

POPULATION- AND FAMILY-LEVEL VARIATION OF BRITTLEBUSH (*ENCELIA FARINOSA*, ASTERACEAE) PUBESCENCE: ITS RELATION TO DROUGHT AND IMPLICATIONS FOR SELECTION IN VARIABLE ENVIRONMENTS¹

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Because leaf pubescence of the desert shrub *Encelia farinosa* increases in response to drought and influences photosynthesis and transpiration, we hypothesized that differences in water availability across the range of this species may result in genetic differentiation for pubescence and associated productivity traits. We examined maternal family variation of pubescence-moderated light absorption (absorptance) in three populations of *E. farinosa*. Absorptance was always greatest for plants from the high-rainfall environment and lowest for those from the driest site, but the rate of absorptance change in response to drought was similar among all populations. Similar patterns were found when we compared families within populations—all genotypes had similar initial leaf absorptances, differentiated very early in seasonal growth, then had concordant changes in absorptance thereafter. However, family-level variance was greatest for plants from the driest site, a region with highly heterogeneous precipitation patterns, whereas low variance was found for plants from the wettest, least heterogeneous site. The concordance of leaf absorptance changes, within and among populations, may be due to integration with other drought-related traits; however, the differences in absorptance values within and among populations suggest that variation of leaf pubescence results from selection associated with geographical and local patterns of water availability.

Key words: absorptance; adaptation; Asteraceae; brittlebush; desert; drought acclimation; *Encelia farinosa*; leaf pubescence; maternal family variance; spatiotemporal heterogeneity.

In arid regions the spatial and temporal heterogeneity of resources can be very high (Noy-Meir, 1973; Le Houérou et al., 1988; Frank and Inouye, 1994). Thus, widely distributed desert species are challenged to adapt to this variability over a broad geographic scale and also on local scales, where unpredictability of limiting resources can be extreme (MacMahon and Schimpf, 1981; Lajtha and Schlesinger, 1986; Le Houérou et al., 1988; Ehleringer, 1994). The influence of heterogeneous water availability is especially important in the evolution of desert plant species because water is the most limiting resource for productivity in desert ecosystems (Noy-Meir, 1973; Fischer and Turner, 1978; Hadley and Szarek, 1981).

For the widespread desert perennial *Encelia farinosa* A. Gray (Asteraceae), traits associated with water use and productivity have been shown to vary on local and regional scales (Cunningham and Strain, 1969; Ehleringer and Cook, 1990; Monson et al., 1992; Sandquist and Ehleringer, 1997, 1998; Housman et al., 2002). One of these traits, leaf pubescence, is important for productivity under hot and dry desert conditions because the highly reflective pubescence decreases absorption of solar radiation and decreases the heat load on a leaf (Ehleringer and Clark, 1988). During drought, each consecutive leaf cohort has a greater density of leaf hairs, which helps maintain leaf temperatures within the narrow range favorable

for photosynthesis while also lowering dependence on water for transpirational cooling (Smith and Nobel, 1977; Ehleringer and Mooney, 1978; Ehleringer, 1983). In the absence of water deficit, however, each cohort will maintain approximately the same, low amount of leaf pubescence (Ehleringer, 1982).

Increasing pubescence during drought is also associated with longer maintenance of the leaf canopy (Sandquist and Ehleringer, 1997). Although this extended activity can enhance productivity by increasing the longevity of daily and seasonal photosynthesis, there are also productivity trade-offs associated with greater pubescence. These include the additional costs for construction of the pubescence and lower rates of photosynthesis from leaf hairs reflecting photosynthetically active radiation (PAR). There is also an opportunity cost because the degree of pubescence cannot be changed after the leaf has expanded and the plant cannot produce newer primary leaves with higher light absorption (lower pubescence). Highly absorptive leaves can be produced only after a plant has become leafless or as small axillary leaves among the larger pubescent leaves (Ehleringer and Björkman, 1978; Ehleringer, 1982). Thus, pubescence constrains maximum PAR absorption if water stress is alleviated in the middle of a drought.

