Intraspecific Variation of Leaf Pubescence and Drought Response in Encelia farinosa Associated with Contrasting Desert Environments

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SUMMARY

Traits associated with leaf energy balance are especially important for desert plants because decoupling leaf and ambient temperatures can be critical for maximizing productivity and survival in these hot, dry regions. Deserts are also one of the most climatically unpredictable and heterogeneous biomes; thus, variation of energy balance characters due either to plasticity or genetic differentiation might also be crucial to the success of desert plant species. In a common garden environment we examined variation in the traits associated with energy balance and productivity in *Encelia farinosa* A. Gray (brittlebush) plants. Comparing two populations from contrasting rainfall and drought climates, we found that plants from the wetter site (Superior, Arizona) always maintained higher leaf absorptances than plants from the more xeric region (Oatman, Arizona) when at similar water potentials. Superior plants also increased stomatal conductance and photosynthesis in response to mid-spring rainfall, whereas Oatman plants did not. Oatman plants, however, tended to have greater leaf areas and continuous spring growth, which made them larger than Superior plants, yet both populations produced the same number of flower heads. The differences for these traits, and the associations among them, agree with predictions based on the contrasting drought and rainfall environments of these two populations. Our results suggest that the differences might represent alternative suites of characters of selective importance for maximizing carbon gain over the climatically variable range of this widespread species. Furthermore, these differences, detected in common environment conditions, might have a genetic basis, which might contribute to a greater potential for local adaptation in this species.

Key words: Desert, drought response, *Encelia farinosa* (brittlebush), energy balance, leaf pubescence.

INTRODUCTION

Variation in physiological traits and their association with other plant characters (morphological and phenological) can play an important role in the performance of species that span broad environmental gradients or highly heterogeneous habitats. Comparing this variation among populations provides a mean to understand better both the roles played by these traits in enhancing the adaptability of the species, and the potential evolution of the character relationships.

Physiological performance in the desert perennial shrub *Encelia farinosa* A. Gray (brittlebush) is

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closely associated with seasonal changes of leaf morphology (Cunningham & Strain, 1969; Odening, Strain & Oechel, 1974; Smith & Nobel, 1977, 1978; Ehleringer & Mooney, 1978; Ehleringer, 1988). In particular, development of highly reflective leaf pubescence decreases both leaf heat-load and the reliance on transpirational cooling for maintenance of favourable leaf temperatures (Ehleringer & Mooney, 1978). However, leaf hairs are costly to produce and they reflect photosynthetically active radiation, which reduces carbon assimilation (Ehleringer & Björkman, 1978; Ehleringer & Werk, 1986). This trade-off should influence variation for the physiological, morphological and phenological traits associated with energy balance and carbon assimilation over the very broad distribution of *E.*

farinosa. Indeed, phenotypic variation has been found for leaf absorptance, water use and timing of leaf loss, and this variation corresponds to regional differences of precipitation and drought duration (Ehleringer, 1988; Sandquist, 1995). However, although there is convincing evidence that decreased radiation absorption due to greater pubescence represents an adaptation to low water availability and high temperatures, little is known about the basis of the geographic variability of this trait, or of that of other physiological and phenological traits associated with it.

Within the broad range of *E. farinosa* there is high geographic variation in mean annual rainfall and drought length. In addition, there is also high interannual variance of water availability. In light of the trade-off associated with leaf pubescence, these spatial and temporal patterns of water availability could affect inter-population genetic differentiation of traits associated with energy balance, water use and productivity. Previous findings do, in fact, suggest that genetic differentiation might play an important role in the capacity of *E. farinosa* to occupy contrasting microclimates. For example, variability of water use has been found in association with isozyme differentiation along microclimatic gradients and may facilitate population structuring over these fairly small spatial scales (Monson *et al.*, 1992; Schuster *et al.*, unpublished). Such genetic variance might also contribute to divergence among regional populations, since selection might vary according to differences in rainfall and drought. However, the high degree of environmental heterogeneity might actually provide a selective basis for greater plasticity, which could preclude genetic differentiation among populations (Bradshaw, 1965; Marshall & Jain, 1968; Cooper & Kaplan, 1982; Seger & Brockmann, 1987; Schmid, 1992). The combination of these alternatives, genetic variability for plasticity, is also an important mechanism of adaptation (Schlichting, 1986; MacDonald, Chinnappa & Reid, 1988; Thompson, 1991).

In this study we examined inter-population variability of traits associated with energy balance, water availability and productivity in *E. farinosa*, since such variability might be crucial to the acclimation and adaptation of this species to the highly heterogeneous desert environment.

Plants from two populations representing contrasting rainfall environments were raised in a common garden: one population originated from a highly variable and dry environment within a zone of unpredictable monsoon activity (Oatman, Arizona), and the other from a less variable, wet environment (Superior, Arizona). We propose that these contrasting climates have given rise to genetic differentiation in leaf absorptance, plant phenology and water-use traits. Thus, plants from the drier, Oatman population were expected to have trait

values associated with lower water availability, such as lower leaf absorptance, foliage densities and stomatal conductance, whereas those of plants from the high rainfall environment, Superior, should have been greater. We also examined how the integration of these traits might form adaptive suites, which in spite of large leaf-level differences might result in a convergence of whole-plant productivity.

