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Genetic Diversity in the Rare California Shrub *Dedeckera eurekensis* (Polygonaceae)

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ABSTRACT. *Dedeckera eurekensis* is a rare, shrubby, perennial endemic to the Mojave Desert of California. Although many thousands of flowers are produced, only about 1% of the ovules mature into viable seeds and no seedlings or juvenile plants are known; hence this species is potentially threatened with extinction. Enzyme electrophoresis was used to determine levels of genetic variation within and between six populations. *Dedeckera* is surprisingly variable genetically as suggested by the relatively high number of alleles per locus (2.6), mean percentage of polymorphic loci (80.5), and mean heterozygosity (0.269). These results stand in contrast to the expectation of limited genetic diversity in other plant species with similar life histories and restricted distributions. A gene duplication has apparently resulted in a third PGM locus, which may be useful in phylogenetic studies of *Dedeckera* and related genera.

Dedeckera eurekensis Reveal & Howell is a rare shrub endemic to the Last Chance, Panamint, Inyo, and White Mountain ranges northwest of Death Valley in Inyo County, California, where it is known from only 12 populations. This monotypic genus was first discovered by Mary C. DeDecker on limestone outcrops in what is now officially known as Dedeckera Canyon located southeast of the Eureka Valley sand dunes. This plant was later named in her honor by Reveal and Howell (1976). *Dedeckera* is most closely related to *Eriogonum* Michx. but is distinguished from it by the lack of a tubular involucre, pubescence type, inflorescence type, and "the presence of a solitary, short-pedicellate flower found at the base of the peduncle" (Reveal and Howell 1976). Studies of seed/ovule ratios in *Dedeckera* have been conducted by Wiens et al. (1988). Although the plants flower prolifically, the percentage of ovules maturing into fully viable seeds averages less than 1%. This exceptionally low ratio is apparently due to the action of embryonic developmental lethals (Wiens et al. 1988). Because *Dedeckera* has no means of vegetative reproduction, viable seed production is extremely limited, and no obviously juvenile plants or seedlings are known, the species may well be moving toward extinction. *Dedeckera* is currently listed under "category 2" on the Federal List of Threatened and Endangered Plants. This category encompasses taxa that are possibly threatened or endangered but for which substantial data on vulnerability or threat are not known.

Given the unusually low reproductive capacity of this species, its limited distribution, and the possible threat of extinction, an electrophoretic study of *Dedeckera* was begun. The goal of this study was to collect baseline genetic data to address questions concerning population dynamics of this evolutionary relict, and to consider questions concerning the biogeography and phylogeny of this species. Data relevant to its reproductive capacity will be considered elsewhere. Previous electrophoretic studies of other narrow endemics such as Torrey pine (Ledig and Conkle 1983) suggested that genetic variation in *Dedeckera* might be limited. If populational bottlenecks have, in the past, severely restricted genetic variation in these plants, homozygosis and inbreeding depression would be expected to contribute to the exeptionally low fecundity.

MATERIALS AND METHODS

Twenty individuals from each of six populations of *Dedeckera* were sampled during July of 1987 (table 1). Approximately 5.0 g of stems with young leaves were clipped from each in-

TABLE 1. Collection data for populations of *Dedeckera eurekensis* examined in this study. [a] UTM = Universal Transverse Mercator Grid System.

Population number and name	Location (all Inyo Co., CA, UTM zone 11[a])
1. Coldwater Canyon	Bishop quadrangle, 384000E (*Wiens 6730*)
2. Dedeckera Canyon (upper)	Last Chance Range quadrangle, 443700E-4101900N (*Wiens 6734*)
3. Bishop	Bishop quadrangle, 385500E (*Wiens 6738*)
4. Gunter Canyon	Bishop quadrangle, 388100E (*Wiens 6739*)
5. Last Chance Mountains	Last Chance Range quadrangle, 442000E-4094800N (*Wiens 6740*)
6. Dedeckera Canyon (lower)	Last Chance Range quadrangle, 443600E-4101300N (*Wiens 6741*)

