

## Characterization of a glabrate *Encelia farinosa* mutant: morphology, ecophysiology, and field observations

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**Abstract.** An individual *Encelia farinosa* (Asteraceae) from Death Valley, California is described that is completely lacking in the dense leaf pubescence covering characteristic of the species. While leaf absorptances to solar radiation of the mutant *E. farinosa* are much greater than those of the wild type, other morphological aspects and photosynthetic characteristics appear to be similar to those typical for *E. farinosa*. Leaf temperatures of mutant and wild type *E. farinosa* in the field are similar, but only because of steeper leaf angles and higher leaf conductances to water vapor in the mutant form. As a consequence of a greater water expenditure for transpirational cooling, the mutant *E. farinosa* becomes deciduous much earlier in the drought period than do the normal pubescent leaved *E. farinosa*.

### Introduction

*Encelia farinosa* Gray (Asteraceae) is a common suffrutescent shrub of the Sonoran Desert. The drought-deciduous leaves are characterized by a dense pubescence on both the upper and lower surfaces (Shreve and Wiggins 1964), which serves to reflect solar radiation (Ehleringer and Björkman 1978a). The leaf pubescence is produced in response to drought and high temperature conditions (Smith and Nobel 1978; Ehleringer 1982). Leaf absorptances to solar radiation in *E. farinosa* over the photosynthetically useful wavelengths (400–700 nm) and over the total solar waveband (400–3,000 nm) can be as low as 29% and 10%, respectively, as a result of the reflective hair covering (Ehleringer, Björkman, and Mooney 1976; Ehleringer and Björkman 1978a). This is in contrast to absorptance values of 85% and 50%, respectively, which are more characteristic of green leaves (Gates 1980; Ehleringer 1981). As a direct consequence of the reduced leaf absorptance, leaf temperature and transpiration rate are reduced, allowing for leaf temperatures more favorable to photosynthesis under high air temperatures and prolonged photosynthetic activity into drought periods in the Sonoran Desert (Ehleringer and Mooney 1978).

Recently, a single mature *E. farinosa* individual was found in Death Valley, California, with leaves that appeared glabrous to the naked eye. In all other respects, this plant appeared identical to the remainder of the *E. farinosa* population. This provided an opportunity to directly compare the significance of leaf pubescence to leaves of

*E. farinosa* in a side by side situation. The study by Ehleringer and Mooney (1978) suggested that leaf pubescence was essential to maximize carbon gain and probably for survival in *E. farinosa*. The question arose, therefore, how could this apparent mutant *E. farinosa* survive? The purpose of the present study was to describe the mutant in terms of leaf morphology and leaf absorptance spectra in order to characterize this individual plant. Then photosynthesis and transpiration measurements of single leaves in the laboratory and water relations and microclimate in the field were investigated to determine how this plant is able to survive the hot, arid conditions of Death Valley.

### Methods and materials

Field observations and ecophysiological measurements were made on the apparently glabrous-leaved *Encelia farinosa* individual (hereafter called *E. farinosa* mutant) and on surrounding pubescent-leaved *E. farinosa* individuals (hereafter called *E. farinosa* wild type) within the Death Valley National Monument, California. The location was at the bottom of a small ravine (600 m elevation) just off of Confidence Wash (long. 116°32' W, 35°50' N). The vegetation consisted primarily of *Atriplex hymenelytra*, *E. farinosa*, and *Viguiera reticulata*. The rocky soils of the area appeared to be volcanically derived.

Measurements of photosynthesis and transpiration were also made in the laboratory in Salt Lake City, Utah. For these measurements, the *E. farinosa* wild type were germinated from seed and grown in 20 l pots outdoors in Salt Lake City, Utah during the summer. At other times of the year plants were grown in a greenhouse which received supplemental lighting from HID lamps to create daily quanta totals of 40–50 mol m<sup>-2</sup> in the 400–700 nm waveband. The *E. farinosa* mutant was propagated by cuttings from the individual in the field and were grown adjacent to the *E. farinosa* wild type. Further propagations were from plants derived from the original cuttings.

Leaf spectral characteristics over the 400–700 nm waveband were measured using an Ulbricht integrating sphere attached to a grating monochromator (Ehleringer 1981). These values are often presented in the text as the integrated 400–700 nm absorptance to sunlight.

Simultaneous measurements of photosynthesis and transpiration were made on attached leaves of plants. The gas exchange system was similar to that previously described by Ehleringer and Björkman (1978b) and Ehler-

inger (1983). The photosynthetic-irradiance response curve was measured by first exposing the leaves to an irradiance of  $2.0 \text{ mmol m}^{-2} \text{ s}^{-1}$  (400–700 nm), a leaf temperature of  $30^\circ \text{C}$ , an ambient  $\text{CO}_2$  concentration of  $320 \mu\text{l l}^{-1}$ ,  $21\% \text{ O}_2$ , and a water vapor pressure deficit of  $1.0 \text{ kPa}$ . After equilibrium had been obtained, the irradiance was reduced in steps. For the temperature dependence of photosynthesis measurements, the standard conditions were the same as for the high irradiance point in the photosynthesis-irradiance response curves. Sample size was 3–4 leaves from different plants.