MATERIALS AND METHODS

Characterization of seed source regions

The range of *Encelia farinosa* spans much of the Mojave and Sonoran Deserts of southwestern North America (Fig. 1). Mean annual rainfall varies by an order of magnitude (Fig. 2), and the average maximum summer drought duration (days between storms $\geqslant 10$ mm) varies from < 45 d to > 160 d (Sandquist, 1995). High temporal variation of these factors accompanies this spatial variability, rainfall being more unpredictable where amounts are low (Hastings & Turner, 1965; Ehleringer, 1985; Comstock & Ehleringer, 1992), while drought length is most unpredictable along the boundary of summer monsoon advancements (Fig. 2). This appears to result from year-to-year variability in the strength (i.e. advancement) of summer monsoons (Ehleringer, 1994).

Seeds of *E. farinosa* var. *farinosa*, an obligate outcrossing composite, were collected (see below) from two natural populations, 'Oatman' and 'Superior', chosen to represent extremely different points along a rainfall gradient in Arizona (Figs 1, 2). Mean annual rainfall increases, and drought length decreases from Oatman to Superior (Fig. 2), and there are also strong differences in seasonal rainfall amounts (climate diagrams, Fig. 1).

Means for annual rainfall and duration of longest drought at the Oatman site (34° 55' N, 114° 25' W, 427 m, Mohave Co., Arizona) are 111 mm and 75 d, respectively. Most precipitation occurs during winter and early spring (Fig. 1). Late spring and early summer rainfall is infrequent, usually totalling < 10 mm, which is considered to be the minimum amount needed to trigger plant growth responses (Beatley, 1974; Ehleringer, 1994). In the summer months of July and August, monsoon precipitation averages 25·3 mm, nearly 23 % of the annual total, but the coefficient of variation (*cv*) for this amount, a measure of its unpredictability, is very high (102 %). The drought period, therefore, encompasses most of late spring and early summer and the date when it ends, at the onset of monsoon precipitation, is highly variable.

By contrast, mean annual precipitation at the Superior site (33° 46' N, 111° 05' W, 914 m, Pinal Co., Arizona) is high (453 mm), and the duration of longest drought is short (45 d). At this site, pre-
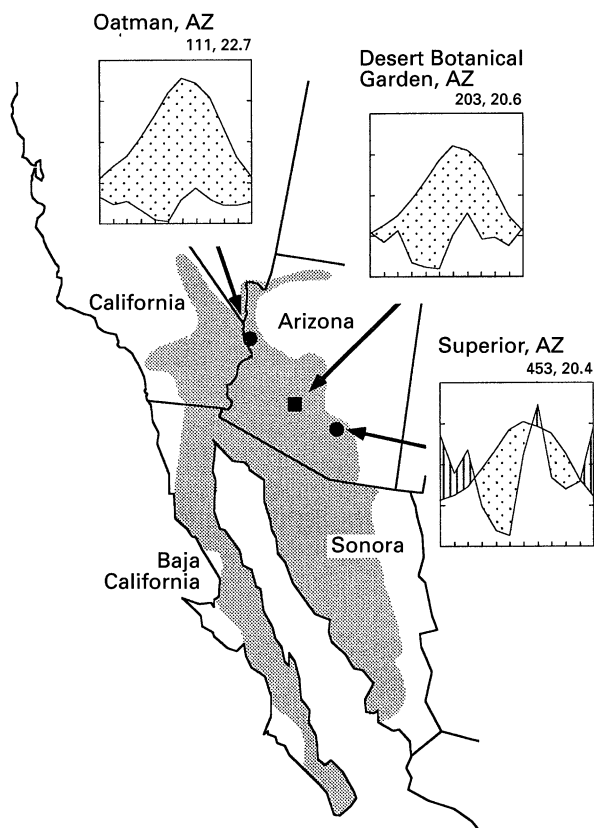
Figure 1. Distribution of *Encelia farinosa* (shaded) in southwestern North America with climate diagrams for seed source localities (Oatman and Superior, Arizona) and the common garden site (Desert Botanical Garden, Phoenix, AZ; weather data from Tempe, AZ). Mean annual precipitation (mm) and temperature (°C) are given at the top right of each climate diagram. Stippled areas represent periods of relative water deficit; hatched areas represent relative water surplus.
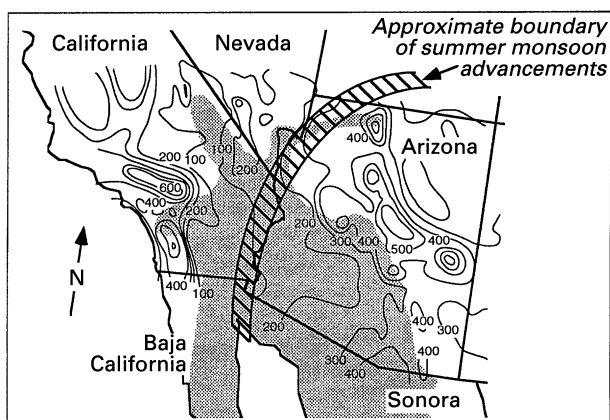

Figure 2. The northern distribution of *Encelia farinosa* (shaded area) with isolines for mean annual precipitation (data period 1931–60). Also shown is the approximate boundary of summer monsoon advancements (hatched area), within which monsoon activity and drought duration are the most unpredictable from year to year.

cipitation exceeds evaporation between November and mid-March; only May and June average < 10 mm of rainfall (Fig. 1). Monsoon rains in July and August contribute more precipitation than any other 2-month period (Fig. 1). The high frequency of late spring storms and strong annual monsoon activities combine to affect a drought regime that is predictably short ($cv = 30\%$).

