

PLANT GENETIC DIVERSITY IN THE CANARY ISLANDS: A CONSERVATION PERSPECTIVE¹

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The Canary Islands are an Atlantic volcanic archipelago with a rich flora of ~570 endemic species. The endemics represent ~40% of the native flora of the islands, and ~20% of the endemics are in the E (endangered) category of the International Union for Conservation of Nature. A review of allozyme variation in 69 endemic species belonging to 18 genera and eight families is presented. The average species-level genetic diversity (H_T) at allozyme loci is 0.186, which is twice as high as the mean reported for endemics of Pacific archipelagos. Possible factors contributing to this higher diversity are discussed, but the reasons remain obscure. An average of 28% of the allozyme diversity within species resides among populations, indicating a high level of interpopulational differentiation. Studies of reproductive biology indicate that many of the endemic species are outcrossers. The high total diversity within species, the relatively high differentiation among populations, and the outcrossing breeding systems have implications for species conservation. Decreased population sizes in outcrossing species would promote biparental inbreeding and increase inbreeding depression. The relatively high proportion of allozyme diversity among populations indicates that the most effective strategy for preserving genetic variation in species is to conserve as many populations as possible. The genetic diversity in many Canary Island endemics is endangered by: (1) overgrazing by introduced animals, such as barbary sheep, goats, mouflons, rabbits, and sheep; (2) interspecific hybridization following habitat disturbance or planting of endemics along roadsides or in public gardens; (3) competition with alien plant species; and (4) decline of population size because of urban development and farming.

Key words: allozymes; conservation; endangered species; Macaronesia; oceanic islands.

Oceanic islands are natural laboratories for studies of plant evolution (Crawford, Whitkus, and Stuessy, 1987; Adersen, 1995; Crawford and Stuessy, 1997). One feature of the floras of oceanic islands is the high number of endemics occurring in small areas. Adaptive radiation into diverse habitats and genetic drift are often considered to be important factors producing such extensive speciation (Crawford, Whitkus, and Stuessy, 1987; Baldwin et al., 1998). Oceanic islands also provide many well-known examples of species extinctions caused primarily by the negative impact of humans (Olson, 1989; Riese-

berg and Swensen, 1996; Cronk, 1997; Maunder, Culham, and Hankamer, 1998; Stuessy et al., 1998; Raven, 1998). About one in six known vascular plant species grows on oceanic islands, and one in three of all known endangered plants is an insular endemic (World Conservation Monitoring Center, 1992). Major factors responsible for the decline of insular biodiversity include massive introductions of alien plants and animals, clearing of climax vegetation for farming and urban development, and environmental degradation of the original ecological niches of endemic species (Parsons, 1981; Olson, 1989; Stone and Stone, 1989; Lawesson et al., 1990; Adersen, 1991; D'Antonio and Dudley, 1995; Rieseberg and Swensen, 1996; Maunder, Culham, and Hankamer, 1998).

The Canaries include seven volcanic islands and four islets; although part of Spain politically, they are near the Western Sahara region. The oldest island, Fuerteventura, is 21 million years (Myr) old and situated only 100 km from the African coast (Carracedo, 1984, 1994). There are at least 14 sea mountains between the Canaries and Portugal, four of them only 40 m below sea level (Nord-sieck and García-Talavera, 1979; Báez and Sánchez-Pinto, 1983; García-Talavera, 1997, 1999). It is likely that these submerged mountains were above sea level during some periods of the early Miocene (Vail and Hardenbol, 1979), and once they are dated, the age of the Canarian biota could be documented as much greater than 21 Myr.

There are approximately 570 endemic plant species

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(Santos-Guerra, 1999, in press) and, despite the short distance to the continent, the percentage of Canarian endemics [40%, Santos-Guerra (1999, in press)] is relatively high and is comparable to the 42% in the Galápagos Islands (Lawesson, Adersen, and Bentley, 1987). It has been estimated that 105 of the Canary Island endemics are endangered and thus have been accorded the "E" (endangered) category established by the International Union for Nature Conservation in 1981 (IUCN, 1981); this number represents about ~20% of the endemic species (Barreno, 1984; Gómez-Campo, 1996).

One of the major biological features of plants on oceanic islands is the high number of woody species in otherwise herbaceous groups (Carlquist, 1974). As in other archipelagos such as Hawaii and the Juan Fernández Islands, a high percentage of the Canary Island endemics (72%) is woody (Aldridge, 1979). Another common feature of plants from oceanic islands is the presence of mechanisms promoting outcrossing (Carlquist, 1965, 1974; Ehrendorfer, 1979; Barrett, 1996, 1998). The floras of the Juan Fernández and Hawaiian archipelagos, for example, have the highest percentages of dioecious species known anywhere on earth (Sakai et al., 1995). In contrast, only 10 dioecious endemic species are known in the Canaries (Francisco-Ortega et al., unpublished data); the Canarian flora is similar to the Galápagos in the rarity of dioecy as a sex expression (McMullen, 1987). However, it is estimated that at least 237 Canarian endemics have unisexual flowers, protandry, heteromorphic styles, or allelic self-incompatibility as mechanisms promoting outbreeding (Francisco-Ortega et al., unpublished data). This estimate is based on limited sampling, and it is likely that future investigations will increase the number of known outcrossing species.