Interpopulation variability of leaf absorptance for *E. farinosa* may result from the balance between these costs and benefits over regional differences in precipitation and drought. In addition, variation at the intrapopulation level might also be present as a result of the interplay between this trade-off and local climatic heterogeneity. Such predictions are analogous to the density of trichomes being involved in (1) defense, in which variation is related to the presence or absence of herbivores (Levin, 1973; Bécerra and Ezcurra, 1986), and (2) thermoregulation, in which variation correlates with elevation

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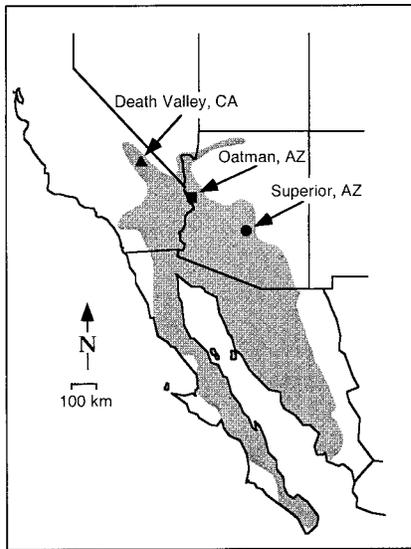


Fig. 1. Distribution of *Encelia farinosa* (shaded area) in southwestern North America and the three populations from which seeds were collected for common environment studies. Rainfall increases and drought length decreases along a northwest to southeast transect that encompasses these three populations (see Table 1).

(Baruch, 1979). For these two selective factors, evolutionary responses of trichome morphology and density, including heritability, have been well documented (e.g., Levin, 1973; Baruch, 1979; Gibson and Maiti, 1983; Vasek, 1986). Despite numerous studies that demonstrate the importance of leaf pubescence for productivity in *E. farinosa*, the genetic basis for phenotypic variation of leaf hair production has not been quantitatively analyzed.

To explore the evolutionary potential of leaf pubescence in *E. farinosa*, we examined the maternal family variability of pubescence-moderated leaf absorptance for three populations that span a broad gradient of water availability. Previous comparisons among populations of *E. farinosa* have shown that the leaf absorptance values of the initial leaf flush can be similar (Sandquist and Ehleringer, 1997, 1998), but after this stage, discrete differences occur. Leaf absorptance is consistently greater for plants from regions of high rainfall relative to those from lower-rainfall environments (Sandquist and Ehleringer, 1997; Housman et al., 2002), and in a preliminary common garden study of *E. farinosa* plants from nine populations, absorptance was correlated to the mean annual precipitation of the seed source regions (Sandquist, 1995). These findings suggest that local adaptation and genetic divergence have given rise to variation of absorptance among populations; however, the implied genetic determination for this variation has never been detailed.

The goals of the present investigation were to (1) determine if differences for leaf absorptance values and responses to drought result from genetic differentiation among populations, (2) examine the degree of family-level variance (V_G) present within populations to see how it might be related to the differences of climatic heterogeneity, and (3) provide insights about the potential selective processes operating within and among populations. We made use of three *E. farinosa* populations from a broad gradient of annual precipitation amount and maximum drought length. At one end of the gradient, where rainfall is low and drought is long, selection should

TABLE 1. Long-term averages for annual precipitation and maximum length of annual drought for sites of the three seed-source populations used in this study. Also given is the coefficient of variation (CV)^a as a measure of the unpredictability of the means. Data were compiled from United States National Weather Service records, 1931–1980.

| Site | Annual precipitation | | Maximum drought duration | |
|--------------|----------------------|--------|--------------------------|--------|
| | Mean (mm) | CV (%) | Mean (d) | CV (%) |
| Superior | 453 | 32 | 45 | 30 |
| Oatman | 111 | 51 | 75 | 71 |
| Death Valley | 52 | 63 | 159 | 39 |

^a CV = (standard deviation × 100)/mean (thus expressed as a percentage).

strongly favor leaf pubescence, thereby reducing genetic variance, specifically, additive genetic variation (V_A), for this trait (Falconer, 1989). However, this environment is also unpredictable, being temporally heterogeneous on both an inter- and intra-annual basis. Thus, a high degree of genetic variability (V_A) may be maintained if disruptive selection is strong and alternative genotypes can survive through unfavorable years (Ellner and Hairston, 1994). At the other end of the gradient, rainfall is high and drought duration is short. Here, pubescence should play a less important role in productivity, and selection for high leaf pubescence should be weaker. However, this expectation does not preclude the possibility of finding reduced variance resulting from either consistency of this selection or via selection for higher PAR absorption (i.e., against high leaf pubescence) (Falconer, 1989).

Knowledge of the genotypic basis for variation of leaf pubescence is necessary so that we may better understand the potential for adaptation and adaptability of *E. farinosa* over its broad geographic range and within highly variable local environments.