Seeds were collected from both populations in March and April 1990. Numerous flower heads per individual were sampled and seeds were bulked by plant. The experimental plants were germinated in the University of Utah glasshouse in September 1990. Lower germination from the Superior population resulted in 10 seedlings from six maternal plants, whereas 20 seedlings germinated from 13 Oatman plants.

The common garden site

All experimental plants were transplanted into the Desert Botanical Garden (Phoenix, AZ) on 31 March 1991. The Garden is within the natural range of *E. farinosa* (Fig. 1) and the research plot was on gravelly soils, typical of *E. farinosa* habitat. The experimental plants were randomly distributed within a large plot of *E. farinosa* plants (26 m × 26 m), all separated by 2 m. This distance is sufficient to preclude root interactions between plants (Ehleringer & Cook, 1990).

Measurements of leaf absorptance and phenological traits were made at intervals of approx. 60 to 90 d from February 1992 to August 1993. With few exceptions, water status and gas exchange measurements were also made on all dates beginning in March of each year.

Physiological and phenological trait measurements

Plant water status was determined by pre-dawn leaf water potential (Ψ_{pd}) using a Scholander-type pressure bomb (PMS, Corvallis, Oregon). Measurements using one or two leaves per plant were made within the 3 h before sunrise.

Leaf absorptance values were always determined from the most recently matured leaf cohort. An older cohort was also measured on one sample date (late February 1992), because these leaves were still fully green and photosynthetically active. This cohort was probably one of the first produced that year; near the beginning of the month.

For each absorptance sample, three fully expanded leaves were removed from every plant. Leaves were stored in plastic bags with a damp paper towel and refrigerated to prevent water loss and pigment degradation before absorptance determinations made in the laboratory. Percentage absorptance was measured with monochromatic 625 nm wavelength light and an Ulbricht-type integrating sphere coated with MgO (Ehleringer, 1981). Absorptance of the 625 nm wavelength most closely approximates the

integrated absorptance of all photosynthetically active radiation (400–700 nm) and is also correlated with absorptance of radiation in the energy spectrum (400–3000 nm).

Measurements of leaf temperature (T_l), maximum stomatal conductance to water vapour (g) and rates of photosynthesis (A) were taken 2–4 h after sunrise, the period of maximum photosynthetic activity for *E. farinosa* (Ehleringer, 1988; Ehleringer & Cook, 1990). Values of T_l, g and A were measured on a single leaf or group of leaves using a portable gas analyser (LiCor 6200; LiCor Instruments, Lincoln, NE, USA). Leaves used were located on the south-eastern part of the upper plant canopy and were of the same cohort used for all other measurements on that date.

Plant height, maximum canopy width and width perpendicular to the maximum width were used to determine plant volume (m³) based on the equation for a half spheroid. The foliage density (m² m⁻³) of a plant was determined from a non-destructive estimation of canopy leaf area (m²) ('Appendix 1') divided by the plant volume. Plant volumes were also used to determine relative growth rates between periods of sampling, i.e. size change relative to the size of the plant at the earlier date. In April 1992, at the peak of flowering, the number of capitula (flower heads) per plant was counted. All heads for which any flowers had reached anthesis, or were about to, were included.

Statistics

Values of Ψ_{pd}, g, plant volume and capitula number required log transformation before statistical analyses, and absorptance values were always arcsine transformed. Foliage density, T_l and A values were not transformed unless otherwise noted.

Longitudinal (time–series) analyses of seasonal plant responses were performed using repeated measures analysis of variance (ANOVAR; JMP 3.0 or 3.1, SAS Institute Inc., 1994). For these analyses the following recommendations of Potvin, Lechowicz & Tardif (1990) were applied. If the data did not conform to the assumption of compound symmetry, based on Mauchly's criterion, comparisons were only made when Huynh–Feldt epsilon (H–F ε) neared unity (> 0·8). In such cases, effects due to month (M) and population-by-month interaction (P × M) were tested using the Huynh–Feldt epsilon correction for F-values and probabilities. Exact F-values and corresponding probabilities for population effects (P), and for M and P × M effects when H–F ε = 1·0, were based on Pillai's trace. If the assumptions of ANOVAR were violated, Wilcoxon non-parametric rank tests were used for population–level comparisons with individuals being ranked on the trait mean taken over all months of interest. The M and P × M effects were incon-

sequential in these situations and therefore not tested. Furthermore, although the design of this study did not allow for a rigorous analysis of within-population variance for trait responses, it has been shown elsewhere (with similar traits) that intrapopulation slopes of response are concordant (Sandquist, 1995).

Post hoc comparisons between populations within a single date of the ANOVAR series were tested by Saterwaite's corrected t-test (Winer, 1971), for which we report the absolute difference between means (D) and least significant difference (LSD) at $P < 0·05$. For two-sample comparisons not associated with a time–series, a Student's t-test or non-parametric rank–sum test (Wilcoxon test) was used. In April 1992, with plant size as the covariate, analysis of covariance (ANCOVA) was used to test differences between populations in flower production.

