Comparative ecophysiology of *Encelia farinosa* and *Encelia frutescens*

I. Energy balance considerations

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Summary. *Encelia farinosa* and *Encelia frutescens* are drought-deciduous shrubs whose distributions overlap throughout much of the Sonoran Desert. During hot and dry periods, leaves of *E. farinosa* utilize increased leaf reflectance to reduce leaf temperature, whereas leaves of *E. frutescens* have substantially higher leaf conductances and rely on increased transpirational cooling to reduce leaf temperature. *E. farinosa* is common on the dry slope microhabitats, whereas *E. frutescens* occurs only in wash microhabitats where greater soil moisture is available to provide the water necessary for transpirational cooling. *E. farinosa* tends not to persist in wash microhabitats because of its greater susceptibility to flashfloods. The consequences and significance of increased leaf reflectance versus increased transpirational cooling to leaf temperature regulation are discussed.

Key words: Adaptation – Carbon isotope ratio – Leaf conductance – Water-use efficiency

Along gradients of increasing aridity in western North America, it is common to observe an increase in the fraction of the species that have reflective leaf surfaces (Coulter et al. 1911; Billings and Morris 1951; Ehleringer 1988). A number of studies have focused on the adaptive value of these changes in leaf spectral characteristics. Perhaps one of the best studied genera is *Encelia*, a genus of 15 suffrutescent, drought-deciduous shrub species, extending from wet, coastal regions to the dry, hot interior deserts and in which increased pubescence is responsible for decreasing leaf absorptance and reducing leaf temperature (Shreve 1924; Cunningham and Strain 1969; Smith and Nobel 1977a; Ehleringer and Mooney 1978; Ehleringer and Clark 1988).

In *Encelia*, there is a progressive replacement of one species by another along a gradient of increasing aridity in both North and South America, such that on drier sites the species possess more pubescent leaves (Ehleringer et al. 1981). Pubescence can be a highly plastic character in pubescent-leaved species with the extent of its development being inversely related to soil water availability (Ehleringer 1982, 1983). Ehleringer and Mooney (1978) demonstrated that leaf pubescence had three major effects in *E. farinosa*: 1) it was an effective means of reducing leaf temperatures and therefore also transpiration rate under water-limiting conditions, 2) given the relatively low temperature optimum for photosynthesis, leaf pubescence by reducing leaf temper-

ature resulted in a higher rate of carbon gain despite reducing the absorbed photon flux, and 3) by reducing leaf temperature, the reflective pubescence provided the leaf with a means of avoiding high, potentially lethal leaf temperatures.

There is, however, a major exception to the general pattern in *Encelia* of increased pubescence in more arid habitats. This is found in the species *E. frutescens*, a green, scabrous-leaved shrub, which is widespread throughout much of the Sonoran Desert, and is sympatric with *E. farinosa* over much of its range (Shreve and Wiggins 1964). From earlier studies of leaf energy balance simulations coupled with physiological measurements, Ehleringer and Mooney (1978) calculated that a green-leaved (high absorptance) genotype with the same characteristics as measured on pubescent-leaved *E. farinosa* would not be able to maintain its leaf area long into the drought period and would be at a selective disadvantage in terms of total carbon gain when contrasted to pubescent (low absorptance) genotypes. Indeed when a mutant glabrate *E. farinosa* was found in Death Valley, this individual plant was unable to maintain leaves beyond the relatively cooler, more moist periods of the year despite being otherwise similar to other *E. farinosa* shrubs in the region (Ehleringer 1983).

Photosynthetic measurements on leaves of *E. frutescens* indicate this species has no ability to thermally acclimate to changes in growth temperature and that both the temperature optimum and upper lethal temperatures are the same as have been measured in *E. farinosa* (Comstock and Ehleringer 1984). Thus, the physiological constraints that necessitate avoidance of high leaf temperatures in *E. farinosa* should also apply to *E. frutescens*. Given this and also the observation that *E. frutescens* has green leaves with an apparent high leaf absorptance, how is it that this species is able to cope in the same macroclimate as *E. farinosa*?

Materials and methods

Field observations and measurements were made on *Encelia farinosa* and *Encelia frutescens* shrubs growing under natural conditions in the Saddle Peak Hills (lat. 35°45′N, long. 116°20′W, 300 m elevation), immediately east of the Death Valley National Monument, California USA. The topography consists of a series of slopes with shallow soils or surface bedrock which feed into active washes of alluvial origin. These washes are part of a larger alluvial drainage

system (bajada), which ultimately feeds into the Amargosa River. The vegetation of the area is typical of the northern portions of the Sonoran Desert, and is dominated by *Ambrosia dumosa, Atriplex hymenelytra, Encelia farinosa, Encelia frutescens, Hymenoclea salsola*, and *Larrea divaricata* (Shreve and Wiggins 1964; Hunt 1966). The vegetation is open; ground cover is less than 20%. For the observations reported in this study, measurements were collected from *E. farinosa* and *E. frutescens* shrubs growing adjacent to each other in a wash.

Leaf conductance to water vapor was measured on attached leaves using a null-balance diffusion porometer, similar in design to that described earlier by Forseth and Ehleringer (1980). The cuvette was of sufficient volume to enclose several leaves; it was made of clear FEP Teflon to allow high photon fluxes upon the leaves during the measurement period and included a Micronel fan to insure adequate ventilation. Additional gas exchange measurements of photosynthesis, leaf conductance and intercellular carbon dioxide concentrations were collected using a portable photosynthesis system (LICOR Instruments, Lincoln, Nebraska USA). Sample size for all gas exchange measurements was four sets of leaves for each species during each sample interval.

