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Intraspecific variation of drought adaptation in brittlebush: leaf pubescence and timing of leaf loss vary with rainfall

Abstract Reflective leaf pubescence of the desert shrub *Encelia farinosa* (brittlebrush) reduces leaf temperature and plant water loss, and is considered adaptive in xeric environments. Yet, little is known about intraspecific variation in this trait. Among three populations in the northern range of *E. farinosa*, which span a very broad precipitation gradient, both leaf absorptance variation and differences in the timing of drought-induced leaf loss were broadly associated with climatic variability. Where mean annual rainfall was greatest, drought-induced leaf loss was earliest, but these plants also had higher population-level mean leaf absorptance values. Higher absorptance increases the relative dependence on latent heat transfer (transpirational cooling), but it also provides greater instantaneous carbon assimilation. Plants at the driest site reached lower leaf absorptance values and maintained leaves longer into the drought period. Lower leaf absorptance reduces water consumption, and extended leaf longevity may buffer against the unpredictability of growing conditions experienced in the driest site. These observations are consistent with a trade-off scenario in which plants from wetter regions might trade off water conservation for higher instantaneous carbon gain, whereas plants from drier regions reduce water consumption and extend leaf longevity to maintain photosynthetic activity in the face of unpredictable growing conditions.

Key words Desert plant adaptation · Drought response · Leaf longevity · Leaf pubescence and absorptance · Water use trade-offs

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Introduction

During drought, the desert perennial shrub *Encelia farinosa* A. Gray produces leaves which are highly pubescent. The amount of pubescence increases for each cohort of leaves produced during soil drying and this reduces the absorption of incident solar radiation. Ultimately, this change can decrease absorption of the visible wavelengths from 85% to 30% (Ehleringer and Björkman 1978). Furthermore, increased pubescence reduces the heat load, which helps maintain leaf temperatures within the photosynthetically stable range while also decreasing reliance on transpirational cooling for avoiding high leaf temperatures (Ehleringer and Mooney 1978). This developmental response has been considered adaptive in water-limited environments because it reduces water loss and permits the maintenance of photosynthetic activity longer into the drought period (Smith and Nobel 1977; Ehleringer and Mooney 1978; Ehleringer 1983). In the Sonoran and Mojave Deserts, where timing of rainfall and duration of drought can strongly affect plant survival and productivity (Hadley and Szarek 1981; Ehleringer 1994), interpopulation variation of pubescence production in *E. farinosa* may result from selective pressures related to climatic variability over its range. In spite of its possible importance, little is known about pubescence variation at the geographic and intraspecific level, or its ecological correlates (Ehleringer and Clark 1988).

Comparisons between pubescent and nonpubescent *Encelia* (*E. farinosa* vs. *E. frutescens*; *E. farinosa* vs. *E. californica*; *E. farinosa* vs. a glabrous-mutant *E. farinosa*) have found that the pubescent form consistently has higher productivity and reproduction under late-spring and summer drought conditions (Ehleringer 1983; Ehleringer 1988; Ehleringer and Cook 1990). However, when water availability is greater, or when drought is ameliorated by rainfall, the benefit of leaf hairs may be offset by costs and constraints associated with their production (Ehleringer and Mooney 1978; Ehleringer

and Werk 1986). Leaf hairs can have high one-time construction costs, and they also continuously reduce photosynthesis by reflecting photosynthetically active radiation. For *E. farinosa*, leaf pubescence can also constrain carbon gain because plants must become dormant, or nearly so, before leaves with higher light absorption and photosynthetic rates can again be produced (Ehleringer 1982). These costs and benefits result in a trade-off that may give rise to geographic variation of *E. farinosa* leaf pubescence based on differences of water availability across the range of this species, the benefit of reduced leaf absorption being lower in regions with greater precipitation.

In this study we examined the geographic variability of plant phenology and leaf absorptance (the percentage of light absorbed) in three populations of *E. farinosa*. These populations spanned a broad water availability gradient that is influenced by precipitation, temperatures and drought longevity (Fig. 1). Based on the relationships between leaf pubescence, productivity and water availability, we hypothesized that this broad gradient would promote regional differentiation in leaf pubescence and phenology. Specifically, we expected plants from regions with greater precipitation to have higher absorptance values since this allows higher instantaneous carbon gains. Plants from drier regions might have lower absorptance values because they rely more on leaf pubescence to maintain a favorable energy balance. Here we report the results of field observations examining the relationships among leaf morphology and plant phenology with respect to potential water use differences. Variation in these relationships and traits may reflect genetic differentiation or plastic responses that allow *E. farinosa* to occupy such a broad climatic range.