RESULTS

Climate variation during study

Air temperatures during this study were similar in 1992 and 1993, and typical of the long-term averages for the Desert Botanical Garden (DBG), our common garden site (Figs 1, 3). These values were also similar to the long-term averages for both the Oatman and Superior regions (Fig. 1). Precipitation, however, was higher from December to March in both years than the long-term means of all sites for these months (Figs 1, 3). In 1992, sporadic rainfall events continued into summer, with the longest period of drought (days between storms ⩾ 10 mm) being only 49 d (2 April–20 May). There was also a strong monsoon period during July and August 1992 (Fig. 4h). In 1993, spring and summer rainfall was scarce (Figs 3, 4h); the longest drought period lasted 150 d (28 March–25 August). Monsoon activity in 1993 was weak, but our sampling finished before any significant summer storms.
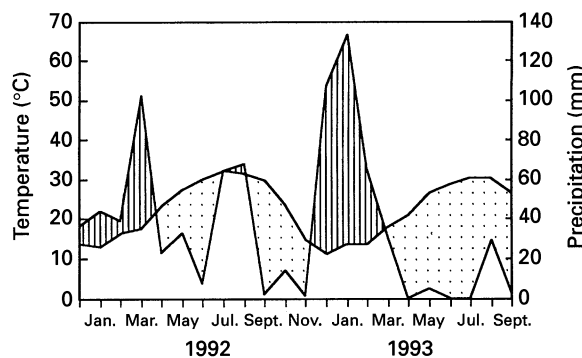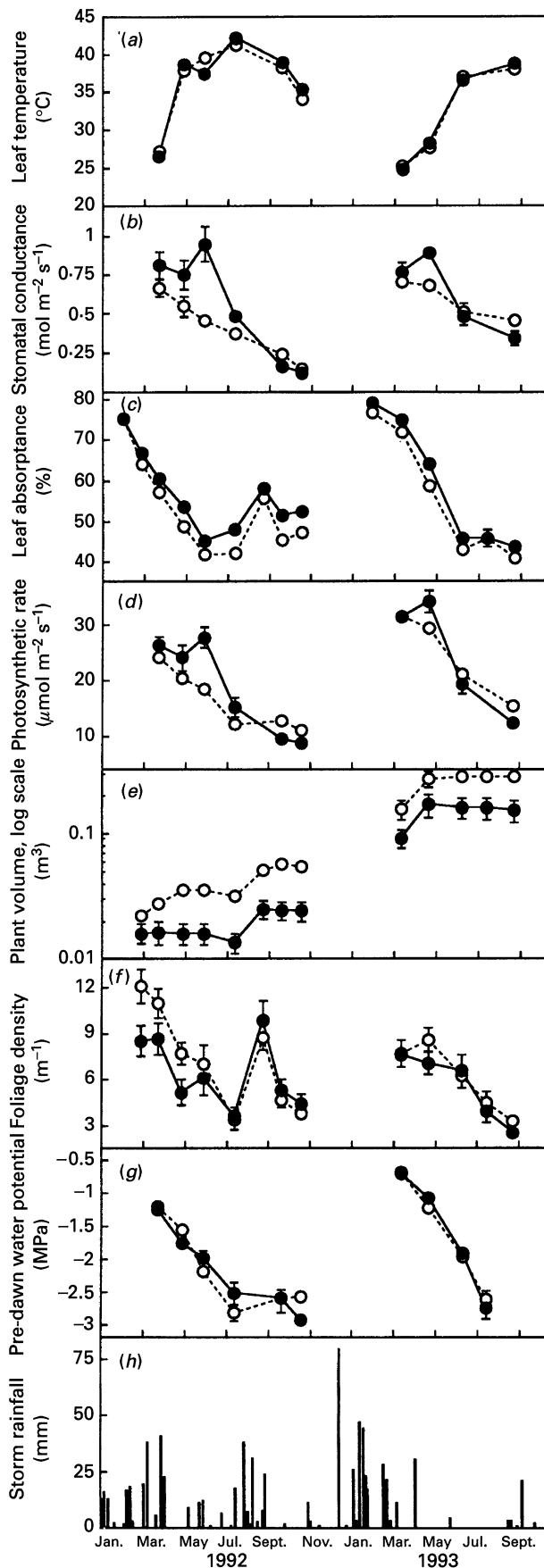

Figure 3. Monthly precipitation and average temperatures at the Desert Botanical Garden in 1992 and 1993. Data are presented in the form of a climate diagram (see Fig. 1).

Water status and energy balance traits

Plant water potential and leaf temperature. From March to July 1992 there were no population–level differences for Ψ_{pd} or T_l (Table 1). Pre-dawn water potential decreased continuously as the water deficit increased (Figs 3, 4), while T_l increased in concordance with increasing air temperatures (Figs 3, 4). During this period, however, populations differed in their patterns of change for both Ψ_{pd} and T_l(P × M effect; Table 1). These differences were apparent during the period of late spring rains (May 1992), when the population ranks for Ψ_{pd} reversed (Superior less negative, Fig. 4g), and leaf temperatures of Superior plants became significantly lower than those of Oatman plants (D = 2·51; LSD = 1·17; P < 0·05) (Fig. 4a).

There were only slight changes of Ψ_{pd} and T_l, in response to 1992 monsoon rainfall (July–September) (Fig. 4). However, these parameters were not measured in August, when the most substantial changes are likely to have occurred. In 1993, Ψ_{pd} and T_l values (and their changes through the prolonged drought) did not differ between the two populations.