dividual, packaged in plastic bags, refrigerated, and soon thereafter shipped (ambient temperature) via express mail to Urbana, Illinois. Protein extraction from leaves was carried out immediately upon arrival. Approximately 1.0 g (wet weight) of leaves were ground to a powder with liquid nitrogen and extracted using a Brinkman Polytron homogenizer. The extraction buffer (pH 7.5) was similar to that reported by Soltis et al. (1983) and was composed of the following: 7 mM Na borate, 2 mM Na bisulfite, 50 mM Na ascorbic acid, 4 mM Na diethyldithiocarbamic acid, 0.4 mM Na_2 EDTA, 0.2 M Tris, 1% 2-mercaptoethanol, and 10% (w/v) polyvinylpyrrolidone (PVP-40). The crude extract was centrifuged at 10,000 *g* at 4°C for 15 minutes. Following centrifugation, the supernatant was transferred to 1.5 ml microcentrifuge tubes and stored at −100°C.

Eight polymorphic enzyme systems coded by 12 presumptive gene loci were used in this study: colorimetric esterase (EST-2, E.C. 3.1.1.1), glutathione reductase (GSR-2, E.C. 1.6.4.2), isocitrate dehydrogenase (IDH-2, E.C. 1.1.1.42), malate dehydrogenase (MDH-1, MDH-2, MDH-4, E.C. 1.1.1.37), menadione reductase (MDR-1, E.C. 1.6.99.2), phosphoglucoisomerase (PGI-2, E.C. 5.3.1.9), phosphoglucomutase (PGM-1, PGM-2, PGM-3, E.C. 2.7.5.1), and shikimate dehydrogenase (SKDH, E.C. 1.1.1.25). Seven loci were monomorphic in all populations: adenylate kinase (ADK-1, E.C. 2.7.4.3), GSR-1, glucose-6-phosphate dehydrogenase (G-6-PDH-1 and G-6-PDH-2, E.C. 1.1.1.49), leucine amino peptidase (LAP, E.C. 3.4.11.1), MDH-3, and PGI-1. The three gel/electrode buffers used to resolve the eight enzyme systems were: 1) Tris-citrate, pH 7.5 (buffer no. 4 in Soltis et al. 1983); 2) histidine-citrate pH 6.0; and 3) lithium-borate pH 8.1 (Ridgeway et al. 1970). The electrode buffer no. 1 was composed of 0.223 M Tris and 0.086 M citric acid. Gel buffer no. 1 was formed by diluting 35 ml of the electrode buffer to 1 liter. Electrode buffer no. 2 was composed of 0.065 M L-histidine (free base), 0.016 M citrate (free acid), and was adjusted to pH 6.0 with citric acid. Gel buffer no. 2 was made up as a 1:6 dilution of the electrode buffer. The electrode buffer no. 3 was composed of 0.06 M LiOH and 0.3 M borate. The gel buffer consisted of 0.03 M Tris and 5 mM citric acid (pH 8.0–8.1). For use, nine parts of the gel buffer were added to one part of the electrode buffer. ADK, GSR, LAP, and PGI were best resolved on buffer no. 1; EST, G-6-PDH, IDH, MDH, and SKDH on buffer no. 2; and MDR and PGM on buffer no. 3.

Enzyme separation was accomplished using 14% starch gels and standard electrophoretic methods as reported in Shaw and Prasad (1970). The enzyme staining protocol for GSR was from Harris and Hopkinson (1976) and the protocol for MDR was from Burdon et al. (1980). All other stains were essentially as in Soltis et al. (1983). Genotypes were inferred directly from enzyme banding patterns because crosses are difficult and genetic analysis in *Dedeckera* is essentially impossible given the extremely low fecundity. For all systems, the most common allele was assigned a mobility number of "100" and other alleles were given numeric designations relative to that band. Genetic variability tabulations, genetic distance, cluster analysis, and other statistical tests of the data were performed using BIOSYS-1 (Swofford and Selander 1981).

RESULTS

Allele frequencies across 12 polymorphic loci for the six populations used in this study are given in table 2. The most variable loci are PGM-3 and SKDH with six alleles each among

TABLE 2. Allele frequencies for six populations of *Dedeckera eurekensis*. See Table 1 for a key to the population numbers.

