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High levels of genetic variation in populations of four dominant aridland plant species in Arizona

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Intrapopulation genetic variation in four dominant, perennial plant species from the deserts of south-western North America was assessed and compared using isozyme techniques. In each of two localities, a warm desert and a cold desert environment, one population of the most common long-lived perennial was compared with a nearby population of a dominant, comparatively short-lived perennial. The warm desert species were *Encelia farinosa* and *Larrea tridentata* while *Gutierrezia microcephala* and *Coleogyne ramosissima* were examined at the cold desert site. All samples were electrophoresed and stained for 18 enzyme systems. Mean values for these four species were 0·173 for gene diversity, 66·9% for polymorphism, and 2·02 for number of alleles per locus. These values are significantly greater than published means from a recent survey of the plant isozyme literature, and are comparable to or higher than levels of genetic variation in other widespread plant species. Differences in level of variation among the species were not significant, thus failing to indicate any relationship between life expectancy and genetic variation. These results demonstrate that aridland plant populations can harbor high levels of genetic variation, and suggest that environmental heterogeneity may be important in the development and maintenance of this diversity.

Key words: evolution; genetic diversity; genetic variation; isozymes; life expectancy; plant ecology; population genetics

Introduction

Evolutionary change is contingent upon the presence of genetic variation, and levels of genetic diversity set limits to the potentials for both response to selection and stochastic differentiation. In a recent review of 653 electrophoretic studies of genetic variation in plants, Hamrick & Godt (1990) demonstrated that a variety of ecological and life-history parameters are significantly correlated with measures of genetic diversity. Strong associations between genetic variation and factors such as breeding system and geographic ranges conform to the expectations of population genetic theory regarding the effects of inbreeding and limited population size (Wright, 1921, 1931). Other relationships, such as regional trends in genetic diversity, and correlations with taxonomic status and life form are generally more difficult to interpret. Continued investigation into these and other associations are important to understand cause and effect relationships between ecological parameters and the maintenance of genetic variation.

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Despite extensive ecological research on plants from arid regions, there is a noticeable lack of information on levels of genetic variation in these systems. Hamrick *et al.* (1979) hypothesized that strong directional selection might result in lower levels of genetic variation in aridland plant populations. Although the results of their survey, as well as those of Nevo *et al.* (1984) exhibited a trend for decreasing genetic diversity with increasing habitat aridity, the number of studies bearing on this question were too few to warrant firm conclusions. More recently, Nevo & Beiles (1988, 1989) documented a trend of increasing population genetic diversity along transects from the outside to the center of the Negev and Sinai Deserts, but these data came primarily from animal species. From both an evolutionary and an ecological perspective, it is important to determine the nature of any possible relationship between arid environments and levels of genetic diversity in plants.

In this study we examined electrophoretic diversity in populations of four dominant, perennial plant species from the deserts of south-western North America. In each of two different localities, one characterized by a warm desert and the other by a cold desert environment, we examined one population of the most common long-lived perennial plant species and another nearby population of a dominant, comparatively short-lived perennial. We compared the resulting genetic diversity statistics to the results of the Hamrick & Godt (1990) survey, and also considered comparisons among these species. We were particularly interested in the relationship between life expectancy and genetic variation, since some data indicate that long-lived perennials support higher levels of intrapopulation genetic variation compared to shorter-lived species (Hamrick, 1979; Hamrick *et al.*, 1979; Mitton, 1983).

The four species examined were woody angiosperms with large geographic ranges. We used similar sampling protocols and sample sizes for each species, and surveyed the same set of isozymes using identical techniques to alleviate problems inherent in comparisons of results from different investigations. The primary questions we addressed were: (1) Do these four species corroborate the suggestion that aridland plants have lower levels of genetic variation compared to plants from other environments? (2) Within these two deserts, do the data suggest a correlation between intrapopulation genetic diversity and life expectancy?

Materials and methods

Study sites and species

The study sites were located in two aridland localities with contrasting environmental conditions, referred to here as the warm and cold desert sites. The warm desert site was located south-west of Oatman, Arizona (Mohave Co., U.S.A.) and 18 km east of the Colorado River at an elevation of 500 m. Mean annual precipitation at nearby Needles, California, is 111·5 mm. Mean monthly temperature is 22·7°C and temperatures seldom drop below freezing. This area is within the Lower Colorado Valley portion of the Sonoran Desert (Shreve & Wiggins, 1964). The cold desert site was located 11·5 km north of Lee's Ferry, Arizona (Coconino Co., U.S.A.), at an elevation of 1340 m, in an area of the Colorado Plateau characterized by a cold desert environment (West, 1983). Mean annual precipitation at nearby Page, Arizona, is 140·9 mm. Mean monthly temperature is 14·5°C and freezing temperatures are common from December through February. This site is 330 km north and east of the warm desert site. Further descriptions of the study sites can be found in Schuster *et al.* (1992*a*).