Stomatal conductance and leaf absorptance. Maximum leaf conductance values (g) during the pre-monsoon period of 1992 were significantly greater for Superior than Oatman plants (Table 1), and g values for Oatman plants decreased consistently, whereas the changes for Superior plants varied (Fig. 4b). Notably, from April to May, the same period that Ψ_{pd} and T_l differences were observed (above), g values increased for Superior plants, but declined for Oatman plants (Fig. 4b). During the monsoon period of 1992, conductance values did not differ between populations (Table 1) and were lower than the minimum pre-monsoon values (Superior: t = 11·26, P < 0·001; Oatman: t = 4·74, P = 0·001). This decrease occurred despite an increase or no change in Ψ_{pd}, and lower leaf temperatures (Fig. 4).

There was also a decline in conductance from March to August 1993 (Fig. 4b). On average, the populations had similar g values (Table 1), but the changes in g differed between populations (Table 1). As in the previous year, the greatest difference was after a late spring rainstorm, when g increased only for the Superior plants ($D_{\log g} = 0·113$; $LSD_{\log g} = 0·074$, P < 0·05). Late into the drought, however, Oatman plants had greater g values (August: $D_{\log g} = 0·132$; $LSD_{\log g} = 0·074$, P < 0·05).

Patterns of leaf absorptance changes throughout

Figure 4. Seasonal changes of physiological, morphological and phenological traits for Superior (●) and Oatman (○) plants raised in the common garden. Shown are the mean values (± 1 SE) for all traits and storm rainfall totals from January 1992 to September 1993.

Table 1. *Summary of analyses of variance with repeated measures (ANOVAR) for morphological and physiological traits compared between two* Encelia farinosa *populations (Oatman, AZ and Superior, AZ)*

	ANOVAR effects					
	Population			Population × month		
	Pillai's trace	F	P	H–F epsilon†	F	P
Pre-drawn water potential (Ψ_{pd})						
1992 Pre-monsoon	< 0·001	0·02	0·879 n.s.	0·916	4·25	0·010 **
1992 Post-monsoon	0·041	1·20	0·282 n.s.	0·056†	1·66	0·208 n.s.
1993 Pre-monsoon‡	0·004	0·11	0·737 n.s.	0·860	0·87	0·447 n.s.
Leaf temperature (T_l)						
1992 Pre-monsoon	0·012	0·34	0·563 n.s.	0·822	3·30	0·033 *
1992 Post-monsoon	0·080	2·42	0·131 n.s.	0·003†	0·08	0·772 n.s.
1993 Pre-monsoon	0·005	0·13	0·718 n.s.	0·823	0·52	0·632 n.s.
Stomatal conductance (g)						
1992 Pre-monsoon	0·309	12·55	< 0·002 **	0·882	2·64	0·062 n.s.
1992 Post-monsoon	0·072	2·17	0·152 n.s.	< 0·001†	0·25	0·615 n.s.
1993 Pre-monsoon	< 0·001	< 0·01	0·945 n.s.	0·950	3·95	0·012 **
Leaf absorptance						
1992 Pre-monsoon§	0·350	15·07	< 0·001 ***	0·853	4·03	0·004 **
1992 Post-monsoon	0·405	19·08	< 0·001 ***	0·914	4·42	0·020 *
1993 Pre-monsoon‖	0·328	13·66	< 0·001 ***	0·855	1·69	0·153 n.s.
Photosynthetic assimilation rate (A)						
1992 Pre-monsoon	0·242	8·96	0·006 **	0·988	4·35	0·007 **
1992 Post-monsoon	0·130	4·19	0·050 n.s.¶	0·017†	0·49	0·488 n.s.
1993 Pre-monsoon	< 0·001	< 0·01	0·997 n.s.	0·833	3·50	0·026 *

† When H–F $\varepsilon = 1$·0, population × month analysis is based on Pillai's trace (see 'Materials and Methods'), thus Pillai's trace value and corresponding F and P values are presented in the table.

‡ March–July only; August values do not correspond to other measurements (see 'Materials and Methods').

§ February–July.

‖ January–August.

¶ Actual P value was 0·0502 and thus is recorded as not significant.

Plants were raised in Phoenix, Arizona at the Desert Botanical Garden research mini-farm (Fig. 1). Population and population-by-month effects are divided into distinct phenological states: 1992 pre-monsoon (March–July) and 1992 post-monsoon (August–October) periods, and 1993 pre-monsoon (March–August) period.

the year were typical of those for *E. farinosa* in other field and common garden studies (Ehleringer, 1982, 1983; Ehleringer & Cook, 1990; Sandquist, 1995). Both populations underwent a continuous decline in absorptance through the pre-monsoon periods (Fig. 4c), although late drought values remained constant as plants neared summer dormancy (May–July 1992; May–August 1993). In August 1992, when drought ended, plants produced new leaves which had greater absorptance values than those of the previous month (July).

Despite their similar overall pattern, mean leaf absorptance values were consistently lower in Oatman plants in both years (Fig. 4c; population effect, Table 1), but the seasonal changes differed only in 1992 when Oatman plants decreased absorptance values more rapidly than Superior plants (Fig. 4c; population-by-month effect, Table 1). Further analysis showed that this latter difference was due to a divergence between population means in late winter. Removal of the first leaf cohort (early February 1992) from the ANOVAR model rendered the population-by-month effect no longer significant, regardless of how many subsequent months were included in the test. The population effect, however, always remained significant ($P < 0$·05). In 1993, absorptance means were already different at the first sampling date (30 January 1993), perhaps as a result of the short rainless period 8–27 December 1992.