Locus	Population 1	2	3	4	5	6
EST-2						
A	1.000	0.333	0.750	0.600	0.400	0.333
B	0.000	0.250	0.000	0.400	0.400	0.333
C	0.000	0.417	0.000	0.000	0.200	0.333
D	0.000	0.000	0.250	0.000	0.000	0.000
GSR-2						
A	0.825	0.842	1.000	0.842	0.800	0.763
B	0.175	0.158	0.000	0.053	0.200	0.237
C	0.000	0.000	0.000	0.105	0.000	0.000
IDH-1						
A	0.950	0.775	1.000	0.900	1.000	0.750
B	0.000	0.225	0.000	0.000	0.000	0.000
C	0.025	0.000	0.000	0.100	0.000	0.250
D	0.025	0.000	0.000	0.000	0.000	0.000
MDH-1						
A	0.737	1.000	0.464	1.000	1.000	1.000
B	0.026	0.000	0.071	0.000	0.000	0.000
C	0.237	0.000	0.464	0.000	0.000	0.000
MDH-2						
A	0.900	0.933	0.950	0.950	0.906	0.750
B	0.100	0.067	0.050	0.050	0.063	0.250
C	0.000	0.000	0.000	0.000	0.031	0.000
MDH-4						
A	0.975	0.800	1.000	1.000	0.781	0.975
B	0.025	0.067	0.000	0.000	0.219	0.025
C	0.000	0.133	0.000	0.000	0.000	0.000
MDR-1						
A	1.000	0.800	1.000	1.000	0.800	0.750
B	0.000	0.175	0.000	0.000	0.200	0.167
C	0.000	0.025	0.000	0.000	0.000	0.028
D	0.000	0.000	0.000	0.000	0.000	0.056
PGI-2						
A	0.350	0.275	0.750	0.425	0.250	0.316
B	0.625	0.575	0.250	0.550	0.406	0.342
C	0.000	0.000	0.000	0.000	0.000	0.237
D	0.025	0.150	0.000	0.025	0.344	0.105
PGM-1						
A	0.150	0.031	0.237	0.075	0.200	0.200
B	0.200	0.531	0.289	0.325	0.033	0.450
C	0.650	0.438	0.474	0.600	0.767	0.225
D	0.000	0.000	0.000	0.000	0.000	0.125
PGM-2						
A	0.625	0.536	0.775	0.600	0.500	0.550
B	0.250	0.250	0.100	0.000	0.000	0.075
C	0.025	0.000	0.125	0.225	0.100	0.275
D	0.100	0.107	0.000	0.175	0.400	0.050
E	0.000	0.107	0.000	0.000	0.000	0.050
PGM-3						
A	0.650	0.588	0.850	0.525	0.214	0.700
B	0.125	0.235	0.000	0.075	0.179	0.075
C	0.050	0.176	0.000	0.050	0.464	0.050
D	0.125	0.000	0.000	0.025	0.000	0.050
E	0.025	0.000	0.150	0.325	0.143	0.100
F	0.025	0.000	0.000	0.000	0.000	0.025
SKDH						
A	1.000	0.533	0.900	0.964	0.500	0.800
B	0.000	0.300	0.100	0.000	0.067	0.025
C	0.000	0.167	0.000	0.036	0.133	0.150
D	0.000	0.000	0.000	0.000	0.033	0.000
E	0.000	0.000	0.000	0.000	0.267	0.000
F	0.000	0.000	0.000	0.000	0.000	0.025

the six populations. GSR-2, MDH-1, MDH-2, and MDH-4 are the least variable, each with three alleles per locus. The monomeric enzyme phosphoglucomutase (PGM) generally exists as a single plastid and cytosolic isozyme in higher plants (Gottlieb 1982). Three loci for PGM are reported here for *Dedeckera*, suggesting that a gene duplication has taken place (fig. 1). Polyploidy is not a likely explanation for this additional isozyme locus because the number of loci for all other enzymes conforms to those reported for diploids (Gottlieb 1982) and the meiotic chromosome count was n = ca. 12.