Microclimatic parameters were monitored using a portable datalogger (Campbell Scientific, Logan, Utah USA). Sensors were scanned at one minute intervals and the data presented are hourly averages. Photon flux was measured with a LICOR quantum sensor (LICOR Instruments, Lincoln, Nebraska USA). Leaf temperatures were measured with 36 gauge copper-constantan thermocouples inserted into the undersides of leaves. Air temperatures were measured at leaf height using 24 gauge thermocouples shielded om direct and reflected solar radiation. The leaf to air water vapor gradient (Δw) was calculated based upon air and leaf temperatures and relative humidity measurements (Vaisala Instruments, Helsinki, Finland), and was corrected for elevation. The water vapor saturation deficit (Δe), defined as the water vapor concentration gradient between air at saturation and at actual relative humidity, was measured in a similar manner.

Leaf water potentials were measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon USA). Sample size was four leaves per measurement interval.

Carbon isotope ratios were measured on dried, ground leaf tissues using an in-vial sealed combustion technique. Isotope ratios were measured on a Finnigan MAT delta E isotope ratioing mass spectrometer. Results are expressed in parts per thousand (‰) relative to the PDB standard.

Long-term estimates of the intercellular carbon dioxide concentration (c_i) were calculated by rearranging the equations originally developed by Farquhar, O'Leary and Berry (1982) as

$$c_i = c_a \cdot (\delta^{13}C_{air} - \delta^{13}C_{leaf} - a)/(b-a) \qquad (1)$$

where c_a is the ambient carbon dioxide concentration (340 µl l^{-1}), $\delta^{13}C_{air}(= -7.8‰)$ and $\delta^{13}C_{leaf}$ are the carbon isotope ratios of the air and leaf, respectively, a is the discrimination associated with the slower diffusion rate of ˋO$_2$ ($a=4.4‰$), and b is the net discrimination against ᴗO$_2$ associated with RuBP carboxylase ($b=27‰$). Relative differences in leaf water-use efficiency (ratio of photosynthesis to transpiration, A/E) were calculated as

$$A/E = (c_a - c_i)/(1.6 \cdot \Delta w) \qquad (2)$$

where 1.6 is the ratio of the diffusion coefficients of water to carbon dioxide in air.

Leaf absorptances were measured using an integrating sphere as described previously by Ehleringer (1981). Leaf size and canopy leaf area index were measured using a leaf area meter (LICOR Instruments, Lincoln, Nebraska USA).

Results

Microhabitat distributions of the two species

Three broad but distinct microhabitat zones can be described for most parts of the Sonoran Desert. First there are slopes, consisting of shallow soils with limited soil development and often having bedrock exposed at the surface. Below the slopes are bajadas, large expansive alluvial fans, consisting of two components: wash and transition zones. Washes are best described as regions of active soil and gravel deposition, soil movement (via flashflooding), and deeper gravelly soils. The transition zone is the stabilized portion of a bajada, originally formed from wash deposits, but in recent times no longer subjected to active soil movement.

Encelia farinosa shrubs are most commonly found on the slopes at elevations ranging from 200–800 m. They rarely occurred in active wash locations subjected to periodic flashflooding, but were frequently found in transition zones where flashflooding no longer occurred (Fig. 1). *E. frutescens* shrubs, on the other hand, were most common in the wash microhabitat, became less frequent in the transition zone, and did not occur on the slopes. Because of the different microhabitat preferences, their distributions overlapped primarily in the transition zone.

There were limited situations in which the two species were found together in the wash microhabitat. In such cases, the *E. farinosa* plants were almost always young (approximately 2–6 years of age). In all cases observed over a seven-year period, the *E. farinosa* shrubs in the wash were eventually wholly or partially covered by gravel and debris from flashfloods. The consequence was that the suffrutescent stems broke (usually near the bases) and the shrubs died. In contrast, when debris from flashfloods covered *E. frutescens* shrubs, the thinner suffrutescent stems were bent and perhaps buried, but usually recovered both by apical and axillary growth.
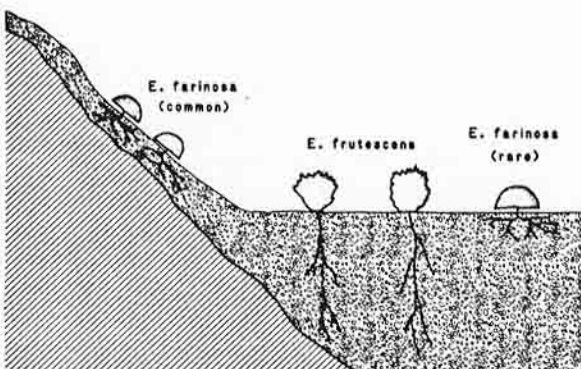

