High Levels of Genetic Polymorphism in the Insular Endemic Herb *Jepsonia malvifolia*

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***Jepsonia malvifolia* is a long-lived perennial herb endemic to the Channel Islands of southern California and Guadalupe Island, Mexico. Twelve populations of *J. malvifolia* on San Clemente Island were surveyed for their genotype at 21 allozyme loci, revealing high levels of genetic polymorphism. For all individuals across San Clemente Island, 95.2% of loci are polymorphic with $A_p = 2.90$ and $H_e = 0.179$. Populations averaged 60.2% polymorphic loci with $A_p = 2.42$ and $H_e = 0.158$. Most variation is found within rather than among populations ($G_{ST} = 0.101$), although differentiation among populations is significant. Genetic identities range from 0.936 to 0.999 with mean $I = 0.975$. There is no significant relationship between genetic and geographic distance. Gene flow among populations is $Nm = 9.5$ based on private alleles and $Nm = 2.2$ based on F_{ST}. Outcrossing rates based on fixation indices average $t = 0.753$, indicating a primarily outcrossed mating system. The genetic variation observed is unusually high for an insular endemic herb and indicates that *J. malvifolia* is unlikely to be endangered by genetic factors.**

Maintenance of genetic variation has become a major focus of conservation programs. Rare and endangered species are susceptible to loss of genetic variation through genetic drift in small populations. This reduces evolutionary potential over the long term because adaptation to a changing environment is only possible with genetic variation (Frankel et al. 1995). Genetic variation may also increase fitness in the short term in spatially or temporally heterogeneous environments, by reducing inbreeding, and by other mechanisms (Huenneke 1991). Understanding the pattern of genetic variation within and among populations of rare species is therefore critical for prioritizing populations for protection, for guiding collection of ex situ material, and for choosing seed sources for reintroduction and restoration.

Geographic range is one of the more important characteristics determining levels of genetic variation within populations, with endemic species averaging fewer polymorphic loci and alleles per locus, and lower expected heterozygosity than species with larger ranges (Hamrick and Godt 1989). Another factor associated with low genetic variation is whether populations occupy an island or a mainland habitat, presumably due to the genetic drift associated with colonization and establishment of island populations. Island populations have less genetic variation (Barrett and Husband 1989; Frankham 1997) and generally experience more inbreeding than mainland populations (Frankham 1998) due to the loss of genetic variation through drift. Moreover, taxa endemic to islands appear to be especially genetically depauperate (DeJoode and Wendel 1992; Frankham 1997; Stuessy et al. 1998, but see Francisco-Ortega et al. 2000). Island populations and insular endemics thus appear to be especially vulnerable to extinction due to genetic factors.

The genus *Jepsonia* (Saxifragaceae) is endemic to the California floristic province (Raven and Axelrod 1978). It has long been considered relictual (Raven and Axelrod 1978) and enigmatic in its relationship with other genera in the Saxifragaceae (Ornduff 1969), although recent molecular studies have elucidated its phylogenetic position (Soltis et al. 1993). *Jepsonia* consists of three allopatric species, all of which are long-lived perennial herbs with $n = 7$, sharing unusual features such as a distylous breeding system, an annual contractile root (a second taproot that moves the base of the stem well below the soil surface during the first few years of growth), adaptation to xeric habitats, and flowering before leaf production. Two of