At each site we located areas dominated by the chosen study species and collected five to 10 fresh leaves from each of 50 contiguous, established individuals for electrophoretic analysis. At the warm desert site, we sampled leaves from *Larrea tridentata* (DC.) Cov. and *Encelia farinosa* Gray. *Larrea tridentata* is an ubiquitous, frequently-dominant evergreen

shrub throughout much of the Sonoran, Mohave and Chihuahuan Deserts (Shreve & Wiggins, 1964). Clonal reproduction allows individuals to persist for at least 700 years, and age estimates of the largest clones exceed 10,000 years (Barbour, 1969; Vasek, 1980). *Encelia farinosa* is a common, drought-deciduous shrub in both the Mohave and Sonoran Deserts; individuals attain ages of 30–50 years at most (Goldberg & Turner, 1986; Turner, 1990).

At the cold desert site we sampled leaves from *Coleogyne ramosissima* Torr. and *Gutierrezia microcephala* (DC.) Gray. *Coleogyne ramosissima* is a dominant plant that often forms pure stands along the margins of the Sonoran, Mohave and Great Basin Deserts (Benson & Darrow, 1957). Individual life-spans can exceed 100 years based on matched photographs (R. Webb, pers. comm.), and one report documented ages up to 240 years based on ring counts (Bounds & West, 1976). *Gutierrezia microcephala* is a common shrub throughout much of arid western North America, especially around disturbed areas. Its maximum life-span has been estimated at 20–30 years (Parker, 1985).

Electrophoresis

Leaves were ground in liquid nitrogen with the grinding buffer of Mitton *et al.* (1979). Samples were stored at −70°C until analysis. Extracts were absorbed onto filter-paper wicks and loaded into 12% starch gels. Three buffer systems were employed to survey 18 different enzyme systems. System 1 was the Histidine II buffer system of King & Dancik (1983). System 2 was the lithium hydroxide, pH 8·1 buffer system of Ridgeway *et al.* (1970). System 3 was a pH 8·0 buffer system with a 0·5 M tris – 0·02 M EDTA – 0·65 m boric acid electrode buffer and a 1 : 9 dilution of the above for the gel buffer. Enzyme systems surveyed were phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGDH), shikimate dehydrogenase (SKD), diaphorase (DIA), acid phosphatase (ACP), malic enzyme (ME), phosphoglucose isomerase (PGI), esterase (EST), superoxide dismutase (SOD), glucose-6-phosphate dehydrogenase (G6PDH), uridine diphosphoglucose-pyrophosphorylase (UDP), malate dehydrogenase (MDH), glutamate dehydrogenase (GDH), aminopeptidase (AMP), glutamate oxaloacetate transaminase (GOT), glycerate dehydrogenase (GLYDH), leucine aminopeptidase (LAP), and alkaline phosphatase (ALKP).

Multiple loci and alleles were numbered sequentially according to speed of anodal migration. Loci were selected for scoring on the basis of clear and consistent interpretability, based on information on enzyme structure and banding patterns (Weeden & Wendel, 1989). Identical standards were loaded on all gels to ensure consistent scoring of allelomorphs.

Data analysis

Data were analysed with the computer package BIOSYS-1 (Swofford & Selander, 1989). For each species we determined the following variability measures: percentage of polymorphic loci (P), using the criterion that the frequency of the most common allele was less than 99%; Nei's (1978) unbiased estimate of gene diversity (H_e), or expected heterozygosity; the mean number of alleles per locus (A); and Wright's fixation index (F), averaged over all loci (Jain & Workman, 1967).

We used t-tests to compare mean levels of variation for the above indices between the long- and shorter-lived species within each site. Our use of a parametric test was based on the observation that gene diversity distributions approach normality above a nominal level (approximately 7·5%), and thus type-I error rates in computer simulations approach values expected with the t-test (Archie, 1985). Individual measures were transformed as arcsine square-roots before analyses, which helped to normalize distributions and equalize

variances (Sokal & Rohlf, 1981). All comparisons were made twice: once using all available data, and a second time using data from only those loci successfully scored in both taxa under consideration.

The mean and standard errors for P, H_e, and A over all four species were then used for comparisons with intrapopulation diversity measures from the survey of Hamrick & Godt (1990). We compared our data with values for all 468 taxa for which comparable data were available (mean values of 34·2, 0·113 and 1·53 for P, H_e, and A, respectively) and also with means for 85 of these 468 taxa with wide geographic ranges (43·0, 0·159, and 1·72, respectively).