In the field several parameters were measured diurnally on the *E. farinosa* mutant and adjacent wild type individuals. The measurements included estimates of leaf conductance to water vapor ( $n=4$ ) with a null balance porometer (Forseth and Ehleringer 1980) except in March when measurements were made with a transit time porometer, and leaf water potential ( $n=2-3$  on the mutant,  $n=3-4$  on the wild type) with a pressure chamber. Several microclimate parameters were measured each minute and averaged over 30 min with a micrologger (Campbell Scientific, Logan, Utah). These included leaf temperatures ( $n=6$ ) of both *E. farinosa* mutant and wild types using 36 gauge thermocouples, air temperature, relative humidity, and quantum flux. Fisheye pictures to characterize the solar radiation regime of the *E. farinosa* mutant were collected using a fisheye conversion lens attached to 35 mm camera. These photographs were analyzed using a computer program which calculated the solar radiation levels and the projected paths of the sun for different times of the year (List 1966).

Leaf angles (using a compass) and sizes (using a ruler) were measured on 25 leaves of both the mutant and wild type forms.

## Results

**Description of mutant.** The apparently glabrous *E. farinosa* mutant was approximately 0.8 m wide and 0.5 m tall, similar to the other *E. farinosa*. It was suffrutescent and had the same hemispherical appearance as the neighboring *E. farinosa* shrubs.

Leaf shape appeared to be identical in the two *E. farinosa* forms (Fig. 1). Leaves were lanceolate to broadly

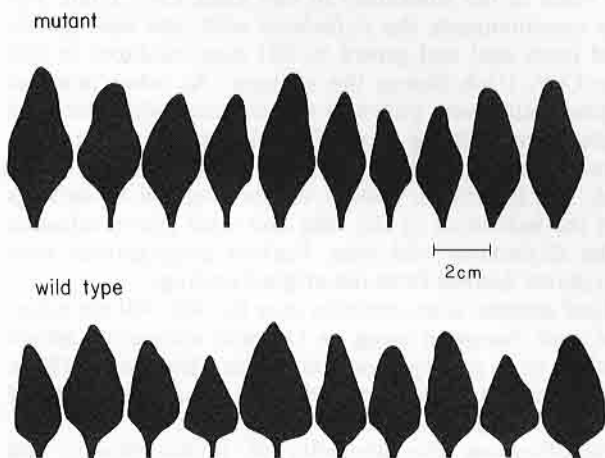


Fig. 1. Representative leaf tracings of the mutant *Encelia farinosa* (top) and wild type *E. farinosa* (bottom) to show the similarity in leaf shapes.

ovate, and were quite different from the glabrate-leaved *Encelia* species (i.e., *E. frutescens* and *E. virginensis*), so that there was no chance for confusion. The leaf sizes were somewhat different. During March, the leaf sizes of the *E. farinosa* mutant and wild types were  $14.4 \pm 0.7 \text{ mm}$  ( $\bar{x} \pm \text{s.e.}$ ) and  $18.2 \pm 0.6 \text{ mm}$ , respectively. Leaf angles were also different, with the mutant having a much steeper leaf angle. Leaf angles averaged  $47.0 \pm 2.9^\circ$  and  $24.6 \pm 2.0^\circ$  for the mutant and wild type, respectively.

Floral morphology appeared to be the same in both *E. farinosa* forms. Each had yellow disk and ray flowers, the same number of ray flowers per head, and multiple flower heads per peduncle. These characters together distinguished *E. farinosa* from other *Encelia* species, and again, it was highly unlikely because of those differences that the mutant represented a hybrid of *E. farinosa* with another *Encelia* species.