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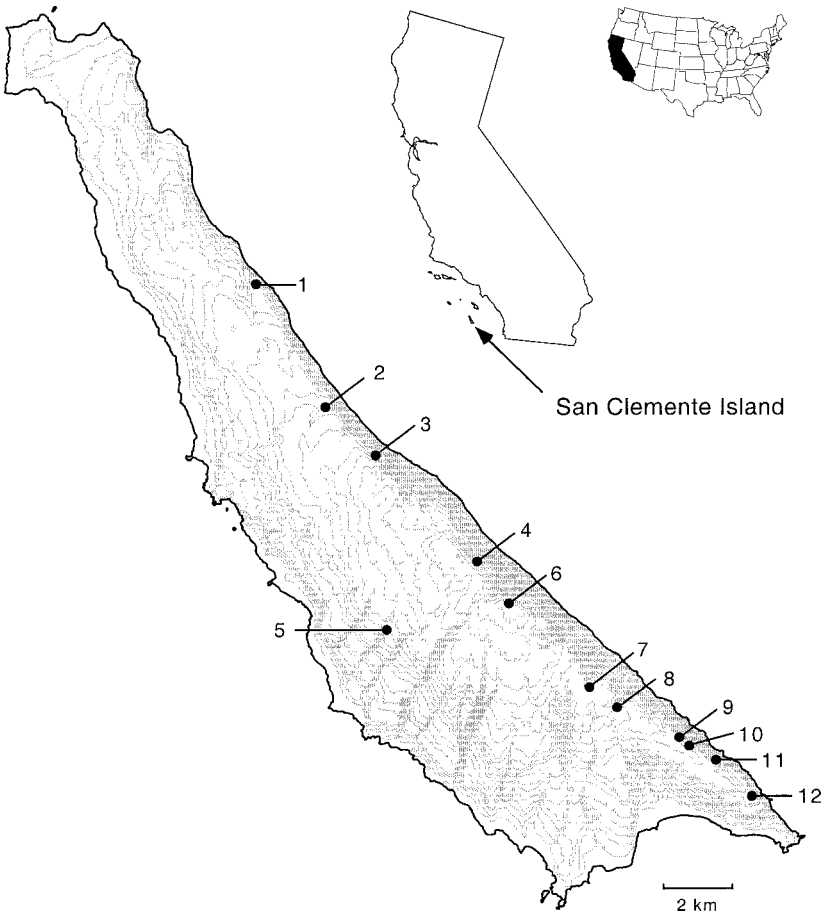

Figure 1. Locations of 12 sampled populations of *J. malvifolia* on San Clemente Island, California.

the species occur in mainland California and adjacent Mexico, while the third, *J. malvifolia* (Greene) Small, is endemic to the Channel Islands of Southern California and Guadalupe Island, Mexico (Ornduff 1969). It is found on five of the eight Channel Islands (Junak et al. 1995; Wallace 1985); on San Clemente Island, populations are found primarily on north-facing slopes at the heads of canyons on the east side of the island.

In this article I report high levels of genetic polymorphism in *J. malvifolia* on San Clemente Island. This study was initiated as part of an investigation of the conservation genetics of rare and endangered plant species of San Clemente Island. The goals of the study were to assess the genetic structure of *J. malvifolia* on San Clemente Island and provide management guidelines based on population genetic data.

Table 1. Genetic variability at 21 loci in 12 populations of *J. malvifolia* on San Clemente Island

Population	N	P	A	A_p	A_e	H_o	H_e	F	t
1 Triangulation Point Jack	30	57.1	1.90	2.58	1.18	0.109	0.149	0.273	0.571
2 Lemon Tank	30	55.0	1.60	2.09	1.17	0.158	0.147	−0.080	1.174
3 Stone Canyon	30	66.7	1.95	2.43	1.26	0.164	0.209	0.203	0.663
4 North Boulders	30	71.4	1.95	2.33	1.22	0.186	0.180	−0.035	1.073
5 Norton Canyon	30	52.4	1.86	2.64	1.20	0.131	0.170	0.235	0.619
6 Vista Canyon	30	47.6	1.67	2.40	1.16	0.092	0.136	0.328	0.506
7 Bryce Canyon	32	66.7	1.81	2.21	1.17	0.109	0.143	0.235	0.619
8 Dead Man's Curve	30	66.7	1.81	2.21	1.18	0.138	0.151	0.081	0.850
9 Canchalagua Canyon	25	72.2	1.89	2.23	1.13	0.091	0.117	0.359	0.472
10 Matriarch Canyon	30	66.7	2.10	2.64	1.21	0.142	0.172	0.174	0.704
11 Knob Canyon	30	52.4	1.90	2.73	1.21	0.141	0.172	0.181	0.693
12 Guds	30	47.6	1.76	2.60	1.17	0.132	0.146	0.096	0.825
Mean		60.2	1.85	2.42	1.19	0.133	0.158	0.171	0.731
(SE)		2.6	0.04	0.06	0.01	0.008	0.007	0.039	0.062
Species	357	95.2	2.81	2.90	1.22	0.134	0.179	—	—

N = sample size; P = proportion of polymorphic loci; A = alleles per locus; A_p = alleles per polymorphic locus; A_e = effective number of alleles; H_o = observed heterozygosity; H_e = expected heterozygosity; F = fixation index; t = outcrossing rate.