Amount and Distribution of Genetic Variation. The genetic variability statistics for all populations are given in table 3. The percentage of polymorphic loci across the six populations ranges from 66.7 to 91.7 with a mean of 80.5. Loci that were monomorphic for all populations were excluded from this analysis. Populations with P values less than 100% indicate that they were monomorphic for at least one locus. Higher levels of polymorphism were seen for the three populations collected from the Last Chance Range (pops. 2, 5, and 6) as compared with those from the White Mountains (pops. 1, 3, and 4)

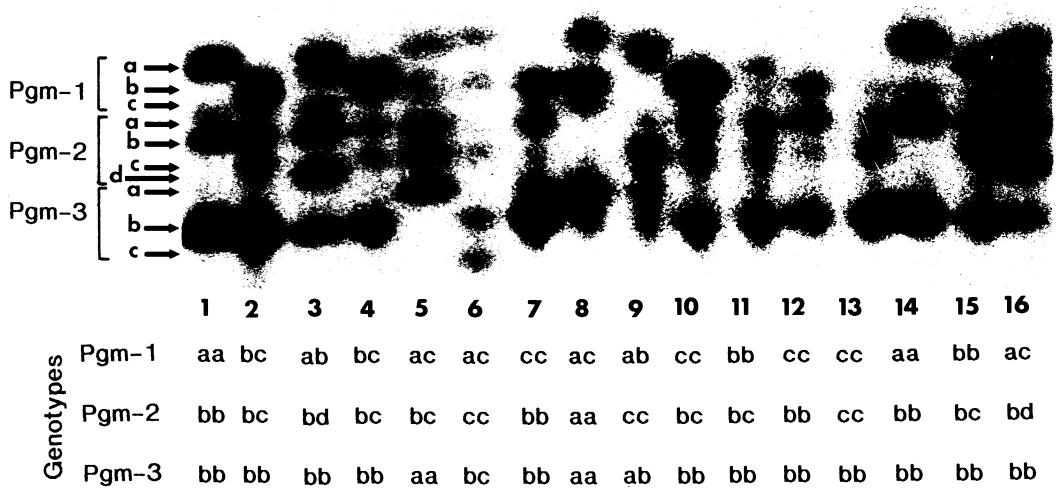

FIG. 1. Electrophoretic phenotypes and genotypes of phosphoglucomutase (PGM) for two populations of *Dedeckera eurekensis*. Lanes 1-4 are from population 1 (Coldwater Canyon), lanes 5-10 from population 2 (Dedeckera Canyon—upper), and lanes 11-16 from population 3 (Bishop). The lowest number of bands observed is three (e.g., lane 7) indicating an individual homozygous at all three loci. Light subbands are present above particularly dark staining bands for homozygotes, such as above PGM-3^{bb} for lane 7. Heterozygote genotypes can be seen at all three loci and are usually present as two equally intense bands.

to the northwest (72.2% vs. 88.9%, respectively). This trend is also seen in the mean number of alleles per locus (2.26 vs. 2.9) and the mean heterozygosity (0.207 vs. 0.331). The percentage of heterozygotes (direct count) per locus across all populations ranged from 0.119 for MDR-1 to 0.583 for PGI-2.

It could be argued that excluding strictly monomorphic loci would bias the estimation of percent polymorphism. To test this, a larger set (27) of loci were examined for polymorphism. This group included the 12 polymorphic loci used for statistical analysis, the seven monomorphic loci, and eight polymorphic loci that were not consistently resolved across all populations. These eight loci were: aconitase (ACO-2), EST-1, EST-3, aspartate amino transferase (AAT-1, AAT-2), IDH-1, and 6-phosphogluconate dehydrogenase (6-PGD-1, 6-PGD-2). Of the total 27 loci, 20 (74%) were polymorphic across all six *Dedeckera* populations. This corresponds closely to the mean value of 80.5% previously cited.

The direct count of the mean percentage of heterozygotes is, for all populations, less than that expected assuming Hardy-Weinberg equilibrium proportions (table 3). To identify significant deviations of heterozygote proportions from those expected under equilibrium, the Fixation Index "*F*" (Wright 1965) was used (table 4). The values of *F* can vary between 1.0 (no heterozygotes) to −1.0 (all heterozygotes). Eight of the 12 loci show significant deviations from expected genotypic proportions in at least one population: EST-2, GSR-2, IDH-2, MDH-2, PGM-1, PGM-2, PGM-3, and SKDH. All deviations represent heterozygote deficiencies except for PGM-2 in population 4. Of the 58 tests conducted, 17 (29%) are significant at the $P < 0.05$ level or less.

Genetic variation within and between populations can be measured using *F*-statistics (Nei 1977; Wright 1978). Table 5 summarizes the *F*-statistics for all loci where F_{IS} is the fixation index within populations, F_{ST} measures the amount of differentiation between populations, and F_{IT} is the total fixation index. For the six *Dedeckera* populations, F_{IS} (0.192) is greater than F_{ST} (0.133), which suggests that more of the total genetic variation is found within populations than among populations, which is generally true for outcrossing species. As indicated by an F_{ST} value of 0.133, however, some degree of differentiation between populations is apparent.