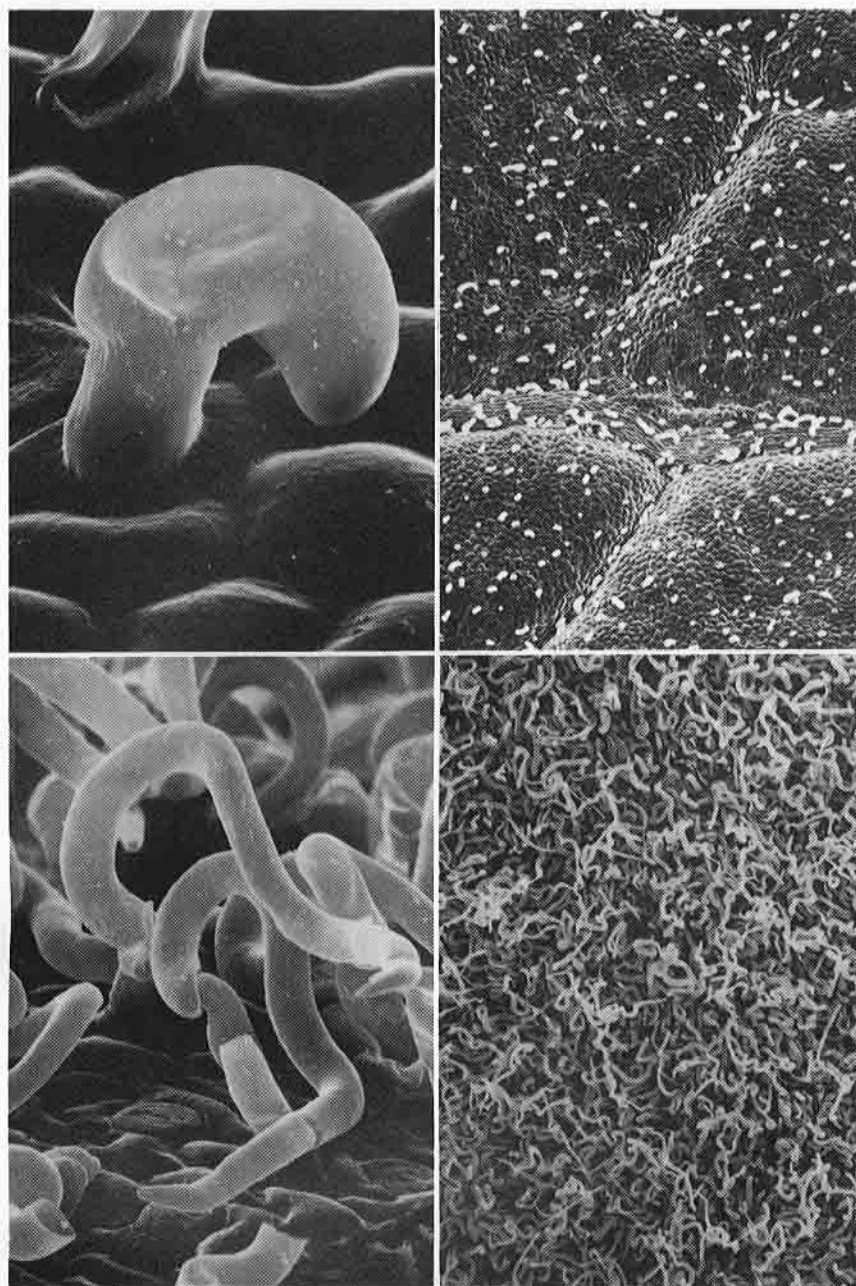
These morphological criteria thus indicated that the glabrate *Encelia* was a mutant of *E. farinosa*, not a member of another *Encelia* species or a hybrid with another *Encelia* species.

The leaf surfaces of both wild type and mutant *E. farinosa* leaves were examined using the scanning electron microscope (SEM). On leaves of the *E. farinosa* wild type, there was a dense mat of long, linear hairs covering the upper and lower surfaces (Fig. 2 bottom left and right plates). The leaf and hair morphology was the same as has been described by Ehleringer and Björkman (1978a). However, in the mutant *E. farinosa*, the situation was quite different. The leaf surface was not glabrous, but instead was covered by what appear to be stubby linear hairs (Fig. 2 top left and right). The bases of the hairs in the two *E. farinosa* forms were similar, but the hair had not elongated to any extent in the mutant form. The hair densities on the *E. farinosa* mutant leaf appeared to be much less dense than on the wild type.

**Spectral characteristics.** The leaf absorbance spectrum for the *E. farinosa* mutant differed greatly from that of the normal *E. farinosa* in that the mutant had much higher absorbances at all wavelengths (Fig. 3). The *E. farinosa* mutant leaf absorbances averaged about 85%, typical for green leaves such as the nearly glabrous *E. californica* (a coastal species). The lower absorbance by *E. farinosa* wild type leaves was due to the increased reflectance caused by the pubescence. There was little difference in the transmittance spectra of the wild type and mutant *E. farinosa* leaves.

There were apparently no plants having leaves with intermediate absorbances within the *E. farinosa* population. The leaf absorbance of mature leaves from individuals in the population were sampled and the data summarized in Fig. 4. The leaf absorbance histogram of the population was bimodal, with peaks at approximately 45% and 60%, both far below the mutant value of 86%. The bimodal frequency distribution of leaf absorbances actually represented the distinct absorbance differences of plants growing in washes (somewhat greater water availability) and those growing on the hillsides (less water availability). This phenomenon has been described by Ehleringer (1982). However, in neither subpopulation were the leaf absorbances at all similar to those of the *E. farinosa* mutant.

Since it was known that the absorbance of *E. farinosa* leaves changed throughout the year with water availability, the seasonal variation in leaf absorbance was measured



**Fig. 2.** Top: SEM micrographs of the mutant *Encelia farinosa* hair (left) and of the adaxial surface of the leaf. Bottom: SEM micrographs of normal *E. farinosa* hairs and of the adaxial surface of the leaf. Magnifications: top left,  $\times 1,280$ ; top right,  $\times 40$ ; bottom left,  $\times 450$ ; bottom right,  $\times 50$ .

for both mutant and wild type forms. Over the course of two years the leaf absorptances of the wild type *E. farinosa* varied from 76% to 45% annually, whereas the leaf absorptances of the *E. farinosa* mutant remained constant at approximately 85% (Fig. 5). The wild type *E. farinosa* remained in leaf throughout the entire period, although during the drought periods the leaf area was very much reduced. In contrast, the mutant dropped its leaves soon after the beginning of each drought period.