Productivity, growth and canopy dynamics

There was an overall decline in maximum photosynthetic rate (A) before the monsoon period each year. The only exceptions, as for T_l and g, were found in May 1992 and April 1993, when A of Superior plants increased (Fig. 4d). Superior plants also had significantly greater photosynthetic rates throughout the pre-monsoon period of 1992 (Table 1) and a different response pattern from that of Oatman plants (Table 1). After monsoon rains, the Oatman plants had slightly greater A values than those of Superior plants (Table 1). Overall A values in 1993 did not differ between populations (Table 1) but, as with g, population values changed over this period. Superior plants had higher A values after the late March storm (April: D = 4·71; LSD = 2·48, $P < 0$·05), but Oatman plants had greater A values in

Desert Botanical Garden
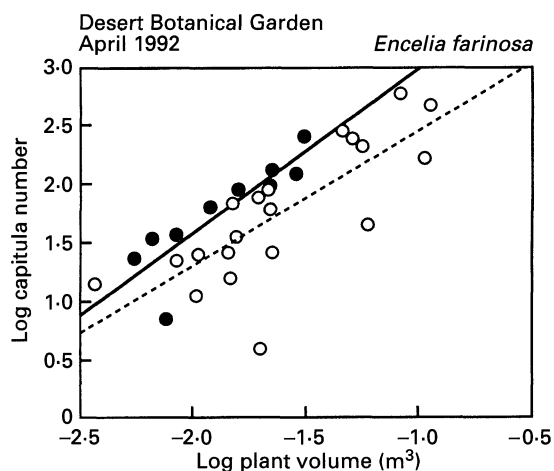April 1992   *Encelia farinosa*

Figure 5. The relationship between capitula number and plant volume (log–log) for Superior (●) and Oatman (○) *Encelia farinosa* plants raised in common environment conditions. Lines are drawn from actual regressions and have significantly different intercepts, but not slopes (see 'Results').

the late drought (August: D = 2·91; LSD = 2·48, $P < 0.05$).

Foliage densities from January to April 1992 were higher for Oatman plants than for Superior plants (Pillai's trace = 0·20, F = 7·08, P = 0·013), but their values declined in similar fashion (Fig. 4f). During this period, plant sizes were not significantly different (Pillai's trace = 0·06, F = 1·70, P = 0·20), although Oatman plants continued to grow, while superior plants did not (Fig. 4e). In May, the two populations did not differ in foliage density (D = 0·94; LSD = 1·98, $P > 0.05$), since there was a slight increase for Superior plants and a continued decline for Oatman plants (Fig. 4f). For the rest of the summer, foliage densities were not significantly different between populations (May–July: Pillai's trace < 0.01, F = 0·07, P = 0·79). After summer monsoon rains, there was an equivalent increase of foliage density in both populations (July–August, P × M: Pillai's trace = 0·02, F = 0·70, P = 0·41), and they maintained similar densities throughout the post-monsoon period (Wilcoxon test = 0·85, P = 0·36). However, Oatman plants again grew for a longer period (Fig. 4e), and by October were significantly larger than Superior plants (t = 2·24, P = 0·03).

The majority of growth, of plants of both populations, took place between January and April 1993 (Fig. 4e). In April 1993, plant sizes were no longer different between populations (t = 1·58, P = 0·12), but by the end of the summer drought, Oatman plants were once again larger (August: t = 2·94, P = 0·006). Throughout this entire period (March–August 1993), foliage densities did not differ between populations (Pillai's trace = 0·01, F = 0·39, P = 0·56) and changes through the prolonged drought were similar (P × M: H–F ε = 0·86, F =

0·86, P = 0·48). There appeared to be a slight increase of foliage density in the Oatman plants from March to April, but the population mean was not significantly different from that of Superior (t = 1·38; P = 0·18).

The numbers of flower heads produced by both populations were similar in 1992. However, because the populations differed in plant size, the flower head counts relative to plant size, were greater for Superior than for Oatman plants (Fig. 5) (ANCOVA: F = 23·39, $P < 0.001$; population effect F = 5·46, P = 0·03).

DISCUSSION

Interpopulation differences of energy balance characteristics

Leaf energy balance is an important component of productivity in desert plants, especially when maximum photosynthetic rates are achieved only within narrow temperature ranges (Gates, 1965; Smith, 1978). Previous studies of *E. farinosa* have shown that leaf pubescence reduces radiation absorption, and is a cost-effective mechanism for maintaining favourable leaf temperatures in very hot, dry, desert climates (Ehleringer & Mooney, 1978; Ehleringer & Werk, 1986). However, we found that the Oatman and Superior populations of *E. farinosa* consistently maintained different absorptance values throughout seasonal changes in water availability. These differences were also associated with variation in other physiological and phenological traits.