In this paper we review the level and apportionment of genetic diversity at allozyme loci for plants endemic to the Canary Islands and consider the conservation implications of the data. Genetic diversity will also be discussed within the context of breeding systems and population sizes of the endemics, and the information interpreted relative to species conservation. The impact of current human activities on the genetic diversity and integrity of species is assessed and some perspectives on in situ and ex situ genetic conservation are presented. A final objective is to evaluate the major intrinsic and extrinsic factors affecting long-term preservation of plants endemic to the Canaries.

GENETIC DIVERSITY IN CANARY ISLAND ENDEMICS

The most recent review of allozyme variability in plants from oceanic islands was by DeJoode and Wendel (1992), while Frankham (1997) compared genetic variation between plants from islands and continents. However, these reviews included almost exclusively species from Pacific archipelagos.

Unless otherwise noted, gene diversity statistics reported in this paper were calculated according to Nei (1973) where H_T is total genetic diversity within a species, H_S is the mean diversity within populations, and G_{ST} is the proportion of the total diversity residing among populations. Family names are given in parentheses in

the text only for those taxa not listed with family designation in any of the tables. The authorities for names are given in the text for those genera and species not listed in the tables.

Total genetic diversity—Allozyme diversities are given for 69 endemic species from 18 genera in the Canary Islands (Table 1). These studies also include several endemic subspecies of *Argyranthemum* (15), *Chamaecytisus proliferus* (6), *Dactylis glomerata* (2), and *Lobularia canariensis* (4). The range of genetic diversities varies from 0.000 for *Sonchus bornmuelleri* Pit. and *S. wildpretii* U.Reifenb. & A.Reifenb. to 0.456 for *Cistus chinamadensis*, with a mean of 0.186. This value is more than twice the average reported by DeJoode and Wendel (1992) for species endemic to oceanic islands ($H_T = 0.064$). Only seven species have H_T values less than 0.050; these are *Androcymbium psammophyllum*, *A. hierrense*, *Argyranthemum maderense* (D. Don) Humphries, *Cheirolophus arbutifolius* (Svent.) Kunkel, *Sonchus acaulis*, *S. gummifer*, *S. tuberifer*, and the aforementioned species of *Sonchus*, in which no diversity was found.

The only other plant groups from oceanic islands with average genetic variation comparable to the Canarian plants are from Hawaii and include *Alsinidendron* H.Mann and *Schiedea* Cham. & Schldl. (both Caryophyllaceae) (Weller, Sakai, and Straub, 1996), and *Metrosideros* Gaertn. (Myrtaceae) (Aradhya, Mueller-Dombois, and Ranker, 1991), although only polymorphic loci were included in the latter study. Weller, Sakai, and Straub (1996) found that levels of genetic variation were strongly correlated with population size, breeding system, and phylogenetic relationships, and it would be of interest to know whether such correlations exist in the Canaries.

Correlation of breeding system and allozyme variation may be examined in Canary Island plants using *Argyranthemum*, *Chamaecytisus proliferus*, *Cistus osbaeckiaefolius*, *Echium*, *Lobularia canariensis*, and *Phoenix canariensis*. These taxa are strictly or predominantly outcrossing (Webb and Shand, 1985; Bramwell, 1972, 1973; Calero and Santos-Guerra, 1993; Cunneen, 1995; Borgen, 1996; Francisco-Ortega et al., 1997) and have high levels of genetic variation. Breeding systems are not known with certainty for other endemics for which allozyme data are available. However, there are strongly suggestive data for several taxa. Continental taxa of *Androcymbium* ($H_T = 0.054$), *Cheirolophus* ($H_T = 0.130$), *Sonchus* ($H_T = 0.104$), *Viola* ($H_T = 0.181$), and the *Dactylis glomerata* complex ($H_T = 0.317$) appear to be predominantly outcrossing (East, 1940; Smith, 1944; Mejías, 1992; Proctor, Yeo, and Lack, 1996; Caujapé-Castells and Pedrola-Monfort, 1997; Garnatje, Susanna, and Messeguer, 1998; J. Caujapé-Castells, Jardín Botánico Viera y Clavijo, personal communication). Mainland species of *Avena* L. ($H_T = 0.176$) are regarded as strictly autogamous (Fryxell, 1957). These data do not indicate a consistent trend for higher diversity in outcrossing compared to selfing species.