MATERIALS AND METHODS

Study species, growth conditions, and protocol—*Encelia farinosa*, brittlebush, is an outcrossing perennial shrub that is widespread throughout the Sonoran and Mojave Deserts of southwestern North America (Fig. 1). Its range encompasses areas where mean annual rainfall can be as low as 25 mm to as great as 500 mm. Average maximum drought length also varies over its distribution, from less than 45 d to at least 160 d (Sandquist, 1995). This geographic variability is accompanied by variability of temporal patterns in precipitation and drought. Annual and seasonal rainfall is most unpredictable where average rainfall is lowest (Hastings and Turner, 1965; Ehleringer, 1985; Comstock and Ehleringer, 1992), while drought length varies in relation to the termination of spring rainfall and the onset of summer monsoon rain (Ehleringer, 1994). The most unpredictable drought length is found where summer monsoons die out in weak years but continue to advance in strong monsoon years. This region is roughly along the boarder of Arizona and California in North America.

Encelia farinosa plants from three natural populations were used as seed sources for our common environment studies. These populations were located at Superior, Arizona; Oatman, Arizona; and Death Valley, California (Fig. 1). Long-term averages and the coefficients of variation (CV) for annual precipitation and maximum drought length at these localities are given in Table 1. The CV represents a measure of the unpredictability of these averages (Hastings and Turner, 1965)—a greater CV value indicating higher year-to-year unpredictability.

Seeds were collected from individual (maternal) plants in spring 1991. Plants raised from the seeds of one maternal plant make up a family, and the relatedness of individuals within each family can range from half sibling to full sibling. Seeds were collected from numerous flower heads throughout the

plant and on two different dates. The seeds were germinated in spring 1992 and raised for 45 d, receiving water twice daily, in the University of Utah greenhouse (Salt Lake City, Utah, USA). Plants were then transplanted in mid-June to large pots containing approximately 55 L of sand. Ten families with eight individuals per family were used for the Oatman and Death Valley populations. For Superior, only five families of eight individuals each could be used because of lower germination rates. The potted plants were randomly arrayed in a uniform open field of the University of Utah Experimental Research Garden.

Plants were watered to pot capacity every day for 1 mo, after which the first leaf absorbance measurements were made (designated "predrought"). Watering was then reduced to once every 5 d for the next 3 wk, with natural precipitation providing additional water on two dates. After this 3-wk period, the "early drought" measurements of leaf absorbance were made. Light rain showers on five of the next 13 d, plus one final water supplement during this period, was the only water input for the next month. By the final date of leaf absorbance measurements ("mid-drought"), plants had not received any water for 20 d. Temperature conditions during the course of the study were within the normal range experienced by all populations, but were most similar to those experienced by plants of the Superior population.

Absorbance, the percentage of light absorbed relative to a MgO standard that absorbs <1%, was measured using an Ulbricht-type integration sphere and a monochromatic wavelength of 625 nm (Ehleringer, 1981). This method closely approximates the integrated absorbance of all photosynthetically active radiation (400–700 nm) and is highly correlated with total solar radiation absorption (400–3000 nm).

On each sample date, one leaf of the most recently matured leaf cohort was removed for determination of leaf absorbance. Leaves were kept in plastic bags and refrigerated until measured. All leaves were measured within 72 h (<72 h), so that the time since leaf removal would not influence absorbance values (Sandquist, 1995). Plants were measured at random among populations.

Among populations analyses—Analysis of variance with repeated measures (ANOVAR; JMP 3.1 statistical package, SAS Institute, 1994) was used to test the overall differences in leaf absorbance among populations (population effect, P), differences in responses to drought (population by drought stage effect, P × D), and effects based on drought stage (D). The recommendations of Potvin et al. (1990) were used for ANOVAR tests. All data conformed to the assumption of compound symmetry based on the Mauchly criterion or had a Huynh-Feldt epsilon (H-F ϵ) that neared unity (>0.95). In the latter cases, drought stage and population by drought stage effects were tested using the Huynh-Feldt epsilon correction for *F* values and probabilities (Potvin et al., 1990). Pillai's trace was always used for population effects and for D and P × D effects when H-F ϵ = 1.0.

Differences among populations for mean leaf absorbance at a single drought stage were tested by the Kruskal-Wallis nonparametric rank test (JMP 3.1, SAS Institute, 1994). This test was chosen because the assumption of homogeneity among group variances was occasionally violated depending on the method used for its determination (see JMP 3.1; SAS Institute, 1994). Note, however, that these differences of variance only slightly influenced, if at all, the assumption of compound symmetry for the ANOVARs.

Within populations analyses—Analysis of variance with repeated measures was also used as one test of the genetic and environmental components of variance for absorbance within populations. Effects due to family (F), drought stage (D), and family by drought stage (F × D) were determined (JMP 3.1, SAS Institute, 1994). This intrapopulation, family-based partitioning of seasonal variances for leaf absorbance provides broad estimates of the genetic variation corresponding to overall leaf absorbance and changes caused by drought (i.e., reaction norms).