Leaf absorptances for both populations decreased proportionately with decreasing water availability (Fig. 6) and seasonal drought (Fig. 4c), yet plants originating from the higher rainfall habitat (Superior) had higher absorptances, even during the most drought-stressed conditions (e.g. summer 1993). These differences in leaf absorptance did not, however, result in different leaf temperatures. The greater heat load associated with higher radiation absorption by Superior plants was apparently dissipated by a higher conductance to water vapour (transpirational cooling) (Raschke, 1960; Gates, 1965; Ehleringer & Mooney, 1978), which also allowed greater light absorption for photosynthesis. This trade-off between leaf absorptance and stomatal conductance is a general phenomenon for this genus (Ehleringer, 1988; Ehleringer & Cook, 1990), although we did not always see higher conductances in the plants with increased energy absorption. In such cases, other energy balance traits (e.g. leaf angles or size) might play an important role (Gates, Alderfer & Taylor, 1968; Parkhurst & Loucks, 1972; Givnish, 1987). Nonetheless, our results show that there are population-specific differences in leaf absorptance values relative to water availability and in associated energy balance and productivity traits.
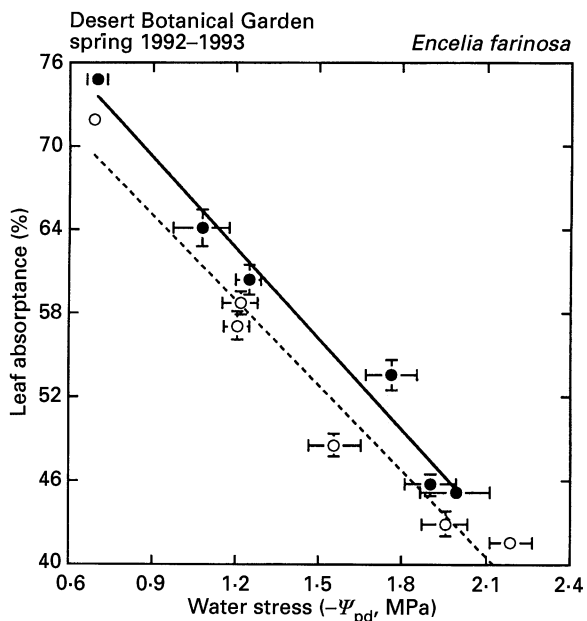
Figure 6. The decrease of leaf absorptance related to changes in water stress for Superior (●) and Oatman (○) plants raised in a common environment. Increasing water stress is represented on the x-axis by the inverse of predawn leaf water potential $(-\Psi_{pd})$. Pre-monsoon values (mean ± 1 SE) for 1992 and 1993 are plotted together with one best-fit line drawn for each population. The lines are not .to indicate regressions, but to show that population changes appear parallel, Superior plants maintaining greater leaf absorptance for any given Ψ_{pd} (see 'Results').
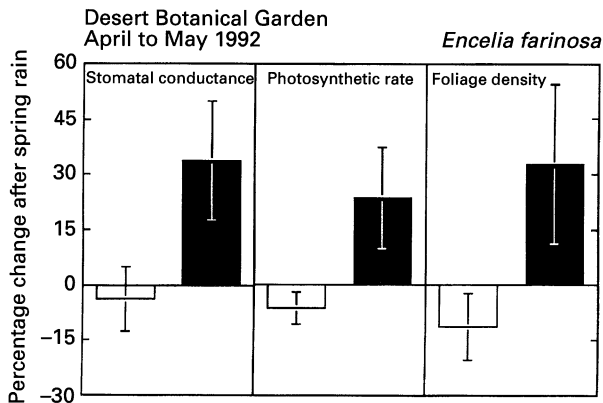

Figure 7. Percentage changes of stomatal conductances, photosynthetic rates and foliage densities after spring rainfall (1992) for Oatman (□) and Superior (■) plants raised in common environment conditions ($\pm$ 1 SE). A similar response was seen in 1993 (Fig. 4).

Potential selection associated with water availability

The variation seen in energy balance might arise from the different selection pressures associated with contrasting drought and precipitation climates (Orians & Solbrig, 1977; Ehleringer *et al.*, 1981; Ehleringer & Werk, 1986). Plants from regions with greater and more predictable rainfall (Superior) might maintain higher leaf absorptance into a

drought, since this provides higher radiation absorption for photosynthesis when rainfall resumes, whereas, in drier regions, where drought is prolonged and summer rainfall is unpredictable (Oatman), lower leaf absorptance reduces water loss and helps to retain leaves and photosynthetic capacity for longer periods of time. Other studies with *Encelia* species also support these inferences. Interspecific comparisons have shown that plants from drier habitats always have lower leaf absorptances (Ehleringer *et al.*, 1981; Ehleringer, 1988; Ehleringer & Cook, 1990), while field observations of *E. farinosa* along moisture or drought gradients indicate differences in water-use patterns (Monson *et al.*, 1992), radiation absorptance, and timing of leaf loss (Sandquist, 1995).

Two additional observations from our study suggest that differences between populations might have resulted from selection involving both the amount and predictability of water availability. During May 1992 and April 1993, stomatal conductances increased for Superior plants, apparently in response to late spring rainfall (Fig. 7). By contrast, leaf conductances for Oatman plants remained constant, or declined. As a result, Superior plants had significantly lower leaf temperatures (May 1992) and greater A values on both dates than did Oatman plants (Fig. 4), while foliage density increased or remained constant, whereas it decreased for Oatman plants (Figs 4, 7). These different responses to spring rainfall are consistent with the hypothesis that plants from wetter regions maintain higher leaf absorptances to take advantage of higher precipitation and an earlier end to drought. However, for this strategy to be selectively important, a short drought should also be predictable, since any exceptionally long drought would strongly select against high leaf absorptances due to leaf loss at an earlier stage of drought, low reproduction and greater mortality (Ehleringer & Werk, 1986; Sandquist, 1995). Indeed, the Superior region, with high precipitation and short droughts, also has low unpredictability for both parameters.