The next consideration is whether genetic diversity is correlated with phylogenetic relationships in Canary Island endemics. Phylogenetic hypotheses based on DNA data are available for *Argyranthemum* (Francisco-Ortega et al., 1997) and the woody *Sonchus* alliance, which in-

TABLE 1. Total genetic diversity (H_T) or mean expected heterozygosity from isozyme data of Canarian plant endemics compared with average values reported for other oceanic islands. Number of loci studied (N_l) are also indicated. Additional genetic statistics can be found in Table 2.

Taxon ^a	Family	H_T	N_l
<i>Androcymbium</i> Willd. (2)	Colchicaceae	0.054	10
<i>Androcymbium psammophilum</i> Svent.	Colchicaceae	0.108	17
<i>Argyranthemum</i> Sch.Bip. ^b (23)	Asteraceae	0.230	17
<i>Avena canariensis</i> Baum, Rajh. & Samps.	Poaceae	0.176	13
<i>Babcockia platylepis</i> (Webb) Boulos	Asteraceae	0.127	13
<i>Brassica bourgeauii</i> (Christ) Kuntze.	Brassicaceae	0.244	11
<i>Chamaecytisus proliferus</i> (L.f.) Link	Fabaceae	0.326	10
<i>Cheirolophus</i> Cass. (10)	Asteraceae	0.130	unknown
<i>Cistus osbaeckiaefolius</i> Christ	Cistaceae	0.333	13
<i>Cistus symphytifolius</i> Lam.	Cistaceae	0.309	13
<i>Cistus chinamadensis</i> Bañares & Romero	Cistaceae	0.456	13
<i>Dactylis glomerata</i> L. ^c	Poaceae	0.317 ^d	8
<i>Echium achanthocarpum</i> Svent.	Boraginaceae	0.235	10
<i>Lactucosonchus webbii</i> (Sch.Bip.) Svent.	Asteraceae	0.051	13
<i>Lobularia canariensis</i> (DC.) Borgen	Brassicaceae	0.278	10
<i>Lolium canariense</i> Steud.	Poaceae	0.104	13
<i>Lolium canariense</i>	Poaceae	0.167	10
<i>Phoenix canariensis</i> Chev.	Arecaceae	0.236	17
<i>Prenanthes pendula</i> Sch.Bip.	Asteraceae	0.079	13
<i>Sonchus</i> L. subg. <i>Dendrosonchus</i> Sch.Bip. ^b (13)	Asteraceae	0.104	13
<i>Sonchus tuberifer</i> Svent.	Asteraceae	0.047	13
<i>Sventenia bupleuroides</i> Font Quer	Asteraceae	0.057	13
<i>Taekholmia</i> Boulos (4)	Asteraceae	0.120	13
<i>Viola palmensis</i> Webb & Berthel.	Violaceae	0.181	11
Mean		0.186	
Average value for other oceanic archipelagos ^e		0.064	

Note: Information on genetic diversity compiled from Batista et al. (1999) for *Cistus* L.; Borgen (1996) for *Lobularia* Desv.; Charmet and Balfourier (1994) for *Lolium* L.; Francisco-Ortega et al. (1992, 1995, 1996a, 1997) for *Argyranthemum*, and *Chamaecytisus* Link; Garnatje, Susanna, and Messegue (1998) for *Cheirolophus*; González-Pérez, Sosa, and Caujapé-Castells (1999) or *Phoenix* L.; Kim et al. (1999) for *Babcockia* Boulos, *Lactucosonchus* (Sch. Bip.) Svent., *Prenanthes* L., *Sonchus*, *Sventenia* Font Quer, and *Taekholmia*; Lázaro and Aguinagalde (1998) for *Brassica* L.; Morikawa and Leggett (1990) for *Avena* L.; Oliveira, Arbones, and Bregu (1995) for *Lolium*; Pedrola-Monfort and Caujapé-Castells (1994, 1996) for *Androcymbium*; Sahuquillo and Lumaret (1995) for *Dactylis* L.; and P. A. Sosa (Universidad de Las Palmas de Gran Canaria, personal communication) for *Echium* L. and *Viola* L.

^a Number of species studied are indicated in parentheses.

^b Includes populations from other Macaronesian islands.

^c There are two endemic forms of *Dactylis glomerata* in the Canaries: *D. glomerata* subsp. *smithii* (Link) Stebb & Zoh., and *D. glomerata* "Canaria type" (Sahuquillo and Lumaret, 1995; Lumaret, 1997).

^d Genetic diversity calculated as mean observed heterozygosity.