Materials and methods

Study sites

Three study sites were chosen which span the northwest to southeast precipitation gradient in the northern range of *E. farinosa* (Fig. 1). In conjunction with this rainfall gradient, the mean annual temperature and duration of drought decrease from northwest to southeast. The arid northwestern site was located in Warm Springs Canyon within Death Valley National Park, California (35°58′N, 116°55′W, 621 m, Inyo County). Mean annual rainfall at the Death Valley National Park Visitors Center (53 km north of Warm Springs Canyon) is 52 mm, and the mean annual temperature is 24.1°C. The mean duration of longest annual drought here is 159 days. At the mid-transect site, Oatman, Arizona (34°55′N, 114°25′W, 427 m, Mohave County), mean annual rainfall is 111 mm, mean annual temperature is 22.7°C, and the duration of the longest annual drought is 75 days (weather data from Needles FAA Airport, California, 23 km southwest of the site). The wettest site, Superior, Arizona (33°46′N, 111°05′W, 914 m, Pinal County) has a mean annual precipitation of 453 mm and a mean annual temperature of 20.5°C. The average maximum drought length is

Fig. 1 Distribution of *Encelia farinosa* (shaded area) in southwestern North America and the three field sites used for study. Also shown are isolines for mean annual precipitation and the mean annual rainfall for the field sites (data period 1931–1960)
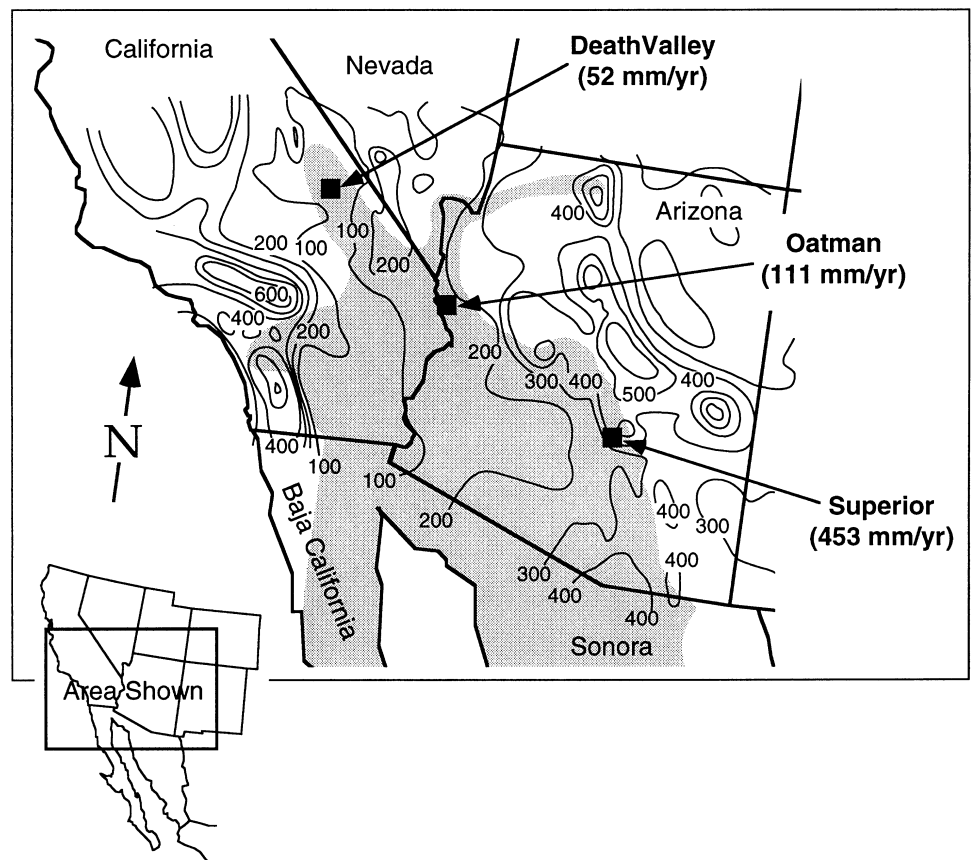
only 45 days (data from Superior, Arizona, 2.6 km north of the site). All data are based on US National Weather Service records for 1930 through 1980.