It might seem curious that the Oatman plants did not respond to spring rains, since short droughts in that region, such as the 49-d drought during this study, are not uncommon (National Weather Service Records, 1930–80). However, the benefit of responding to these rainfall events might be insignificant relative to the potential cost of maintaining that capacity during long droughts (complete leaf loss, minimal reproduction, death; Ehleringer & Werk, 1986; Sandquist, 1995). It might also be that a greater summer rainfall is required to elicit a response. In either case, high unpredictability for drought amelioration and for amount of rainfall might be one selective mechanism favouring a more drought-tolerant strategy in Oatman plants.

Variation of productivity and fitness related to different life history strategies

Evidence based on carbon gain at the whole-plant level also shows interpopulation level divergence of traits associated with productivity and fitness. Superior plants often had higher photosynthesis (Fig. 4*d*), which when integrated over an entire day or season, could result in significantly greater carbon gain for plants of this population. Oatman plants, however, maintained greater canopy areas (foliage density × plant size) during most periods when Superior plants had higher *A* values (March–July 1992) (Fig. 4). These contrasts suggest that the lower *A* values of Oatman plants might have been offset by the maintenance of a greater photosynthetic surface area (Comstock, Cooper & Ehleringer, 1988).

Both alternatives provide a means of high spring-time carbon gain, yet we observed that only Oatman plants continued to grow during this period. Superior plants did not increase in size, even when photosynthetic rates substantially increased (e.g. May 1992), but did produce a proportionately greater number of capitula than did Oatman plants (Fig. 5). Both populations, however, had the same average number of capitula per plant at the end of the growing season, because Oatman plants were larger.

As with differences in the leaf-level energy balance traits, the contrasts of whole-plant carbon gain, growth and flowering patterns might accompany different life-history strategies related to the predictability of resources. A 'complete' switch to flowering without continued vegetative growth has previously been proposed for plants growing in predictable environments, whereas continuation of growth, and overlap with flower production, is expected in unpredictable environments (Cohen, 1976; Bazzaz *et al.*, 1987). Such variance in the affiliation between growth and flowering is often found among annual species that experience different degrees and timing of environmental stress (e.g. Fox, 1989; Geber, 1989, 1990; Aronson *et al.*, 1992), and a similar evolutionary process might have given rise to the divergent patterns found between the two *E. farinosa* populations. One population potentially increased productivity and fitness via continued growth and greater plant size (Oatman), whereas the other did so through higher instantaneous carbon gains and immediate allocation to flowers (Superior). The concordance we found, among trait patterns and their association with the environmental variability, provides compelling evidence in support of the proposition that Superior plants employ a somewhat opportunistic strategy of carbon gain (Orians & Solbrig, 1977; Bazzaz *et al.*, 1987), which may be favoured in environments where water availability is predictable yet still limiting, or where competition for resources is very high (Cohen, 1970; Fowler,

1986), whereas in the unpredictable and dry Oatman environment, a more conservative strategy of survival and/or tolerance might provide the greatest fitness advantage to plants (Cohen, 1970; Orians & Solbrig, 1977; Aronson *et al.*, 1992).

In conclusion, we have found that there are population-specific differences in energy balance and productivity traits within *E. farinosa*. Although we could not assess the degree to which plasticity or genotype-by-environment effects might affect these differences, it is clear that there is likely to be some genetically-based component in this variation. Furthermore, these results agree with predictions of how the populations should vary based on the climatic differences between them, and suggest that the interpopulation level variation might result from local adaptation. They also coincide with the findings of Monson *et al.* (1992) who suggested that selection had given rise to microscale differentiation for *E. farinosa* water-use patterns. Together, these findings suggest that there might be a high degree of genetic variance in *E. farinosa*, which – by allowing a greater diversity of character combinations and environmental responses – could account, in part, for the ubiquity of this species throughout the Mojave and Sonoran Deserts of southwestern North America.

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APPENDIX 1

Canopy leaf area per plant was estimated using the following formula,

canopy leaf area (m²) =

$$\left(\frac{S}{9 \times 10^4}\right) \sum_{i=1}^{3} \left[L_i \left(\left(0.106 \sum_{j=1}^{3} w_{ij}\right) + \left(0.006 \sum_{j=1}^{3} w_{ij}^2 \right) \right) \right], \quad (1)$$

where S is total number of stems, L_i is number of leaves for stem i, and w_{ij} is leaf width (mm) for leaf j of stem i. Three stems ($i = 1, 2, 3$) were subjectively chosen to represent the diversity of stems on the plant and, for these, an estimation of stem leaf area was made by counting leaf number (L_i) on that stem and measuring leaf widths (w_{ij}) of three leaves on the stem ($j = 1, 2, 3$). These three leaves were subjectively chosen to represent the variance of leaf sizes on the stem. The coefficients 0.106 and 0.006 are based on a binomial regression for the conversion of leaf width (mm) to leaf area (cm²). This regression was empirically determined from measurements of leaf widths and areas of 762 leaves collected during March and May 1992. The intercept was forced through zero, thus none appears in eqn (1). The coefficient of determination for this relationship was $R^2 = 0.985$ ($P < 0.001$). Finally, the denominator (9×10^4) is from conversion of cm² to m² (1×10^4) multiplied by nine (9). Nine is the product of denominators from $L/3$, for each leaf measured (j) representing one-third of the leaves on a stem, and $S/3$, for each stem measured (i) representing one-third of the stems on a plant. This non-destructive estimate of foliage density compared well with two other methods for measuring foliage density (Sandquist, 1995).