^e Value from DeJoode and Wendel (1992).

cludes six genera (Kim et al., 1996). Levels of allozymic variation in species of *Argyranthemum* and the woody *Sonchus* alliance are not related to their positions in the DNA phylogenies. For example, species of *Argyranthemum* with relatively basal positions [*A. haemotomma* (Lowe) Lowe, *A. maderense*, *A. winteri* (Svent.) Humphries, and *A. tenerifae* Humphries], have H_T values ranging from 0.011 for *A. maderense* to 0.097 in *A. haemotomma* (Francisco-Ortega et al., 1997). Species in relatively derived positions [*A. dissectum* (Lowe) Lowe, *A. frutescens* (L.) Sch.Bip., *A. lidii* Humphries, and *A. webbii* Sch. Bip.], display a similar range of allozyme variation, with H_T values from 0.020 in *A. dissectum* to 0.118 in *A. webbii* (Francisco-Ortega et al., 1997). If there were loss of variation due to drift or founder events associated with recent speciation, then the more recently derived species would be expected to display lower allozyme diversity than basal taxa. Clearly, this is not the case.

Consider next correlations between allozymic diversity and population size. Allozyme data are available for only 22 taxa with large population sizes [more than >2500 individuals, Francisco-Ortega and Santos-Guerra (in press)]. These are from *Argyranthemum*, *Chamaecytisus*,

Cistus, *Echium*, *Phoenix*, the woody *Sonchus* alliance, and *Viola*. Mean total diversity for these 22 species is 0.146 with a range from 0.037 to 0.370 (Francisco-Ortega et al., 1996c, 1997, unpublished data; Kim et al., 1999). Mean allozyme diversity for species consisting of populations with fewer than 100 plants is 0.097 with a range from 0.000 to 0.360. A Mann-Whitney test (Snedecor and Cochran, 1989) revealed no significant difference between the two groups. Thus, although more commonly occurring species have higher average levels of genetic variation than rarer taxa, there is a wide range of variation in each group. It seems, therefore, that factors other than breeding system and population size are responsible for higher mean genetic diversity in the Canary Islands than in Pacific archipelago endemics.

A possible explanation for the higher diversities in Canarian endemics compared to Pacific Island endemics is that some of them represent old lineages that took refuge in Macaronesia during glaciations and desertifications in Europe and northern Africa after the Miocene. This hypothesis seems plausible given the considerable ages of some islands. The assumption is that allozyme variation would increase with time via mutation, and thus

the older taxa would be more diverse (Witter and Carr, 1988). However, phylogenetic studies of several groups do not support great ages for the endemics. The woody *Sonchus* alliance occupies a derived position in a molecular phylogeny of subtribe Sonchinae, with several Mediterranean species sister to the rest of the tree (Kim et al., 1996). Molecular phylogenies of the tribe Anthemideae are also concordant with the hypothesis that the insular endemics are younger elements; *Argyranthemum* is in a highly derived position within a clade of Mediterranean species (Francisco-Ortega et al., 1997; Watson, Evans, and Boluarte, 2000). Molecular phylogenies of other groups that include both continental and insular species [i.e., the *Aeonium* Webb & Berthel. alliance (Crassulaceae), *androcybium*, *Asteriscus* Mill. (Asteraceae), the *Bencomia* Webb & Berthel. alliance (Rosaceae), *Echium*, *Isoplexis* (Lindl.) J. C. Loudon (Scrophulariaceae), *Ixanthus* Griseb. (Gentianaceae), *Pinus* L. (Pinaceae), and *Tinguarra* Parl. (Apiaceae)] likewise indicate that most Macaronesian endemics occupy derived positions relative to their Mediterranean relatives (Böhle, Hilger, and Martin, 1996; Mes, VanBrederode, and 't Hart, 1996; Carvalho and Culham, 1998; VanHam and 't Hart, 1998; Caujapé-Castells et al., 1999; Francisco-Ortega et al., 1999; Thiv, Struwe, and Kadereit, 1999; Wang et al., 1999; Downie, Katz-Downie, and Spalik, 2000; Helfgott et al., 2000). The only known exceptions are the endemic genus *Plocama* Aiton (Rubiaceae) and the rare Tenerife endemic *Lavatera phoenicea* Vent. (Malvaceae). The former is in a basal position relative to a group comprising mainly Mediterranean taxa of the subfamily Rubioideae, and *L. phoenicea* is basal to all species of the *Lavatera* L.—*Malva* L. complex (Ray, 1995; Bremer, 1996; Fierrez-Aguilar et al., 1996; Andersson and Rova, 1999).

Another possible explanation for Canary Island endemics having greater diversity than species in Pacific archipelagos is that they originated from multiple introductions of continental taxa. The close proximity of the Canaries to a continental source area makes this more feasible than for more highly isolated Pacific islands. It has been suggested that in certain periods of the Quaternary the sea dropped at least 120 m below the current level (Carracedo et al., 1997; García-Talavera, 1997, 1999) and that the African coast was only 60 km from the island of Fuerteventura. This short distance would have facilitated multiple introductions of taxa into the Canaries and thus genetic bottlenecks associated with the colonization of these islands may have been less extreme than for remote archipelagos such as Hawaii. Molecular phylogenies indicate that even the most morphologically diverse endemic groups such as the woody *Sonchus* alliance (Kim et al., 1996) and *Argyranthemum* (Francisco-Ortega et al., 1997) are monophyletic. This does not mean, however, that there could not have been several dispersal events of continental ancestral taxa prior to or in the early stages of the origin and radiation of insular endemics.