At each study site, 50–100 mature *E. farinosa* plants were tagged for repeated measurements. Plots were located on rocky, south-facing slopes and *E. farinosa* was always the dominant shrub in nearly monospecific coverage. Every 60–90 days, visits were made to the Oatman and Superior sites in 1990 (March–November) and to all three sites in 1991 (April–September). In 1992, visits to the Death Valley site were made at approximately 90-day intervals from March through September.

Phenological measurements

Plant height, maximum width and width perpendicular to the maximum width were measured during each visit. These parameters were used to calculate plant size (m^3) based on the equation for a half spheroid. Canopy status was estimated (visually) based on a five-scale index: 0 = no leaves, 1 = 1–25% leaf cover, 2 = 26–50% leaf cover, 3 = 51–75% leaf cover, 4 = 76–100% leaf cover. In the second spring of annual surveys, plant death during the previous year was recorded.

Leaf absorptance measurements

Leaves were collected on every sample date for determination of leaf spectral absorptance. From every plant, three fully expanded leaves of the most recently matured cohort were removed, stored in plastic bags with a damp towel, and kept refrigerated in the dark until absorptance measurements were made in the laboratory (measurements were usually made within 7 days of collection, and storing leaves for up to 10 days, under conditions that maintained high water contents, had no obvious effect on absorptance values).

Leaf discs 1 cm in diameter, cut from between the midrib and margin, were placed in an Ulbricht-type integration sphere with their adaxial surface towards a monochromatic 625-nm beam of light. This wavelength correlates highly with the integrated leaf absorptance of radiation in the photosynthetically active range (400–700 nm) and the energy spectrum (400–3,000 nm) (Ehleringer 1981). The difference between light detection within the sphere when the leaf is in place versus that in its absence is the percent of light absorbed by the leaf (absorptance).

Results

Climate variation

Rainfall during 1990–1992 was greater than the corresponding long-term averages for every site (Fig. 2). Precipitation at Superior exceeded the long-term average by 46% in 1990, largely as a result of a single, strong August storm (Fig. 2). In 1991, there was high rainfall in March, but April through early July were very dry. Precipitation thereafter, through the last month of observations (September), was near normal.

Rainfall in 1990 at Oatman was sporadic but resulted in a near-average total annual amount (Fig. 2). Precipitation from February through December was below average, but this was interspersed by high rainfall in May and September. In 1991, abnormally high precipitation between January and March (185% above average) was followed by extreme drought through September.

Death Valley had a sporadic rainfall pattern in 1991. In 4 of the first 6 months there was no precipitation, and for all but 2 months of the year, precipitation was below
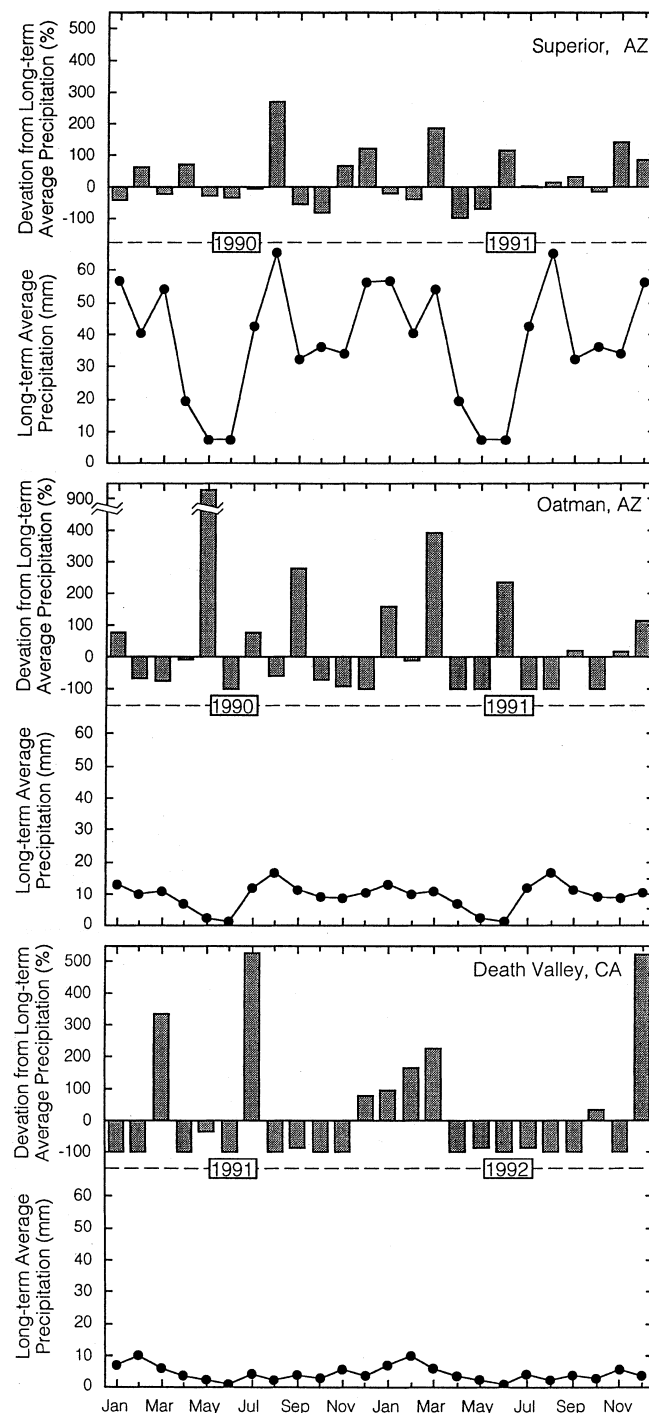
Fig. 2 Rainfall for 1990–1992 and departures from long-term means at the three field sites. The upper-half of each panel shows percent deviation from average monthly rainfall for the years of this study, and the lower-half of each panel shows long-term (1930–1980) average monthly rainfall for each site. Data are from the National Weather Service weather stations at Superior, Arizona, (*Superior*), Needles FAA Airport, California (*Oatman*), and Death Valley Visitors Center, California (*Death Valley*)