Materials and Methods

Leaf tissue was sampled from 12 populations spanning the range of *J. malvifolia* on San Clemente Island (Figure 1, Table 1). Twenty-five to 32 individuals were haphazardly sampled from each population. Leaves were stored in plastic bags and kept moist and cool until they were transported to the laboratory, where they were stored at 5°C.

Electrophoretic methods followed Soltis et al. (1983). Leaf tissue was crushed in phosphate extraction buffer (Conkle et al. 1982) and stored at −80°C until electrophoresis was conducted. Three buffer systems were used to resolve loci coding for 15 enzymes. Aspartate aminotransferase (Aat), shikimate dehydrogenase (Skd), and triose-phosphate isomerase (Tpi) were resolved using a Tris-citrate, pH 6.3/6.7 buffer system (Selander et al. 1971) with 13.0% starch gels. Alcohol dehydrogenase (Adh), aldolase (Ald), diaphorase (Dia), fructose-1,6-diphosphatase (Fdp), glyceraldehyde-3-phosphate dehydrogenase (G3p), isocitrate dehydrogenase (Idh), malate dehydrogenase (Mdh), malic enzyme (Me), 6-phosphogluconate dehydrogenase (Pgd), and phosphoglucomutase (Pgm) were resolved using a morpholine citrate, pH 6.1 buffer system (Clayton and Tretiak 1972) with 13% starch gels. Menadione reductase (Mr) and phosphoglucose isomerase (Pgi) were resolved using a lithium hydroxide pH 8.1/8.5 buffer system (Ridgeway et al. 1970) with 13% starch gels. Staining recipes for all enzymes followed Soltis et al. (1983), except for diaphorase (Murphy et al. 1990). Loci were numbered sequentially with the most anodally migrating enzyme designated "1".

Data were analyzed using the computer program Genestrut (Constantine et al. 1994). The percentage of polymorphic loci (P), mean number of alleles per locus (A), and per polymorphic locus (A_p), effective number of alleles (A_e), observed heterozygosity (H_o), and expected heterozygosity (H_e) were calculated. Loci were considered polymorphic if more than one allele was detected. Levels of genetic variation were calculated for individual populations and for all individuals pooled across all populations on San Clemente Island. Fixation indices (F), reflecting deviations from

Table 2. Matrix of Nei's (1972) genetic identities (above diagonal) and geographic distances (in kilometers below diagonal) among the 12 populations of *J. malvifolia* on San Clemente Island

Population	1	2	3	4	5	6	7	8	9	10	11	12
1 Triangulation Point Jack		0.944	0.944	0.982	0.994	0.993	0.984	0.981	0.996	0.972	0.994	0.976
2 Lemon Tank	3.1		0.982	0.959	0.955	0.951	0.960	0.972	0.952	0.948	0.959	0.973
3 Stone Canyon	4.9	1.8		0.968	0.959	0.955	0.964	0.971	0.957	0.936	0.963	0.963
4 North Boulders	8.9	6.0	4.0		0.976	0.987	0.997	0.992	0.984	0.966	0.979	0.986
5 Norton Canyon	9.6	6.5	4.9	2.9		0.989	0.977	0.975	0.988	0.959	0.999	0.968
6 Vista Canyon	11.6	8.6	6.6	2.8	4.1		0.988	0.983	0.994	0.979	0.988	0.976
7 Bryce Canyon	14.1	11.0	9.2	5.2	5.9	2.5		0.996	0.989	0.972	0.978	0.989
8 Dead Man's Curve	15.1	12.2	10.2	6.2	6.7	3.5	4.0		0.991	0.978	0.980	0.993
9 Canchalagua Canyon	16.8	13.8	12.0	8.0	8.7	5.3	3.0	1.8		0.982	0.993	0.977
10 Matriarch Canyon	17.3	14.4	12.6	8.6	9.2	5.8	3.4	2.4	0.6		0.964	0.971
11 Knob Canyon	18.4	15.5	13.7	9.6	10.3	6.9	4.6	3.6	1.7	1.1		0.968
12 Guds	19.9	17.0	15.0	11.0	11.7	8.4	6.0	5.0	3.0	2.6	1.5	