Apportionment of genetic diversity among populations—Knowing the distribution of diversity within and among populations of a species is important for conservation because it provides useful guidelines for the preservation of genetic diversity within the species as a

whole. If a large proportion of the diversity resides among populations, then more populations must be conserved than if each population contains much of the species-level diversity (Hamrick et al., 1991; Hamrick and Godt, 1996). G_{ST} values provide a measure of the percentage of total species diversity residing among populations; these values are available for 23 taxa endemic to the Canaries. From 0.0 to 77.3% of the diversity resides among populations of the 23 species (Table 2), with a mean value of 28.06%. This contrasts with the mean of 17.9% for endemic outcrossing species (Hamrick and Godt, 1997). The mean for the Canary Island plants is very similar to the value calculated for 30 species from the Juan Fernández Islands (D. J. Crawford et al., unpublished data).

Given the high mean genetic differentiation among conspecific populations, an important question is how the diversity is distributed geographically within and among islands in the archipelago. Multivariate analyses of allele frequencies show that for some taxa most populations from the same island cluster together. Good examples are *Chamaecytisus proliferus* (Francisco-Ortega et al., 1992), *Dactylis glomerata* (Sahuquillo and Lumaret, 1995), and *Lobularia canariensis* (Borgen, 1996). The subspecies of these three species complexes always group together by island origin. By contrast, the most extreme example of lack of correlation is the six genera of the woody *Sonchus* alliance where none of the isozyme groups obtained by cluster analysis was related to island origin (Kim et al., 1999).

With regard to single islands, patterns of allozyme variation do not correlate with the ecology and geography of populations. Rather, within-island patterns of isozyme diversity are mosaic. The only exception is *Avena canariensis*, in which Morikawa and Leggett (1990) reported a relationship between populations clustered by allozyme similarities and soil conditions. The apparent lack of geographical correlates of allozyme diversity within some species has implications for conservation because it precludes making a priori assumptions that preservation of a population from a given island or an area on an island will conserve a high proportion of the diversity from that area.

The high G_{ST} values detected for the Canarian endemics indicate that, despite being predominantly outcrossing, there have been low levels of gene flow among populations. The results also indicate that preservation of high levels of variation within endemic species will require the conservation of a high proportion of the native populations.

LOSS OF PLANT GENETIC DIVERSITY IN THE CANARY ISLANDS

Biological processes and species attributes important for the conservation of Canary Island endemics are similar to those shaping allozyme diversity within and among populations; they include migration, selection, breeding system, and population size. Human activities in the Canaries have had a large influence on these factors, particularly during the last 30 yr (Kämmer, 1979; Aguilera et al., 1994). Approximately 1.6 million people inhabit the islands, with a yearly influx of ~9 million visitors. This

TABLE 2. Population diversity and genetic differentiation of Canary Island plant endemics. H_S = mean genetic diversity within populations; D_{ST} = mean genetic diversity among populations; G_{ST} = proportion of among population genetic diversity relative to the total genetic diversity; N_P = number of populations. Values are based on Nei's statistics (Nei, 1973) except for *Lobularia canariensis*, which are based on Wright's F statistics (Wright, 1965). See Table 1 for reference information.

Taxon	H_S	D_{ST}	G_{ST} (%)	N_P
<i>Androcymbium hierrense</i> A. Santos	0.056	~0	~0	3
<i>Androcymbium psammophilum</i> Svent.	0.108	0	0	2
<i>Androcymbium psammophilum</i>	0.052	~0	~0	2
<i>Babcockia platylepis</i>	0.059	0.068	53.8	2
<i>Chamaecytisus proliferus</i>	0.328	0.056	12.6	175
<i>Cistus osbaeckiaefolius</i>	0.252	0.082	20.9	4
<i>Cistus symphytifolius</i>	0.241	0.069	17.6	4
<i>Cistus chinamadensis</i>	0.262	0.195	39.2	2
<i>Echium acanthocarpum</i>	0.235	~0	~0	2
<i>Lobularia canariensis</i>	0.518	0.222	38.1	19
<i>Phoenix canariensis</i>	0.205	0.030	12.8	3
<i>Prenanthes pendula</i>	0.057	0.021	27.1	2
<i>Sonchus acaulis</i> Dum.—Cours.	0.030	~0	~0	4
<i>Sonchus brachylobus</i> Webb & Berthel.	0.059	0.068	53.5	3
<i>Sonchus canariensis</i> (Sch.Bip.) Boulos	0.028	0.064	69.6	6
<i>Sonchus congestus</i> Willd.	0.026	0.026	50.1	5
<i>Sonchus gonzalezpadroni</i> Svent.	0.056	0.023	29.4	2
<i>Sonchus gummifer</i> Link	0.032	0.005	14.2	3
<i>Sonchus hierrensis</i> (Pit.) Boulos	0.038	0.129	77.3	2
<i>Sonchus ortunoi</i> Svent.	0.075	0.013	14.3	3
<i>Sonchus palmensis</i> (Sch.Bip.) Boulos	0.052	0.035	40.1	3
<i>Sonchus pinnatifidus</i> Cav.	0.253	0.163	39.2	2
<i>Taekholmia pinnata</i> (L.f.) Boulos	0.095	0.110	53.6	3
<i>Viola palmensis</i>	0.166	0.015	10.0	8