Fig. 1. Distribution patterns of *Encelia farinosa* and *Encelia frutescens* in wash and slope microhabitats within the Sonoran Desert
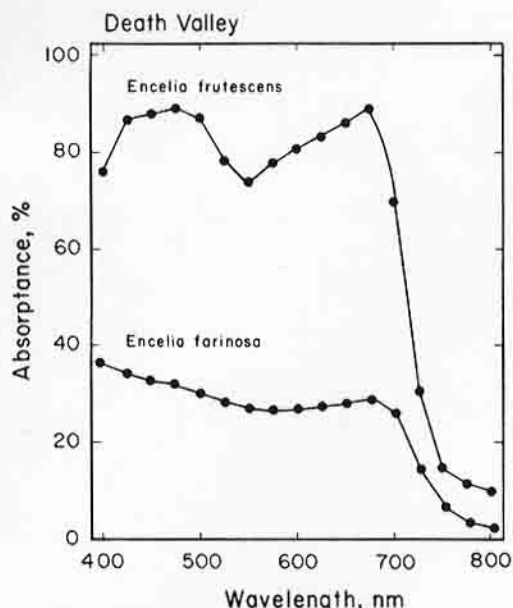
Death Valley

Fig. 2. Leaf absorptance of *Encelia farinosa* and *Encelia frutescens* from the Saddle Peak Hills, adjacent to Death Valley National Monument, California

Given the opportunity, the two species will freely hybridize. These hybrids are clearly recognizable by their intermediate leaf size, leaf shape and leaf absorptance. At this site, approximately 1–2% of the *Encelia* along the washes and in the transition zone appeared to be of hybrid origin. Without exception, hybrids occurred at the lower edge of the transition zone.

Leaf characteristics

Leaf absorptances were significantly different between *E. farinosa* and *E. frutescens* (Fig. 2). *E. frutescens* leaves exhibited absorptances in the 400–800 nm band that were typical of green leaves measured from a large number of species. Leaf absorptances in the 400–500 nm and 600–700 nm waveband were near 90% and when the absorption spectrum was integrated against the solar spectrum at the earth's surface, the integrated leaf absorptance was 85%. Leaf reflectance and transmittance were 11% and 4%, respectively, again typical of most green leaves (data not shown). In sharp contrast, the leaf absorptance over the 400–800 nm waveband was very much reduced in *E. farinosa* being 31% (Fig. 2), as previously shown by Ehleringer and Björkman (1978). This reduced absorptance was associated with a high leaf reflectance and not by an increased transmittance. The data presented in Fig. 2 were from leaves collected in early summer. Leaf absorptances of *E. frutescens* leaves collected at several times during the year did not show significant variation through time (data not presented). Again in contrast, *E. farinosa* leaves are known to have different absorptances through the year depending on soil water availability and this pattern was in fact observed (Ehleringer 1982, 1983, 1985).

E. farinosa leaves were much larger than *E. frutescens* leaves both in terms of width and area (Table 1). There are also large difference in specific leaf area (13.4 vs. 7.1 mg cm^{-2}), but these differences arose because of the dense pubescence layer on upper and lower leaf surfaces of *E. farinosa*. Ehleringer and Cook (1984) demonstrated

Table 1. Leaf and canopy characteristics of *Encelia farinosa* and *Encelia frutescens* measured in mid spring at the Saddle Peak Hills, California. Data are means ± 1 standard error with sample sizes in parentheses

	Encelia farinosa	*Encelia frutescens*
leaf width (mm) ($n = 50$)	18.1 ± 0.7	8.8 ± 0.3
leaf area (cm^2) ($n = 25$)	4.18 ± 0.20	1.17 ± 0.07
specific leaf area (mg cm^{-2}) ($n = 25$)	13.4 ± 0.3	7.1 ± 0.1
leaf angle (°) ($n = 50$)	27.4 ± 2.2	24.8 ± 2.3
leaf area index ($n = 10$)	1.31 ± 0.09	1.50 ± 0.24
root/shoot ratio ($n = 10$)	0.23 ± 0.03	0.42 ± 0.04

that if this pubescence layer was removed that specific leaf area in *E. farinosa* remained constant at approximately 7 mg cm^{-2} over a wide range of leaf absorptances.

Leaf angles were very similar between the two species (Table 1), and therefore the amount of solar radiation incident on the leaf surfaces of the two species during the day should also be similar. However, because of the large differences in leaf absorptance in the 400–800 nm waveband (Fig. 2), which will translate into large absorption differences over the entire solar band (Ehleringer 1981), the total solar radiation absorbed will be much less in the pubescent-leaves species *E. farinosa* than in *E. frutescens*.

Leaf area indices were low in both species, despite the fact that precipitation in the year when these measurements were collected was above average (Table 1). Although leaf area indices of the two species were not different, there were significant differences in the root/shoot ratios. *E. farinosa* allocated a higher fraction of its biomass to aboveground components (specifically to stems/twigs) than did *E. frutescens*. Root to shoot ratio differences are considered further by Ehleringer and Cook (1988), where data indicate that *E. farinosa* primarily stored nitrogen and carbohydrate reserves for growth in stems and twigs, whereas *E. frutescens* primarily stored these reserves in its roots.

Gas exchange and microclimate

Three days, representing early (April 7), mid (May 2), and late spring (May 25) conditions, are presented to illustrate the comparative leaf gas exchange and water potential patterns of the two species.

Over the growing season, air temperature and humidity patterns progressively changed in a semipredictable pattern. Daytime air temperatures increased from approximately 20–25 C in early spring, to 25–30 C in midspring, and finally to 30–40 C in late spring (Fig. 3). Δe exhibited a similar pattern, reaching peaks of 25–30 mbar bar^{-1} in early spring, 30–35 mbar bar^{-1} in mid spring, and 50–70 mbar bar in late spring (Fig. 3).