Genetic Similarity among Populations. Several genetic similarity and distance measures

TABLE 3. Genetic variability at 12 loci in *Dedeckera eurekensis*. [a] A locus is considered polymorphic if more than one allele was detected. [b] Unbiased estimate (Nei 1978).

Population number and name	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic[a]	Mean heterozygosity ($\bar{H}$)	
				Direct count	Hardy-Weinberg expected[b]
1. Coldwater Canyon	18.8	2.6	75.0	0.218	0.264
2. Dedeckera Canyon (upper)	14.8	2.7	91.7	0.384	0.428
3. Bishop	15.8	1.9	66.7	0.211	0.256
4. Gunter Canyon	16.3	2.3	75.0	0.194	0.287
5. Last Chance Mountains	13.3	2.7	83.3	0.318	0.413
6. Dedeckera Canyon (lower)	16.7	3.3	91.7	0.293	0.444
Means	16.0	2.6	80.5	0.269	0.348

were employed for all pairwise comparisons of the six populations. The matrix of genetic identities (Nei 1978) and genetic similarities (Rogers 1972) is shown in table 6. Rogers' genetic similarity values range from 0.7 between populations 3 and 5 to 0.866 between populations 1 and 4. Values using Nei's genetic identity are consistently higher than the previous measure and ranged from 0.855 (populations 3 and 5) to 0.974 (populations 2 and 6).

UPGMA cluster analysis (Sneath and Sokal 1973) was used to produce phenograms from several genetic identity and distance matrices. The phenogram shown in figure 2 used Rogers' (1972) similarity measure and had a cophenetic correlation of 0.715 and a percent standard deviation (Fitch and Margoliash 1967) of 4.2. Among all genetic identity and distance measures tested, the topologies of the resulting UPGMA phenograms differed only in the placement of population 4 (Gunter Canyon). In figure 2, this population is shown as being most similar to Coldwater Canyon and Bishop. The six populations cluster in two groups, one comprising the three populations from the White Mountains and the other three populations from the Last Chance Range. The cluster analysis based upon genetic distance suggests that geographically proximal populations are more similar genetically than those that are geographically distant. It would be instructive to obtain additional material of *Dedeckera* from the Panamint and Inyo mountains to test further this apparent correlation.

TABLE 4. Fixation indices (F) for the six *Dedeckera* populations showing deviations from Hardy-Weinberg genotype proportions. Genotypes were pooled into three classes, homozygotes for the most common allele, common/rare heterozygotes, and rare homozygotes plus other heterozygotes. Dashes indicate monomorphic loci. [a] = $P < 0.05$; [b] = $P < 0.01$; [c] = $P < 0.001$.

Locus	Population					
	1	2	3	4	5	6
EST-2	—	0.234	0.556	1.000[a]	−0.250	1.000[b]
GSR-2	0.134	0.208	—	0.240	0.583[a]	0.563[b]
IDH-2	−0.039	0.283	—	−0.111	—	0.467[a]
MDH-1	0.343	—	−0.394	—	—	—
MDH-2	0.444[a]	−0.071	−0.053	−0.053	−0.079	−0.067
MDH-4	−0.026	−0.184	—	—	−0.280	−0.026
MDR	—	0.392	—	—	0.167	0.042
PGI-2	−0.028	−0.225	−0.333	−0.162	0.045	0.338
PGM-1	−0.320	−0.190	0.420[a]	0.811[c]	0.102	0.132
PGM-2	0.161	0.089	−0.204	−0.074[a]	0.195	0.018[b]
PGM-3	−0.014[a]	0.378[a]	0.608[b]	0.262	0.375[b]	0.284[b]
SKDH	—	−0.115	0.630[b]	−0.037	0.797[c]	0.108

TABLE 5. Summary of *F*-statistics for all loci.

