genetic identity values among some species/subspecies of endemic plant genera/species in the archipelagos of Hawaii and the Canary Islands.

Plant group	Archipelago	No. of taxa	Genetic identity			Reference
			Mean	Min.	Max.	
<i>Tetramolopium</i>	Hawaii	6	0.95	0.87	1.00	Lowrey & Crawford 1985
<i>Bidens</i>	Hawaii	18	0.96	0.89	1.00	Helenum & Ganders 1985
<i>Wilkesia</i>	Hawaii	2	0.97	-	-	Witter & Carr 1988
<i>Dubautia</i> , n=14	Hawaii	6	0.69	0.43	0.93	Witter & Carr 1988
<i>Dubautia</i> , n=13	Hawaii	9	0.95	0.73	1.00	Witter & Carr 1988
<i>Dubautia scabra</i>	Hawaii	2	0.98	-	-	Witter & Carr 1988
<i>Argyranthemum</i>	Canary Islands	26	-	0.89	-	Franciso-Ortega et al. 1994, 1995
<i>Lobularia canariensis</i>	Canary Islands	5	0.76	0.70	0.83	This paper

$F_{IS}=0.222$ , indicates an overall excess of homozygotes, which is also expressed by the fixation indices. «Inbreeding» in small populations will often result in an excess of homozygotes. Homozygote excess is common in insect-pollinated herbs (Brown 1979) and has even been reported in obligate outcrossers like *Silene dioica* (Westerbergh & Saura 1992). Although self-compatible, the subspecies of *L. canariensis* are all highly outcrossing (Borgen 1987). The distribution pattern, with extremely localized and relatively small populations, results in crosses between neighbours that in many cases are «sisters», i. e. biparental inbreeding (Brown et al. 1989), and thus an excess of homozygotes is to be expected, particularly in investigations based on seed progeny like this one.

Hierarchical F-statistics on a geographic scale show F-values of 0.386 for the comparison population-archipelago, 0.350 for population-island, and 0.054 for island-archipelago. On a taxonomic scale, the F-values are 0.369 for population-species, 0.331 for population-subspecies, and 0.056 for subspecies-species. The observed differentiation pattern suggests partitioning among populations irrespective of island or taxon. Restricted gene flow among the populations, combined with drift in small populations, has apparently resulted in genetic differentiation but mainly at the population level. At least part of this differentiation has occurred within a relatively long historical perspective but as genetic identities between pairs of populations are highly variably, some populations have apparently been isolated for a considerable period of time, while others may not. Although not very well correlated with morphological differentiation patterns or geographical distances within the archipelago, the genetic differentiation is to a certain extent correlated with geological age and stability of the habitats.

In conclusion, a high level of genetic variation is observed in *L. canariensis*, and the differentiation among the Canarian populations is substantial. However, the data do not identify clear taxonomic and geographic patterns. Genetic drift is one of the most powerful evo-

lutionary processes that may lead to rapid genetic change and is, in combination with selection, often cited as one of the main processes behind adaptive radiation on oceanic islands (cf. Crawford, Witkus & Stuessy 1987). Data for *L. canariensis* demonstrate the importance of the population as the main unit in evolution and also the need to distinguish between those processes that result in evolution at the population level and those that eventually result in speciation. The many instances of low genetic identities between pairs of populations of *L. canariensis* in the Canary Islands contrast with the high genetic identities reported for many other groups of endemic plants on oceanic islands. Substantial geological evidence supports a much older origin for at least parts of the Canarian archipelago than most other oceanic archipelagos, for instance Hawaii. These data thus support the view that time is a critical factor for allozyme divergence. The data also indicate that a small amount of inter-insular gene flow may occur. In a system of relatively small and normally isolated populations, small amounts of gene flow may counterbalance the effects of inbreeding and drift and retard the differentiation of distinct genetic as well as morphologically recognizable taxonomic units.

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# Appendix 1.