Given the large differences in leaf absorptances measured between the two species, it was anticipated that leaf temperatures of the two species would also be significantly different. However, actual diurnal leaf temperature measurements on adjacent *E. farinosa* and *E. frutescens* shrubs indicated remarkably similar leaf temperature readings. In early spring, leaf temperatures of the two species were up to several degrees below air temperature and were within 1 C of each other (Fig. 3). Even though air temperatures
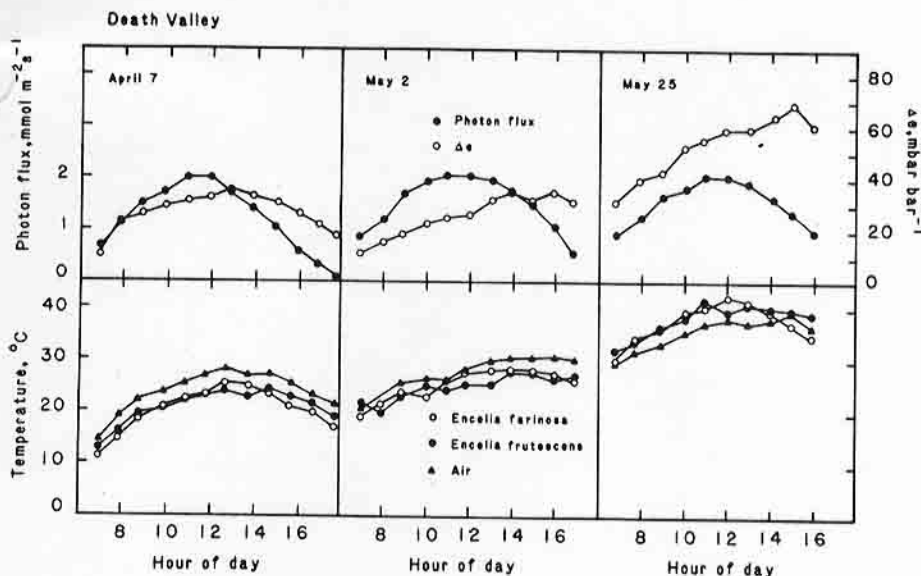
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Fig. 3. Photon flux (400–700 nm), air water vapor saturation deficit (Δe), and air and leaf temperatures of *Encelia farinosa* and *Encelia frutescens* from the Saddle Peak Hills, adjacent to Death Valley National Monument, California under early spring (April 7), midspring (May 2), and late spring (May 25) conditions
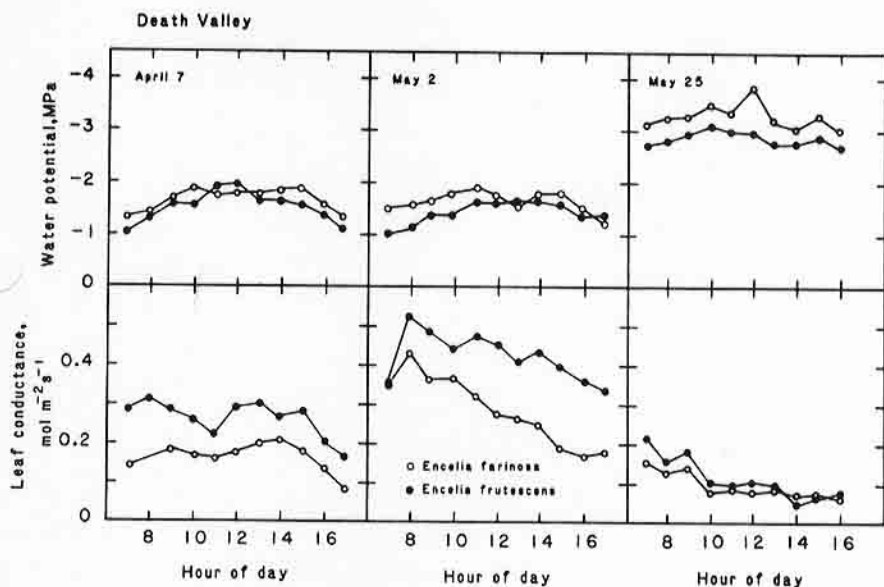

Fig. 4. Leaf water potential and leaf conductance to water vapor of *Encelia farinosa* and *Encelia frutescens* from the Saddle Peak Hills, adjacent to Death Valley National Monument, California under early spring (April 7), midspring (May 2), and late spring (May 25) conditions

were several degrees higher in mid spring, leaf temperatures of both species were again below air temperature and again within approximately 1 C of each other (Fig. 3). Under late spring conditions when air temperatures ranged from 35–40 during midday, leaf temperatures were slightly above air temperature. Yet still leaf temperatures of *E. farinosa* and *E. frutescens* were almost exactly the same (Fig. 3).

If leaf temperatures are similar for the two species, despite large differences in the amount of solar radiation absorbed, then it must be that latent heat loss (transpiration) is greater in leaves of *E. frutescens* than in those of *E. farinosa*. Diurnal observations of leaf conductance confirmed this prediction. Leaf conductances to water vapor were substantially higher in *E. frutescens* leaves than in *farinosa* leaves under early and mid spring conditions and slightly higher under late spring conditions (Fig. 4). On any single day, leaf conductances were also a reliable indicator of the transpiration rate for both species, since leaf temperatures and therefore Δw values were similar be-

tween the two species. During early and mid spring observation periods, the difference in leaf conductances (and therefore transpiration rates) was approximately 30–50%, and appeared to remain constant through the day. From Fig. 4, it is evident that stomata on both *E. farinosa* and *E. frutescens* leaves responded to changes in Δw. On both days leaf water potentials changed little during the day, yet leaf conductances in both species decreased during the day as Δw increased.