*The wash as a protective location.* The possibility existed that the mutant *E. farinosa* was able to survive because it occurred in a wash, protected from the intense solar radiation normally received by more exposed plants in this habitat. To determine whether or not this was the case, fisheye pictures which yield a hemispherical projection of the sky were taken from the position of the mutant *E. farinosa*

(Fig. 6). These pictures were then analyzed to determine how much less daily solar radiation the mutant *E. farinosa* received than did plants occurring on a flat, horizontal surface. During the growing season (February to May) and on into the drought period (June to October) the total daily solar radiation received by the mutant was virtually the same as that received on an open, horizontal surface. Less solar radiation was received in the wash by the mutant when the sun was at its lowest declination, but this was also the time of lowest daily solar radiation totals, lowest photoperiod, and coolest air temperatures. Thus, I conclude that the reason why the mutant was able to survive was not because it was protected by and receiving less solar radiation in the wash.

*Gas exchange characteristics.* Having established that the mutant and wild type *E. farinosa* forms were morphologi-



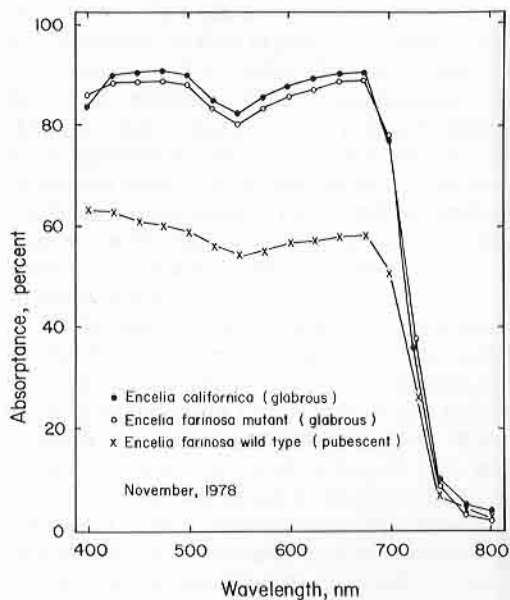


Fig. 3. Leaf absorbance spectra between 400–800 nm for leaves of *Encelia californica*, a glabrous mutant *E. farinosa*, and a normal pubescent *E. farinosa*

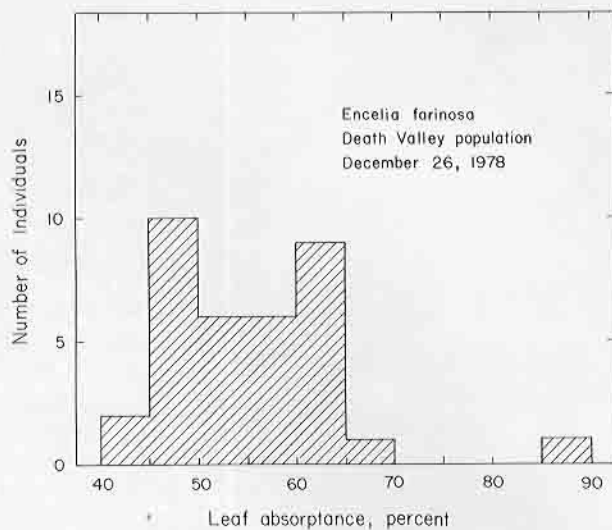


Fig. 4. Histogram of leaf absorbances to solar radiation in the 400–700 nm waveband for the Death Valley population of *Encelia farinosa* with the glabrous mutant *E. farinosa* individual

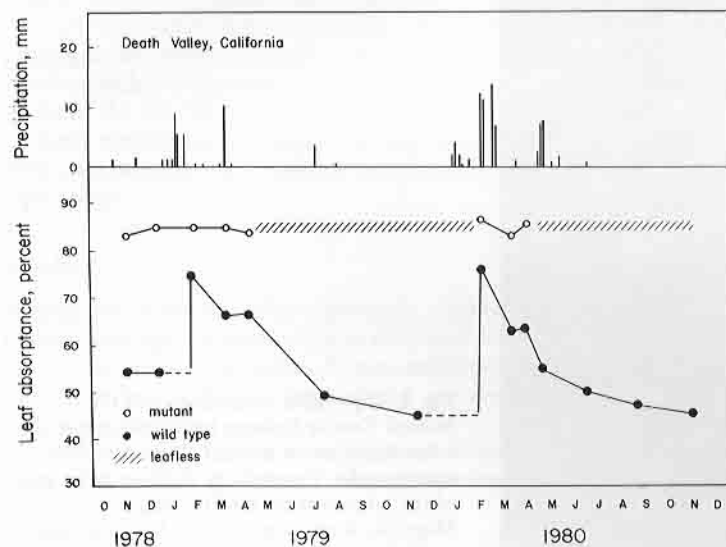


Fig. 5. Top: Time course of precipitation in Death Valley, California. Bottom: Time course of leaf absorbances to solar radiation in the 400–700 nm waveband for the mutant *Encelia farinosa* and the wild type *E. farinosa*. Sample size is 4–5 for the mutant and 10–50 for the wild type

cally similar except for the difference in leaf pubescence. Physiological parameters relating to photosynthesis and transpiration were measured on the mutant *E. farinosa* in Salt Lake City to see if they were also similar.