average (Fig. 2). However, rainfall in March 1991 was high (335% above average) and there was a rare summer storm in July (25 mm). The rainfall pattern in 1992 was more typical for this region – winter storms with summer drought. Precipitation from January–March 1992 was above average by 149%, but this was followed by virtually no rainfall (0.8 mm) for the next 6 months.

It is important for this study that there was at least one prolonged drought within the 2 years of study at each site (in 1991 for Superior and Oatman and in 1992 for Death Valley). These droughts provide the basis for observations of drought-specific responses discussed in later sections.

Leaf absorptance and timing of deciduousness

The highest mean leaf absorptance values for each population (ca. 71–76%) were measured in early spring (March 1990 and 1992) and were comparable among all three populations (Fig. 3). Leaf absorptances may have been slightly higher on dates earlier than those sampled, but the values measured were close to or equalled the maximum leaf absorptances found in previous studies (Ehleringer 1982, 1983). Furthermore, common-environment studies have shown that maximum leaf absorptances are similar for these three populations (Sandquist and Ehleringer 1997).

Leaf absorptance changes through the season followed a pattern typical for *E. farinosa* (Ehleringer and Björkman 1978) (Fig. 3). Mean leaf absorptance steadily decreased throughout the season when there was no additional rainfall. Rainfall which came after plants had become deciduous resulted in the production of new and green leaves (e.g., August–September 1990 at Superior; Fig. 3), and when rainfall came during mid-spring, leaf absorptances stayed constant. In conjunction with these changes of leaf absorptance, foliage cover was generally greater during months when leaf absorptance was higher (Pearson product-moment correlations: Superior, $r = 0.781$, $P < 0.005$, $n = 11$ months; Oatman $r = 0.942$, $P = 0.058$, $n = 4$; Death Valley, $r = 0.988$, $P < 0.001$, $n = 8$), but within a sample period there was no consistent correlation between foliage cover and absorptance.

Although all populations followed a similar overall pattern of leaf absorptance changes, there were notable population-specific behaviors. Superior plants maintained relatively high leaf absorptances through spring 1990, possibly as a result of late-spring rains; however, many became leafless in early summer and almost all plants were deciduous by August (Fig. 3). Thereafter, a large summer storm (222 mm, August 12–16) induced a new flush of highly absorptive leaves.