Even though shrubs of both species were sampled at the same wash location, leaf water potentials were not necessarily equivalent. Under early spring conditions, leaf water potentials measured throughout the day on both species averaged −1.7 MPa and varied less than 0.4 MPa (Fig. 4). However, by mid spring, consistent differences in leaf water potential of 0.2–0.5 MPa had developed between the two species, with leaf water potentials being consistently higher in *E. frutescens*. By late spring when leaf water potentials had decreased to nearly −3 MPa, the difference

in leaf water potentials between the two species had increased to 0.3–0.8 MPa.

The differences in leaf water potential evident later in the season suggested that rooting depths of *E. frutescens* shrubs were deeper than those of *E. farinosa* shrubs. Add to this the significantly higher transpiration rate of *E. frutescens* shrubs, and it is clear that this species must be tapping a larger, more reliable water source than available to *E. farinosa* shrubs, even though both species grow adjacent to each other. Root excavation studies were not feasible, but recent flashfloods had eroded edges of the transition zone in several places and had exposed a number of *E. farinosa* and *E. frutescens* root systems. In these exposed root systems, the maximum rooting depths of *E. farinosa* shrubs were not deeper than 80 cm. In contrast, rooting depths of *E. frutescens* were all beyond 300 cm (the maximum exposure cut observed).

Intercellular carbon dioxide and water-use efficiency

Earlier studies of the intrinsic photosynthetic characteristics of *E. farinosa* (Ehleringer and Björkman 1978; Ehleringer and Cook 1984) and *E. frutescens* (Comstock and Ehleringer 1984) had suggested that photosynthetic capacities of the two species were similar. Moreover, when pubescence effects on specific leaf area differences between the two species were taken into consideration, there were no differences in the carboxylation efficiency (slope of the linear portion of the photosynthetis versus intercellular carbon dioxide concentration (c_i) response curve) between leaves of the two species over a wide range of leaf water potentials. These results infer that under field conditions, it would be expected that photosynthesis should be higher in *E. frutescens* leaves than *E. farinosa* leaves, because of the higher leaf conductances and therefore expected higher intercellular carbon dioxide concentrations.

Diurnal measurements on leaves of both species in early spring (but with unusually low leaf water potentials on this date because of lower than average rainfall) indicated that higher leaf conductances in *E. frutescens* resulted in higher net photosynthetic rates (Fig. 5). On average, calculated c_i values from these observations were also higher in *E. frutescens* leaves than in those of *E. farinosa*. As leaves of both species maintained the same leaf temperature on this day, the higher c_i values indicated that water-use efficiency was lower in *E. frutescens* than in *E. farinosa*. Given c_i values from Fig. 5 and the average Δw for both species of 36 mbar bar^{-1} between 0900–1400, the estimated water-use efficiency during this period was 1.60 and 1.22 for *E. farinosa* and *E. frutescens*, respectively. It would appear that the higher photosynthetic rate in *E. frutescens* comes at a substantial cost in terms of the amount of water lost per unit carbon gain.

Long-term estimates of c_i can be obtained from leaf carbon isotope ratios. $\delta^{13}C$ ratios of *E. farinosa* leaves are more positive than those of *E. frutescens* (Table 2), supporting the field observation of a higher c_i value in *E. frutescens* leaves. The carbon isotope ratio values presented predict that the long-term c_i values for the two species were 218 and 242 µl l^{-1} for *E. farinosa* and *E. frutescens*, respectively. While these c_i values were lower than those measured by gas exchange techniques in Fig. 5 (248 and 270 µl l^{-1}), the differences in c_i values between the two species were very similar.
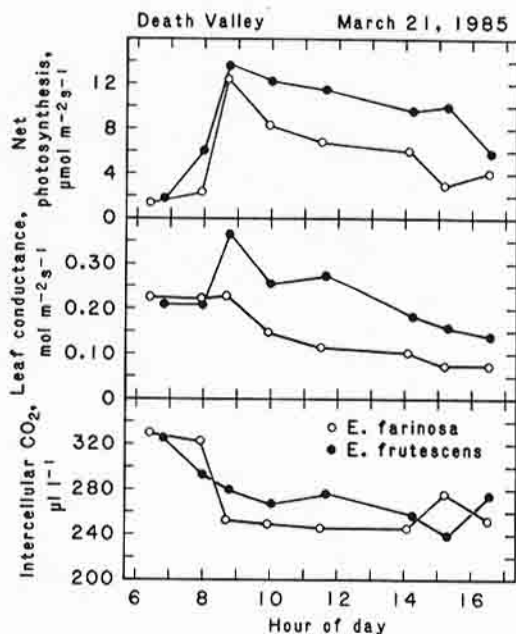