## Allele frequencies in 19 populations of *Lobularia canariensis*

Locus	Population								
	1	2	3	4	5	6	7	8	9
<b>AMP-1</b>									
(N)	9	25	31	19	20	30	21	35	21
A	.000	.000	.048	.000	.000	.017	.167	.329	.000
B	.278	.280	.468	.237	.025	.050	.048	.286	.000
C	.111	.260	.274	.289	.000	.017	.548	.257	.833
D	.500	.460	.161	.368	.450	.833	.143	.086	.167
E	.111	.000	.048	.105	.450	.083	.095	.043	.000
F	.000	.000	.000	.000	.075	.000	.000	.000	.000
<b>AMP-2</b>									
(N)	9	25	31	19	20	30	21	36	21
A	.278	.120	.032	.132	.000	.433	.024	.056	.310
B	.278	.460	.290	.421	.325	.117	.405	.167	.405
C	.389	.420	.661	.289	.675	.433	.214	.542	.262
D	0.56	.000	.016	.158	.000	.017	.357	.236	.024
<b>GPI-1</b>									
(N)	11	25	31	19	20	32	20	36	21
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<b>GPI-2</b>									
(N)	11	30	31	21	20	32	20	36	21
A	.000	.000	.016	.000	.000	.000	.000	.000	.000
B	.455	.117	.532	.405	.400	.078	.000	.014	.000
C	.500	.850	.000	.000	.000	.000	.000	.000	.881
D	.000	.000	.355	.429	.475	.813	.125	.847	.000
E	.000	.000	.081	.095	.000	.016	.000	.000	.000
F	.045	.033	.000	.000	.125	.000	.775	.139	.119
G	.000	.000	.016	.071	.000	.094	.100	.000	.000
<b>IDH-1</b>									
(N)	11	39	31	19	20	30	21	34	21
A	.000	.000	.210	.026	.050	.033	.000	.088	.571
B	.909	.936	.790	.974	.950	.567	.881	.721	.429
C	.091	.064	.000	.000	.000	.400	.119	.191	.000
<b>MDH-4</b>									
(N)	11	33	31	19	20	32	21	36	21
A	.000	.015	.000	.000	.000	.000	.000	.000	.000
B	1.000	.985	1.000	1.000	1.000	.797	1.000	.931	.595
C	.000	.000	.000	.000	.000	.203	.000	.069	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.405
<b>PGM-1</b>									
(N)	11	29	29	19	20	32	21	28	20
A	.000	.000	.017	.000	.000	.000	.000	.000	.000
B	.318	1.000	.569	.000	1.000	.938	1.000	.893	1.000
C	.682	.000	.414	1.000	.000	.063	.000	.107	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000
<b>PGM-2</b>									
(N)	11	29	29	19	20	32	21	36	20
A	.000	.000	.000	.000	.000	.000	.048	.083	.050
B	1.000	.931	.000	.000	.050	.906	.952	.917	.650
C	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.828	1.000	.950	.063	.000	.000	.300
E	.000	.034	.103	.000	.000	.000	.000	.000	.000
F	.000	.034	.069	.000	.000	.031	.000	.000	.000
<b>PGD-1</b>									
(N)	11	38	31	21	20	32	21	36	21
A	.000	.000	.016	.000	.000	.000	.000	.000	.000
B	.000	.000	.871	.143	.950	.813	.786	.000	.024
C	1.000	.961	.113	.643	.050	.188	.214	.986	.976
D	.000	.039	.000	.214	.000	.000	.000	.014	.000
<b>TPI-1</b>									
(N)	11	25	31	19	20	32	21	36	21
A	.136	.000	.000	.000	.000	.000	.048	.000	.333
B	.000	.000	.016	.026	.000	.156	.881	.111	.000
C	.864	1.000	.984	.974	1.000	.844	.048	.736	.595
D	.000	.000	.000	.000	.000	.000	.000	.014	.000
E	.000	.000	.000	.000	.000	.000	.000	.069	.071
F	.000	.000	.000	.000	.000	.000	.024	.069	.000



Population

10	11	12	13	14	15	16	17	18	19
25	50	17	36	38	47	45	25	35	25
.000	.080	.000	.000	.000	.000	.100	.000	.014	.000
.060	.420	.088	.000	.171	.000	.000	.000	.143	.000
.400	.500	.176	.000	.579	.000	.144	.000	.586	.280
.360	.000	.706	.750	.145	.213	.656	.880	.257	.560
.180	.000	.000	.250	.105	.755	.100	.100	.000	.160
.000	.000	.029	.000	.000	.032	.000	.020	.000	.000
25	50	17	36	37	47	45	25	32	25
.000	.220	.000	.000	.000	.000	.056	.500	.438	.480
.280	.560	.353	.292	.095	.638	.489	.460	.125	.160
.680	.200	.500	.542	.824	.298	.433	.040	.359	.300
.040	.020	.147	.167	.081	.064	.022	.000	.078	.060
24	51	17	25	31	47	48	34	34	28
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
24	51	17	25	31	47	48	34	34	28
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
.021	.245	.265	.000	.000	.021	.031	.000	.632	.661
.000	.000	.000	.000	.032	.362	.521	.853	.338	.000
.875	.441	.706	.920	.871	.000	.000	.000	.029	.268
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
.104	.294	.029	.080	.081	.500	.448	.147	.000	.054
.000	.020	.000	.000	.016	.117	.000	.000	.000	.018
25	50	17	36	42	46	44	34	34	31
.000	.000	.000	.000	.000	.011	.000	.029	.000	.000
.860	.810	.441	.986	.976	.402	.250	.735	.088	.177
.140	.190	.559	.014	.024	.587	.750	.235	.912	.823
25	50	17	36	43	47	47	34	34	22
.000	.000	.000	.000	.000	.000	.106	.000	.000	.000
1.000	1.000	1.000	.958	1.000	1.000	.894	1.000	1.000	.977
.000	.000	.000	.042	.000	.000	.000	.000	.000	.023
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
25	51	17	36	41	41	35	33	32	31
.000	.010	.000	.000	.000	.000	.000	.273	.000	.000
1.000	.912	1.000	1.000	.976	.110	.157	.727	.703	.710
.000	.078	.000	.000	.012	.890	.843	.000	.297	.290
.000	.000	.000	.000	.012	.000	.000	.000	.000	.000
25	51	17	36	41	41	46	33	32	31
.000	.000	.000	.111	.049	.159	.359	.061	.016	.000
.000	.029	.176	.306	.354	.159	.337	.485	.078	.242
.000	.000	.000	.000	.000	.622	.152	.000	.000	.000
1.000	.971	.824	.583	.451	.061	.130	.455	.906	.694
.000	.000	.000	.000	.000	.000	.022	.000	.000	.065
.000	.000	.000	.000	.146	.000	.000	.000	.000	.000
25	51	17	35	35	49	45	34	34	31
.000	.000	.000	.000	.000	.000	.000	.000	.162	.000
.140	.578	.176	.086	.543	.122	.556	.103	.456	.065
.840	.422	.824	.829	.457	.878	.444	.897	.382	.903
.020	.000	.000	.086	.000	.000	.000	.000	.000	.032
25	51	17	25	40	47	48	34	34	29
.000	.069	.000	.000	.000	.000	.000	.000	.000	.052
.040	.000	.000	.000	.000	.000	.000	.000	.353	.000
.940	.931	1.000	.980	1.000	1.000	1.000	1.000	.647	.828
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
.020	.000	.000	.020	.000	.000	.000	.000	.000	.121
.000	.000	.000	.000	.000	.000	.000	.000	.000	.000