Changes in leaf absorptance for 1991 at Superior were similar to those during the early months of 1990; absorptance values rapidly declined from April to July. Rain in July and August may have allowed some persistence of leaf activity, and even induced reactivation of
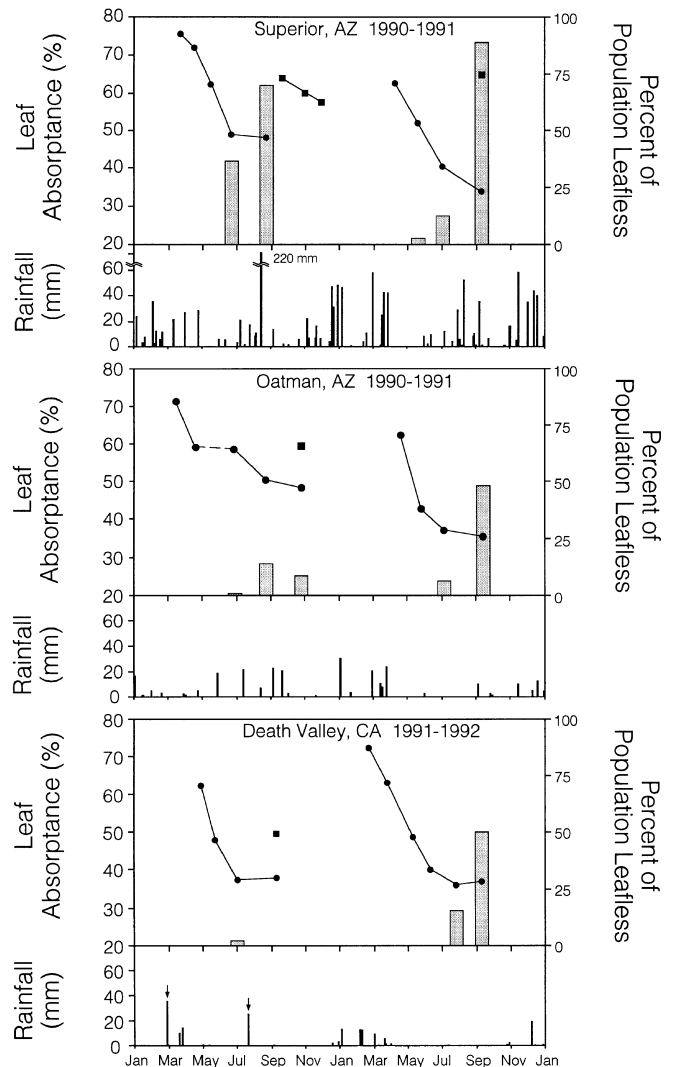
Fig. 3 Leaf absorptance changes and rainfall for 1990–1991 at the Superior and Oatman sites, and for 1991–1992 at the Death Valley site. *Upper panels* Mean leaf absorptance values for active *E. farinosa* plants on each sample date. *Circles* are means for plants that had not yet become leafless at the date of sampling. *Squares* are means for plants that had become dormant but produced new leaves after summer rainfall. Standard errors of the means are smaller than symbols. The *shaded histogram bars* represent the proportion of each population that was leafless at the time of sampling. *Lower panels* Precipitation totals for rainstorm events throughout the sample periods. Totals for each "event" are calculated from the sum of consecutive days with rainfall. Data are from the National Weather Service weather stations near each site (see Materials and methods). The *arrows* on the Death Valley precipitation record indicate storms that were not recorded at the Death Valley Visitors Center due to missing records. The rainfall totals on these dates are taken from the National Weather Service weather station at Shoshone, California

one plant (Fig. 3), but by September, the majority of the population was leafless.

Leaf absorptance responses for Oatman in 1990 showed the influences of two large rainfall events (Fig. 3). After a late-spring rainstorm (May 28–29), leaf absorptance values were the same as in the previous month, although this may have resulted from a flush of new leaves. A different set of summer storms between

September 4 and 22 caused both the persistence of low-absorptance leaves and a new flush by some previously leafless plants. In 1991, the leaf absorptances declined consistently and most Oatman plants were leafless in September.

The Death Valley population showed a consistent pattern of leaf absorptance change in both years of sampling with nearly all plants maintaining activity throughout the summer (Fig. 3). In 1991, a rare July rainstorm (25 mm) allowed plants to maintain activity into September at absorptance values similar to those found 45 days previously. The single plant that had become leafless by July flushed new green leaves. In 1992, there was no rainfall between early April and late October, yet more than 85% of the population maintained leaves after 3 months of drought (April–July), and over half the population had leaves in September, more than 6 months after the last precipitation event.