Fig. 5. Net photosynthesis, leaf conductance to water vapor, and intercellular carbon dioxide concentrations of *Encelia farinosa* and *Encelia frutescens* from the Saddle Peak Hills, adjacent to Death Valley National Monument, California under spring conditions
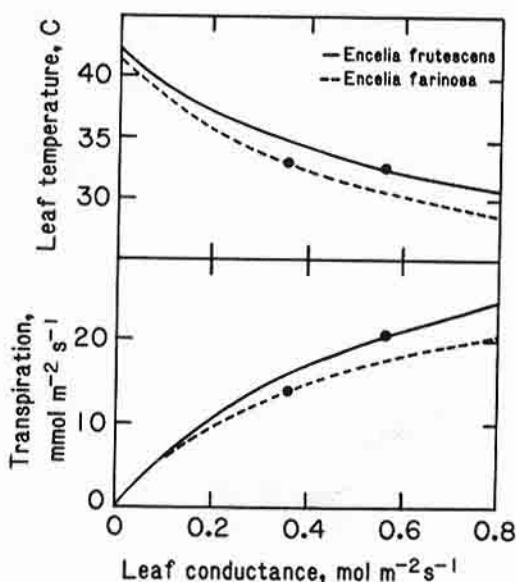

Fig. 6. Simulation results for leaf temperature and transpiration rate of *Encelia farinosa* and *Encelia frutescens* leaves as a function of the leaf conductance to water vapor. Simulation conditions were similar to mid to late spring field conditions and included: air temperature of 35 C, soil temperature of 55 C, 10% relative humidity, total solar radiation of 1000 W m^{-2}, wind speed of 1 m s^{-1}, leaf absorptances (400–3000 nm) of 32% and 50%, and leaf widths of 1.8 cm and 0.9 cm for *Encelia farinosa* and *Encelia frutescens*, respectively. Dots on simulation curves represent the expected operational maximum conductances for a leaf water potential of −20 bars and a Δw of 45 mbar bar^{-1} (based on data from Comstock and Ehleringer 1984 and Ehleringer and Cook 1984)

Leaf temperature and energy budget

Leaf energy budget models as originally developed by Rashke (1960) and Gates (1962, 1980) can be used to explore the interactions between various modes of energy ex-

change and leaf temperature. Leaf energy exchange equations were used to calculate energy budget relationships between leaf temperature, transpiration rate and leaf conductance to water vapor. Specifically, measured leaf morphological and spectral characteristics (Fig. 2, Table 1) were used in simulations to calculate how leaf temperature and transpiration rate in the two species changed as a function of leaf conductance to water vapor.

The simulations showed that at any leaf conductance value, leaf temperatures were always lower in *E. farinosa* than in *E. frutescens* and transpiration rates were always higher in *E. frutescens* (Fig. 6). Given the lower leaf absorptance in *E. farinosa*, equivalent leaf temperatures can only be maintained if leaf conductance and therefore transpiration rates were substantially higher in *E. frutescens* leaves. The closed circles in Fig. 6 indicate the mean maximum leaf conductances expected for the two species at midday under mid spring conditions. Figure 6 (top) shows that under these leaf conductances, leaf temperatures of the two species will indeed be equal. However, there is a substantial cost to *E. frutescens* in terms of water loss rates associated with maintaining equal leaf temperatures. Figure 6 (bottom) shows that transpiration rate in *E. frutescens* will be higher (21 vs 13 mmol m^{-2} s^{-1}).

Discussion

Leaf temperature and metabolism

There are temperature constraints that limit the range over which *Encelia* species are able to operate. While both *E. farinosa* and *E. frutescens* occur in a hot desert region, their temperature optima for photosynthesis are 25–30 C, photosynthetic rates decrease rapidly above the temperature optima, and lethal leaf temperatures occur in the vicinity of 46–48 C (Ehleringer and Björkman 1978; Comstock and Ehleringer 1984). These physiological limitations, for which there appears to be little acclimation potential, should limit carbon acquisition in these *Encelia* to cool and moderate air temperatures. However, these species do not necessarily avoid periods of the year when air temperatures are high (40–50 C). When adequate soil moisture is available both species will maintain high rates of metabolic activity as well as extensive vegetative growth and reproductive activity (Ehleringer and Mooney 1978; Ehleringer 1985; Comstock and Ehleringer 1986).

In order to maintain these high rates of metabolic activity, leaf temperatures need to be decoupled from air temperatures during hot conditions. At air temperatures above 30 C, photosynthetic performance of both *Encelia* species is enhanced by having an under-temperature (leaf temperature less than air temperature). At leaf temperatures greater than 30 C, the leaf is operating above the thermal optima for photosynthesis, and the net carbon gain benefits should be proportional to the leaf under-temperature. Smith (1978) has shown that both transpiration and spectral changes can be used to produce leaf under-temperatures. His simulation results indicate that increased leaf size can amplify the leaf under-temperature if spectral changes are used to reduce the amount of radiation absorbed. Interestingly, leaf size in the species with high leaf reflectance, *E. farinosa*, is significantly larger than in *E. frutescens*.

What is of importance is that high, potentially lethal temperatures be avoided and that leaf temperatures be maintained at levels that allow greater carbon gain. It is perhaps surprising that both species are able to maintain similar leaf temperatures in the same microclimate, even though leaf spectral characteristics are so different.

Transpirational cooling to avoid high leaf temperatures

High transpiration rates in desert plants have been known since the pioneering studies of Maximov (1929). Perhaps the first investigator to link high transpiration rate with plant function was Lange (1959), who suggested that evaporative cooling resulting from the high transpiration rates of *Citrullus colocynthis*, *Abutilon muticum* and *Chrozophora senegalensis* leaves in the Sahara Desert was an essential feature for avoiding lethal leaf temperatures. More recently, Althawadi and Grace (1986) verified the high transpiration rates in *C. colocynthis* leaves under field conditions (approximately 9 mmol m^{-2} s^{-1}, which was sufficient to reduce leaf temperatures to as much as 2 C below air temperature).