In addition, an estimate of quantitative genetic variance (V_G) for leaf absorbance within each population was determined for each drought stage. The least squares method, Model II ANOVA, was used to determine family-based variance components (V_G) (Falconer, 1989; JMP 3.1, SAS Institute, 1994). From these, maximum and minimum values of broad-sense heritabilities were calculated based on the possible range of individual relatedness being half-

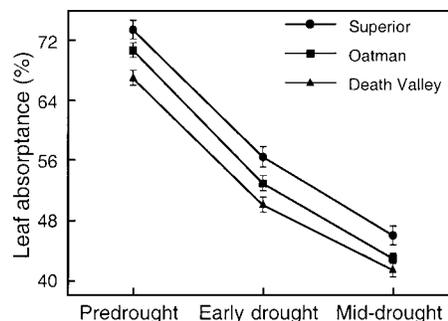


Fig. 2. Mean leaf absorbance at different drought stages for three populations of *Encelia farinosa* growing under common environment conditions. Leaf absorbance values differed among populations ($P < 0.001$) and among drought stages ($P < 0.001$), but the population by drought stage interaction was not significant ($P = 0.06$), indicating that the slopes of response to drought were similar among populations.

sib to full-sib (*E. farinosa* is an obligate outcrosser). In the strictest sense, this estimate of V_G includes one-fourth additive genetic variance (V_A) plus 1/16 of the epistatic effects, if any. However, dominance variance (V_D) and maternal effects confound this strict interpretation of V_A , and our design, unfortunately, does not allow for the determination of these factors. Therefore, our calculation of the intraclass correlation (t) is based only on family variance (V_G) divided by the total variance. This value is then used to estimate the broad-sense heritability (H^2) as $4t$ (Falconer, 1989).

Intrapopulation phenotypic correlations of leaf absorbance (pairwise comparisons among drought stages) were determined with the Pearson product-moment correlation (JMP 3.1, SAS Institute, 1994). Estimates for family mean correlations among drought stages were based on the Pearson product-moment correlation among mean leaf absorbance values for each family (Via, 1984).

RESULTS

Interpopulation variation of leaf absorbance—Mean leaf absorbance values decreased for all populations over the course of drought (Fig. 2), but these means were already different on the first sampling date (predrought). The fact that population means had differentiated while water and temperature stress were lowest suggests that plants at this stage may have experienced some degree of water stress or that these changes may take place, not in response to drought, but as a predetermined aspect of plant development that may differ at the population level—a possibility that deserves additional study. Because of this early deviation among populations, we could not directly address questions regarding the initiation of leaf absorbance differences among populations. Our results are confined to the questions of variability for overall leaf absorbance and the rate of change during drought.

Populations differed for overall leaf absorbance as indicated by a significant population effect in the among-populations ANOVAR ($F_{2,22} = 32.01$; $P < 0.001$). However, the rates of absorbance responses to drought (i.e., slopes in Fig. 2) did not differ among populations ($F_{4,44} = 2.47$; $P = 0.06$). Further examination showed that leaf absorbance means were significantly different among populations at all three periods of sampling (predrought $H = 50.05$, $P < 0.001$; early drought $H = 51.8$, $P < 0.001$; mid-drought $H = 33.9$, $P < 0.001$), with relative ranks remaining constant throughout the drought period. Superior plants always maintained the greatest leaf absorbance and Death Valley plants the lowest (Fig. 2).

Intrapopulation variation of leaf absorbance—Leaf absorbance variation due to family effect was significant within

TABLE 2. Family, drought stage, and family by drought stage effects on leaf absorptance values within each *Encelia farinosa* population. Shown are the *F* values and significance levels for family, drought stage, and family by drought stage effects (df = 4, 2, and 8 for Superior and 9, 2, and 18 for both Oatman and Death Valley, respectively) based on an analysis of variance with repeated measures. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001. NS = not significant.

| Site/statistic | Leaf absorptance sources of variation | | |
|---------------------------------|---------------------------------------|---------------|-------------------------|
| | Family | Drought stage | Family by drought stage |
| Superior | | | |
| <i>F</i> | 1.985 NS | 651.0*** | 1.350 NS |
| <i>P</i> | 0.121 | <0.001 | 0.236 |
| Oatman^a | | | |
| <i>F</i> | 2.058* | 1250.0*** | 1.231 NS |
| <i>P</i> | 0.047 | <0.001 | 0.250 |
| Death Valley^a | | | |
| <i>F</i> | 2.682* | 946.0*** | 1.190 NS |
| <i>P</i> | 0.010 | <0.001 | 0.279 |

^a For Oatman and Death Valley, H-F ϵ = 0.96 and 0.99, respectively. Thus, *F* values and probabilities for drought stage and family by drought stage effects are based on the Huynh-Feldt correction (Potvin et al., 1990).

the Oatman and Death Valley populations, but not the Superior population (Table 2). All three populations had significant differences in leaf absorptance due to drought stage, but the family by drought stage effect was not significant within any population (Table 2). The latter result suggests that differentiation is low among families for leaf absorptance changes through drought; however, some variation may exist because family-level reaction norms for absorptance response to drought occasionally crossed (data not shown).