represents an underestimate because it includes only non-Spanish tourists (Anonymous, 1997; Instituto Canario de Estadística, www.istac.rcanaria.es). There has been increased road building, farming activities, and urban development, all of which have an impact on the population genetic structure of plants.

Population size, breeding systems, and genetic drift—

Small populations are likely to become extinct because they are prone to genetic drift and inbreeding depression (Ellstrand and Elam, 1993; Frankham, 1998). In addition, differences between the effective and census sizes of populations have a greater effect on stochastic fluctuations of gene frequencies in small than in large populations (Nunney and Elam, 1994). Small differences in population features such as age structure, sex ratios, or progeny production will have a greater impact on the spatial and temporal genetic structure of small populations as compared to large ones (Wright, 1931; Gale and Lawrence, 1984; Ellstrand and Elam, 1993; Nunney and Elam, 1994).

One of the main objectives of a conservation program is to define a "Minimum Viable Population" size (MVP). This value will indicate which populations are in need of conservation measures in order to ensure long term survival (Pavlik, 1996). The MVP depends on several factors such as breeding system, ecology, and propagation ability, and it is usually considered to range between 50 and 2500 individuals (Mace and Lande, 1991; Given, 1994).

There are at least 38 Canarian endemics at the lowest level on the MVP "scale" with fewer than 50 individuals per population and 300 total plants; therefore, they should have the highest priority for plant genetic conservation

(Francisco-Ortega and Santos-Guerra, in press). This high priority list includes three species from Macaronesian genera [*Isoplexis*, *Normania* Lowe, (Solanaceae) and *Pericallis* D. Don (Asteraceae)] and four species from genera restricted to the Canaries [*Bencomia* and *Kunkeliella* Stearn (Santalaceae)]. A second category for genetic conservation includes species with 50–500 plants per population and 2500 or fewer total plants. There are 49 endemics in this category, including six species of the Macaronesian genera *Argyranthemum*, *Isoplexis*, *Monanthes* Haw. (Crassulaceae), and *Pericallis*, and four species of the Canarian genera *Kunkeliella* and *Parolinia* Webb (Brassicaceae) (Francisco-Ortega and Santos-Guerra, in press).

Reduction in population sizes in the predominantly outcrossing plant groups in the Canaries may lead to increased inbreeding depression and lowered fitness. This in turn would lower their ability to compete with introduced species, to cope with disturbed habitats, and to adapt to natural changes in the environment (Ellstrand and Elam, 1993; Ferson and Burgman, 1995; Menges, 1998; Frankham, 1998).

Genetic migration: hybridization and extinction—

Human activities have enhanced genetic migration by eliminating many of the previous ecological and geographical barriers separating populations and species. Congeneric endemic species in oceanic islands tend to hybridize easily once external barriers are removed because postmating isolation is typically weak (Crawford, Whitkus, and Stuessy, 1987; Baldwin et al., 1998). Marrero-Rodríguez (1992) distinguished three major groups of congeneric endemics in the Canaries based on the strength of interspecific barriers to hybridization. The first

group includes species that are very rarely sympatric, but that form natural hybrids easily if grown together. This group includes genera such as *Limonium* Mill. (Plumbaginaceae) and the *Bencomia* alliance. The second group has species that may be sympatric and form hybrid swarms in their natural habitats; good examples are in *Argyranthemum* (Humphries, 1975, 1976), *Carlina* L. (Asteraceae) (Marrero-Rodríguez, 1989), *Echium* (Bramwell, 1972, 1973), and *Micromeria* Benth. (Lamiaceae) (Pérez-DePaz, 1978). The third group includes species, that although sympatric, rarely form hybrid swarms. Natural hybrids can be found but extensive backcrossing rarely occurs because of hybrid sterility. Included in this category are species of the *Aeonium* alliance, the woody *Sonchus* alliance, and *Euphorbia* L. (Euphorbiaceae).