Peak photosynthetic rates in the mutant *E. farinosa* averaged  $53.1 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  ( $\bar{x} \pm \text{s.e.}$ ), at a leaf temperature of  $30^\circ \text{C}$ , and normal atmospheric conditions (Fig. 7). Photosynthesis decreased in response to decreased quantum flux, and was not saturated at the highest irradiances measured. The leaf conductance to water vapor averaged  $31.2 \pm 1.3 \text{ mm s}^{-1}$  at the highest irradiances. Changes in the leaf conductance to water vapor paralleled those of photosynthesis as irradiance was decreased. As a consequence, the intercellular  $\text{CO}_2$  concentration was  $256 \mu\text{l l}^{-1}$ .

Photosynthesis at high irradiances in the *E. farinosa* mutant was strongly temperature dependent at low and

high leaf temperatures, although the photosynthetic rate was relatively constant near the temperature optimum (Fig. 8). The temperature optimum was between  $28\text{--}30^\circ \text{C}$ . At the temperature optimum, the photosynthetic rate averaged  $51.9 \pm 0.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , the leaf conductance to water vapor averaged  $31.2 \pm 1.8 \text{ mm s}^{-1}$ , and the intercellular  $\text{CO}_2$  concentration averaged  $257 \mu\text{l l}^{-1}$ . All of these values were similar to those measured in the photosynthesis-irradiance response experiments. The photosynthetic rate was greater than 90% of the maximum over a temperature range of  $17\text{--}36^\circ \text{C}$ . However, the photosynthetic rate dropped off quickly above  $36^\circ \text{C}$ , reaching half maximum capacity at  $43^\circ \text{C}$ .

*Field observations of microclimate and water relations.* Field measurements are presented for three days during the winter-spring growing season. These are February 22, 1982,

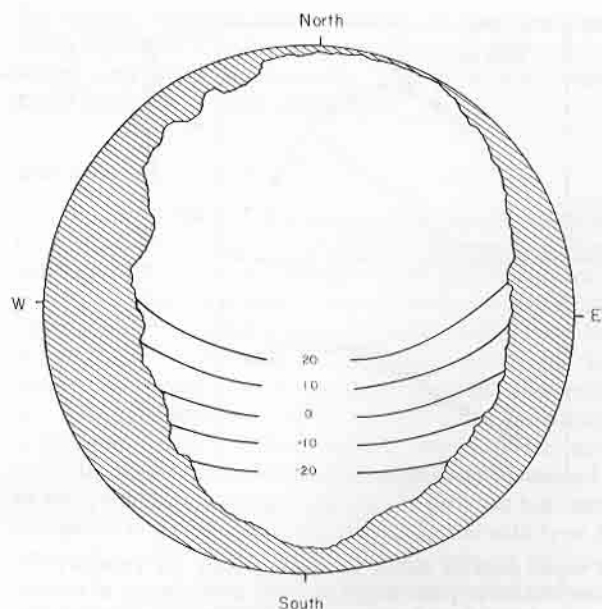


Fig. 6. Fisheye picture of the sky taken from the position of the mutant *Encelia farinosa* in Death Valley. The lines represent the path of the sun through the sky for different solar declinations.

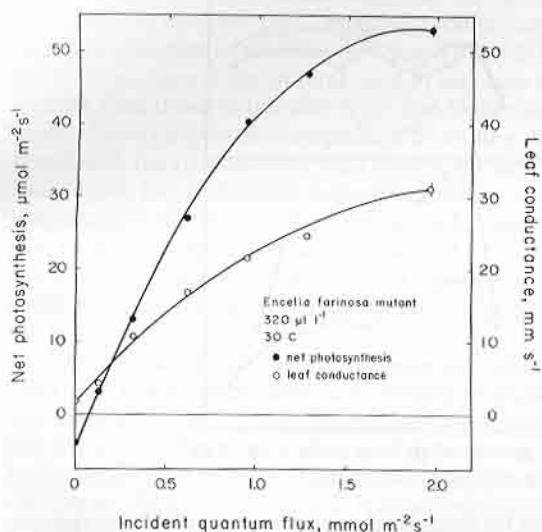


Fig. 7. The response of net photosynthesis and leaf conductance to changes in water vapor to net incident quantum flux (400–700 nm) for intact leaves of the mutant *Encelia farinosa*. These curves are representative of the response curves measured. Vertical bars represent  $\pm 1$  standard error for a sample size of three. Experimental conditions were an ambient  $\text{CO}_2$  level of  $320 \mu\text{l l}^{-1}$ ,  $30^\circ \text{C}$  leaf temperature, and a VPD of 1 kPa. Leaf water potential was  $-1.4 \text{ MPa}$ .

March 21, 1980, and April 21, 1982. Some explanation is necessary for these dates. 1980 was a relatively dry year and comparative data could only be collected in March. 1981 was an extremely dry year and both *Encelia* had very few leaves at any time. 1982 was yet a different year. Rains came early in December, 1981, and were followed by warm temperatures and a dry period through the beginning of March, 1982. March and April, 1982 were relatively cool and wet, followed by a very hot May.