Results

Twenty-six to 30 putative enzyme loci were observed for the species under consideration (Table 1), although many were not resolved due to problems with weak expression, poor resolution, or uninterpretable phenotypes. The numbers of successfully resolved loci were: 21 in *Encelia farinosa*, 20 in *Larrea tridentata*, 15 in *Gutierrezia microcephala*, and 23 in *Coleogyne ramosissima*. Despite reports of polyploid races in *L. tridentata* and *G. microcephala* (e.g. Solbrig, 1960; Hunziker *et al.*, 1972), individuals in these populations exhibited typical diploid banding patterns. The number of banding zones interpreted as distinct loci for each enzyme system was generally consistent across the species. Observed differences in six systems (PGM, UDP, EST, DIA, GOT, LAP) may have resulted from poor enzyme activity, or possibly differential gene duplication and/or silencing (Gottlieb, 1982).

Substantial amounts of electrophoretic variation were observed in all four taxa (Table 2). Mean values for gene diversity, polymorphism and alleles per locus for these aridland plants were all significantly greater ($p < 0·05$) than mean values based on 468 plant taxa reported by Hamrick & Godt (1990). The observed values were also greater than the means based on 85 widespread species, but the difference was significant only for per cent polymorphic loci ($p < 0·05$).

Genetic variation measures in the long-lived *Larrea tridentata* were the lowest among the four species examined (Table 2). The co-occurring and shorter-lived *Encelia farinosa* exhibited the highest levels of intrapopulation variation, but the differences between these two species were not statistically significant. There was no corresponding trend for genetic variation measures in the longer-lived *Coleogyne ramosissima* to be less than in the shorter-lived *Gutierrezia microcephala*. The population of *G. microcephala* exhibited an excess of heterozygotes compared to Hardy-Weinberg expectations, while the other three species exhibited slight deficiencies, but none of the fixation indices differed significantly from zero. Differences in the fixation index between species at each site were also non-significant. The values in Table 2 represent data for all surveyed loci: statistics based only on loci successfully scored for both species in each comparison were not substantially different, and also exhibited no significant differences among species.

Discussion

The results indicate that these aridland plant species are genetically quite variable, which does not support the argument that such species should be less variable than plants from more mesic environments. In fact, these reported levels are significantly higher than average values from a recent survey of genetic variation in 468 plant taxa. We conclude that there is abundant variation within these plant populations which may facilitate response to natural selection and environmental change, and permit processes such as genetic structuring and differentiation. Other data are accumulating that also indicate high levels

Table 1. *Enzyme systems and loci surveyed, buffer systems employed, and results obtained for population samples from four species of dominant aridland plants*

Enzyme system*	Buffer system*	Locus	Results† Warm desert species *Encelia farinosa*	Warm desert species *Larrea tridentata*	Cold desert species *Gutierrezia microcephala*	Cold desert species *Coleogyne ramosissima*
PGI	2	1	+	+	+	+
		2	+	+	+	+
PGM	1	1	+	+	+	+
		2	0	+	−	+
UDP	1	1	+	+	+	+
		2	0	+	0	−
6PGDH	1	1	−	+	−	+
		2	−	−	−	+
SKD	1	1	+	+	−	+
MDH	2	1	+	−	+	+
		2	+	−	+	−
EST	3	1	+	−	−	+
		2	+	+	−	+
		3	−	−	−	+
SOD	3	1	+	+	−	+
		2	−	+	−	+
DIA	1	1	+	+	+	+
		2	+	0	−	−
GDH	2	1	+	+	+	+
G6PDH	3	1	+	+	−	−
ACP	1	1	−	−	−	−
		2	+	−	+	+
AMP	2	1	+	−	+	+
		2	+	−	−	−
ME	1	1	+	+	+	+
GOT	2	1	+	+	−	+
		2	0	+	+	−
GLYDH	2	1	+	+	+	+
LAP	2	1	−	−	+	+
		2	0	+	+	+
ALKP	2	1	+	+	−	+

* Enzyme and buffer systems descriptions in text.
† +, Successfully scored loci; −, unresolved loci; 0, loci not observed.

of genetic variation within aridland plant populations (Parker & Hamrick, 1992; Schuster *et al.*, 1992*a*; Schuster *et al.*, 1992*b*).