Hardy–Weinberg equilibrium, were calculated and outcrossing rates (t) were estimated using $t = (1 - F)/(1 + F)$ (Weir 1990). The partitioning of genetic diversity within and among all populations was analyzed using F statistics (Nei 1973). Nei's (1978) unbiased genetic identity (I) was calculated for pairwise comparisons of populations. The relationship between genetic and geographic distance on San Clemente Island was tested using Mantel (1967) analysis. A cluster analysis was performed using the unweighted pair group method (UPGMA) and Rogers's (1972) genetic distance. Gene flow was estimated using Wright's (1951) formula, $Nm = (1 - F_{ST})/4F_{ST}$, with F_{ST} considered equivalent to G_{ST} (Nei 1977). A second estimate was based on the frequency of private alleles (alleles found in a single population; Slatkin 1985).

Results

Enzyme electrophoresis resulted in clear and consistent staining for 15 enzymes encoded by 21 putative loci: *Aat, Adh, Ald-1, Ald-2, Dia-1, Dia-2, Dia-3, Fdp, G3p, Idh, Mdh-1, Mdh-2, Mdh-3, Me, Mr, Pgd-1, Pgd-2, Pgi, Pgm, Skd,* and *Tpi.* All enzymes migrated anodally.

All loci except *Fdp* are polymorphic in at least one population (95.2%; Table 1). Totaled across all populations, 59 alleles were detected on San Clemente Island. Most loci have one common allele in all populations and from one to four alternative alleles. The average number of alleles per polymorphic locus is 2.90, and overall expected heterozygosity for San Clemente Island is 0.179.

Populations contain from 10 to 14 polymorphic loci, with an average number of alleles per polymorphic locus of 2.42 and average expected heterozygosity of 0.158. Populations contain 12 to 23 alternative alleles ranging in frequency from 0.017 to 0.607 in populations (mean $q = 0.138$). Only eight alleles are unique to single populations (seven different ones); all occur at frequencies of less than 0.05.

Mean fixation indices (F) for island populations range from −0.080 to 0.359 with a mean F of 0.171 ($n = 12$), indicating a deficiency of heterozygotes relative to Hardy–Weinberg expectations. Forty-one of 137 fixation indices for individual loci are significant; 29 of these (70.7%) are positive. Outcrossing rates (t) based on fixation indices range from 0.472 to 1.174 (mean $t = 0.731$; Table 1), indicating a predominantly outcrossed mating system.

Genetic identity values were generally high. Genetic identities for pairs of populations ranged from 0.936 to 0.999 with a mean of 0.975 (Table 2). The phenogram produced by UPGMA cluster analysis depicts a relatively close genetic relationship among all populations (Figure 2). No significant relationship exists between genetic and geographic distance ($P = .8540$, $n = 12$; Mantel 1967).

Mean F_{IS}, representing average deviation from Hardy–Weinberg expectations within populations, is low (mean $F_{IS} = 0.144$, $P < .01$; Table 3). Differentiation of populations is relatively low, but significantly different from 0 (mean $F_{ST} = 0.101$, $P < .01$). Of the total gene diversity found on San Clemente Island, 89.9% is found within populations and 10.1% is found among populations (mean $H_S = 0.177$, mean $D_{ST} = 0.020$, mean $H_T = 0.197$, $G_{ST} = 0.101$).

Gene flow among San Clemente Island populations was $Nm = 9.5$ using Slatkin's (1985) method based on eight private alleles with an average frequency of 0.026. Wright's (1951) method yielded an estimate of $Nm = 2.2$.