One of the best-known examples of human influence on genetic migration is found in *Argyranthemum*, a Macaronesian genus of 24 species (Francisco-Ortega et al., 1997). *Argyranthemum frutescens* is a weed that disperses easily along roads, and it hybridizes with other endemic congeners. Hybrid swarms with *A. coronopifolium* (Willd.) Humphries, *A. foeniculaceum* (Willd.) Sch.Bip., *A. broussonetii* (Pers.) Humphries, and *A. vincentii* A.Santos & E. Feria occur along roads on Tenerife (Humphries, 1975, 1976; Brochmann, 1984, 1987). It is uncertain to what extent these hybrid swarms are leading to introgressed variants outside the areas immediately surrounding the roads.

Hybrids have been reported between endemics and alien continental species. *Arbutus canariensis* Veill. (Ericaceae), *Phoenix canariensis*, and *Senecio teneriffae* Sch. Bip. (Asteraceae) hybridize with introduced *A. unedo* L. (Salas-Pascual, Acebes-Ginovés, and DelArco-Aguilar, 1993), *P. dactylifera* L. (Morici, 1998; González-Pérez, Sosa, and Caujapé-Castells, 1999), and *S. vulgaris* L. (Gilmer and Kadereit, 1989), respectively. One of the most commonly occurring hybrids is between *P. canariensis* and the introduced date palm (*P. dactylifera*) (Morici, 1998; González-Pérez, Sosa, and Caujapé-Castells, 1999).

Hybridization between widespread and rare taxa may contribute to the extinction of endangered species (Levin, Francisco-Ortega, and Jansen, 1996; Rhymer and Simberloff, 1996; Rieseberg and Swensen, 1996; Maunder, Culham, and Hankamer, 1998). Several examples from continental and insular areas supporting this view include *Margyricarpus* Ruíz & Pav. (Rosaceae) in the Juan Fernández Islands (Crawford et al., 1993), *Rubus* L. (Rosaceae) in Hawaii (Howarth, Gardner, and Morden, 1997; C. M. Morden, University of Hawaii, personal communication), and *Spartina* Schreb. (Poaceae) in California (Dahler and Strong, 1997). If this process continues it will likely play a major role in the genetic erosion of some rare species in the Canaries. From a conservation perspective, gene flow involving small populations can have two effects. If hybrids and their progeny are vigorous and fertile, the rare species could be assimilated.

In other circumstances, gene flow could prevent local differentiation or adaptation, thus leading to diminished fitness through outbreeding depression (Templeton, 1986; Ellstrand and Elam, 1993; Storfer, 1999). This process will usually occur when the source population of the more common native or invasive is genetically depau-

perate and there is substantial immigration into the small target populations (Ellstrand and Elam, 1993).

A recent trend has been to use Canarian endemics as ornamentals for gardening programs in the archipelago, with endemic species extensively planted along the main interdistrict roads of the islands and in major public gardens. These programs often involve moving species between islands. For example, *Echium decaisnei* Webb and *Argyranthemum pinnatifidum* (L. f.) Lowe are planted in public gardens on Tenerife although they are native to Gran Canaria and Madeira, respectively. Endemics from at least 14 genera are planted in gardens (Francisco-Ortega and Santos-Guerra, in press); species within each of these genera hybridize very easily, and even intergeneric hybrids have also been reported for some groups.

PROSPECTS FOR PLANT GENETIC CONSERVATION IN THE CANARY ISLANDS

In situ conservation—In the last 30 yr there have been substantial efforts to establish ex situ and in situ conservation programs directed towards protection of genetic diversity in Canarian endemics. Approximately 50% of the area of the islands is officially protected by a network of four national parks and 141 nature reserves (Martín-Esquivel et al., 1995; National Law 12/1994 of nature reserves of Canaries). These reserves contain 83 of the 87 rarest endemic species (Francisco-Ortega and Santos-Guerra, in press); their primary function is to protect the original habitats of the endemics. However, recently “genetic rescue” programs have been implemented to protect particular endemics. These programs have been directed particularly at the edges of the National Park of Caldera de Taburiente (Palomares-Martínez, 1993) and in some areas of the National Parks of Garajonay (Bañares-Baudet, 1990) and Cañadas del Teide (Bañares-Baudet, Castroviejo, and Real, 1993; Marrero-Gómez and Bañares-Baudet, 1996). They involve transplanting individuals or taking seeds from areas with large population sizes to zones with few or no plants of the target species.

From a genetic conservation perspective, these procedures may entail some risks (Leberg, 1990; Leberg et al., 1994; Green and Rothstein, 1998; Storfer, 1999), particularly if the source population is poorly sampled (Robichaux, Friar, and Mount, 1997). The consequences of gene flow and genetic bottleneck resulting from these transplantations on the genetic structure of particular populations are unknown, but possible results include decreased fitness through outbreeding or inbreeding depression and reduction of local variation (Fahselt, 1988; Leberg, 1990; Ellstrand and Elam, 1993; Robichaux, Friar, and Mount, 1997; Storfer, 1999). The eventual outcome of this process will be homogenization of allele frequencies and a severe reduction in genetic diversity among populations. The allozyme data clearly show that most of the Canarian groups follow a mosaic-like pattern of ecogeographical variation with relatively high differentiation among populations. This pattern could be altered if genetic migration exceeds rates occurring naturally without human intervention. Even transplanting individuals to areas where the target species no longer exists should be done only as a last resort, and always keeping in mind the risks associated with having the new populations as

possible sources of genes for neighboring populations of the same or different species.