Locus	F_{IS}	F_{IT}	F_{ST}
EST-2	0.479	0.590	0.213
GSR-2	0.364	0.398	0.053
IDH-1	0.250	0.349	0.133
MDH-1	−0.088	0.255	0.315
MDH-2	0.022	0.074	0.054
MDH-4	−0.206	−0.066	0.116
MDR-1	0.189	0.275	0.106
PGI-2	−0.024	0.089	0.110
PGM-1	0.273	0.349	0.105
PGM-2	0.045	0.120	0.079
PGM-3	0.292	0.388	0.136
SKDH	0.327	0.445	0.176
Means	0.192	0.299	0.133

DISCUSSION

Endemic taxa may be ancient and restricted to a small portion of their previous range such as the genetically homogeneous Torrey pine (Ledig and Conkle 1983). Conversely, endemics may differentiate rapidly and recently as with *Stephanomeria malheurensis* Gottlieb, which apparently arose from the progenitor species *S. exigua* Nutt. subsp. *coronaria* (Greene) Gottlieb (Gottlieb 1973a). The mean proportion of polymorphic loci in *S. malheurensis* is 0.12 as compared with 0.6 in the progenitor. Although originally considered a derivative of *Clarkia rubicunda* (Lindl.) Lewis & Lewis, the serpentine endemic *C. franciscana* Lewis & Raven was later found to be more distantly related to the former (Gottlieb 1973b, 1974). With the exception of GOT, *C. franciscana* was monomorphic for all isozyme loci examined (Gottlieb 1973b). The two known populations may represent the sole relicts of a formerly more widespread ancestral species. This range truncation, in combination with its selfing breeding system, probably accounts for the near lack of genetic variation in this species.

A summary of genetic diversity levels for plants and their associations with ecological traits and life history variables was reported by Hamrick et al. (1981). Considering the categories employed by Hamrick et al. (1981), *Dedeckera* would be categorized as a long-lived, perennial dicot, endemic to a xeric habitat, sexually reproducing and outcrossed via pollinating insects (Wiens et al. 1986). According to this summary, this plant would, on average, have ca. 37% polymorphic loci, 1.57 alleles/locus, and a heterozygosity level at ca. 0.13. As shown in table 3, genetic variation in *Dedeckera* greatly exceeds these averaged values. Therefore, other factors are apparently influencing the genetic structure of *Dedeckera* populations.

Genetic Diversity, Longevity, and Breeding System. Among higher plants, genetic variation is strongly influenced by the breeding system with the highest levels of polymorphism found among long-lived, outcrossing perennials (Hamrick et al. 1981). The inbreeding or dominance hypothesis described by Ledig (1986) presents the situation as a "vicious circle" for plants with high genetic loads such as forest trees. If inbreeding occurs, deleterious genes are present in the homozygous condition for a large proportion of loci in the F_1 progeny. Plants with these genotypes are competitively inferior and die before reproducing, usually during embryogenesis. This mutational load thus "drives" the breeding system to outcrossing, with the serious drawback that deleterious recessive genes are maintained in the population in the heterozygous state. The high "cost" of these genes is manifested by embryo mortality (Wiens et al. 1987). High genetic loads may result directly from the formation of sex cells from so-

TABLE 6. Genetic identity and similarity coefficients for six *Dedeckera* populations. Above diagonal: Nei (1978) unbiased genetic identity. Below diagonal: Rogers (1972) genetic similarity.

Population number and name	1	2	3	4	5	6
1. Coldwater Canyon	—	0.922	0.969	0.969	0.900	0.926
2. Dedeckera Canyon (upper)	0.792	—	0.893	0.949	0.941	0.974
3. Bishop	0.848	0.728	—	0.946	0.855	0.918
4. Gunter Canyon	0.866	0.809	0.824	—	0.944	0.972
5. Last Chance Mountains	0.762	0.819	0.700	0.800	—	0.913
6. Dedeckera Canyon (lower)	0.784	0.838	0.752	0.827	0.783	—