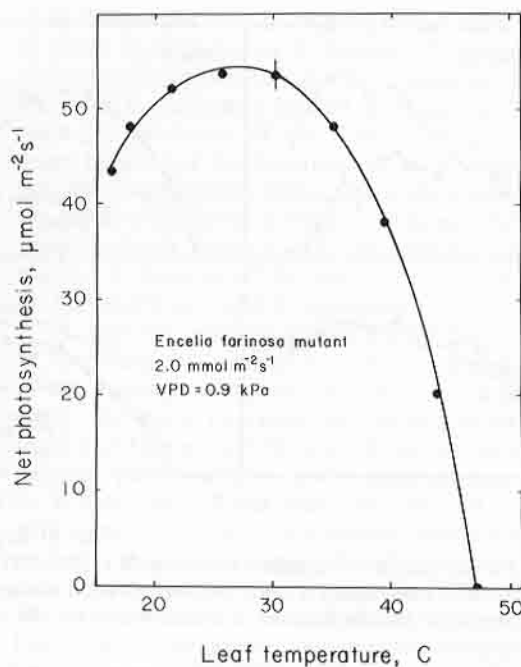


Fig. 8. The response of net photosynthesis to changes in leaf temperature for intact leaves of the mutant *Encelia farinosa*. This curve is representative of the response curves measured. Vertical bars represent  $\pm 1$  standard error for a sample size of four. Experimental conditions were an ambient  $\text{CO}_2$  level of  $320 \mu\text{l l}^{-1}$ , a quantum flux (400–700 nm) of  $2 \text{ mmol m}^{-2} \text{s}^{-1}$ , and a VPD of 0.9 kPa. Leaf water potential was  $-1.4 \text{ MPa}$ .

The three days of field measurements presented illustrate the comparative performances of mutant and wild type forms under three spring-time combinations of drought: low soil water availability and high atmospheric vapor pressure deficits (VPD) (February 22), moderate soil water availability and high atmospheric VPDs (March 21), and moderate soil water availability and low atmospheric VPDs (April 21).

February 22 was characterized by warmer than normal air temperatures, which ranged from  $24$ – $29^\circ \text{C}$  through the midday hours (Fig. 9). Leaf temperatures of both forms were below air temperature; the difference between leaf and air temperature averaged  $-1.6$  and  $-2.1^\circ \text{C}$  for the mutant and wild type forms, respectively. VPD reached a maximum of 3.5 kPa, and averaged 3.13 kPa through the midday hours. Midday leaf water potentials were very similar in both mutant and wild type forms and were in the  $-2.6$  to  $-2.9 \text{ MPa}$  range (Fig. 10). In the early morning and later afternoon hours, leaf water potentials of both forms were below  $-2.0 \text{ MPa}$ . Leaf conductances of both forms increased initially in the morning, but in response to the increases in VPD, decreased after 1000. The maximum leaf conductances on this day were  $3.9 \pm 0.1$  and  $3.3 \pm 0.1 \text{ mm s}^{-1}$  for the *E. farinosa* mutant and wild type, respectively.

On March 21, the air temperature ranged from  $24$ – $29^\circ \text{C}$ , more typical for this time of the year (Fig. 9). Leaf temperatures were again below air temperature, averaging under temperatures of  $-4.1$  and  $-2.4^\circ \text{C}$  for the mutant and wild type forms, respectively. Since the relative humidity was low (11% at midday), the VPD reached a maximum of 3.5 kPa and averaged 3.04 kPa through the

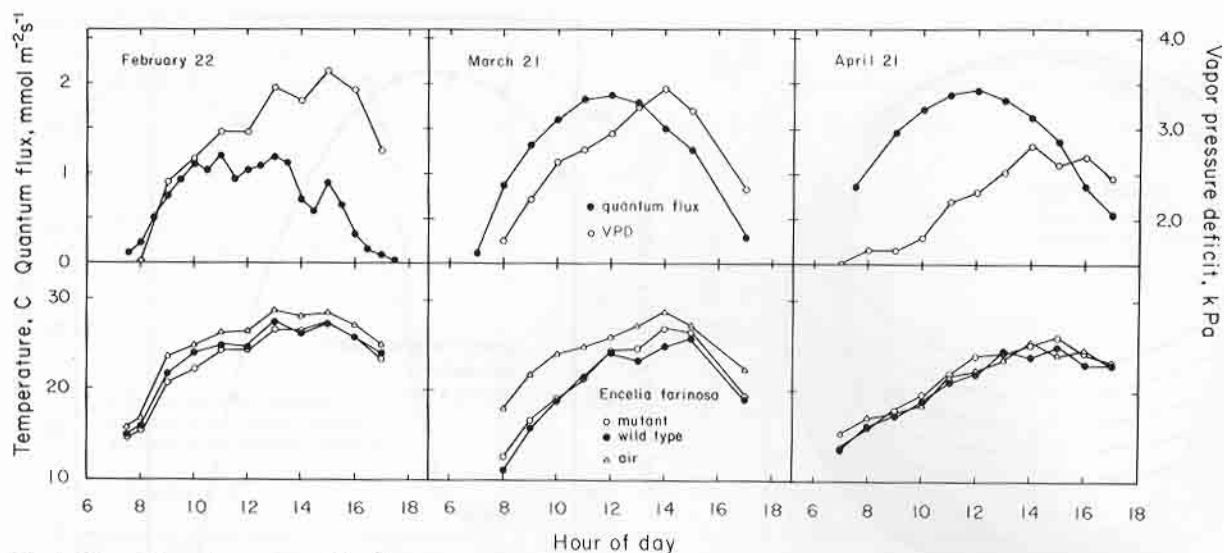


Fig. 9. Top: Diurnal courses of incident quantum flux (400–700 nm) and vapor pressure deficit in Death Valley for February 22, 1982, March 21, 1980, and April 21, 1982. Bottom: Diurnal courses of air temperature at plant height and leaf temperatures of mutant and wild type forms of *Encelia farinosa* in Death Valley for the same dates as above. Leaf temperatures are means of a sample size of six