Clearly, the best strategy for in situ conservation of genetic diversity in endemics of the Canary Island is preservation of natural habitats. Elimination of many introduced animals and plants should have higher priority than transplanting endemics. For example, large numbers of two species of mammals introduced into two major national parks in 1972 still remain there. The “Barbary Sheep” (*Ammotragus lervia* Pallas) is in the National Park of Caldera de Taburiente, and the “Corsica Mouflon” (*Ovis ammon musimom* Schreber) is present in the National Park of Cañadas del Teide. These two species, which have a very negative impact on the native flora, exist primarily for the hunting pleasure of a small percentage of the islands’ population (Rodríguez-Luengo and Rodríguez-Piñero, 1990).

Ex situ conservation—Seeds of most of the endemics withstand low humidity and temperatures and are therefore suitable for conservation in seed banks (i.e., Maya, Monzón, and Ponce, 1988; Reghunath et al., 1993; Francisco-Ortega et al., 1994). Possible exceptions are members of Aquifoliaceae, Lauraceae, Myricaceae, Myrsinaceae, Oleaceae, Sapotaceae, and Ternstroemiaceae. These species are arborescent and occur mainly in the subhumid ecological zone known as the “laurel forest” (*Prunella lauretea azoricae* Oberd.) (Santos-Guerra, 1990).

Most efforts at ex situ genetic conservation via seed banks have been undertaken in the Botanic Garden Viera y Clavijo, Gran Canaria (Maya, 1990), in Viceconsejería de Medio Ambiente del Gobierno de Canarias, and in the Escuela Técnica Superior de Ingenieros Agrónomos, Madrid (Gómez-Campo, 1973). Extensive seed banks with multiple populations for each species presently exist only for species of *Argyranthemum*, *Avena canariensis*, members of *Beta* L. sect. *Patellares* Tranzschel (Chenopodiaceae), *Chamaecytisus proliferus*, the *Gonospermum* Less. alliance (Asteraceae), and *Phoenix canariensis* (Baum et al., 1975; Morikawa and Leggett, 1990; Ford-Lloyd, Jackson, and Santos-Guerra, 1982; Olivier and Cordier, 1987; Francisco-Ortega et al., 1990, 1996b; R. Febles, Botanic Garden Viera y Clavijo, personal communication). Additional seed collections are needed to sample adequately the gene pool of most endemic species.

In this paper we have discussed how studies of genetic variation in populations and species of plants, when taken together with other biological aspects of the taxa, are important for understanding the factors responsible for the genetic erosion and extinction of Canary Island endemics. As indicated by Gray (1996), two major factors shape genetic diversity in plant populations: “(1) the intrinsic biological properties of the species and (2) extrinsic dynamic processes which affect species.” Plant genetic conservation strategies must take both factors into consideration. The Canarian endemics have several intrinsic attributes (Pavliv, 1996) indicating high potential for long-term genetic conservation. These include woodiness, high genetic diversity, high fecundity, and high survival of propagules in the seed bank. However, any effort for the implementation of conservation strategies will fail if the extrinsic factors outweigh the intrinsic ones.

Several contemporary extrinsic events contribute to genetic erosion and are obstacles to the establishment of genetic conservation policies in the Canary Islands. Of these, the four most important are (1) endemics competing with exotic plant invaders for resources (Kunkel, 1973a, b, 1976; Dickson, Rodríguez, and Machado, 1987), (2) introduced animals feeding on native plants (Rodríguez-Luengo and Rodríguez-Piñero, 1987, 1990; Rodríguez-Piñero, Rodríguez-Luengo, and Domínguez, 1987; Nogales, Valido, and Medina, 1995), (3) hybridization of rare endemics with widespread native or alien species as a result of corridor formation by clearance of original vegetation, road building (Levin, Francisco-Ortega, and Jansen, 1996; Rhymer and Simberloff, 1996), or transplantations for gardens, and (4) continuous decline of population sizes as native habitats are lost to urban development and agriculture (Santos-Guerra, Beltrán, and Ruiloba-Santana, 1985; Aguilera et al., 1994). The key to the preservation of the unique plant heritage of the Canary Islands depends almost entirely on how the present generation of Canarians chooses to deal in the short term with these four major issues.

Note Added in Proof: Programs to transplant rare Canary Island endemics in national parks have been reviewed by park botanists. Currently these programs are very limited and use strict sampling techniques. In order to preserve the genetic structure of the populations, some of the taxa previously planted have been eliminated (Bañares-Baudet et al., in press).

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