These transpiration rates in *C. colocynthis* are somewhat less than the 11–14 mmol m^{-2} s^{-1} measured by Smith (1978), which were sufficient to lower leaf temperatures to as much as 18 C below air temperature for a number of Sonoran Desert species (including *E. farinosa*). While the Smith (1978) data represent maximum transpiration rates following rainfall events, they are nonetheless strongly indicative of the high transpiration rates that can occur in Sonoran Desert shrubs during active vegetative growth periods (Smith and Nobel 1977a, b; Comstock and Ehleringer 1986). In the present study, transpiration rates were 13–15 mmol m^{-2} s^{-1} for *E. frutescens* leaves in mid spring, and for *E. farinosa* approximately 60–70% of these values.

Transpiration versus reflectance as a means of regulating leaf temperature

High transpiration rates need not be the only mechanism for avoiding high leaf temperatures. Lowering leaf temperatures by reducing the amount of solar radiation absorbed is another viable mechanism, and this can be accomplished either by a decreased leaf absorptance and/or an increased leaf angle. The data presented in this study indicate that while leaf absorptances differed, leaf angles were not different between the two species. The leaf absorptance differences in the 400–700 nm waveband of 31% and 85% for *E. farinosa* and *E. frutescens* translate into leaf absorptances in the 400–3000 nm waveband (total solar) of 11% and 50%, respectively. However, a more reasonable total solar leaf absorptance for *E. farinosa* during the late spring is 32%.

In terms of maintaining similar leaf temperatures, this one-third reduction of leaf absorptance in *E. farinosa* versus *E. frutescens* is approximately equivalent to a one-third increase in transpiration rate in *E. frutescens*. Both sides of the energy budget equation are in balance at the same leaf temperature. In one species, the amount of energy absorbed is decreased, while in the other, the amount of energy dissipated is increased. In other words, the increased solar radiation absorption by *E. frutescens* leaves can be offset by having a latent heat loss rate that is one-third higher than in *E. farinosa*.

Tradeoffs involving decreased leaf absorptance versus increased latent heat loss have several carbon and water balance ramifications. First, the investment in producing a reflective surface, such as the dense pubescence layer of

Table 2. Leaf carbon isotope ratios and the predicted intercellular to atmospheric carbon dioxide ratio (c_i/c_a) and intercellular carbon dioxide concentration (c_i). Predicted c_i/c_a and c_i values are based on equations from Farquhar, O'Leary and Berry (1982)

	$\delta^{13}C$ (‰)	c_i/c_a	c_i (μl l^{-1})
Encelia farinosa	−26.7	0.64	218
Encelia frutescens	−28.3	0.71	242

E. farinosa, is a fixed cost as opposed to the continual cost of maintaining higher transpiration rates each day. However, the pubescence can represent a substantial carbon investment as it has been shown that in a low absorptance leaf the hairs represent approximately 55% of the total leaf mass (Ehleringer and Cook 1984). Using a production-value approach, Ehleringer and Werk (1986) calculated that the production cost of a lightly pubescent leaf (such as that of *E. frutescens*) is only 49% of that cost necessary to produce a heavily pubescent leaf (such as that of *E. farinosa*). When calculations of the time needed to recover this additional investment were made, it was estimated that the extra cost of pubescence in a leaf can be recovered with approximately eight days of photosynthesis. Second, the decreased leaf absorptance necessarily means that water loss rates are less than would occur in a green leaf (at the same leaf conductance), and so that by limiting soil moisture depletion, gas exchange activity can be extended over a longer period of time (assuming soil water is not consumed by neighboring individuals). While it is not necessarily the case that this extension of activity will always result in a greater net carbon gain, it may be the only viable option for shrubs growing on shallow soils with very limited soil water availability.

One immediate consequence of enhancing transpiration rates to cool a leaf is that the leaf will necessarily be operating at a lowered leaf water-use efficiency. Given similar leaf temperatures, an increase in transpiration rate must result from increased leaf conductance, which in turn implies a higher intercellular CO_2 concentration (c_i) and therefore a lower water-use efficiency (equation 2). The carbon isotope ratio data (Table 2) confirmed that a necessary consequence of enhanced transpirational cooling in *E. frutescens* was a decreased water-use efficiency. However, these data do not necessarily dictate that absolute photosynthetic rates differ between the two species. Differences in the initial slope of the net photosynthesis versus c_i response curve (carboxylation efficiency) could offset the predicted increase in photosynthetic rate expected with an increased c_i value. For instance, a greater carboxylation efficiency could allow a leaf to operate at a lower c_i value (therefore higher water-use efficiency), yet still have the same photosynthetic rate as a leaf with a lower carboxylation efficiency but a higher c_i value (and also a lower water-use efficiency). No field observations of carboxylation efficiency are available for *E. farinosa* and *E. frutescens* under similar conditions, but laboratory-based studies on both species suggest that there are no differences carboxylation efficiency between species (Ehleringer and Cook 1984; Comstock and Ehleringer 1984). Thus, the lower water-use efficiency of *E. frutescens* is likely to result in higher rates of carbon gain.