Estimates of intrapopulation genetic variance for leaf absorptance were also determined for all drought stages (Table 3). Superior plants never had a significant family-based variance component for leaf absorptance, a result that corresponds with the lack of a family effect in the ANOVA for this population (Table 2). However, because of the small number of maternal families used from this population, this result should not be interpreted as indicating a complete absence of such variation ($V_G + V_M$). For Oatman and Death Valley populations, family-level variance was a significant component of the phenotypic variance but not for every drought stage (Table 3). Only the early drought sample had a significant intraclass correlation for Oatman plants, while both early drought and mid-drought leaf absorptances for Death Valley had significant intraclass correlations (Table 3). The phenotypic variance of predrought leaf absorptance did not have a significant family component in any of the populations (Table 3).

Heritability estimates (H^2) were calculated for leaf absorptances when intraclass correlations were significant (Table 3). The maximum values, based on half-sib relatedness among progeny from each maternal parent, were generally high. Minimum H^2 values, based on an assumption of full-sib relatedness, were 0.462 for Oatman plants at the early drought stage and 0.586 and 0.232 for Death Valley plants at the early and mid-drought stages, respectively (Table 3). These minimum values, however, are only approximate because V_G calculated from full-sib-related families includes one-quarter dominance effects.

TABLE 3. Estimates of variance components and broad-sense heritabilities for leaf absorptance of each *Encelia farinosa* population at three drought stages. Heritability ranges are based on full-sib relatedness (minimum value) to half-sib relatedness (maximum value) within families (see Materials and Methods). * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001. NS = not significant.

| Site/absorptance stage | Variance components | | Intraclass correlation | Heritability |
|------------------------|---------------------|-----------------|------------------------|--------------|
| | Family (V_G) | Total (V_P) | | |
| Superior | | | | |
| Predrought | 0.284 | 11.954 | NS | — |
| Early drought | 2.978 | 20.637 | NS | — |
| Mid-drought | 1.800 | 14.700 | NS | — |
| Oatman | | | | |
| Predrought | -0.462 | 17.883 | NS | — |
| Early drought | 3.915 | 16.933 | 0.231** | 0.462–0.925 |
| Mid-drought | -0.356 | 7.588 | NS | — |
| Death Valley | | | | |
| Predrought | 0.015 | 23.127 | NS | — |
| Early drought | 3.102 | 10.582 | 0.293*** | 0.586–1.172 |
| Mid-drought | 1.723 | 14.858 | 0.116* | 0.232–0.463 |

Within all three populations, predrought leaf absorptance did not correlate with values at later drought stages (Table 4). All three populations, however, had significant phenotypic correlations between early and mid-drought leaf absorptance. Significant family mean correlations (*P* < 0.05) were also observed among these periods for the Superior and Death Valley populations, while for the Oatman population this family correlation was significant at *P* = 0.059 (Table 4).

DISCUSSION

Trade-offs associated with leaf pubescence and differences in soil-water availability over the broad range of *E. farinosa* should affect leaf absorptance variation among populations. In this study, we examined the degree of variation present within populations, the relationships associated with drought and regional differences in water availability, and the potential genetic basis (which may include maternal effects) for leaf absorptance differentiation. We found that leaf absorptance differences among populations had a potential genetic basis (Fig.

TABLE 4. Phenotypic correlations (above diagonal) and genetic maternal (family) correlations (below diagonal) of leaf absorptance values among drought stages within each *E. farinosa* population. Correlations are based on Pearson product-moment correlations. † *P* < 0.06; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

| Site/absorptance stage | Absorptance stage | | |
|------------------------|-------------------|---------------|-------------|
| | Predrought | Early drought | Mid-drought |
| Superior | | | |
| Predrought | — | 0.144 | -0.051 |
| Early drought | 0.765 | — | 0.550*** |
| Mid-drought | -0.020 | 0.908* | — |
| Oatman | | | |
| Predrought | — | 0.086 | 0.202 |
| Early drought | 0.476 | — | 0.344** |
| Mid-drought | 0.067 | 0.614† | — |
| Death Valley | | | |
| Predrought | — | 0.004 | 0.094 |
| Early drought | 0.193 | — | 0.270* |
| Mid-drought | 0.289 | 0.725* | — |

2) and that intrapopulation genetic variance (family level) for leaf absorptance was present in two of three populations surveyed (Table 3). In contrast, there was no apparent genetic variation for the rate of leaf absorptance change through the drought period either among populations (Fig. 2) or within them (Table 2). These results suggest that these populations have become genetically differentiated for the overall value of leaf absorptance, but not for the relative rate of leaf absorptance reduction during drought.