The lowest mean leaf absorptance found on a single date was similar for all three sites (Superior = 35%, $n = 6$; Oatman = 35%, $n = 49$; Death Valley = 36%, $n = 44$, Fig. 3), but these values were determined from only those plants that retained leaves. While this indicates that some plants within each population could reach very low absorptances, a distinct difference was found among populations when considering the minimum leaf absorptance values observed for each plant within a population (i.e., the values prior to canopy loss regardless of when it occurred). On average, Death Valley plants reached lower absorptances (mean $\pm$ 1SE 35.1 $\pm$ 0.51%, $n = 52$) than plants from Oatman (38.5 $\pm$ 0.63%, $n = 99$) or Superior (44.1 $\pm$ 1.46%, $n = 57$) (Kruskal-Wallis $H = 38.12$, $P < 0.001$). This also shows that the average plant from Superior became leafless at a higher leaf absorptance value than those of Oatman, followed by Death Valley.

Superior plants also became leafless sooner after the last significant rainstorm (> 10 mm, sensu Ehleringer 1994) than Oatman or Death Valley plants (Figs. 3, 4). For periods of prolonged drought at Superior, 40% of the population was leafless after 50 days in 1990, and 86% after 158 days in 1991. A 160-day drought period was necessary before 50% of the Oatman plants became leafless (April–September 1991), and for Death Valley plants nearly 200 drought days passed before 50% were leafless (February–September 1992). Acclimation by changes in leaf canopy area was similar for all three populations, each reducing the average canopy area to a ranking of 1 (1–25% coverage) within 90 days of the onset of drought. Of further note is that rainfall prior to these drought periods was highest at Superior and lowest at Death Valley. These results indicate that there was earlier leaf loss and higher minimum absorptance values in the habitat where rainfall was greatest. That is, plants which maintained higher leaf absorptances, and thus morphologically acclimated the least over the drought period, became leafless earlier (Fig. 4). This pattern, seen among populations, was also evident within the Superior and Oatman populations, as shown in Fig. 5
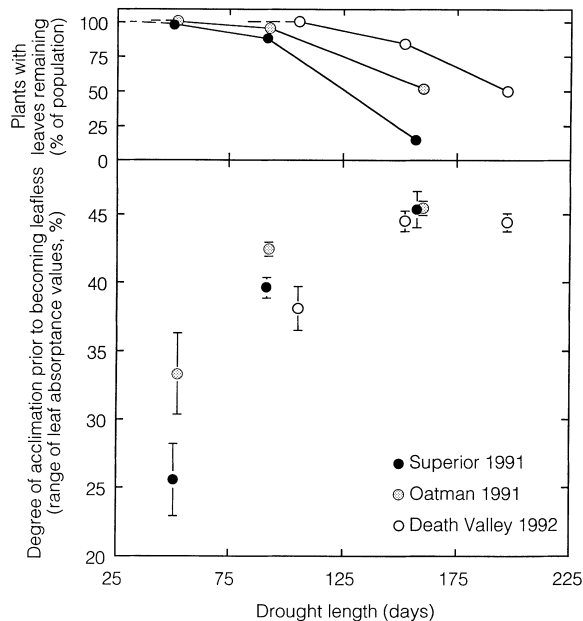
Fig. 4 The relationships of leaf absorptance acclimation and timing of leaf loss for *E. farinosa* of three different populations. The *lower panel* depicts the group means for individual plant leaf absorptance acclimation (maximum–minimum ± 1SE) achieved during drought. Each symbol represents a group of plants that became leafless before the next sample period. The range of absorptances (acclimation) is plotted in relationship to the last recorded date of activity after the onset of the drought period (i.e., days since the last rainfall ≥ 10 mm). The range value and days since rainfall are, therefore, minimum estimates. The *upper panel* shows what percentage of each population was still active on those respective dates. Note that the first plants to become deciduous for each population do so at very different leaf absorptance ranges (Death Valley > Oatman > Superior), and while the maximum range is similar for all populations (ca. 45%), there are differences among the population in how many plants achieve this range (Death Valley > Oatman > Superior)
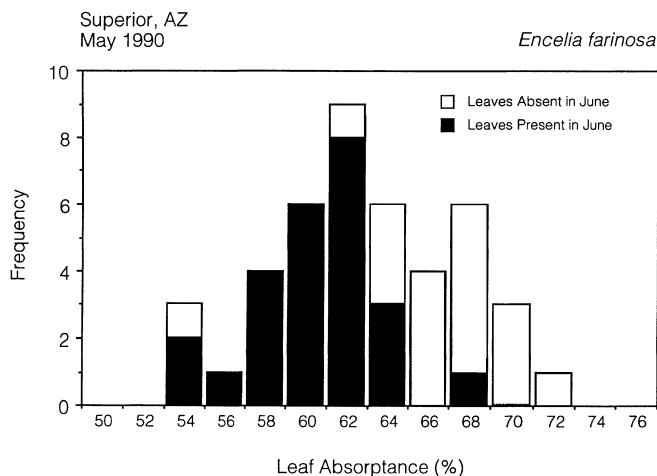
Fig. 5 The distribution of leaf absorptance values, and the canopy fate in the following month, for the Superior population of *E. farinosa* plants in May 1990. The histogram is partitioned into plants that continued activity into the following month (*filled bars*) and those that became leafless prior to the next month (*open bars*). Plants which remained active until June had lower mean leaf absorptances (mean $\pm$ 1 SE: 60.0 $\pm$ 0.65%, $n = 25$) than plants which were leafless in June (65.5 $\pm$ 0.93, $n = 18$; $t = 5.05$, $P < 0.001$)