Members of the *farinosa* clade within *Encelia* that occur in warm deserts utilize increased reflectance to regulate leaf temperature (Ehleringer and Clark 1988). This group includes *E. canescens*, *E. densifolia* Clark sp. nov., *E. palmeri*, and *E. farinosa*. The same appears to hold for the primitive members of the *frutescens* clade (*E. ravenii* and *E. actonii*). Data from this study have shown that *E. frutescens*, the most advanced member of the *frutescens* clade does not follow this pattern, but instead this species uses transpirational cooling as an alternative to increased reflectance. It is not clear that *E. frutescens* is the only *Encelia* member capable of utilizing transpirational cooling in warm desert habitats to regulate leaf temperature. The other two advanced members of the *frutescens* clade, *E. resinosa* Clark sp. nov. and *E. virginensis*, also lack reflective pubescence (Ehleringer and Cook 1987). While data are unavailable, it is possible that both of these species also rely on transpirational cooling to regulate leaf temperatures.

Microhabitat distribution

Since both species support equivalent canopy sizes, *E. frutescens* can only maintain higher water loss rates if shrubs are located in a microhabitat capable of providing the necessary additional soil water. Soils on the slopes are too shallow and lack the large water-holding capacity necessary to support transpirational demands of *E. frutescens*. On the other hand, wash sites with their deeper, gravelly soils and greater water availability at deeper depths are more likely to be able to provide sufficient amounts of soil water for *E. frutescens*. Root systems in *E. frutescens* penetrate deep into the wash soils, but there is no evidence that this species is phreatophytic as has been suggested for *Citrullus colocynthis*, the cucurbit from Saudi Arabia that appears to rely on transpirational cooling (Althawadi 1985, cited in Althawadi and Grace 1986).

Certainly a number of Sonoran Desert tree species in the wash (*Chilopsis linearis*, *Prosopis glandulosa*, *Olneya tesota*, and possibly *Acacia greggii*) do have roots penetrating to the water table (Nilsen, Sharifi and Rundel 1984). Yet these tree species apparently do not rely on transpirational cooling to the same extent that *E. frutescens* does, since maximum transpiration rates of these phreatophytes was 8 mmol m^{-2} s^{-1} or less (Nilsen et al. 1983, 1984). In addition, other perennial species within the wash microhabitat, such as *Eriogonum fasciculatum*, *Hyptis emoryi*, and *Mirabilis tenuiloba*, do not appear to maintain transpiration rates of similar magnitude to those reported here for *E. frutescens* (Smith and Nobel 1977a; Smith and Osmond 1987). Thus, although the wash zones may be the only microhabitat capable of supplying sufficient amounts of soil water to maintain transpirational cooling in *E. frutescens* over extended periods, not all species occupying this zone utilize this means of reducing leaf temperature. In fact, the only other species from this area that appears to rely on transpirational cooling to reduce leaf temperatures might be the short-lived and prostrate perennial, *Heliotropium curassavicum*. Mooney (1980) reported that the upper lethal leaf temperature for this species under midsummer conditions was near 48 C. Summer air temperatures in the desert close to the soil surface will usually exceed 50 C throughout much of the day. Thus, it is perhaps not surprising to have reported transpiration rates in *H. curassavicum* approaching 30 mmol m^{-2} s^{-1} (Roy and Mooney 1982).

While inadequate soil moisture availability on the slopes is the most likely explanation for the restriction of *E. frutes-*

cens to wash microhabitats, it does not provide a reciprocal explanation for the lack of *E. farinosa* in wash microhabitats. The lack of *E. farinosa* in wash microhabitats is likely due to its intolerance of periodic flashflooding. Seedlings of both *Encelia* species can get established in the active wash, yet *E. farinosa* shrubs appear to be more susceptible to being covered by flashflood debris. Mineral and carbohydrate reserves to initiate growth and for reproduction are primarily stored in the thick stems of *E. farinosa* as opposed to the root system in *E. frutescens* (Ehleringer and Cook 1988). Since *E. farinosa* stems are easily broken (common name of the shrub is "brittle bush"), mortality associated with stem breakage is the likely explanation of why individual *E. farinosa* do not persist within the wash. If a species, such as *E. frutescens* is using transpirational cooling to regulate leaf temperatures, then one would expect that the stomata on such species should be less sensitive to changes in humidity than other species less dependent on transpirational cooling. That is, as Δw increased during the day, stomata should remain open or respond less than in leaves of species not so dependent on transpirational cooling. This is exactly what has been observed. Stomata of *E. frutescens* are much less sensitive to Δw than are those of *E. farinosa* (Ehleringer, unpublished observations). Direct comparisons with other wash-habitat species are not possible because data were not collected under similar experimental conditions. However, it is nonetheless evident from the data available that at midday Δw values for mid to late spring conditions that *E. frutescens* leaves maintained higher leaf conductances than other wash-habitat perennials, including *Acacia greggii, Eriogonum inflatum, Hymenoclea salsola, Olneya tesota,* and *Prosopis glandulosa* (Nilsen et al. 1983; Nilsen et al. 1984; Smith and Osmond 1987). Thus, at the time when conditions are driest and transpirational cooling most effective, species other than *E. frutescens* appear to be closing their stomata rather than keeping them open.

The genus *Encelia* appears to be ideally suited for studies linking habitat distribution and functional morphology. While previous studies of this genus have focused on variation in leaf pubescence and how changes in this morphological character can be selectively advantageous across aridity gradients, the present study documents that on a finer distribution scale, analyses of the tradeoffs involved between morphological and physiological characters can contribute to our understanding of the factors involved in determining plant adaptation and distribution limits.

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