Leaf pubescence and environmental variability—A consistent pattern observed in comparisons among *Encelia* species is that plants from regions of high precipitation always have greater leaf absorptance than those of drier regions (Ehleringer, 1985). This pattern has also been found within *E. farinosa* (Sandquist and Ehleringer, 1997, 1998; Housman et al., 2002), and because leaf absorptance variation affects differences in productivity (Ehleringer, 1983; Ehleringer and Cook, 1990), divergence among populations may represent local adaptation to soil-water availability.

This conclusion implies that strong selective pressures have given rise to differences in leaf absorptance among populations, but such selection should reduce the genetic variance within populations (Falconer, 1989). Our results, however, indicate that family-based (genetic or maternal) variation may persist within some populations (Tables 3 and 4), suggesting that either (1) selection has not been strong enough or consistent enough to eliminate genetic variance for leaf absorptance, (2) prevalence of dominance and maternal effects overwhelm selective influences, or (3) local spatial/temporal heterogeneity is great enough to support polymorphic populations (e.g., Ellner and Hairston, 1994). Furthermore, the amount of this genetic variance appears to be related to the unpredictability of the environments from which these populations originated. Family-level variance was greatest where temporal (and presumably spatial) heterogeneity of precipitation is high (Death Valley) and least where heterogeneity of precipitation is low (Superior) (Tables 1 and 4). This result is consistent with predictions based on the relationship between genetic variance and environmental heterogeneity, but it must also be viewed with caution because of the small maternal family-level sample size of the Superior population. Nonetheless, because broad-scale differentiation among populations is correlated with soil-water availability, one might also predict that the same mechanisms of selection could contribute to variation within populations, especially where precipitation is highly variable. That is, within a population some plants may be adapted to low levels of water availability and others adapted to higher levels. This suggestion seems to contradict a general evolutionary pattern in which genotypes that do well across all climates (high plasticity), but do best in neither extreme, should be favored in heterogeneous environments based on a greater geometric mean fitness (Marshall and Jain, 1968; Cooper and Kaplan, 1982; Seger and Brockmann, 1987). However, diverse genotypes within a population could persist if disruptive selection is strong enough and the genotypes that are not favored in a given year have some means of surviving through those unfavorable years (Ellner and Hairston, 1994).

A slight variation of this same mechanism is evident when populations of highly heterogeneous environments never reach equilibrium because there is greater incidence of catastrophic events (e.g., drought) during which genotypes that are at a competitive disadvantage under normal climatic conditions

could realize greater relative fitness. It is also possible that strong selection, based on microclimatic variation, could maintain highly localized population structuring over short distances (Levin, 1973; Monson et al., 1992), and if gene flow is not constrained by such localization, the genetic variation of the progeny from a maternal plant (as used in this study) may be greater than that of the natural population (in which variance is reduced by selection within each microclimate). In this case, our results would instead represent the possible evolutionary potential of the population.

Finally, measurements of genetic variance must also take into consideration genotype-by-environment interactions because the observed genetic variance can be dependent on the environment (Gupta and Lewontin, 1982; Mitchell-Olds and Rutledge, 1986). Indeed, our study was done in only one environment, one that had fairly high water availability and cooler temperatures than the drier populations might experience during normal years. It was, therefore, more similar to the selective regime of the wetter population (Superior) and thus may have lowered the observed family variance for this population. However, it should also be recognized that higher-than-average water availability is also an important component for selection in dry regions and may be one of the agents that maintains genetic variance within populations like Oatman and Death Valley.

Our investigation was not designed to determine the mechanism responsible for maintenance of genetic variance within these populations, but it does demonstrate the following for leaf absorptance of *E. farinosa*: (1) genetic variance potentially does exist, (2) it may be related to the degree of environmental heterogeneity, and (3) from this variation there may be the potential for local adaptation.