for Superior plants: those with the highest leaf absorptance in May 1990 were leafless by June 1990.

Growth and mortality

From 1990 to 1991, Superior plants increased in volume by an average of 400%, yet, in spite of above-average rainfall at this site in 1990, mortality was 14%. Plants from Oatman showed virtually no change in volume (decreasing −2% on average) and mortality was 10%. In the Death Valley population, plants increased by an average of 150% from 1991 to 1992 and there was no mortality.

Discussion

The model in Fig. 6 conceptualizes the relationships among important leaf-level productivity components for the desert shrub *E. farinosa*. These relationships, which ultimately influence fitness, illustrate some of the mechanisms available for balancing responses to different degrees of water limitation. One component, leaf pubescence, has been shown to be adaptive in environments of low water availability and high temperatures (Smith and Nobel 1977; Ehleringer and Mooney 1978). This trait, however, can have both positive and negative

Fig. 6 A conceptual model of the relationships among productivity components for *E. farinosa* (*g* stomatal conductance, c_i intercellular CO_2 concentration, *E* transpiration, T_l leaf temperature). *Plus* and *minus symbols* do not necessarily indicate causal relationships, but rather the general relationships among components

effects on primary productivity (Fig. 6), and the degree of its importance for enhancing productivity and fitness should depend on regional differences of precipitation and drought.

The responses to drought we observed among three populations show that leaf absorptance and timing of leaf loss differed as predicted for these contrasting environments. These differences appeared as a trade-off between higher leaf absorptances to increase photosynthesis and lower absorptance with sustained leaf maintenance into drought (e.g., Figs. 4, 5), and suggest that there are also differences among these populations in water use patterns. These results may indicate an underlying genetic differentiation (see Sandquist and Ehleringer 1997) but, alternatively, could be the result of environmental differences among the study sites.

Previous studies have shown that leaf absorptance is positively associated with stomatal conductance and transpiration (Ehleringer and Mooney 1978; Ehleringer 1988), mechanisms of latent heat transfer. In arid regions (e.g., Death Valley), low absorptance by leaves of some *E. farinosa* genotypes might result from selection associated with reducing water loss, including a decreased dependence on transpirational cooling. In wetter and cooler environments, such as Superior, plants may be able to rely on latent heat transfer to a greater degree, and therefore maintain leaves with higher absorptance. In fact, selection in this wetter region may actually operate to reduce leaf pubescence in order to increase light absorption and photosynthetic carbon gain. These alternatives exemplify how, over the distribution range of *E. farinosa*, differences in climate and selection are likely to result in geographic variation in relationships between productivity and water use.

Associated with the differences in leaf absorptance, plants of the Superior population may use water more rapidly than plants of Oatman, and Death Valley plants use water most frugally (see Sandquist and Ehleringer 1997). Such variation is similar to that found for *E. farinosa* over a local topographical and moisture gradient (Monson et al. 1992), and for interspecific comparisons of glabrous and pubescent species of *Encelia* (Ehleringer 1988). Monson et al. (1992) also found genetic (isozyme) variation among slope and wash subpopulations and suggested that the physiological and phenological differences were due to local adaptation.