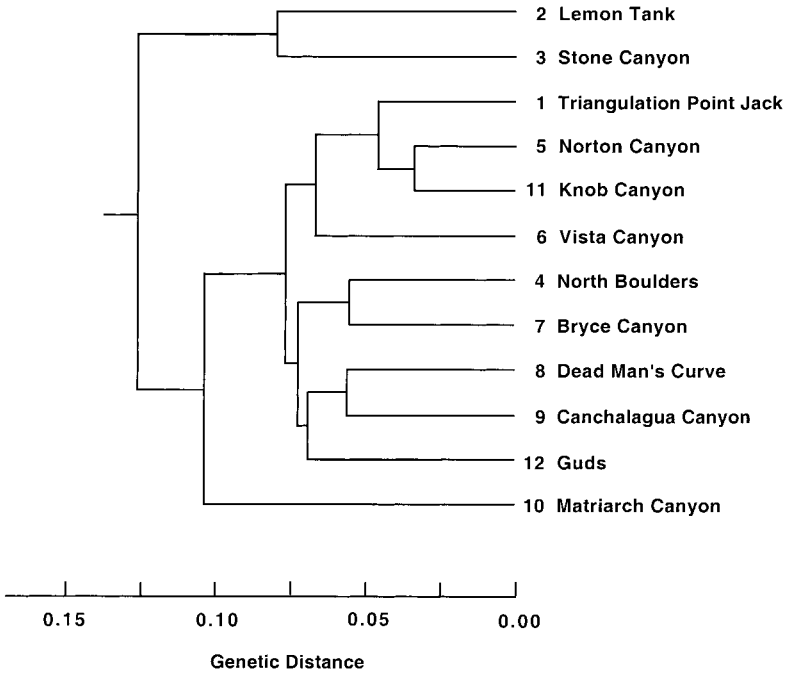

Figure 2. Cluster analysis of 12 populations of *J. malvifolia* on San Clemente Island, California, using the UPGMA method and Rogers's (1972) genetic distance values.

Table 3. Summary of *F* statistics at 20 polymorphic loci of *J. malvifolia* on San Clemente Island

Locus	F_{IS}	F_{ST}	F_{IT}
Aat	0.231	0.110[a]	0.316
Adh	0.721	0.044[a]	0.733
Ald-1	0.441	0.007[a]	0.445
Ald-2	0.482	0.013[a]	0.488
Dia-1	0.042	0.042[a]	0.086
Dia-2	0.106	0.018	0.121
Dia-3	0.141	0.241[a]	0.348
G3p	0.000	−0.001	−0.001
Idh	0.706	0.284[a]	0.789
Mdh-1	−0.003	0.003	0.000
Mdh-2	0.038	0.043[a]	0.079
Mdh-3	−0.011	0.009	−0.003
Me	−0.012	0.153[a]	0.143
Mr	−0.026	−0.019	−0.006
Pgd-1	0.077	0.014[a]	0.090
Pgd-2	0.145	0.164[a]	0.286
Pgi	0.059	0.122[a]	0.174
Pgm	0.071	0.018[a]	0.088
Skd	0.347	0.034[a]	0.369
Tpi	0.000	0.000	0.000
Mean	0.144	0.101[a]	0.230

[a] F_{ST} values significantly different from 0 ($P < .01$).

Discussion

Genetic Variation

Jepsonia malvifolia exhibits extremely high levels of genetic variation. Plant species generally maintain considerably less variation both within taxa (average P = 50.5%, A = 1.96, H_e = 0.149) and within populations (average P = 34.2%, A = 1.53, H_e = 0.113; Hamrick and Godt 1989). The high genetic variation in *J. malvifolia* is particularly surprising for an insular endemic species because narrow geographic range is usually associated with low genetic variation (Hamrick and Godt 1989). There have been few reports of rare plant species maintaining equal or higher levels of variation than *J. malvifolia* (see below).

The breeding system of a species has been shown to be a major determinant of patterns of genetic variation in plants (Hamrick and Godt 1989). Outcrossing species have significantly higher levels of genetic variation within populations and less differentiation among populations than inbreeding species. *J. malvifolia* appears to be a primarily, although not exclusively, outcrossing species (average t = 0.753 calculated from fixation indices). This indirect estimate is supported by experimental evidence regarding the mating system of *J. malvifolia.* The genus *Jepsonia* is unique in the Saxifragaceae in exhibiting heterostyly, a floral polymorphism in which different individuals have different forms of flowers. The floral polymorphism is typically accompanied by a self-incompatibility system that prevents self-fertilization or matings among similar floral forms. In *J. malvifolia,* only partial self-incompatibility is present, with self-pollination and own-form pollination resulting in 13–17% of the seed set from compatible pollinations (Ornduff 1970). Self-incompatibility in *J. malvifolia* is weaker than in the other two species of this genus, consistent with the observation that insular species generally exhibit less self-incompatibility (Baker 1955; Barrett 1996). The weaker self-incompatibility of *J. malvifolia* may have been selected due to insufficient pollination with compatible pollen, which has been observed in the long-styled forms in experimental populations (Ornduff 1970). Although no specific information is available for *J. malvifolia,* the mainland species of *Jepsonia* are pollinated primarily by syrphids and halictid bees (Ornduff 1970). Depauperate pollinator faunas are common on islands, and lower visitation rates have been documented in some species (Barrett 1996).