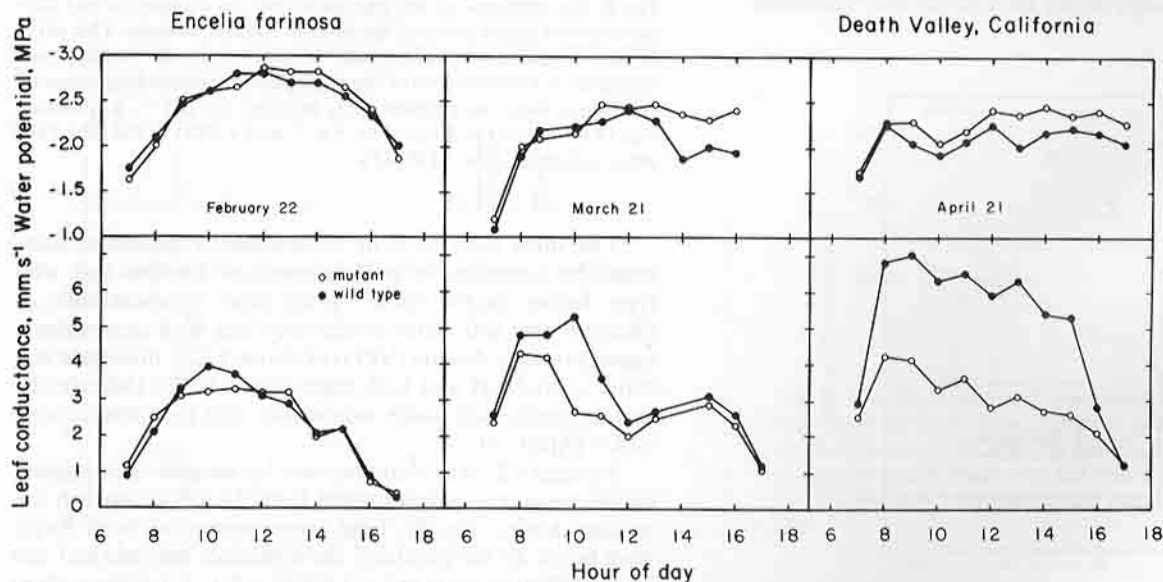


Fig. 10. Diurnal courses of leaf water potential and leaf conductance to water vapor for mutant and wild type forms of *Encelia farinosa* in Death Valley on February 22, 1982, March 21, 1980, and April 21, 1982. Data presented are means

midday hours. Midday leaf water potentials were again similar in the two *E. farinosa* forms; values at midday were in the  $-2.2$  to  $-2.5$  MPa range (Fig. 10). Leaf conductances on both forms increased in the early morning, reaching maximums of  $5.3 \pm 1.0$  and  $4.3 \pm 0.6 \text{ mm s}^{-1}$  for the *E. farinosa* mutant and wild type, respectively (Fig. 10). Leaf conductances decreased sharply as VPD increased; stomates reopend partially in the late afternoon in response to a decrease in VPD.

The weather on the April 21 measurement date was cooler and wetter than normal for that time of the year. It was moderately windy, in contrast to the two previous dates which were calm. The maximum air temperature was  $25^{\circ}\text{C}$  and ranged between  $18$ – $25^{\circ}\text{C}$  through the midday hours (Fig. 9). Most likely as a consequence of the higher

wind speeds, leaf temperatures were similar to air temperatures throughout the day. The relative humidity was similar to that of the two previous dates (14% at midday), but since the air temperatures were lower, VPDs never exceeded 2.8 kPa and averaged 2.38 kPa through the midday hours. The lower VPDs when combined with higher leaf water potentials ( $-2.0$  to  $-2.4$  MPa) resulted in higher leaf conductance values than on either of the two previous dates (Fig. 10). The maximum leaf conductances to water vapor were  $7.0 \pm 0.5$  and  $4.2 \pm 0.3 \text{ mm s}^{-1}$  for the *E. farinosa* mutant and wild type, respectively. The highest leaf conductances were again measured early in the morning and decreased continually through the day as VPD gradually increased.

Comparative measurements could not be made later in

the season, because when midday air temperatures rise much above 30°C (after mid-April), the *E. farinosa* mutant leaves very quickly senescence. This senescence was hastened by low leaf water potentials.