Cause and effect relationships among measures of genetic variation and ecological and environmental parameters are difficult to assess (Hamrick, 1982). However, we feel that a hypothesis of lower genetic variation in aridland plants due to directional selection is untenable in our study areas. Spatially, these aridlands are characterized by differences in substrate, soil structure, slope and aspect that create a mosaic of microhabitats and vegetation patterns (Parker, 1991). These sites also experience temporal heterogeneity in precipitation, the most important requirement for plant growth in arid environments. There is a significant, negative correlation between annual precipitation amount and predictability in the western United States (Ehleringer, 1985; Comstock & Ehleringer,

Table 2. *Levels of genetic variation and inbreeding coefficients for populations of four dominant aridland plant species (S.E.M. in parentheses;* n = *50 for each species)*

Species	Gene diversity†	Polymorphism‡	Alleles per locus	Fixation index
Warm desert				
Encelia farinosa	0·210 (0·048)	78·9	2·28 (0·21)	0·096 (0·178)
Larrea tridentata	0·134 (0·047)	50·0	1·80 (0·22)	0·077 (0·283)
Cold desert				
Gutierrezia microcephala	0·180 (0·052)	60·0	2·00 (0·26)	−0·049 (0·088)
Coleogyne ramosissima	0·168 (0·044)	78·9	2·00 (0·15)	0·046 (0·192)
Mean	0·173 (0·016)*	66·9 (7·19)*	2·02 (0·10)*	0·042 (0·032)

† Unbiased estimate of Hardy-Weinberg expected heterozygosity (H_e; Nei, 1978).
‡ Loci considered polymorphic if the frequency of the most common allele was < 0·99.
* Values significantly greater than mean values for 468 plant taxa surveyed by Hamrick & Godt (1990).

1992), and hence extreme temporal variation at these desert locations. Theoretical and empirical studies have indicated that such environmental heterogeneity can lead to the maintenance of high levels of intrapopulation genetic variation (Hedrick *et al.*, 1976; Ewing, 1979; Gillespie & Turelli, 1989). In addition, individual heterozygosity may be important for the ability to survive under such stressful conditions (Parsons, 1987; Rainey *et al.*, 1987; Mopper *et al.*, 1991).

The wide geographic ranges and ubiquity of these species suggest large interbreeding population sizes which may facilitate the maintenance of high levels of genetic variation. Our results are also indicative of species with predominantly outbreeding mating systems, and in fact *E. farinosa* is considered to be an obligate outcrosser (Kyhos *et al.*, 1981). While Solbrig (1960) suggested that the flowers of *G. microcephala* are mechanically adapted for outbreeding, the mating systems of this species, *L. tridentata* and *C. ramosissima* have received little experimental attention.

These high levels of intrapopulation variation are not likely to be spurious. The populations we studied were all sampled within the central portions of the species' ranges. Preliminary data on genetic diversity in additional populations of two of these species (*E. farinosa* and *G. microcephala*) indicate that these reported values are typical (W. Schuster, unpubl. obs.). Our sampling scheme (50 contiguous individuals) might have resulted in the oversampling of family-groups due to the structure frequently found in plant populations (Schaal, 1980; Linhart *et al.*, 1981). In this case, a wider sampling would have resulted in even higher estimates of variation. In addition, these population estimates may be indicative of overall genetic variation at the species level. The survey of Hamrick & Godt (1990) reported a strong positive correlation between intrapopulation and species-level variation.

We did not find positive correlations between measures of genetic variation and life expectancy, as have occasionally been reported for other species (Hamrick, 1979; Hamrick *et al.*, 1979; Mitton, 1983). While individuals of long-lived species may well experience greater environmental variation during a lifetime compared to shorter-lived plants, it is difficult to predict whether this will select for individuals with greater genetic variation (Mitton, 1983), or against genetically-extreme individuals, thus reducing population genetic variance (Schuster *et al.*, 1992*b*). One major difficulty with such comparisons is the wide inter-locus variance in measures of genetic diversity that severely restricts the ability of surveys to detect significance differences (Nei & Roychoudhury, 1974). Notwithstanding these difficulties, factors other than life-span may well have more important influences on levels of genetic variation. Hamrick (1979) suggested that

correlations between life expectancy and genetic variation may be due to underlying correlations with mating systems or taxonomic groupings.

These results further our understanding of ecological and evolutionary phenomena in aridland plant populations and suggest important interactions between environmental heterogeneity and genetic variation. More detailed studies must be done to understand these relationships fully, quantifying temporal and environmental heterogeneity (e.g. coefficient of variation of annual precipitation) and correlating these with levels of intrapopulation genetic variation. Depending on the mechanisms responsible for generating and maintaining genetic variation in these species, we might predict range-wide correlations between measures of environmental heterogeneity and levels of genetic variation, genetic heterogeneity among contrasting sites in close proximity, and/or more highly heterozygous individuals in more stressful microsites and habitats. Experimental manipulations and studies of selection on known genotypes could be particularly instructive. This paper has established the potential importance of such studies by demonstrating the existence of abundant genetic markers with which to study ecological diversification and evolutionary mechanisms in these aridland plants.

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