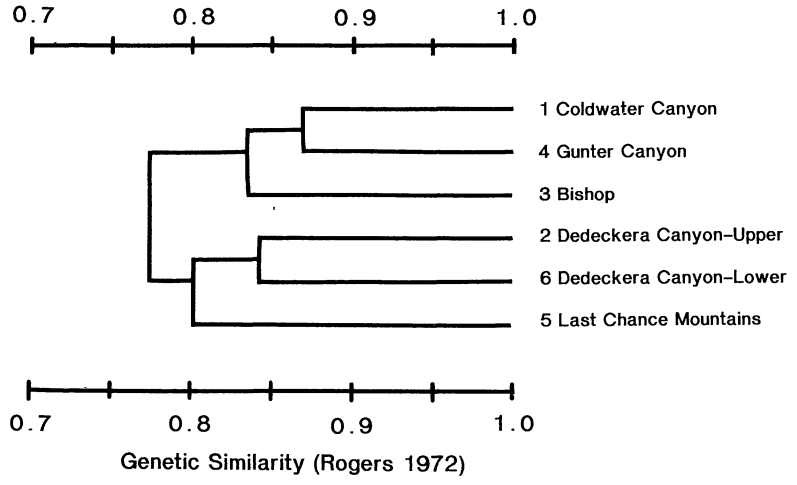

FIG. 2. UPGMA phenogram showing relationships among the six *Dedeckera* populations based upon the genetic similarity measure of Rogers (1972).

matic cells following many mitotic divisions. The older the meristem that forms the reproductive cells, the more probable that mutations have accumulated (Klekowski et al. 1985). Preliminary analyses of growth rings in *Dedeckera* showed that the stems were at least 130 years old. It is likely these stems are much older since new shoots appear continually to replace older stems as they die (Owen, Pollack, Wiens, unpubl. data).

Distribution of Genetic Variation. Cluster analysis suggested an association between geographical proximity and genetic similarity. The F_{ST} value indicates that the majority of genetic variation resides within, not between populations. These results are compatible with a scenario of a previously more widespread taxon whose range has severely contracted, possibly relatively recently. Since genetic differentiation between populations is low, some degree of gene flow is probably occurring. Studies to determine the relative frequencies of allogamous and geitonogamous pollinations are planned that will contribute information relevant to the distribution of genetic variation in populations.

Significant deviations (nearly all heterozygote deficiencies) from Hardy-Weinberg genotype proportions (table 4) were seen in 17 of the 58 (29%) fixation index tests. These heterozygote deficiencies are not confined to a small number of loci but occur in eight of the 12 loci examined. In addition to inbreeding as an explanation for these deficiencies, differential selection (here differential lethality among seedlings and/or juvenile plants) could also contribute to skewed genotype proportions in adult populations. Greater numbers of heterozygotes were recorded from the three Last Chance Range populations compared with those from the White Mountains. The former mountain range is considerably more arid and hotter than the latter, hence it is tempting to interpret this as evidence that heterosis provides a mechanism for survival in severe environments. One possible explanation that involves selection is that greater vegetative fitness is gained given particular combinations of genetic traits (overdominance). These genotypes would, however, have extremely low heritability.

Phylogenetic Affinities. Reveal and Howell (1976) suggest that *Eriogonum* (sect. *Corymbosum* Benth. in DC.) are the most likely living relatives of *Dedeckera*. Despite some degree of morphological similarity, the affinities between these two groups are tentative at best. A number of other genera in subfamily Eriogoneae occur in the southwestern U.S. and have been considered as possible relatives of *Dedeckera*. These include the genus *Chorizanthe* R. Br. ex Benth. (and its segregate genera *Centrostegia* Gray ex Benth. and *Mucronea* Benth. in DC.) and *Oxytheca* Nutt. A scenario of the early evolution of the subfamily was proposed by Reveal and

Howell (1976) and involved the perennial genera *Chorizanthe, Eriogonum* (certain species), *Dedeckera,* and *Harfordia* Greene & Parry.

The presence of a gene duplication in *Dedeckera* for phosphoglucomutase (fig. 1) may provide a potentially useful genetic marker for testing hypotheses regarding phylogenetic relationships. Duplications at the PGM locus were used to elucidate relationships among sections in the genus *Clarkia* Pursh (Soltis et al. 1987) and among genera related to *Layia* Hook. & Arn. (subtribe Madiinae Benth. & Hook.) in the Asteraceae (Gottlieb 1987). Duplications of gene loci are relatively infrequent, but when present can be used to group taxa into monophyletic assemblages (Gottlieb 1983). In addition to *Dedeckera,* several other genera in subfamily Eriogoneae are narrow endemics, such as *Gilmania* Cov., which is also known only from Inyo County, California. Knowledge of the distribution of the PGM duplication among perennial species of *Corizanthe,* known to have species disjunct in North and South America, would offer further avenues of inquiry into the phylogeny of *Dedeckera* and related genera.

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