We suggest that the differences in leaf absorptance patterns found among the three populations examined in this study can be explained in light of the relationships between water availability, water use, carbon gain, and leaf absorptance (Fig. 6). The expenditure of water tends to be greater in wetter environments and can even be favorable as a component of enhanced growth (McKell et al. 1960; Farris 1987; Monson et al. 1992) or competitive advantage (Cohen 1970; Fowler 1986). Furthermore, a higher leaf absorptance increases carbon gain. Thus in wetter environments, such as Superior, greater reliance on transpirational cooling and less leaf pubescence might be expected – even during drought if
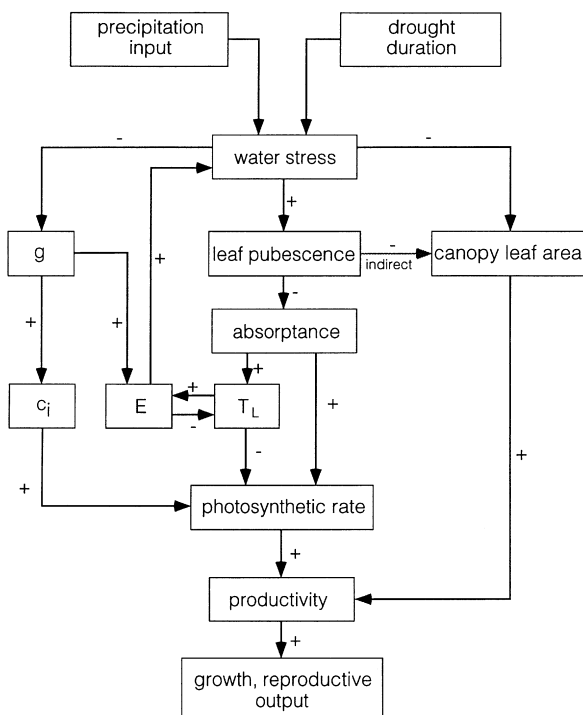
water limitations are generally short in duration (Orians and Solbrig 1977). In dry regions, where water availability for transpirational cooling is limited, leaf pubescence provides an alternative mechanism for maintaining favorable leaf temperatures.

In addition to the changes in mean values across the gradient studied here, the range of individual leaf absorptances increased as precipitation decreased (Fig. 4). In desert regions, where the intra- and interannual water availability becomes more unpredictable as precipitation decreases (Comstock and Ehleringer 1992; Ehleringer 1994), greater phenotypic flexibility may be advantageous as a means of buffering the plant against unpredictable growing conditions (Bradshaw 1965; Marshall and Jain 1968; Sultan 1987; Schlichting 1989).

Interestingly, there was extreme variation in growth among the populations, and this was not associated with the different leaf absorptance patterns. Mortality was unexpectedly greatest where rainfall was highest even in a year when precipitation was above average. Inferences made from such patterns are tenuous, and additional factors, such as timing of rainfall, competition, nutrient availability, and plant history should be considered (Ehleringer 1994). However, our results might indicate that drought-associated mortality is most prevalent in wetter regions, even though the absolute length of the drought is substantially shorter (Fig. 3).

Predictability of drought amelioration may play an integral part in the differentiation of these populations and their responses. Plants in the Superior population rarely experience a sustained drought: on average the longest annual drought is only 45 days. By maintaining high leaf absorptances throughout the initial weeks of a drought, and deferring the cost of structural investment in leaf pubescence, these plants may forgo acclimation in "anticipation" of receiving summer rainfall prior to reaching a critically low water status, and leaflessness. At the other extreme, patterns of leaf absorptance, and hence water use, seen for Death Valley plants may exemplify a response based on a predictable absence of late-spring and summer precipitation. These interpopulation alternatives in phenological, morphological, and physiological responses concur with other observations of, and evolutionary predictions for, responses in stochastic environments, such as patterns of flowering and senescence by desert annuals (Cohen 1976; Fox 1989; Aronson et al. 1992), community-level variation (Bazzaz and Wayne 1994) and variation among desert plant life forms (Orians and Solbrig 1977).

In conclusion, the variation we found for leaf absorptance and canopy retention among *E. farinosa* populations appears to correspond to regional differences in precipitation and drought length. Furthermore, the trade-off between higher leaf absorptances and earlier leaf loss during drought (Fig. 4), which is also found *within* populations (Fig. 5), indicates that broad phenotypic variation can also exist within populations.

The causal mechanisms responsible for leaf absorptance variation, both within and among populations, is poorly understood, and although this study could not discriminate among possible mechanisms, recent studies suggest that there is at least some genetic determination for differences in water use and energy balance traits among *E. farinosa* populations (Monson et al. 1992; Sandquist 1995; Sandquist and Ehleringer 1997). Our findings may reflect the results of selection based on variation in water availability, which has given rise to divergence of the leaf absorptance "adaptation" within this species.

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