In contrast to the variation in mean leaf absorptance, family variation for the slope of leaf-absorptance reduction during drought was very low at both the inter- and intra-population levels. This low variability might result from the importance of coupling leaf absorptance changes with other physiological and developmental characters that also change in response to reduced soil water. Indeed, Ehleringer and Cook (1984) showed that reductions in both leaf absorptance and stomatal limitations were correlated to the rate of decrease in water availability (i.e., water potential). Strong selection for drought-response trait associations could indirectly reduce the variance of the leaf absorptance response. Such low genetic variability would still allow among-environment difference as seen in field observations (Sandquist and Ehleringer, 1998; Housman et al., 2002), but it would preclude strong differentiation in a common environment unless maternal effects are rather strong.

The observation that leaf absorptance reduction rates are invariable while mean leaf absorptance values are distinctly different raises the question as to when leaf absorptance differentiation takes place? Results from the interpopulation comparison suggest that this departure must occur very early in development because differentiation had already taken place prior to the earliest measurements. This implies that the interpopulation differences resulted from a genetically controlled divergence of leaf absorptance during the initial leaf flushes, or if populations start with the same leaf absorptance values (as in Sandquist and Ehleringer, 1997), the differences would result from leaf absorptance changes that take place very early and under generally favorable conditions.

Intrapopulation patterns may also indicate that differentiation takes place during early development, albeit at a slightly

later period than among populations, which might be expected for more closely related plants. We found that family-level genetic variation in leaf absorptance was present only after the predrought stages, and there were no correlations between predrought and early drought leaf absorptance values. These two patterns imply that changes of leaf absorptance that take place between pre- and early drought result in the differences among genotypes and support the proposal that the leaf absorptance variation is manifested during early canopy development or very early within a drought.

In summary, this study has shown that the interpopulation variation of mean leaf absorptance may result from genetic differences among population (although maternal effects can not be ruled out completely). This variation also conforms to expected differences based on geographic variation of water availability, higher leaf absorptance values being found in wetter environments. However, there appeared to be no variation for the rate of leaf absorptance reduction during drought. These findings suggest that selection based on soil-water availability may have given rise to genetic differences for leaf absorptance in *E. farinosa*, but that the rate of leaf absorptance reduction during drought is constrained, perhaps due to correlations between leaf absorptance and other drought-response traits.