Hamrick and Godt (1989) identified a number of other species characteristics associated with high levels of genetic variation in plants. Some of these are exhibited by *J. malvifolia*: sexual reproduction, a long-lived perennial herbaceous habit, and late successional status. Several other characteristics of *J. malvifolia* are atypical; endemic, dicotyledonous species with gravity-dispersed seeds usually have low levels of genetic variation. However, since Hamrick and Godt's (1989) analysis only explained 24% of the observed variation in levels of genetic variation, it is not too surprising to find species that don't fit the typical profile of a genetically diverse taxon.

Genetic Differentiation

Most variation is found within rather than among populations of *J. malvifolia* on San Clemente Island (G_{ST} = 0.101), although differentiation among populations is significant. This level of differentiation among populations is low for plant species (mean G_{ST} = 0.224; Hamrick and Godt 1989), but is consistent with characteristics such as an outcrossing breeding system and late successional status. It is also consistent with the indirect estimate of gene flow based on private alleles (Nm = 9.5), which indicates sufficient gene flow to reduce population differentiation. It should be noted that the G_{ST} value calculated for *J. malvifolia* in this study may be an underestimate for the species as a whole because populations from only one island were sampled. Inclusion of populations from the four other Channel Islands on which it occurs and from Guadalupe Island may reveal greater overall differentiation among populations of this insular endemic species.

Comparison with Other Plants

Island plants generally have been found to have reduced levels of genetic variation. DeJoode and Wendel (1992) reviewed data from 69 insular endemic plants in 16 genera, mainly from Pacific archipelagos, and found lower than average species-level values of genetic diversity (P = 0.25, A = 1.32, H_T = 0.064). Frankham (1997) reviewed comparisons of closely related insular endemic and mainland plant taxa and found that the insular endemic species is nearly always less heterozygous than its mainland congener. Endemic species of the Juan Fernandez archipelago, Chile, generally exhibit low genetic variation (Stuessy et al. 1998). Curiously, endemic plants of the Canary Islands are more genetically variable (H_T = 0.186 for 69 species in 18 genera) than species of other island archipelagos (H_T = 0.064), possibly due to the greater age of these islands compared to their Pacific counterparts and because of their proximity to a continental source of migrants (Francisco-Ortega et al. 2000). Although little work has been conducted on plant genetic diversity on California's Channel Islands, insular endemic subspecies of *Delphinium variegatum* have fewer polymorphic loci and alleles per locus than their mainland congener (Dodd and Helenurm, in press), and endemic varieties of *Malacothamnus fasciculatus* tend to have low levels of genetic variation (Swensen et al. 1995). Thus *J. malvifolia* appears to be a remarkable exception to a general rule of reduced genetic variation on islands, particularly since the data are from only one island rather than several in an archipelago.

Levels of genetic diversity in plant species are also associated with family. A review of genetic diversity in 507 plant species (Hamrick and Godt 1996) indicates that families with predominantly herbaceous species (such as the Saxifragaceae) have less genetic diversity and higher genetic differentiation than families with predominantly long-lived, woody perennials. Saxifragaceae was not included in this analysis due to a low number of allozyme studies. Allozyme studies of Saxifragaceae have revealed a wide variety in levels of genetic variation. No genetic variation was detected in *Bensoniella oregona* (Soltis et al. 1992) or in three of the four taxa of *Sullivantia* (Soltis 1982), a genus very closely