## Discussion

The genus *Encelia* is characterized by species with leaves that range in hairiness from lightly to heavily pubescent. While the genus occurs throughout the arid regions of western North America and portions of South America, the less pubescent leaved species normally occur only on the wetter sites. *E. farinosa* is a heavily pubescent leaved species, occurring in the driest portions of the Sonoran Desert. The pubescence serves to reflect solar radiation and is thought to be a critical feature necessary for survival in its dry, hot desert habitat (Ehleringer and Mooney 1978). In this paper, an apparent mutant *E. farinosa* has been described. It is morphologically similar to the wild type *E. farinosa* (i.e., the remainder of the *E. farinosa* population) in all respects, except that it lacks the dense leaf pubescence. (It also lacks any stem pubescence.) As a consequence, leaf spectral characteristics of the mutant and wild type *E. farinosa* are quite different.

The mutant *E. farinosa* appears able to survive because of several differences in leaf energy budget characteristics: 1) leaf conductance to water vapor in the field is greater than that of the wild type, especially under conditions of high soil moisture availability and low VPDs; 2) leaf angles are twice as steep in the mutant; and 3) leaf sizes are slightly smaller than those of the wild type. The higher leaf conductance allows for greater transpirational cooling. When combined with the reduced heat load associated with its steeper leaf angles, the *E. farinosa* mutant is able to maintain leaf temperatures similar to those of the wild type. However, this is not accomplished without a cost. The tradeoff in water expenditure (mutant) against increased reflectance (wild type) results in different lengths of activity within the year.

If one assumes that each *E. farinosa* individual of equivalent size has an equivalent soil volume to exploit during the growing season, then the mutant must be expending this water at a faster rate than wild type forms, especially in the earlier part of an average growing season when VPDs are lowest. As a consequence, it is expected that the mutant should drop its leaves earlier into the drought period. This is indeed the observation, and is clearly shown in Fig. 5. While this implies that the mutant has less time available for carbon gain and that each leaf probably gains less carbon during the season, it is not sufficient proof. It is possible that since the mutant leaf does not reflect quanta (as occurs in the wild type leaf), that these quanta might be used in photosynthesis if the leaf is not light saturated. What is needed to resolve this question is a detailed analysis of daily carbon gain over the entire year for both forms, taking into account the differential soil water depletion rates.

Ehleringer and Björkman (1978b) showed that except for differences in leaf absorptance, the photosynthetic characteristics of *E. californica* (glabrous, coastal species of more mesic habitats) were not different from those of *E. farinosa* (pubescent, interior species). The current study suggests that there may be a small difference in the intrinsic photosynthetic capacities of the *E. farinosa* mutant and the wild type *E. farinosa*. The maximum photosynthetic capaci-

ty of the mutant may be slightly higher than that observed in either *E. californica* or *E. farinosa*. The maximum photosynthetic rate of the mutant was  $52 \mu\text{mol m}^{-2} \text{s}^{-1}$ , whereas leaves of *E. californica* peaked at  $46 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Ehleringer and Björkman 1978b). There were also similar differences in the leaf conductances to water vapor. It is quite possible that this 13% difference in photosynthetic rate was the result of different growth conditions. The shape of the photosynthesis temperature dependence curve for the mutant *E. farinosa* is the same as has been measured in both *E. californica* and *E. farinosa*.

A broader ecological question to be asked with the *E. farinosa* mutant has to do with the adaptive significance of the pubescence and the evolution or adaptive radiation within the genus into drier and more arid habitats. Ehleringer and Mooney (1978) argued that as far as leaf energy balance, photosynthetic, and transpiration considerations, an *E. farinosa* leaf was the same as an *E. californica* leaf with variable amounts of a blanket reflector (pubescence), and also that the presence of pubescence would result in enhanced daily carbon gain under water limited conditions. This was because the pubescence reflected quanta (reduced heat load) from leaves, reducing leaf temperature. When temperatures were above the photosynthetic temperature optimum, the reduction in leaf temperature caused by the presence of pubescence resulted in a higher photosynthetic rate and also an increase in water use efficiency. More recently, Ehleringer and Cook (unpublished data) have extended this by showing that as leaf water potentials declined in long term soil water depletion cycles, photosynthesis became saturated at high irradiances. This implies a much greater water use efficiency for pubescent leaves than previously thought. The occurrence of a glabrate-leaved *E. farinosa* mutant in the interior desert provides us a rare opportunity to demonstrate the adaptive benefit of leaf pubescence in a direct way. The results of this study allow us to conclude that the glabrate-leaved mutant is able to maintain similar leaf temperatures as observed in the pubescent-leaved individuals, but only if leaf angles are significantly steeper and also transpiration cooling is greater. On a seasonal basis the consequence is that the mutant has a much shorter period for carbon gain. It should be mentioned at this point that *E. frutescens* is a glabrate-leaved shrub occurring in some of the same macro-habitats as *E. farinosa*. On a micro-habitat scale though, *E. frutescens* occurs only in washes with much higher water availability. Leaf conductances and transpirational cooling are also much higher in *E. frutescens* than in *E. farinosa* (Ehleringer and Cook, unpublished data).

The data from this study suggest that the *E. farinosa* mutant is expected to have a lower seasonal carbon gain than *E. farinosa* wild type in a dry desert habitat, and that the same should also be true for the *E. californica*. Transplant garden experiments are currently under way with *E. californica*, *E. frutescens* and both mutant and wild type forms of *E. farinosa* to determine the daily and seasonal carbon gain, fecundity, and mortality patterns.

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