LITERATURE CITED

- BARUCH, Z. 1979. Elevational differentiation in *Espeletia schultzii* (Compositae), a giant rosette plant of the Venezuelan paramos. *Ecology* 60: 85–98.
- BECERRA, J., AND E. EZCURRA. 1986. Glandular hairs in the *Arbutus xalapensis* complex in relation to herbivory. *American Journal of Botany* 73: 1427–1430.
- COMSTOCK, J. P., AND J. R. EHLERINGER. 1992. Plant adaptation in the Great Basin and Colorado Plateau. *Great Basin Naturalist* 52: 195–215.
- COOPER, W. S., AND R. H. KAPLAN. 1982. Adaptive “coin-flipping”: a decision-theoretic examination of natural selection for random individual variation. *Journal of Theoretical Biology* 94: 135–151.
- CUNNINGHAM, G. L., AND B. R. STRAIN. 1969. An ecological significance of seasonal leaf variability in a desert shrub. *Ecology* 50: 400–408.
- EHLERINGER, J. 1981. Leaf absorptances of Mohave and Sonoran Desert plants. *Oecologia* 49: 366–370.
- EHLERINGER, J. 1982. The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *American Journal of Botany* 69: 670–675.
- EHLERINGER, J. 1983. Characterization of a glabrate *Encelia farinosa* mutant: morphology, ecophysiology, and field observations. *Oecologia* 57: 303–310.
- EHLERINGER, J. 1985. Comparative microclimatology and plant responses in *Encelia* species from contrasting habitats. *Journal of Arid Environments* 8: 45–56.
- EHLERINGER, J. R. 1994. Variation in gas exchange characteristics among desert plants. In D.-E. Schulze and M. M. Caldwell [eds.], *Ecophysiology of photosynthesis*, 361–392. Springer-Verlag, New York, New York, USA.
- EHLERINGER, J. R., AND O. BJÖRKMANN. 1978. Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa*. *Oecologia* 36: 151–162.
- EHLERINGER, J. R., AND C. CLARK. 1988. Evolution and adaptation in *Encelia* (Asteraceae). In L. D. Gottlieb and S. K. Jain [eds.], *Plant evolutionary biology*, 221–248. Chapman and Hall, New York, New York, USA.
- EHLERINGER, J. R., AND C. S. COOK. 1984. Photosynthesis in *Encelia farinosa* Gray in response to decreasing leaf water potential. *Plant Physiology* 75: 688–693.
- EHLERINGER, J. R., AND C. S. COOK. 1990. Characteristics of *Encelia* species differing in leaf reflectance and transpiration rate under common garden conditions. *Oecologia* 82: 484–489.
- EHLERINGER, J. R., AND H. A. MOONEY. 1978. Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. *Oecologia* 37: 183–200.
- ELLNER, S., AND N. G. HAIRSTON, JR. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *American Naturalist* 143: 403–417.
- FALCONER, D. S. 1989. Introduction to quantitative genetics. Longman, New York, New York, USA.
- FISCHER, R. A., AND N. C. TURNER. 1978. Plant productivity in the arid and semiarid zones. *Annual Review of Plant Physiology* 29: 277–317.
- FRANK, D. A., AND R. S. INOUE. 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. *Journal of Biogeography* 21: 401–411.
- GIBSON, P. T., AND R. K. MAITI. 1983. Trichomes in segregating generations of sorghum matings. I. Inheritance of presence and density. *Crop Science* 23: 73–75.
- GUPTA, A. P., AND R. C. LEWONTIN. 1982. A study of reaction norms in natural populations of *Drosophila pseudoobscura*. *Evolution* 36: 934–948.
- HADLEY, N. F., AND S. R. SZAREK. 1981. Productivity of desert ecosystems. *BioScience* 31: 747–753.
- HASTINGS, J. R., AND R. M. TURNER. 1965. Seasonal precipitation regimes in Baja California, Mexico. *Geografiska Annaler* 47A: 204–223.
- HOUSMAN, D. C., M. V. PRICE, AND R. A. REDAK. 2002. Architecture of coastal and desert *Encelia farinosa* (Asteraceae): consequences of plastic and heritable variation in leaf characters. *American Journal of Botany* 89: 1303–1310.
- LAJTHA, K., AND W. H. SCHLESINGER. 1986. Plant responses to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2: 29–37.
- LE HOUÉROU, H. N., R. L. BINGHAM, AND W. SKERBEK. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15: 1–18.
- LEVIN, D. A. 1973. The role of trichomes in plant defense. *Quarterly Review of Biology* 48: 3–15.
- MACMAHON, J. A., AND D. J. SCHIMPF. 1981. Water as a factor in the biology of North American desert plants. In D. D. Evans and J. L. Thames [eds.], *Water in desert ecosystems*, 114–171. Dowden, Hutchinson, Ross, Stroudsburg, Pennsylvania, USA.
- MARSHALL, D. R., AND S. K. JAIN. 1968. Phenotypic plasticity of *Avena fatua* and *A. barbata*. *American Naturalist* 102: 457–467.
- MITCHELL-OLDS, T., AND J. J. RUTLEDGE. 1986. Quantitative genetics in natural plant populations: a review of the theory. *American Naturalist* 127: 379–402.
- MONSON, R. K., S. D. SMITH, J. L. GEHRING, W. D. BOWMAN, AND S. R. SZAREK. 1992. Physiological differentiation within an *Encelia farinosa* population along a short topographic gradient in the Sonoran Desert. *Functional Ecology* 6: 751–759.
- NOY-MEIR, I. 1973. Desert ecosystems: environment and procedures. *Annual Review of Ecology and Systematics* 4: 25–51.
- POTVIN, C., M. J. LECHOWICZ, AND S. TARDIF. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71: 1389–1400.
- SANDQUIST, D. R. 1995. Ecotypic differentiation and physiological adaptability of brittlebush (*Encelia farinosa*) in relationship to environmental diversity. Ph.D. dissertation, University of Utah, Salt Lake City, Utah, USA.
- SANDQUIST, D. R., AND J. R. EHLERINGER. 1997. Intraspecific variation of leaf pubescence and drought response in *Encelia farinosa*. Genetic differentiation associated with contrasting desert environments. *New Phytologist* 135: 635–644.
- SANDQUIST, D. R., AND J. R. EHLERINGER. 1998. Intraspecific variation of drought adaptation in brittlebush: leaf pubescence and timing of leaf loss vary with rainfall. *Oecologia* 113: 162–169.
- SAS INSTITUTE. 1994. JMP statistics and graphics guide. SAS Institute, Cary, North Carolina, USA.
- SEGER, J., AND H. J. BROCKMANN. 1987. What is bet-hedging? In P. H. Harvey and L. Partridge [eds.], *Oxford surveys in evolutionary biology*, 182–211. Oxford University Press, Oxford, UK.
- SMITH, W. K., AND P. S. NOBEL. 1977. Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. *Ecology* 58: 1033–1043.
- VASEK, F. C. 1986. Evolutionary modification in *Clarkia*. I. Selection for hairlessness. *American Journal of Botany* 73: 517–523.
- VIA, S. 1984. The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. *Evolution* 38: 896–905.