related to *Jepsonia* (Soltis et al. 1993) in which the species are highly self-fertile and narrowly distributed (Soltis 1981). Very low levels were observed in the fourth taxon of *Sullivantia* (Soltis 1982), *Conimitella williamsii* (Soltis and Soltis 1991), and *Tellima grandiflora* (Rieseberg and Soltis 1987). Levels of genetic variation more typical of flowering plants have been documented in *Elmera racemosa* (Soltis and Soltis 1991), in six species of *Heuchera* (Ness et al. 1989; Soltis 1985; Wolf et al. 1990), and in *Tolmiea menziesii* (Soltis and Soltis 1989). In contrast, a very high level of genetic variation has been reported in *Saxifraga aizoides* (mean P = 78.2%, mean A = 2.7, and mean H_e = 0.40 in a survey of 10 loci encoding eight enzymes; Lutz et al. 2000). Thus two of the genetically most polymorphic rare plant species now known are from the Saxifragaceae, although this family also supplies many examples of no detectable allozyme variation.

Although the high level of genetic polymorphism in *J. malvifolia* is surprising and unusual, it is not unique. There have been two other reports of narrowly distributed species with high levels of genetic variation: *Daviesia suaveolens* (Fabaceae; mean P = 82.5, mean A = 2.6, mean H_e = 0.27; Young and Brown 1996) and *Rutidosis leptorrhynchoides* (Asteraceae; mean P = 83.3, mean A = 2.5, mean H_e = 0.21, although this study was based on only nine loci representing five enzymes; Young et al. 1999).

Management Guidelines

San Clemente Island has a long history of feral goat grazing and sheep, cattle, and pig ranching, resulting in overgrazing, subsequent erosion, and loss of shrub and tree cover. It has been owned by the U.S. government and operated by the U.S. Navy since the early 1930s, providing active naval training and support activities. The recent elimination of goats, the last remaining large herbivores on the island, has permitted vegetative recovery (Kellogg and Kellogg 1994). However, a number of introduced plant species threaten the native vegetation (including grasses such as *Avena* spp., *Bromus* spp., *Ehrharta calycina,* and *Piptantherum miliaceum,* and other species such as *Asphodelus fistulosus, Foeniculum vulgare,* and *Carpobrotus* spp.), and military activities have increased the frequency of fires and trampling of vegetation. Because the island will continue to experience heavy use for military purposes, management guidelines are required to satisfy the twin demands of military exercises and plant conservation.

Overall *J. malvifolia* on San Clemente Island does not appear to be threatened by genetic factors. It is clearly not genetically depauperate; the high proportion of polymorphic loci and the number of alleles per locus indicate greater than average evolutionary potential. In addition, levels of heterozygosity in populations (together with the outcrossing mating system) do not suggest potential problems with inbreeding. If population sizes (currently ranging from about 100 to 1000 individuals) can be maintained or increased, there would appear to be little cause for concern regarding the long-term persistence of this species.

There are no obvious grounds for prioritizing populations. Populations are relatively similar in levels of genetic variation when all measures of genetic variation are considered. For example, even though Matriarch Canyon contains more alternative alleles than other populations and Vista Canyon contains fewer, both populations are intermediate in expected heterozygosity. Moreover, all populations fall within a narrow range in the effective number of alleles.

Consideration of the distributions and frequencies of alleles also does not reveal an obvious way to prioritize populations. If alleles are categorized as widespread versus local (found in only one or a few adjacent populations) and as common versus rare (frequencies less than 0.05) following Marshall and Brown (1975), then all four categories of alleles are found in *J. malvifolia,* although far from equally. Nearly 80% of the alleles (47 of the total 59 alleles) are widespread on San Clemente Island; 41 of these are common and 6 are always rare. The remaining 20% of the alleles (12 of 59) are locally distributed; only one of these is found at a frequency of greater than 0.05 in a population, while 11 are always rare. Thus only one population (Matriarch Canyon) contains a common allele (q = 0.35) that is not also found in many other populations. Rare alleles occur in all populations.

No single population contains all the variation observed on San Clemente Island, and low but significant differentiation exists among populations. The loss of any one population is unlikely to represent a significant loss of genetic diversity because the majority of alleles are found in more than one population and locally distributed alleles (including the eight private alleles) tend to occur at low frequencies. However, ex situ collections will need to include many populations to capture all of the genetic variation on the island.

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